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

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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 *Xenicibis* 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 2*a–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 2*e*), 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 2*h*). It has a subtriangular section and weakly developed articular surfaces.

The radius (figure 2*h*) 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

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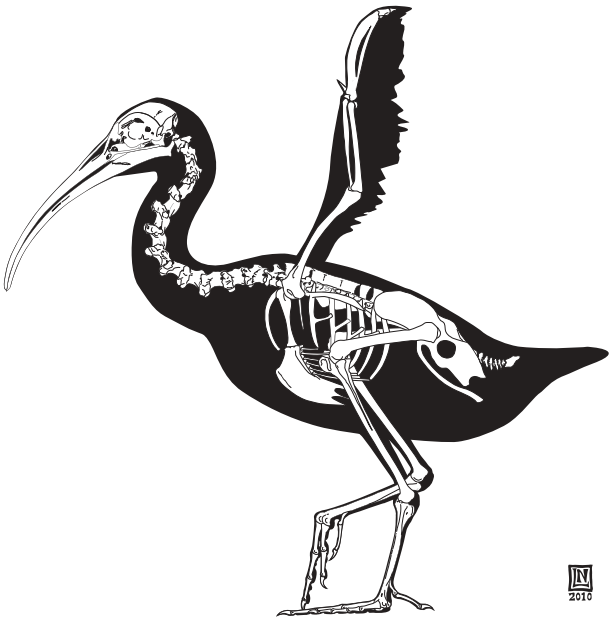

Figure 1. Skeletal reconstruction of *Xenicibis xympithecus* based on USNM 460349 and fossils from the Red Hills Fissure cave deposits, Saint Andrews Parish, Jamaica.

slender and nearly straight (figure 2*h*). 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 dorsoventrally flattened and the articulation for the ulnare is reduced.

The humerus (figure 2*h*) is typical 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 3*e*) and furcula (figure 3*f*) are large and robust. The sternal carina (figure 3*g*), 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 3*a*,*b*), but the tip is knob-like, as in *Apteribis*, rather than spatulate. The parietals and frontals (figure 3*d*) are thickened by a honeycomb of cancellous bone. The vertebrae and notarium are robust, but otherwise unremarkable. The hindlimb (figure 3*h–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 3*k*,*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 antebrachium 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: Gonodactyloidea); 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 4*a*); a fracture callus indicates healing although the bones failed to knit. The second specimen (USNM 460349) is a carpometacarpus (figure 4*b*) 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,

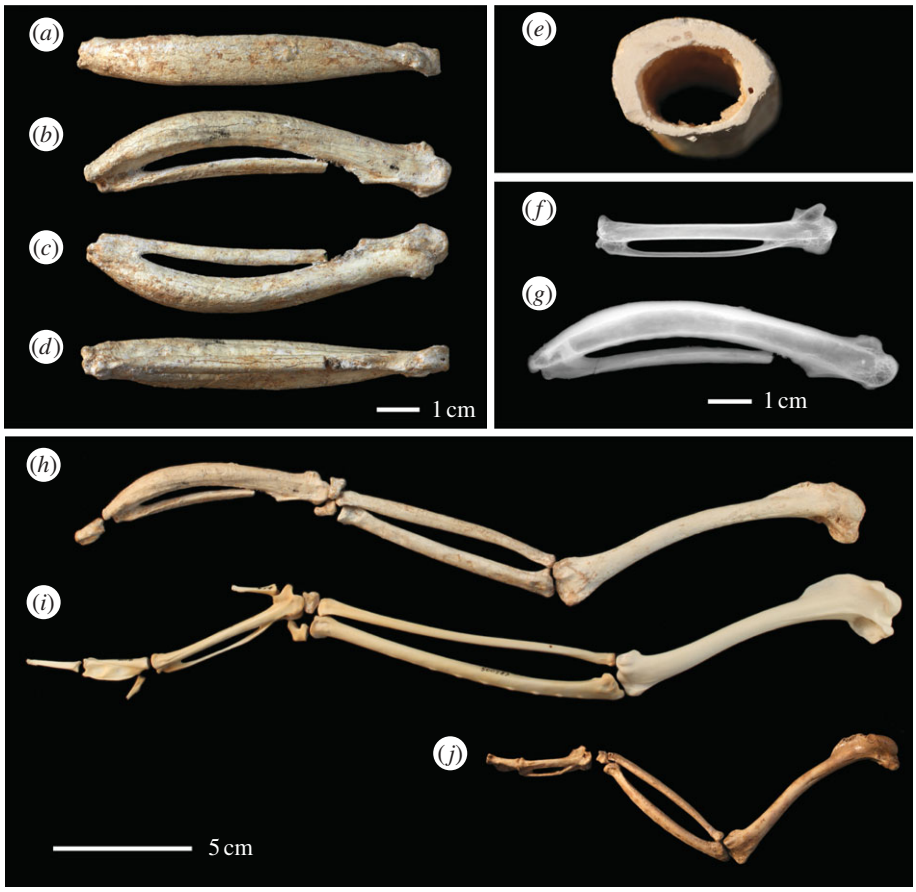

Figure 2. Wing skeleton of *X. xympithecus* compared with *Eudocimus albus* and *Apteribis glenos*. (*a*) Left carpometacarpus (USNM 543067) in cranial view, (*b*) dorsal view, (*c*) ventral view and (*d*) caudal view. (*e*) Major metacarpal (USNM 543074) sectioned at midlength (note the greatly thickened anterior wall). (*f*) Radiograph of carpometacarpus of *Eudocimus* compared with (*g*) *Xenicibis* (USNM 543067). (*h*) Composite left wing of *Xenicibis* (USNM 543067-543073) compared with (*i*) *Eudocimus* (USNM 266467) and (*j*) *Apteribis*.

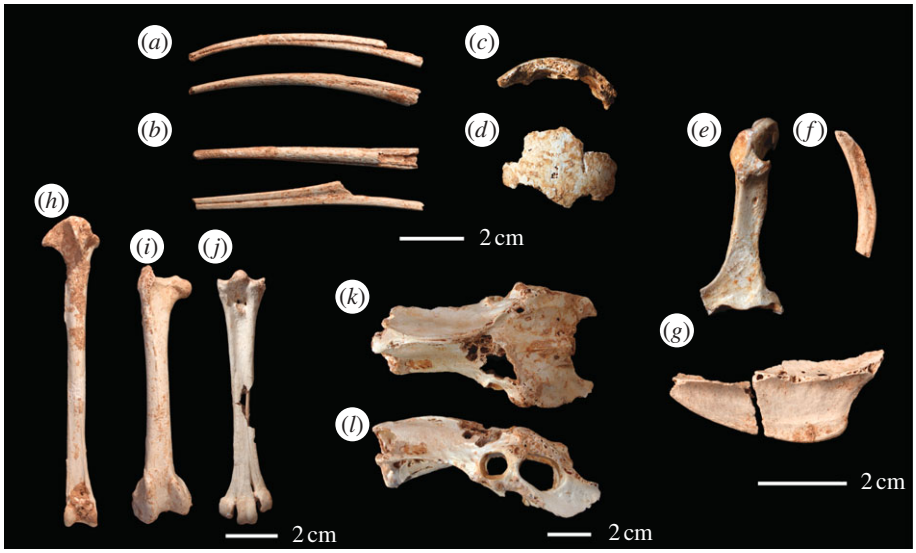

Figure 3. Selected skeletal elements of *X. xympithecus* from the Red Hills Fissure cave deposits, representing multiple individuals. Skull elements: (*a*) rostrum (USNM 543075) and mandible (USNM 543076) in lateral view and (*b*) dorsal view; (*c*) cranial cap (USNM 543077) in left lateral view and (*d*) dorsal view. Pectoral girdle: (*e*) coracoid (USNM 543078), (*f*) clavicle (USNM 543079) and (*g*) two fragments of sternal carina (USNM 543081 and 54080). Hindlimb: (*h*) tibiotarsus (USNM 543084), (*i*) femur (USNM 543083) and (*j*) tarsometatarsus (USNM 543085). Pelvis (USNM 543082): (*k*) dorsal view and (*l*) lateral view.

including screamers (Anhimidae), some jacanas (*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*),

Figure 4. Fossils of *Xenicibis* showing evidence of trauma. (*a*) Fractured left humerus (USNM 543086 and 543087) showing fracture callus (fc): (i) photograph; (ii) radiograph. (*b*) Carpometacarpus of *Xenicibis* (USNM 460349) with rugose fracture callus on anterior, dorsal and ventral surfaces of the major metacarpal: (i) photograph; (ii) radiograph showing development of callus inside the medullary cavity.

geese and swans (Anserinae), the solitaire (*Pezophaps*), sheathbills (*Chionis*), some guans (*Crax*) and stone curlews (*Burhinus*) [11,12,15]. The jacanas *Actophilornis* and *Irediparra* have, instead of a spur, a radius that is expanded into a triangular blade (fig. 1F in [16]). Although field observations are limited, these structures function for intraspecific combat in jacanas [15], sheathbills [15], waterfowl [5,12] and the solitaire [11], and such conflicts can end in serious injury or even death [5,11,12]. In some cases (e.g. swans), these weapons can be employed in defence of eggs and young [17]. Thus, although the morphology of *Xenicibis* is unique, the use of the wing as a weapon is widespread in birds, and would not be entirely unexpected.

While no living ibis shows adaptation of the wing for combat, ibises are highly territorial during nesting and feeding [6,18], and disputes frequently escalate to fights. Of particular note is the fact that *Plegadis* has been seen to grasp its opponent with the bill and then strike with the wings [19]. In many species, intraspecific combat involves access to mates, but 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.

Another possibility is that the manus was employed in defence. *Xenicibis* is unusual in that it became flightless in the presence of predators that could potentially have preyed on its eggs or young. Among these would have been the Jamaican yellow boa *Epicrates subflavus* (which can reach up to 2.0 m in length [20]), the small, extinct monkey *Xenothrix mcgregori* [21], and over a dozen species of Falconiformes, including hawks, kites, falcons and caracaras [22]. *Xenicibis* is also unusual because, whereas in most flightless birds the young are precocial [2], the young of ibises stay in the nest and are fed by the parents until old enough to walk about on their own, although before actually fledging [5]. 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.

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