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AN IBIS-LIKE BIRD (AVES: CF. THRESKIORNITHIDAE)
FROM THE LATE MIDDLE EOCENE OF MYANMAR

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Abstract — A distal tibiotarsus of an ibis-like bird is described from upper middle Eocene deposits of the Pondaung Formation, central Myanmar. The new fossil is the first bird described from the Pondaung fauna and the first from Myanmar. It is here tentatively assigned to the family Threskiornithidae based on the combination of characters exhibited by the specimen. The Pondaung bird may represent the oldest ibis in Asia.

INTRODUCTION

Knowledge of Mesozoic birds from Asia (e.g., Zhou and Hou, 2002) has increased dramatically, but the fossil record of Cenozoic birds in Asia has increased little since Rich et al. (1986) reviewed the record. It is still particularly poor in southeast Asia. Cheneval et al. (1991) provided a detailed description of the Miocene Li Mae Long avifauna from Thailand, but no other Tertiary bird fossils have been described from southeast Asia since 1986, and fossil avians are still unknown from most Southeast Asian countries.

The oldest bird currently known from Southeast Asia is the pelecaniform *Protoplotus beauforti* from Sumatra (Lambrecht, 1931). The holotype and only known specimen of *P. beauforti* is likely Paleocene in age (Whateley and Jordan, 1989) rather than Eocene-to-Miocene as elsewhere reported (Van Tets et al., 1989). Eocene birds from China include falconiforms, anseriforms (Rich et al., 1986), a charadriiform (Hou and Ericson, 2002), and a purported ibis (Hou, 1982). Recent work by researchers from Japan, France, and the United States on primates and other mammals from the middle Eocene Pondaung Formation (reviewed in Ciochon and Gunnell, 2002)

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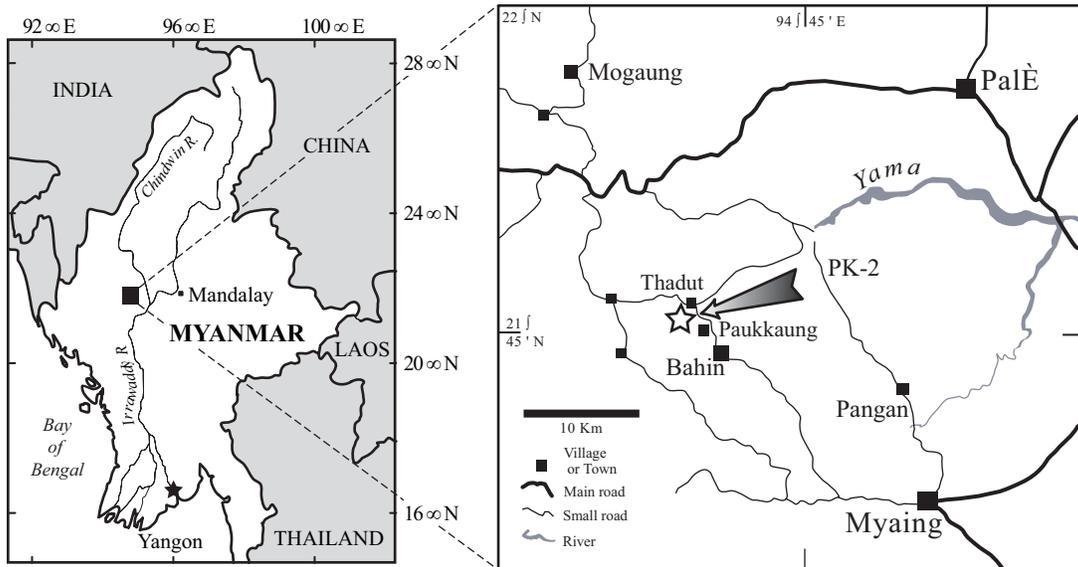


FIG. 1 – Map showing the position of PK-2, locality for the Pondaung bird, and selected local villages. Modified after Gunnell et al., 2002.

has produced the first fossil bird from Myanmar (Burma) and one of the oldest birds in southeast Asia. This bird is represented by a single partial bone, but it is nevertheless an important record.

GEOLOGIC SETTING

The Pondaung Formation of central Myanmar (Fig. 1) has produced a diverse mammalian fauna and less well known reptilian and gastropod remains (Colbert, 1938; Hutchison and Holroyd, 1996; Tsubamoto et al., 2000; Aung Naing Soe et al., 2002; Hutchison et al., 2004; Head et al., 2005), all of latest middle Eocene age (Holroyd and Ciochon, 1994; Tsubamoto et al., 2002). The Pondaung Formation is about 2000 m thick and is divided into informal lower and upper members (Aye Ko Aung, 1999). The vertebrate-bearing upper member (approximately 500 m of the formation) is largely composed of fine- to medium-grained sandstones and mudstones. The depositional environment of the Pondaung Formation was interpreted as a freshwater lagoon by Aye Ko Aung (1999), but is more likely a set of deposits associated with meandering rivers, marshes, and delta plains (Stamp, 1922; Aung Naing Soe et al., 2002). More detailed locality maps and discussion of other vertebrate localities are found in Gunnell et al. (2002).

SYSTEMATIC PALEONTOLOGY

Class AVES
 Order CICONIIFORMES
 Family cf. THRESKIORNITHIDAE

Specimen.— National Museum of Myanmar, Paleontology Specimen NMMP-KU 1301, a right distal tibiotarsus. Casts of NMMP-KU 1301 reside in the collections of the Primate Research

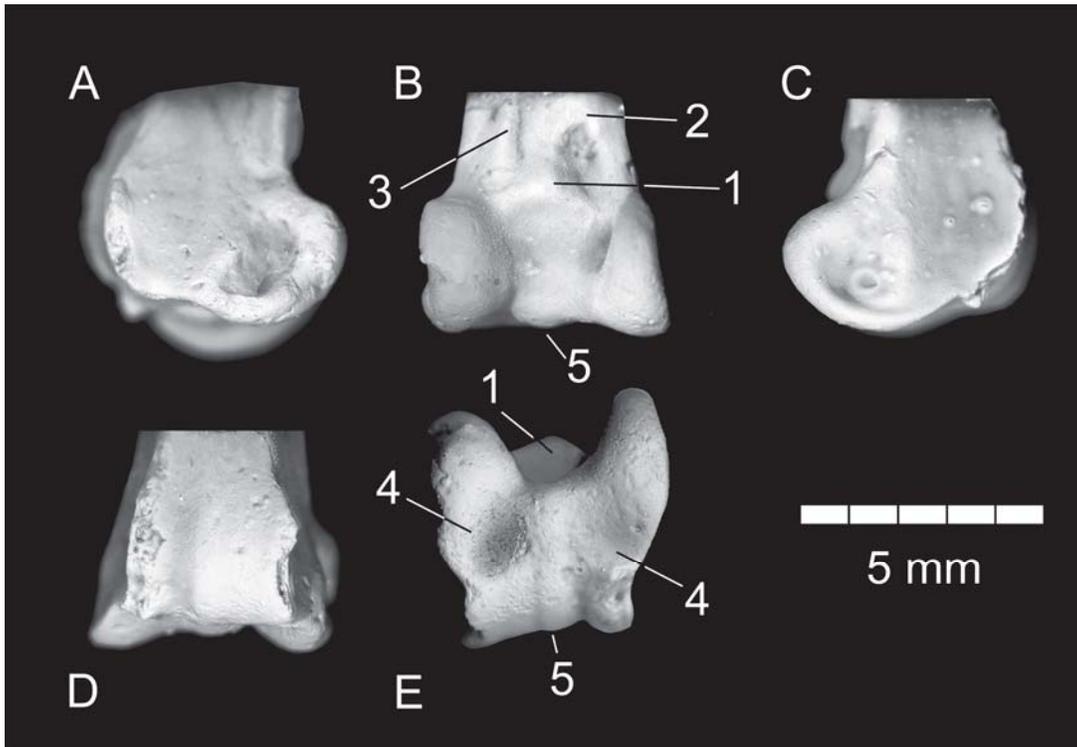


FIG. 2 – The Pondaung bird NMMP-KU 1301. A, lateral view. B, anterior view. C, medial view. D, posterior view. E, distal view. Morphological features: 1, intercondylar prominence; 2, supratendinal bridge; 3, lateral attachment of the extensor retinaculum; 4, depressions/pits; and 5, ridge in articular surface for the tibial cartilage.

Institute (Kyoto, Japan), University of California Museum of Paleontology (Berkeley, USA), and University of Michigan Museum of Paleontology (Ann Arbor, USA).

Fossil Locality.— PK2, northwest of Paukkaung village, at approximately 21° 45' 16" N 94° 39' 14" E, Paukkaung township, central Myanmar (Fig. 1), “upper member” of the Pondaung Formation, latest middle Eocene.

Description.— The specimen is a right distal tibiotarsus (Fig. 2). It is missing only a little of the medial and lateral edges of the articular surface for the tibial cartilage. The tibial shaft is broken proximal to the medial attachment site of the extensor retinaculum.

In anterior view the medial condyle is about one-half the width of the lateral condyle. The medial condyle is wide distally and narrows considerably proximally. At its lateral proximal end is a fossa, medial to the intercondylar prominence and excavated into the lateral side of the medial condyle. The fossa is ovate in outline and about one half the proximodistal length of the medial condyle. The intercondylar prominence is large, broad, and subpyramidal, with a flat distal face, and it is situated at the midpoint between the proximal ends of the condyles. The supratendinal bridge is not wide. The distal opening of the extensor canal (at the distal edge of the supratendinal bridge) is subcircular and opens distally into a broad extensor groove (with the lateral side formed by the intercondylar prominence), which is directed distomedially toward the medial condyle. The distal edge of the supratendinal bridge of the extensor canal is proximal (about 2 mm) to the medial condyle. The finger-like ridge of the lateral attachment site of the extensor retinaculum is situated in between the intercondylar prominence and the proximal end of the lateral condyle. The distal margin of the tibiotarsus is undulatory with two ridges formed by the condyles, and a central ridge

present in the articular surface for the tibial cartilage. There is no obvious peroneous groove on the lateral edge of the tibial shaft.

In distal view the medial condyle extends only slightly anterior to the level of the lateral condyle. The intercondylar incisure has an asymmetrical U-shape. There are two pits on the distal end of the tibiotarsus. The medial pit is less distinct, and is situated just posterior to the anteroposterior midpoint of the distal end of the bone. The lateral pit is larger, deeper, and extends somewhat more anterior than the medial pit. The pits are separated by the ridge that runs posteriorly and proximally up the articular surface for the tibial cartilage. The articular surface for the tibial cartilage is not uniformly concave since the ridge separates the articular surface into a more distinctly concave medial portion and a flatter lateral portion.

In posterior view the posterior face of the tibiotarsus is much narrower than the anterior face. The lateral side of the articular surface for the tibial cartilage flattens proximally and ends proximal to the proximal level of the condyles.

In lateral view the lateral epicondylar depression is proximodistally elongate, with its long axis angled somewhat anteroproximal-to-posterodistal. The lateral epicondylar depression does not extend posterior to the anteroposterior midpoint of the distal end.

In medial view the medial surface is nearly flat, and it is slightly concave in its posterior half. Both the medial and lateral epicondyles are small. The medial epicondylar depression is about the same size as the lateral one, and it is not very distinct except at its anterior end.

DISCUSSION

The Pondaung bird differs from all other birds in the following combination of characters of the tibiotarsus: (1) presence of an ossified supratendinal bridge; (2) a large subpyramidal intercondylar prominence located midway between the lateral and medial condyles; (3) distal edge of the supratendinal bridge at the same proximodistal level as the intercondylar prominence; (4) presence of a large intercondylar incisure; (5) lateral attachment site of the extensor retinaculum finger-like and located midway between the intercondylar prominence and the lateral condyle; (6) distal face of the tibiotarsus with medial and lateral pits that extend medially and laterally, notching the edges of the medial and lateral condyles; (7) presence of a ridge in the articular surface for the tibial cartilage; and (8) small size overall.

The astragalus is completely fused to the tibia and the supratendinal bridge is completely ossified, indicating that the specimen represents an adult individual. Nearly all of the characters present in the Pondaung bird are, individually, homoplastic across neornithine birds. However, the combination of characters in the specimen can significantly narrow its identification. The presence of two pits on the distal end of the tibiotarsus is present in flamingos, some ciconiiforms, gruids, and other groups. The two pits are deeper and more distinct in phoenicopterid and palaelodid flamingos than observed in the Pondaung bird. The Pondaung bird also lacks the bony ridge separating the medial condyle from the distal opening of the tendinal groove, considered a characteristic of flamingos (Rasmussen et al., 1987). The Pondaung bird differs from gruids in having a ridge running through the articular surface for the tibial cartilage, and a subpyramidal intercondylar prominence located midway between the condyles (more lateral in gruids).

The Pondaung bird and gruids share a similar conformation of the distal condyles and a finger-like lateral attachment site for the extensor retinaculum. The distal end of the lateral attachment site of the extensor retinaculum is lateral to the intercondylar prominence in the Pondaung bird rather than proximal to it as in phoenicopterids and some gruiforms. The intercondylar incisure is not round or subtrapezoidal as in Ciconiidae or flamingos (Olson and Feduccia, 1980). The ridge in the articular surface for the tibial cartilage is present in a form similar to the Pondaung bird in *Palaelodus ambiguus*, but not other species of *Palaelodus* (e.g., *P. wilsoni*).

The Pondaung bird and at least some species of extant threskiornithids share the presence of the two pits on the distal end of the tibiotarsus, the distal rims of the condyles notched by these pits, a ridge in the articular surface for the tibial cartilage, the presence of a subpyramidal inter-

condylar prominence positioned midway between the condyles, and a similar morphology of the condyles. The ridge in the articular surface for the tibial cartilage is absent in the threskiornithid genus *Geronticus*, but present in *Plegadis*, *Eudocimus*, and *Theristicus* (although not as prominent as the state in the Pondaung bird). The Pondaung bird differs from extant ibises in having a more distinct raised area for the lateral attachment of the extensor retinaculum, but the state in the Pondaung bird is similar to some geranoidid gruiforms and *Palaelodus ambiguus* (but not other species of *Palaelodus*). The distal edge of the supratendinal bridge is proximal, opening lateral to the intercondylar prominence, rather than medial to the prominence as in extant threskiornithids. The Pondaung bird is also smaller than extant threskiornithids, but approximately the same size as the earliest known ibis *Rhynchaetites*.

The combination of characters in the Pondaung bird appears to fit best with allocation to Threskiornithidae, although not as part of the crown-clade of that family. It is possible that the Pondaung bird may be related to some other clade of neornithine bird, in particular to some extinct gruiform groups (i.e. ergilornithids and geranoidids) and phoenicopteriforms, but the data at hand appear to support allocation of the Pondaung bird to the ciconiiforms and in particular the threskiornithid lineage.

The fossil record of ibises is rather poor, with some taxa having been misplaced in Threskiornithidae (Olson, 1981). The oldest fossils attributed to threskiornithids are from China (Hou, 1982) and Germany (Peters, 1983). *Minggangia changgouensis* is a purported ibis from the late Eocene of China (Hou, 1982). Hou (1982) compared *Minggangia* with *Ibidopsis hordwelliensis*, considering both as ibises. There is a great degree of similarity between the tibiotarsus of both taxa. However, Cracraft (1973) moved *Ibidopsis* from the Threskiornithidae to the Rallidae. The primitive subcircular lateral condyle (lateral view) present in *Minggangia*, *Ibidopsis*, and rails (absent in the Pondaung bird and in threskiornithids) is consistent with placement of those fossil taxa within Rallidae, rather than with the threskiornithids. While the skull and other characters of *Rhynchaetites messelensis* (from Messel in Germany) clearly support identification of *Rhynchaetites* as an ibis, it too shares the primitive subcircular medial condyle (Mayr, 2002: fig. 6). Since the Pondaung bird does not have a rounded medial condyle of the tibiotarsus, but shares a flattened distal face of the tibiotarsus with living threskiornithids, it appears that the Pondaung bird may be more closely related to the crown clade of Threskiornithidae than is *Rhynchaetites*.

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