



A night heron (Ciconiiformes, Ardeidae) and a stork (Ciconiidae) from the Pliocene of Myanmar (Burma)

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ABSTRACT

Two new avian specimens from the Pliocene part of the Irrawaddy sediments of central Myanmar represent the youngest known fossil records of birds from Myanmar (Burma) that previously was restricted to one specimen of an ibis from the middle Eocene. The age of the Sulegon-1 fossil locality is likely from the later part of the Pliocene based on the presence of the suid *Sivachoerus prior*, the anthracotheriid *Merycopotamus dissimilis*, and the Sumatran rhinoceros *Dicerorhinus* sp. cf. *D. sumatrensis*. The distal tarsometatarsus is from a night heron (Ardeidae: Nycticoracini) and exhibits derived (and primitive) features consistent with night herons, but not other groups of ardeids, including the absence of a lateral deflection of trochlea III and a trochlear furrow extending to the proximal plantar end of trochlea III. The night heron fossil is not distinguishable from some species of *Gorsachius* and *Nycticorax* and may derive from one of the extant species in Southeast Asia. The other specimen (a distal tibiotarsus) represents a taxon of stork (Ciconiidae: cf. Leptoptilini) and displays many characters associated with that group (including a large centrally positioned intercondylar tubercle, a rounded intercondylar fossa, and distally notched trochlear rims). This stork is smaller than the 'giant' storks known from the Plio-Pleistocene of Asia and Africa, and may represent a relative of one of the large extant Asian storks. The inferred paleohabitat of the Sulegon locality as a tidal deltaic habitat is consistent with the lifestyle of both the extant night herons and large storks that occur in southeastern Asia today.

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INTRODUCTION

Neogene and Pleistocene birds from South and Southeast Asia are relatively rare in the published fossil record. Recent reports of new taxa and specimens from the Pleistocene of Indonesia (Meijer et al., 2013) are beginning to fill in both a taxonomic, as well as biogeographic picture of this historically complex region, and Meijer (2014) recently reviewed the fossil record of insular portions of Southeast Asia. Prior to those new finds, rather limited published pre-Quaternary specimens from the Siwalik Hills in India and Pakistan (e.g., Davies, 1880; Harrison and Walker, 1982), the Eocene lignite mines in India (e.g., Mayr et al., 2007), the early Miocene of Thailand (Chenval et al., 1991), a single specimen from the Eocene of Myanmar (Stidham et al., 2005), the skeleton of the pelecaniform *Protoplatus* from Indonesia (Van Tets et al., 1989), and Oligocene avian tracks from Indonesia (Zonneveld et al., 2011) are the majority of records from the region. However, ongoing field work continues to produce Neogene and Quaternary avian material in southern Asia (e.g., Stidham et al., 2014, Forestier et al., 2015), adding to the known avian fossil material that was first published in the late nineteenth century. Despite that growing body of research, at present there remains only a single avian specimen (originally identified as an ibis relative) published from the middle Eocene of Myanmar (Burma) (Stidham et al., 2005).

Adding to that sparse record from Southern Asia (and Myanmar), we report two new avian specimens from the Pliocene of Myanmar. These new fossils record the presence of what likely are a stork (Ciconiidae) and a night heron (Ardeidae), and furthermore, those fossils may derive from species that occur in the same geographic area today. The discovery of apparent relatives of extant birds in the Pliocene of Myanmar contrasts with that of the stratigraphic sequence's mammalian fossil record (where most of the mammals known are from extinct groups, with the exception of early

representatives of the Sumatran rhino), but is consistent with the Quaternary Liang Bua site in Indonesia, largely composed of extant avian taxa (Meijer et al., 2013).

The pre-Quaternary record of herons, while extending back into the Paleogene, is rather sparse (Scofield et al., 2010; Worthy et al., 2013). While some Paleogene specimens have been allocated as night herons (Scofield et al., 2010), none of those specimens are from Asia. The fossil record of pre-Quaternary ardeids in Asia includes an unnamed bittern from the Miocene of Mongolia (Zelenkov, 2011), *Nyctisoma robusta* from the middle Miocene of Mongolia (Elzanowski and Zelenkov, 2015), *Nyctanassa kobdoena* from the early Pliocene of Mongolia (Kurochkin, 1976; Zelenkov, 2013), the early Miocene *Proardeola walkeri* from Thailand (Cheneval et al., 1991), a Miocene indeterminate vertebral centrum from China (Hou, 1987), and the middle Miocene *Ardea sytchevskaiae* from Mongolia (Zelenkov, 2011). Only one of those fossils is from southeastern Asia (Thailand).

Large-bodied storks are known from several sites across southern and eastern Asia in the Pliocene and Pleistocene. Traditionally, the larger storks (species of *Jabiru*, *Ephippiorhynchus*, and *Leptoptilos*) have been placed within Leptotilini. However, molecular phylogenetic analyses do not consistently support the monophyly of Leptotilini (Slikas, 1997, 1998), and a recent morphological analysis (de Pietri and Mayr, 2014) demonstrated only weak bootstrap support for the group as whole. The large-bodied storks include the very large (or even 'giant') storks of *Leptoptilos falconeri* (Harrison, 1974; Louchart et al., 2005) from India (and elsewhere), *L. robustus* from Flores Island, Indonesia (Meijer and Due, 2010; Meijer et al., 2013), *L. titan* (Wetmore, 1940) from Java, Indonesia, and *L. lüi* from northeastern China (Zhang et al., 2012). The largest of these extinct storks have been hypothesized to stand 1.8 to 2 meters tall (Louchart et al., 2005; Meijer and Due, 2010). Some fossil

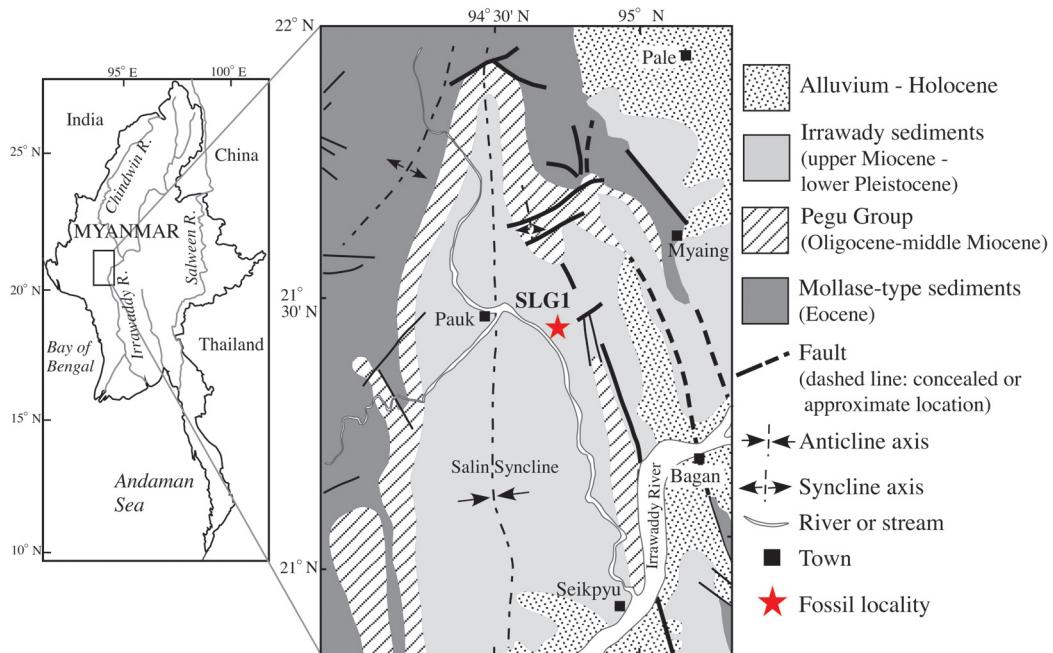


FIGURE 1. Map of Myanmar showing the SLG1 fossil locality (star) and geological map around the SLG locality (Geological map: after The Geological Map of Burma, 1: 1000,000 map; Earth Sciences Research Division, 1977).

material also has been allocated to the extant species of *L. dubius* (Louchart et al., 2005) from India, and two species (*Ephippiorhynchus* cf. *asiaticus* and cf. *L. dubius*) were identified from the Trinil site on Java (Weesie, 1982). Recently, the age of the *L. robustus* type locality was revised to an (older) age of more than 50 ka (Sutikna et al., 2016).

Geological Setting

The Neogene Irrawaddy sediments (= Fossil wood Group: Theobald, 1869; = Irrawaddian Series: Noetling, 1900; = Irrawaddy Formation: Aung-Khin and Kyaw-Win, 1969; = Irrawaddy Group: Bender, 1983) are widely distributed along the Irrawaddy River (= Ayeyarwady River) in central Myanmar (Figure 1). They are mainly composed of fluvial sediments that are characterized by the abundance of silicified fossil woods, and the thickness has been estimated to be 2,000 to 3,000 m (Bender, 1983; Wandrey, 2006). The Irrawaddy sediments have been traditionally subdivided into the “Lower Irrawaddy” and “Upper Irrawaddy” based on the lithological and paleontological criteria (Stamp, 1922; Colbert, 1938; Bender, 1983). The Lower Irrawaddy consists of cross-bedded sandstones, gravels, and pebbly red mudstone layers with carbonate and iron concretions. The Upper Irrawaddy consists of abundant gravels and poorly consolidated sandstones with few red mudstone layers.

The geological age of the Irrawaddy sediments has been estimated by the correlation of the vertebrate faunas with those of the Siwalik Group of Indo-Pakistan. The Lower Irrawaddy has been correlated to the upper Miocene to lower Pliocene Dhok Pathan Formation of the Siwalik Group, although the base of the Lower Irrawaddy probably extends to the middle Miocene because the base yields some taxa of the Chinji Formation of the Siwalik Group (Cotter, 1938; Bender, 1983; Chavasseau et al., 2006). The Upper Irrawaddy has been conventionally correlated to the lower Pleistocene (Colbert, 1938, 1943; Bender, 1983). However, its fauna shows close resemblance to the faunas of the Tatrot and Pinjor Formations of the Siwalik Group, suggesting an upper Pliocene to lower Pleistocene correlation for the Upper Irrawaddy sediments (Zin-Maung-Maung-Thein et al., 2008).

The new bird specimens come from the Irrawaddy sediments at the SLG1 locality (21°21'02"N; 94°40'12"E), Sulegon Village (SLG = Sulegon), Pauk Township, Magway (= Magwe) Region, western part of central Myanmar (Figure 1; Zin-Maung-Maung-Thein et al., 2010; Tsubamoto et al., 2012). Geologically, it is located in the eastern part of the N-S trending axis of the Salin Syncline (Figure 1). The upper Miocene to the lower Pleistocene massive sandstones and gravels of the Irrawaddy sediments are exposed in the central

part, whereas the Miocene to Eocene deposits crop out in the eastern and western limbs of the syncline (Figure 1). The sediments of the syncline are estimated to be more than 9,000 m thick, containing lithic sandstones that alternate with the transgressive shallow marine shales (Trevena et al., 1991). The sedimentary facies and paleocurrent studies indicate a presence of north to south prograding tidal deltas (Rodolfo, 1975; Trevena et al., 1991). The SLG1 locality yielded some molluscan fossils, such as the freshwater gastropod *Melannoides* and freshwater bivalves *Radiatula* and *Parreysia* (Ugai et al., 2006).

The SLG1 locality has produced two bird bones, in addition to a larger sample of mammalian fossils. The Irrawaddy sediments at the SLG1 locality are assigned to the Upper Irrawaddy sediments. The sediments at the locality produced several mammalian fossils represented by indeterminate Bovidae, the suid *Sivachoerus prior*, the anthracotheriid *Merycopotamus dissimilis*, the rhinoceros *Dicerorhinus* sp. cf. *D. sumatrensis* sp., and the proboscidean *Stegodon* sp. (Zin-Maung-Maung-Thein et al., 2010; Tsubamoto et al., 2012). This faunal assemblage has been correlated with the Tatrot and Pinjor Formations of the Siwalik Group, suggesting an age of the Pliocene to early Pleistocene (Zin-Maung-Maung-Thein et al., 2010). The presence of *Sivachoerus prior* potentially indicates a solely Pliocene age of this fauna (Tsubamoto et al., 2012), but Barry and others (2013) state the stratigraphic range of that species as 3.5 to 2.1 Ma, Pliocene to early Pleistocene. The stratigraphic range of the anthracotheriid *Merycopotamus dissimilis* in Pakistan is 7.8 – 3.3 Ma (Barry et al., 2013), and the oldest *Dicerorhinus* sp. cf. *D. sumatrensis* from Myanmar is thought to be approximately 3 Ma (Zin-Maung-Maung-Thein et al., 2010). Furthermore, Badgley et al. (2008) hypothesized that the *Merycopotamus* lineage may have survived to 2.2 Ma, as opposed to its last recorded appearance datum at 3.3 Ma. Given those various stratigraphic ranges across Asia, it would seem likely that the Sulegon-1 locality sediments and fossils derive from the later part of the Pliocene (~3 – 4 Ma).

Repository Information

The designation “NMMP-KU-IR” stands for the National Museum of Myanmar Paleontology-Kyoto University-Irrawaddy. The fossil bird specimens currently are housed in Southern Branch, the National Museum and Library Department (formerly Department of Archaeology), Ministry of Cul-

ture, Yangon, Myanmar. These specimens were collected by the Kyoto University (Japan) and Myanmar Government Joint Paleontological Expedition in February 2005. MVZ – Museum of Vertebrate Zoology, University of California, Berkeley, USA. NMNH – National Museum of Natural History, Washington, D.C., USA.

SYSTEMATIC PALEONTOLOGY

Order CICONIIFORMES Bonaparte, 1854

Family ARDEIDAE Leach, 1820

Tribe cf. NYCTICORACINI Bock, 1956

Figure 2

Specimen. NMMP-KU-IR 0343 is a distal tarsometatarsus.

Description. The specimen is the distal end of a right tarsometatarsus broken near where the facet for metatarsal I would be positioned (Figure 2). The distal mediolateral width of the specimen is 10.1 mm, and the mediolateral width of trochlea III is 3.1 mm. The specimen is fractured through the shaft near its preserved midpoint, and the distal and lateral portions of trochlea IV are missing. The trocheleae have a spongy appearance that could indicate a subadult ontogenetic age of this individual, or could be the result of wear or even acid etching (e.g., from the action of a carnivore’s digestive system).

Trochlea II extends distal to trochlea IV, and it is much wider (mediolaterally) than trochlea IV. The area where the dorsal opening of the distal foramen should be is obscured, but the plantar opening is small and near the same proximodistal level as the proximal end of the plantar ridge extending from the base of trochlea II. The furrow on trochlea III extends from the plantar proximal end onto the dorsal surface, but the furrow does not reach the dorsal proximal end. The furrow is restricted to the plantar surface in trochlea II. Proximal to the plantar base of trochlea II is a short ridge and groove that are oriented from distomedial to proximolateral (Figure 2.5). The medial side of trochlea II is concave, and in dorsal view, the proximal end of trochlea II distinctly projects medial to the medial edge of the shaft. In distal view, trochlea III extends plantar to trochlea II, and the dorsal part of trochlea II is mediolaterally wider than its plantar portion. The lateral side of the shaft proximal to trochlea IV is relatively flat, and there is a slight ridge extending proximal from the lateral proximal base of the broken trochlea IV. The lateral intertrochlear incision is relatively shallow compared to the distal extension of the preserved part of trochlea IV. The proximal end of the specimen is near where the facet for

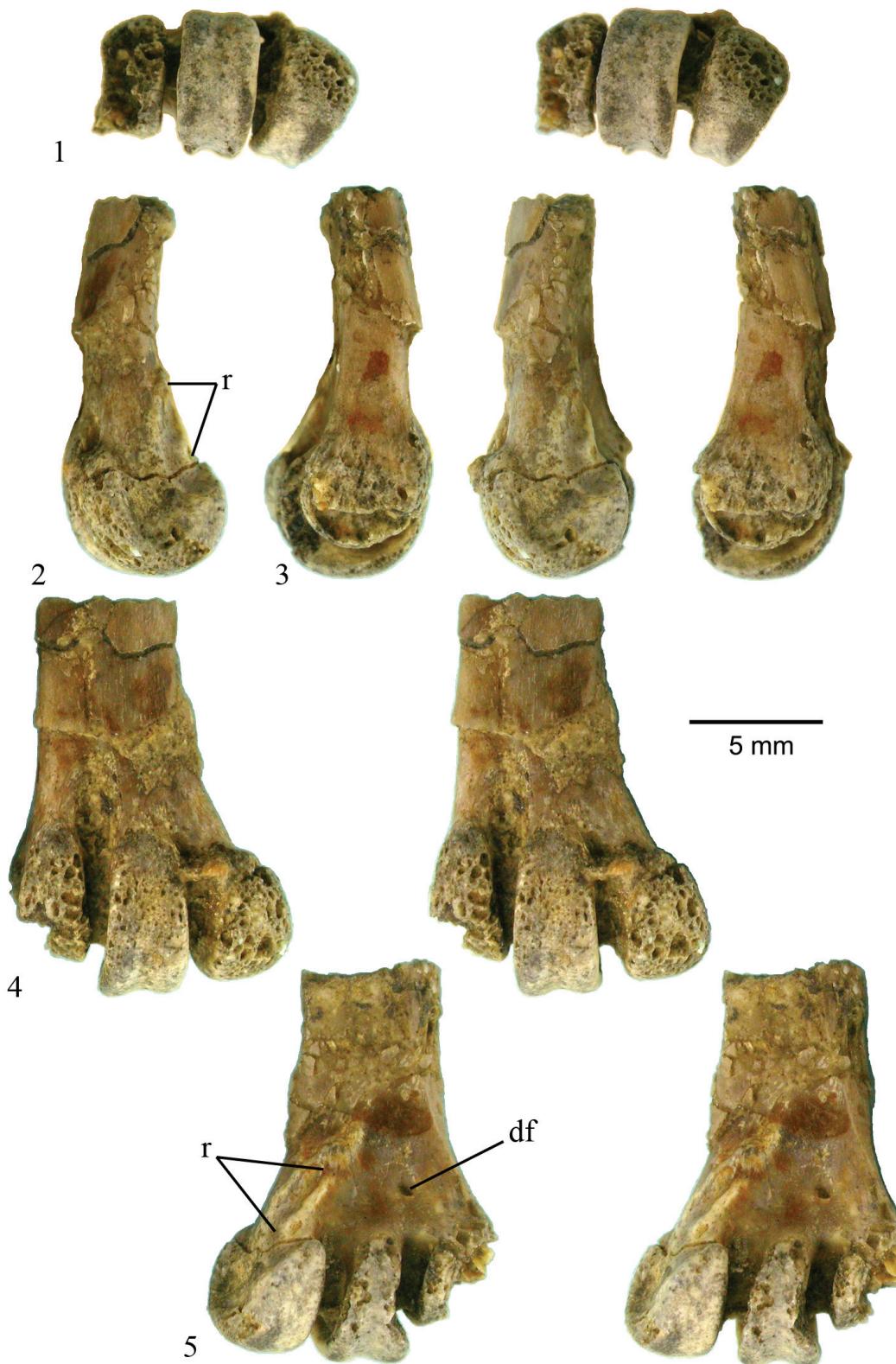


FIGURE 2. Stereophotograph pairs of the night heron distal tarsometatarsus (NMMP-KU-IR 0343) from the SLG1 locality, Myanmar. **1**, distal view; **2**, medial view; **3**, lateral view; **4**, dorsal view; **5**, plantar view. Abbreviations: df – distal foramen; r – ridge.

metatarsal I would be, and it is not clear if the facet was present or not.

Comparisons. Scofield et al. (2010) and Worthy et al. (2013) utilized many tarsometatarsus characters in their analyses of fossil heron and bittern specimens. Several of these characters are present and observable in this fossil. Trochlea IV is damaged, but the preserved portion of the dorsal aspect does not preserve any evidence of a trochlear furrow (Scofield et al., 2010; Worthy et al., 2013; character 1), although a furrow may have been present in the missing portion. The trochlear furrow of trochlea III is strong all the way to its proximal plantar end (Scofield et al., 2010; Worthy et al., 2013; character 2 - state 2). That state does not occur in *Ardea* and *Egretta* (Scofield et al., 2010). The area where the dorsal opening of the distal foramen would be is obscured in the fossil (Scofield et al. 2010; character 3). The dorsal opening of the foramen is either absent or very small (states 0 or 1) because it likely would be visible if it was large. The obscured dorsal opening (if present) of the distal foramen means that characters 3, 4, and 5 cannot be assessed. Trochlea III is oriented in parallel with the shaft of the tarsometatarsus (Scofield et al., 2010; Worthy et al., 2013; character 6 - state 0). That state is present in *Nycticorax*, *Nyctanassa*, *Pilherodius*, and *Tigrisoma*, and absent in *Ardea*, *Egretta*, *Botaurus*, *Ixobrychus*, and *Cochlearius* (Scofield et al., 2010). Trochlea II protrudes abruptly (with the dorsomedial proximal edge extending distinctly medially) from the medial side of the shaft (Scofield et al., 2010; Worthy et al., 2013; character 7 - state 2). That state is present in the night herons, *Pilherodius*, and *Tigrisoma*, and is absent in other herons (Scofield et al., 2010). The plantar rim of trochlea IV is missing, and character 8 of Worthy et al. (2013) cannot be coded. Although broken, it does not appear that trochlea IV protrudes laterally beyond the shaft, or only protruded very slightly (Scofield et al., 2010; character 8 - state 0; Worthy et al., 2013; character 9 - state 0 or 1). That morphology is present in *Nycticorax*, *Nyctanassa*, *Ardea ibis*, *Pilherodius*, *Botaurus*, *Ixobrychus*, and *Cochlearius*, and absent in *Egretta*, other species of *Ardea*, and *Tigrisoma* (Scofield et al., 2010). Worthy et al. (2013) consider their version of the character as variable within night herons (i.e., states 0 and 1). The length of trochlea IV is very short distal to the intertrochlear incision relative to the width of the lateral intertrochlear incision (Worthy et al., 2013; character 10 - state 0). That state is present in night herons, *Ardea*, *Botaurus*,

Egretta, and others (Worthy et al., 2013). It is unclear if there was a facet for metatarsal I since the bone is broken near where that facet would occur (Scofield et al., 2010; character 9; Worthy et al., 2013; character 11). The area between where the metatarsal I facet and the plantar base of trochlea II appears to be relatively flat, although the bone is broken through the shaft in that area (likely state 0 of character 12 of Worthy et al., 2013). Given the published phylogenetic distribution of those characters (above), the combination of features preserved in the Sulegon fossil are consistent only with *Nycticorax*, *Nyctanassa*, and *Pilherodius*. Those three taxa form a clade in Scofield and coauthor's (2010) work and suggests that this fossil belongs to that clade (which includes the night herons). However, Worthy et al. (2013) did not recover a monophyletic grouping of the night herons. Instead, they form a paraphyletic stem at the base of Ardeidae (Worthy et al., 2013).

The Myanmar fossil is very similar to *Nycticorax caledonicus pelewensis* and *Gorsachius melanolophus*. The distal mediolateral width of *N. caledonicus pelewensis* (MVZ 95061) is 10.5/10.7 mm (left/right side) with a trochlea III width of 3.0 mm (left and right sides). That is close to the 10.1 and 3.1 mm equivalent measurements in the Sulegon fossil. There are no recognizable morphological differences with *Gorsachius melanolophus* (USNM 488330), except that the fossil is very slightly larger than the extant specimen (distal mediolateral width is 9.7/9.6 mm and trochlea III mediolateral width 5.2/5.3 mm). With those measurements, the proportions of the trochlea III as compared to the width of the distal end appear more consistent between the Myanmar specimen and *Nycticorax* rather than that in *Gorsachius*. *Nycticorax nycticorax hoactli* has a plantar end of trochlea III wider than the fossil, and the dorsal proximal end is pointed (unlike the fossil). The early Pliocene purported night heron, *Nyctanassa kobdoena* from Mongolia, has deeper and wider intercondylar incisions than the states in the Sulegon specimen, and its generic assignment is in question (Zelenkov, 2013). The Myanmar fossil is much bigger than *Ixobrychus* spp., and the second trochlea in those species is relatively smaller than the state in the fossil. *Tigrisoma mexicanum* (MVZ 85515) has a fossa around the distal foramen (dorsal side) that is much deeper than that in the fossil (no depression visible). *Tigrisoma* also has a ridge on the plantar base of trochlea II that is more elongate, and overall the species is larger than the fossil. The ridge proximal to the plantar side of

trochlea II is more robust in *Egretta i. intermedia* (MVZ 124052) and *E. novaehollandiae* (MVZ 143281). In *Botaurus lentiginosus* (MVZ 151604), the proximal plantar end of trochlea III is very wide (vs. the more narrow condition in the fossil), and trochlea IV is projected more laterally than the fossil (also in *Bulbulcus i. ibis* MVZ 164538). The proximal end of trochlea III in *Bulbulcus i. ibis* is more pointed than the condition in the fossil. *Buteorides anthonyi* (MVZ 74758) is similar in morphology to the fossil but is smaller (distal mediolateral width 7.0 mm).

Family CICONIIDAE Sundevall, 1836

Figure 3

Specimen. NMMP-KU-IR 0355 is a crushed left distal tibiotarsus.

Description. The specimen is crushed mediolaterally, but has a preserved mediolateral width of 18.3 mm (and a maximum preserved craniocaudal depth of 27.4 mm). The proximal end of the ossified supratendinal bridge is obscured, and the extensor groove is not clearly visible (Figure 3). The lateral condyle extends proximal to the medial condyle. The intercondylar tubercle (= tuberculum ligamenti tibiometatarsale intercondylare of Smith et al. [2013] and tubercle for the attachment of ligamentum meniscotibiale intertarsi of Zinoviev [2013]) is larger and roughly in the shape of a rounded square in outline. It is clearly visible in distal view within the intercondylar incision, and the tubercle is at the same proximodistal level as the distal edge of the ossified supratendinal bridge. The tubercle projects far cranially and can be seen in lateral view extending cranial to the proximal end of the lateral condyle. The medial surface of the medial condyle is deeply concave, and there is a raised area (not quite an epicondyle) adjacent to the proximal end of the medial condyle. There is no evidence of a groove for m. fibularis on the cranial-lateral corner of the shaft, but there is a short proximally directed ridge proximal and slightly lateral to the intercondylar tubercle (presumably for attachment of the extensor retinaculum). The extensor groove opens distally into the intercondylar incision (fossa), and the distal edge of the intercondylar tubercle forms part of the proximal edge of that incision (fossa). The intercondylar fossa cuts into the lateral surface of the medial condyle and appears to indent the medial side of the lateral condyle just distal to the intercondylar tubercle. The result is that the proximal end of the medial condyle appears to narrow proximally (in cranial view), while the lateral condyle extends to join with the intercondylar tubercle. The lateral condyle is

deeply concave on its lateral face, and there is a low craniocaudally elongate ridge that maybe equivalent to a lateral epicondyle in that concave area. Near the craniocaudal midpoint of the distal edge of the lateral condyle is a shallow notch that extends onto the distal face of the bone. The area where a corresponding notch would be (if present) on the medial condyle is broken with a chip of bone missing. The distal face of the specimen is fractured, and bone near the center is missing. The intercondylar incision appears to have extended to the distal face, but the preserved articulation for the tibial cartilage on the caudal face is relatively flat except for a slightly concave area preserved on the medial edge. Though broken, it appears that the proximal end of the articulation for the tibial cartilage extended medially and laterally well beyond the shaft of the tibiotarsus, and that articulation's proximal end has a rounded outline. The caudal part of the preserved shaft is crushed, and it appears that some bone is also missing from the area since it is much narrower than the cranial portion (even given the crushing of the entire specimen).

Comparisons. The stork specimen shares the presence of a large centrally positioned intercondylar tubercle, large size, semi-rounded intercondylar fossa, and other features with extant (and extinct) storks. However in general, the Sulegon stork has more square profile to the intercondylar tubercle (than the more mediolaterally elongate state in many storks) and has a less pronounced medial epicondyle (than the state in many storks, see below for details). It might represent an undescribed species, but as the specimen is preserved, that cannot be definitively determined.

The stork *Anastomus l. lamellaigerus* (MVZ 133407) is much smaller than the fossil. In addition, the intercondylar tubercle is larger and more rounded than the state in the fossil. *Ciconia abdimii* (MVZ 133692) is much smaller than the fossil. Its medial epicondyle is much larger than the fossil, and its intercondylar tubercle is not as prominent and rounded as the state in the fossil. The lateral epicondylar fossa is deeper in the fossil than in *Ciconia*. *Ephippiorhynchus senegalensis* (MVZ 140361) is approximately the same size as the fossil. In cranial view, the medial condyle differs from the fossil since its proximal end is more triangular in shape/outline, and there is a pit on the proximal end of the lateral condyle that appears to be absent in the Sulegon specimen. In *Jabiru mycteria* (MVZ 133932), the intercondylar tubercle is more elongate, and the medial epicondyle is much larger

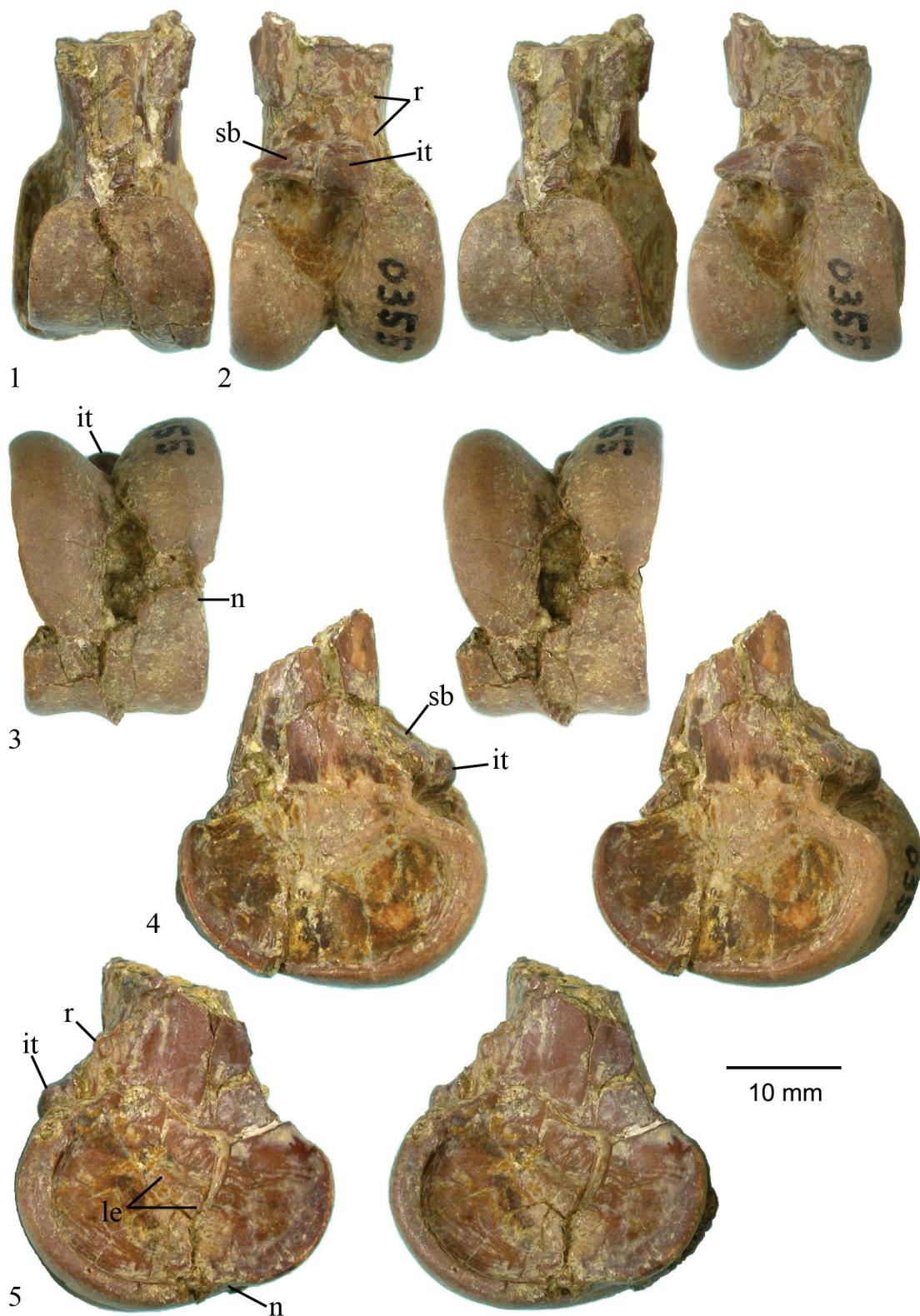


FIGURE 3. Stereophotograph pairs of the stork distal tibiotarsus (NMMP-KU-IR 0355) from the SLG1 locality, Myanmar. **1**, caudal view; **2**, cranial view; **3**, distal view; **4**, medial view; **5**, lateral view. Abbreviations: it – intercondylar tubercle; le – lateral epicondyle; n – notch; r – ridge; sb – supratendinal bridge.

than in the Myanmar fossil. In *Leptoptilos crumeniferus* (MVZ 134058), the intercondylar tubercle is more elongate, and the medial epicondyle is larger than the states in the fossil. *Mycteria americana* (MVZ 24920) is smaller than the Sulegon specimen, its intercondylar tubercle also is mediolaterally elongate, and the medial epicondyle is larger too.

Louchart et al. (2005) provides a thorough review of the fossil record of large-bodied storks, but that review does not illuminate any individual characters that would help to narrow the identification of this fossil specimen to species level. Furthermore, the recent phylogenetic analysis of storks by de Pietri and Mayr (2014) includes a single tibiotarsus character (the presence or absence of the intercondylar tubercle), and as a result does not aid in the taxonomic or phylogenetic placement of the Myanmar specimen within Ciconiidae.

The Myanmar specimen lacks the medial projection (cranial view) just proximal to the medial condyle that is illustrated for specimens referred to *Leptoptilos falconeri* from the Pliocene (Louchart et al., 2005, figure 1). That morphology results in a concave medial margin of distal end of the bone in *L. falconeri*, and there is a flat (or flatter) margin in the Myanmar specimen and *L. dubius*. Specimens of *L. robustus* do not preserve that region of the bone (Meijer and Due, 2010). In addition, with a larger sample size of the extant species, that character might be found to be variable, as so many other characters within stork species are variable (e.g., Louchart et al., 2005). It appears that the intercondylar tubercle is a bit more laterally positioned in the Myanmar specimen as compared to the more central position in fossil *Leptoptilos* (Louchart et al., 2005; Meijer and Due, 2010), but that could be the result of the mediolateral crushing that the Sulegon specimen experienced.

The (uncrushed) distal craniocaudal depth of the distal tibiotarsus is smaller in the Myanmar specimen (27.4 mm) than the specimens referred to *L. falconeri* (larger than 30 mm; Louchart et al., 2005, figure 5). Overall, the Myanmar specimen is similar in size (distal depth 27.4 mm and distal crushed mediolateral minimum width of 18.3 mm) with the extant species in *Ephippiorhynchus*, *Leptoptilos*, and *Jabiru* (Louchart et al., 2005, table 2). Given that the new fossil is mediolaterally crushed, the ratio of the distal depth to distal width cannot be calculated accurately (as preserved it is 1.49), and thus the ratio cannot be compared directly to that of *Ephippiorhynchus* and *Leptoptilos* (e.g., Louchart et al., 2005). Given the distal depth of the bone

and a likely increase in its distal width (by 2 mm or so) when uncrushed, the fossil probably would fall into the *Ephippiorhynchus* and *Leptoptilos dubius* portion of the graph provided by Louchart et al. (2005, figure 5), but not into the region occupied by the 'giant' extinct storks. The Myanmar fossil is relatively close in size with the holotype of *Cryptociconia indica* (Harrison, 1974) that was reassigned as *Leptoptilos dubius/falconeri* by Louchart et al. (2005), and correspondingly appears to fall outside of the size range for the very large or 'giant' storks of the Neogene and Pleistocene (e.g., *L. falconeri*, *L. titan*, and *L. robustus*). There are no hindlimb limb bones known from *L. lüi*, and thus no comparisons can be made to the Sulegon specimen. However, given the very large size of the distal humerus in *L. lüi* (Zhang et al., 2012), it is very unlikely that this smaller leg bone belongs to the same species. In summary, there are no features preserved that distinctly suggest a phylogenetic position of this specimen with a particular genus group (i.e., *Ephippiorhynchus* or *Leptoptilos*), but its large size is suggestive that it belongs among the taxa placed in Leptoptilini. In addition given its smaller overall size (compared to the 'giant' storks), it is possible that the Myanmar specimen is referable or related to extant species that occur in Asia today.

DISCUSSION

The Sulegon night heron specimen (as preserved) is not readily distinguishable from that of *Nycticorax caledonicus* and *Gorsachius melanophous*, and it is possible that the fossil derives from one of those species, other species in those genera, a currently unknown extinct species in the night heron group, or even an extinct species of *Nyctanassa* (a group from North America). Species of the night herons *Nycticorax* and *Gorsachius*, and the large storks *Leptoptilos* and *Ephippiorhynchus* occur in Myanmar (and more broadly in southeastern Asia) today, occupying mangrove, swamps, marshes, and wet areas in forested habitats (Robson, 2008). Given the inferred tidal delta depositional environment of the fossil-bearing sediments (above), the presence of a night heron and a stork is not unexpected in that paleoenvironment. Hopefully, future finds of large, but not 'giant' storks in southeastern Asia will aid in the reconstruction of the evolutionary history of the region's extant species, but this stork fossil demonstrates that smaller-sized species occurred at the same time as the very large species in southern Asia. Furthermore, the presence of relatives or members of extant lin-

eages of birds in the Pliocene of Myanmar potentially may indicate some level avifaunal stability over the last few million years, but the story of the evolutionary history of birds in the region will be written with future avian fossils.

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