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Hanneke J. M. Meijer [a] [b] [f] , Thomas Sutikna [c] [d] , E. Wahyu Saptomo [c] , Rokhus Due Awe [c] ,
Jatmiko [c] , Sri Wasisto [c] , Helen F. James [a] , Michael J. Morwood [d] & Matthew W. Tocheri [e]

[a] Division of Birds, Department of Vertebrate Zoology , National Museum of Natural History,
Smithsonian Institution , Washington , D.C. , 20013-7012 , U.S.A.

[b] Naturalis Biodiversity Center , Darwinweg 2, 2333 , CR Leiden , The Netherlands

[c] The National Research and Development Centre for Archaeology , Jl. Raya Condet Pejaten
No. 4, Jakarta , 12510 , Indonesia

[d] GeoQuEST Research Centre, School of Earth and Environmental Sciences , University of
Wollongong , Wollongong , New South Wales , 2522 , Australia

[e] Human Origins Program, Department of Anthropology , National Museum of Natural History,
Smithsonian Institution , Washington , D.C. , 20013 , U.S.A.

[f] Institut Català de Paleontologia Miquel Crusafont , 08193 Cerdanyola del Vallès,
Barcelona , Spain
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LATE PLEISTOCENE–HOLOCENE NON-PASSERINE AVIFAUNA OF LIANG BUA (FLORES, INDONESIA)

HANNEKE J. M. MEIJER,*,[1,2,†] THOMAS SUTIKNA,[3,4] E. WAHYU SAPTOMO,[3] ROKHUS DUE AWE,[3] JATMIKO,[3] SRI WASISTO,[3] HELEN F. JAMES,[1] MICHAEL J. MORWOOD,[4] and MATTHEW W. TOCHERI[5]

[1]Division of Birds, Department of Vertebrate Zoology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A., hanneke.meijer@icp.cat; jamesh@si.edu;
[2]Naturalis Biodiversity Center, Darwinweg 2, 2333 CR Leiden, The Netherlands;
[3]The National Research and Development Centre for Archaeology, Jl. Raya Condet Pejaten No. 4, Jakarta 12510, Indonesia, thomasutikna@yahoo.com; wahyu_saptomo@yahoo.com; ako_jatmiko90@yahoo.com; sriwasisto@yahoo.com;
[4]GeoQuEST Research Centre, School of Earth and Environmental Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia, mikem@uow.edu.au;
[5]Human Origins Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013, U.S.A., tocherim@si.edu

ABSTRACT—Liang Bua, a limestone cave on the Indonesian island of Flores, has a depositional sequence that spans the last 95,000 years and includes well-preserved faunal remains. Birds are well represented throughout the stratigraphic sequence at Liang Bua. Here, we present the results of the first comprehensive study of avian remains retrieved from Sector XI, a 2 m by 2 m archaeological excavation along the east wall of the cave. A total of 579 specimens were identified as avian, with 244 belonging to at least 26 non-passerine taxa in 13 families. The late Pleistocene assemblage (23 taxa) includes the first recorded occurrence of vultures in Wallacea, as well as kingfishers, snipes, plovers, parrots, pigeons, and swiftlets. Together, these taxa suggest that during this time the surrounding environment was floristically diverse and included several habitat types. Two of these taxa, the giant marabou *Leptoptilos robustus* and the vulture *Trigonoceps* sp., are extinct. Eight taxa were identified in the Holocene assemblage, and five of these were also present in the late Pleistocene. Imperial pigeons *Ducula* sp. and the Island Collared Dove *Streptopelia* cf. *bitorquata* appear only in the Holocene assemblage. The differences in faunal composition between the late Pleistocene and Holocene assemblages may reflect a change in avifaunal composition due to climatic and environmental changes near the Pleistocene–Holocene transition, possibly amplified by impacts associated with the arrival of modern humans; however, the small Holocene sample prevents a firm conclusion about faunal turnover from being made.

INTRODUCTION

Wedged between the large continental landmasses of Indo-Malaysia and Australasia, Wallacea constitutes a transitional faunal zone containing species of both Indo-Malayan and Australasian origins (Wallace, 1869; Mayr, 1944; Coates and Bishop, 1997). In addition, the isolation of the Wallacean islands resulted in the evolution of many endemic species. For birds alone, Wallacea hosts 249 endemic species (Coates and Bishop, 1997). Despite harboring exceptional levels of species richness and unique biotic assemblages (Myers et al., 2000), Wallacean biogeography remains poorly known because of the lack of well-supported phylogenies of Wallacean taxa and their continental relatives, uncertainties about the geological history of the region, and the patchy fossil record.

Excavations at Liang Bua on the Indonesian island of Flores (Fig. 1) have revealed a stratigraphic sequence that spans the last 95,000 years and contains large numbers of well-preserved faunal remains (Morwood et al., 2004; Roberts et al., 2009; van den Bergh et al., 2009; Westaway et al., 2009a). The late Pleistocene layers bear evidence of an insular fauna with many likely endemics, including pygmy elephants (*Stegodon florensis insularis*), small-bodied hominins (*Homo floresiensis*), Komodo drag-

ons (*Varanus komodoensis*), giant marabou storks (*Leptoptilos robustus*), and a diverse set of murid and chiropteran taxa (Brown et al., 2004; Morwood et al., 2004, 2005; van den Hoek Ostende et al., 2006; van den Bergh et al., 2008, 2009; Hocknull et al., 2009; Morwood and Jungers, 2009; Meijer and Due, 2010; Meijer et al., 2010). Of these likely endemics, only the rats, bats, and Komodo dragons continue into the Holocene layers that also document many new arrivals, including modern humans, pigs, civet cats, macaques, and porcupines (Hocknull et al., 2009; van den Bergh et al., 2009).

Liang Bua's faunal record provides an opportunity to reconstruct past biodiversity and the processes that gave rise to current distribution patterns in a biodiversity hotspot. To date, the remains of *H. floresiensis*, *S. florensis insularis*, and *V. komodoensis* have received considerable attention and overshadowed other important components of the Liang Bua faunal assemblage (Brown et al., 2004; Morwood et al., 2004, 2005; Larson et al., 2007; Tocheri et al., 2007; van den Bergh et al., 2008, 2009; Hocknull et al., 2009; Jungers et al., 2009; Morwood and Jungers, 2009). Birds can be fairly specific in their habitat requirements (Rasmussen et al., 1987), and thus can provide important insights into the paleoenvironment that these birds shared with *Homo floresiensis*.

Here we present the first faunal analysis of the bird remains from Liang Bua using the assemblage from Sector XI, a 2 × 2 m area that was excavated in 10-cm spits to 9 m depth in 2004 and yielded additional hominin remains attributed to the

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*Corresponding author.
†Current address: Institut Català de Paleontologia Miquel Crusafont, 08193 Cerdanyola del Vallès, Barcelona, Spain.
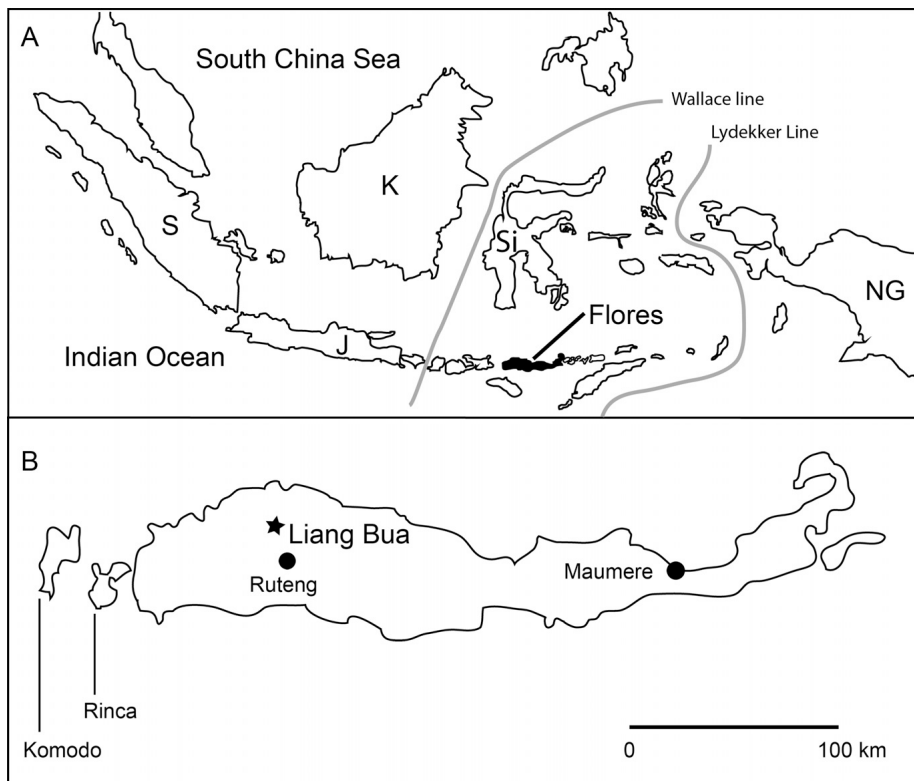
FIGURE 1. Map of Indonesia. **A**, location of Flores within Insular Southeast Asia. Gray lines denote the western and eastern limits of Wallacea by respectively the Wallace Line and the Lydekker Line; **B**, map of Flores with the location of Liang Bua. **Abbreviations**: **J**, Java; **K**, Kalimantan; **NG**, New Guinea; **S**, Sumatra; **Si**, Sulawesi.

holotype of *H. floresiensis*, as well as additional individuals (Brown et al., 2004; Morwood et al., 2004, 2005; Morwood and Jungers, 2009). This sector preserved both Holocene and late Pleistocene deposits, which occur above and below a distinctive layer of black tuffaceous silts (BTS), respectively (Roberts et al., 2009; Westaway et al., 2009b). Sector XI forms the southeast corner of a 4 × 4 m excavation in conjunction with Sectors VII, XV, and XVI (to the north, west, and northwest, respectively). Eight main stratigraphic units are now recognized within this 4 × 4 m square and six of these are present in Sector XI: Unit 1 (Spits 1–10), Unit 2 (Spits 11–15), Unit 3 (Spits 16–30), Unit 6 (Spits 31–37), Unit 7 (Spits 38–53), and Unit 8 (Spits 54 and lower). Units 7 and 8 are Pleistocene deposits that occur clearly beneath the BTS, whereas Units 3 through 1 are Holocene deposits that occur above the BTS (Morwood et al., 2009; Morwood and Jungers, 2009; Roberts et al., 2009; Westaway et al., 2009b). Unit 6 encompasses an erosional boundary of the BTS and thus may contain a mix of Pleistocene and Holocene bone deposits. Avian remains are represented throughout and provide an important record of faunal events and taphonomic processes in and around Liang Bua, as well as the first reported paleontological record for Pleistocene birds in Wallacea.

MATERIALS AND METHODS

The Sector XI excavations yielded 579 bird bones, many of which are incomplete or fragmentary. These remains were recovered both in situ and through dry and wet sieving through 2 mm mesh, and were first identified as avian by R.A.D. and subsequently studied in more detail by H.J.M.M. Of these 579 elements, 167 consist of less diagnostic elements such as phalanges, vertebrae, and (long) bone fragments that could not be assigned below Aves. This paper treats only the non-passerines. Passerines will be treated elsewhere.

Taxonomic Identification

All material is housed at the National Research and Development Centre for Archaeology in Jakarta, Indonesia. Specimens were given a provisional registration number 'LB-Av-XX,' where 'LB' refers to Liang Bua, and 'Av' to Aves, and cataloged. Subsequently, bones were identified by reference to the avian skeleton collection at the Smithsonian Institution's National Museum of Natural History (NMNH) in Washington, D.C. Comparative material examined (Appendix 1) included skeletons of resident and migrant land bird species from Flores and adjacent regions (following Coates and Bishop, 1997; Verhoeye and Holmes, 1998; Mees, 2006). The systematic framework follows Howard and Moore's Checklist (Dickinson, 2003), except for Turnicidae, for which there is now strong support for placing them in Charadriiformes (Baker et al., 2007). Osteological terminology primarily follows Baumel and Witmer (1993) and also Howard (1929). Measurements were taken according to von den Driesch (1976). Juveniles were identified based on the porosity and texture of the bone surfaces. Average body mass (in grams) of each species was obtained from the literature (Dunning, 2008). In order to characterize the range of habitats represented (Sánchez-Marco, 1999) in the late Pleistocene and Holocene assemblages, each species was scored for habitat preference according to the 18 habitat types known to occur in Wallacea as listed in Coates and Bishop (1997). In cases where a species occurs in more than one habitat, each habitat was scored as 1/n. Adding up the scores for each habitat for the whole assemblage results in a habitat spectrum for each assemblage.

Taphonomic Analysis

Specimens were examined for signs of predation (digestion marks [following Andrews, 1990], gnawing marks, and cut marks) and other signs of postmortem bone modification. Bone

TABLE 1. Birds identified from Liang Bua's Sector XI deposits.

Taxon		NISP (relative abundance)					
		8	7	6	3	2	1
Anatidae	Anatidae, gen. et sp. indet.		1 (0.8%)				
Ciconiidae	*Leptoptilos robustus*†		22 (17.6%)	1 (6.3%)			
Accipitridae	*Haliastur* cf. *indus*		3 (2.4%)				
	Trigonoceps sp.*		17 (13.6%)	1 (6.3%)			
	Accipiter sp.	2 (5.1%)					
	Aquila sp.		1 (0.8%)		1 (3.4%)		
Rallidae	*Gallirallus* sp.		1 (0.8%)				
	Porzana sp.	2 (5.1%)					
Charadriidae	*Pluvialis fulva*		4 (3.2%)				
Scolopacidae	*Gallinago* sp.	10 (26%)	6 (4.8%)	1 (6.3%)			
	Actitis hypoleucos		2 (1.6%)				
Turnicidae	*Turnix* sp.	3 (7.7%)					
Columbidae	Columbidae, gen. et sp. indet.	1 (2.6%)		1 (6.3%)			1 (9%)
	Streptopelia cf. *bitorquata*						3 (30%)
	aff. *Macropygia/Ptilinopus*	2 (5.1%)	1 (0.8%)				
	Macropygia sp.	3 (7.7%)	2 (1.7%)				
	Ptilinopus sp.	1 (2.6%)					
	Ducula sp.				1 (3.4%)		
Psittacidae	*Geoffroyus* cf. *geoffroyi*		5 (4%)		2 (6.9%)		
Tytonidae	*Tyto* sp.(†)		5 (4%)				
Strigidae	Strigidae, gen. et sp. indet.					1 (14%)	
	Otus sp.		1 (0.8%)				
Apodidae	*Collacalia esculenta*	2 (5.1%)	2 (1.6%)				1 (10%)
	Aerodramus cf. *fuciphagus*	3 (7.7%)	49 (39.2%)	12 (75%)	25 (86%)	6 (86%)	5 (50%)
Alcedinidae	Halcyoninae, gen. indet.	3 (7.7%)	1 (0.8%)				
	Halcyon sp.	7 (18%)	2 (1.6%)				
Total		39	125	16	29	7	10

Number of identified species (NISP) and relative abundance (in parentheses) are organized by stratigraphic units 8–1. †, extinct species; (†), possibly extinct species; *, does not presently occur on Flores.

weathering stage (BWS) was scored according to Behrensmeyer (1978), where 0 represents the bone surface showing no sign of cracking or flaking at all, and 5 represents a bone falling apart in situ.

RESULTS

Taxonomic Identification

Of the 579 elements, 168 were identified to the order Passeriformes (songbirds) and 226 were identified to non-passerine genera or, when possible, species. The non-passerine remains represent at least 26 taxa in 13 families (Table 1). Additionally, 18 bones clearly belong to a large bird but were too fragmentary to assign at or below the family level. Twenty-three taxa were recorded in the Pleistocene sediments (Units 8–7), and eight in the Holocene (Units 3–1). Five taxa were present in both time periods.

SYSTEMATIC PALEONTOLOGY

AVES Linnaeus, 1758
ANSERIFORMES Wagler, 1830
ANATIDAE Leach, 1819
Gen. et sp. indet.
(Fig. 3A)

Referred Material—A distal right tarsometatarsus including trochlea metatarsi III and IV (LB-Av-388).

Horizon—Late Pleistocene (Spit 44).

Remarks—Although damaged, the trochlea metatarsi II is likely to have been shorter than trochlea metatarsi IV, which in turn is shorter than trochlea metatarsi III and inflated in lateral view. The foramen vasculare distale is set distally and the sulcus running proximomedially from the foramen is pronounced. Plantarly, the foramen vasculare distale opens into a groove that runs to the incisura intertrochlearis lateralis. This diagnoses the fossil

as anatid (Livezey, 1986; Worthy and Lee, 2008), but the fragment does not allow identification to genus level.

CICONIIFORMES Bonaparte, 1854
CICONIIDAE Gray, 1840
LEPTOPTILOS Lesson, 1831
LEPTOPTILOS ROBUSTUS Meijer and Due, 2010
(Fig. 3B)

Referred Material—A distal left tibiotarsus (LB-Av-155), a left proximal carpometacarpus (LB-Av-1), a left femur (LB-Av-140), and a distal left ulna (LB-Av-154) from Sector XI were previously described (Meijer and Due, 2010). We refer the following additional bones to *L. robustus*: the tip of a maxilla (LB-Av-2), a left and a right proximal scapula (LB-Av-126 and LB-Av-145), two furculae (LB-Av-139 and LB-Av-190; Fig. 3B), humeral (LB-Av-107) and ulnar (LB-Av-134, LB-Av-135, LB-Av-148 and LB-Av-156) fragments, a right proximal radius (LB-Av-115), two right ossi carpi radiales (LB-Av-105 and LB-Av-106), a distal right femur (LB-Av-149), long bone fragments (LB-Av-180), and four phalanges (LB-Av-141, LB-Av-142, LB-Av-181, and LB-Av-185).

Horizon—Late Pleistocene (Spits 52, 50, 48–43, and 36).

Remarks—At least two individuals (minimum number of individuals [MNI] = 2) are represented by the remains, based on the two right ossi carpi radiales. The maxillary tip is 18.6 mm long and the most proximal foramen neurovasculare ends rostrally in a small sulcus. The cristae tomiales are not distinct and the rostrum maxillare is flat, similar to extant *Leptoptilos*. The distal right femur (LB-Av-149) agrees well with LB-Av-140 (Meijer and Due, 2010). The radius (LB-Av-115) is slightly larger in size than *L. crumeniferus*. The cotyla humeralis is subcircular. Although damaged, the tuberculum bicipitalis radialis appears well developed and pneumatized. It differs in size from *Trigonoceps*, the only other large bird in the sequence, and in having a subcircular cotyla humeralis as in other storks, as opposed to
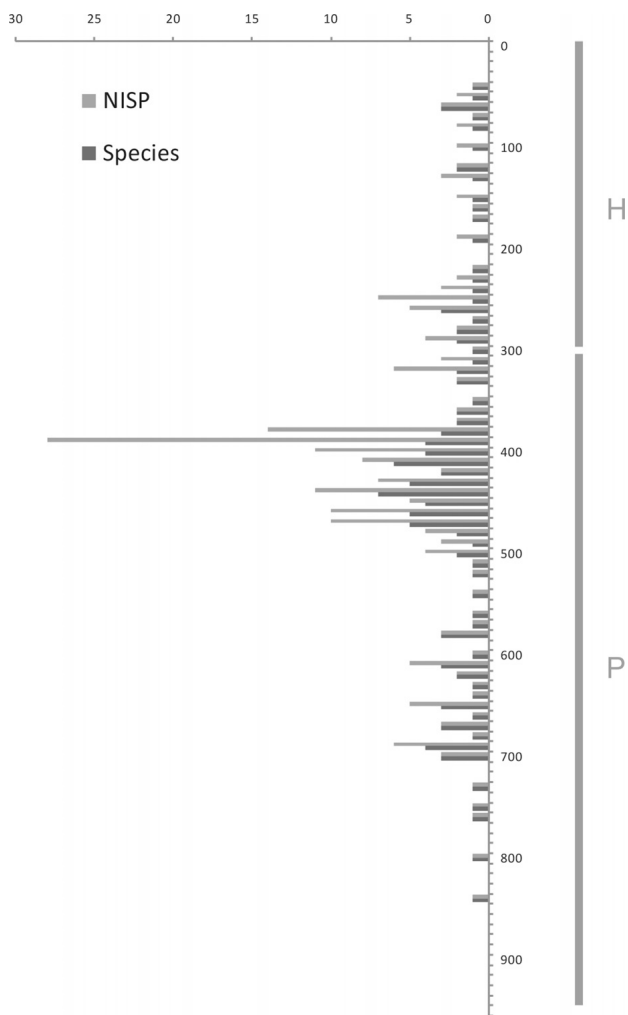
FIGURE 2. The abundance of bird remains and bird species by depth. Light gray bars denote number of identifiable specimens (NISP); dark gray bars denote the number of species at a given depth. Depth is given in cm. Holocene and Pleistocene levels are indicated by 'H' and 'P,' respectively.

and blunt, similar to that in other *Leptoptilos*. A humeral fragment, consisting of only the caput humeri (LB-Av-107), is preliminary referred to *L. robustus* because of its large size (mediolateral width of 37.6 mm). LB-Av-156 is a right ulnar midshaft fragment wherein the margo cranialis and a distinct nutrient foramen on the margo cranialis are visible on the specimen. Caudally, five papillae remigalis caudalis are visible. At the height of the foramen, the shaft measures 17.4 mm in diameter, compared with 15.5 and 17.2 mm in two *L. crumeniferus* specimens (USNM 489396 and USNM 489395, respectively). Ulnar fragments (recognized by the presence of papillae remigalis caudalis) with similar shaft curvatures as *L. crumeniferus* were found in Spits 46 (LB-Av-134), 48 (LB-Av-135), and 52 (LB-Av-148). The ossi carpi radiales are roughly triangular in shape. The dorsal surface bears a distinct and large pneumatic foramen in both specimens, similar to extant Leptoptilini. On the ventral surface, the facies articularis radialis is well developed and elongate. The facies articularis ulnaris is less elongate but distinctly deep in the center. Four phalanges terminales (LB-Av-141, LB-Av-142, LB-Av-181, and LB-Av-185) are stout and flattened (and therefore distinctly different from the other large-bodied bird *Trigonoceps* sp.) and show distinct sulci neurovasculari on the medial and lateral sides of the corpus phalangis.

ACCIPITRIFORMES Vieillot, 1816
ACCIPITRIDAE Vigors, 1824
HALIASTUR Selby, 1840
HALIASTUR cf. *INDUS* (Boddaert, 1783)
(Fig. 3C)

Referred Material—A distal left humerus (LB-Av-130), a proximal left humerus (LB-Av-193), and a distal right tarsometatarsus (LB-Av-342).

Horizon—Late Pleistocene (Spits 46 and 44).

Remarks—The remains represent at least one individual (MNI = 1). The distal humerus has a distinct fossa brachialis and a square-like processus supracondylaris dorsalis (Fig. 3C), which resembles that in *Haliastur indus* rather than in *Haliastur sphenurus*. Lateral to the fossa brachialis, the shaft is narrow and continues into the ridge-like tuberculum supracondylare ventrale. This feature distinguishes it from *Milvus* as well as *H. sphenurus*, in which the shaft bordering the fossa brachialis laterally is wider. The proximal humerus lacks the crista bicipitalis and the caput humeri, but agrees in overall morphology with both *Haliastur* and *Milvus*. However, considering its provenance from the same spit as the distal humerus (Spit 44), it likely belongs to the same individual, and is for now also referred to *Haliastur* cf. *indus*. The tarsometatarsus is similar in size to *H. indus*, and shares with that species a more distal position of small foramen vasculare distale (the foramen attains a more proximal position in *H. sphenurus*) and a less distally projecting trochlea metatarsi II (more distally projecting in *H. sphenurus*). Both the distal humerus and tarsometatarsus agree best in morphology with *H. indus* but are consistently larger than *H. indus* and in the size range of *H. sphenurus*. Sexual dimorphism in size can be significant in Accipitridae, but considering the morphological similarities, the fossils are referred to *Haliastur* cf. *indus*.

TRIGONOCEPS Lesson, 1842
TRIGONOCEPS sp.
(Fig. 3D)

Referred Material—Tip of a maxilla (LB-Av-422), a right (LB-Av-104) and a left distal tibiotarsus (consisting of two fragments, LB-Av-128 and LB-Av-132), a proximal right tarsometatarsus (LB-Av-119), a left and a right distal radius (LB-Av-530 and LB-Av-194), a left and a right os metacarpale major (LB-Av-120 and LB-Av-122), a fragment of a left distal coracoid (LB-Av-146), a fragmentary sternum (LB-Av-137), a distal fragment of a right

subtriangular in *Trigonoceps*. In both scapulae, the facies articularis humeralis is large with a distinct tuberculum coracoideum proximal to it. The acromion is damaged in both specimens, but appears well pronounced. The space between the facies articularis humeralis and the acromion is concave. In size, both scapulae are larger than *L. crumeniferus*, and in the size range of *L. dubius*. The specimens differ from *Trigonoceps* in several respects: larger size, a shorter and less expanded acromion (much more expanded and further projecting in *Trigonoceps* specimens), and the surface between the facies articularis humeralis and the acromion is concave (flat in *Trigonoceps*). The furcula (LB-Av-190) lacks the proximal halves of both claviculae (Fig. 3B). LB-Av-139 consists of only the left clavicula and the apophysis furculae. Both specimens are larger than *L. crumeniferus*, with LB-Av-139 being larger than LB-Av-190. In both specimens, the dorsal edge of the clavicula is sharp and ridge-like. The apophysis furculae is wide and flat (Fig. 3B), and in LB-Av-190 both claviculae join at the apophysis at an approximate angle of 75° (>90° in *Trigonoceps*). Although damaged in both specimens, the synostosis interclavicularis appears not to have been elongated or to project much ventrally (as it does in *Trigonoceps*) but is short

humerus (LB-Av-131), a right proximal scapula (LB-Av-189), and two phalanges (LB-Av-110 and LB-Av-151).

Horizon—Late Pleistocene (Spits 51, 49–47, 45, 44, 42, 41, 38, and 33).

Remarks—The tip of a maxilla (LB-Av-422) is high, has a distinct outer ridge, and a pronounced crista tomialis, in which it resembles *Trigonoceps* and *Torgos*. Both tibiotarsi agree with Aegypiinae, as opposed to other Accipitridae, in lacking a well-developed tuberculum retinaculum m. fibularis (Fig. 3D) and in having a more laterally placed distal opening of the tendinal canal. The tuberositas retinaculi extensori is positioned close to the tendinal bridge as in *Gyps* and *Trigonoceps*, and the specimens share a shallow distal surface between the internal and external condyles with *Gyps* and *Trigonoceps* (deeper in *Torgos* and *Gypaetus*). A proximal right tarsometatarsus (LB-Av-119) has a very short crista hypotarsi medialis that does not extend distally to the foramina vascularia proximalia, unlike *Gyps*. On the facies cranialis, the area proximal to the tuberositas m. tibialis cranialis bears a depression in *Torgos*, which is absent in *Gyps*, *Trigonoceps*, and LB-Av-119. In addition to these morphological similarities with *Trigonoceps*, the Liang Bua specimens also agree in size with *Trigonoceps*, which is distinctly smaller than *Gyps* and *Torgos*. Two distal radii (LB-Av-194 and LB-Av-530) are heavily pneumatized and a strong ridge separates the facies articulare ulnare from the depressio ligamentosa. LB-Av-194 differs from LB-Av-530 in having a much wider facies articulare ulnare, and a much less pronounced scar for the ligamentum radio-radiocarpale dorsale, and is large in size overall. However, the shape of the distal radius is variable in Aegypiinae and the described characteristics fall within the intraspecific variation observed in skeletons of extant species. The significant pneumatization of the radii agrees with larger Aegypiinae species and the specimen is therefore preliminarily referred to the same species represented by the other bones described above, assuming that *Trigonoceps* on Flores was as morphologically variable as extant vultures. Two ossi metacarpales majores (LB-Av-120 and LB-Av-122) lack both proximal and distal articular surfaces, but agree in overall morphology and size with *Trigonoceps*. A fragment of a distal coracoid (LB-Av-146) displays a long and narrow sternal facet. A fragmentary sternum (LB-Av-137), distal humeral fragment (LB-Av-131), a proximal scapula (LB-Av-189), and two phalanges (LB-Av-110 and LB-Av-151) all agree with *Trigonoceps* as well. Although this material was retrieved from a range of depths, at least one individual is represented (MNI = 1). Because the current range of the genus is restricted to Africa, and the only species within the genus, *Trigonoceps occipitalis*, is considered endemic to Africa, we refrain from assigning the Liang Bua specimens to species level until more material is recovered and analyzed.

ACCIPITER Brisson, 1760
ACCIPITER sp.
(Fig. 3E)

Referred Material—A left proximal carpometacarpus (LB-Av-492) and a distal right carpometacarpus (LB-Av-496).

Horizon—Late Pleistocene (Spits 64 and 60).

Remarks—The proximal carpometacarpus has a well-developed processus metacarpalis I and a deeply excavated area between the processus pisiformes and the processus metacarpalis I (less deep in Falconiformes) that undercuts the ventral ridge of the trochlea carpalis (Fig. 3E). The fossa infratrochlearis is deep and the ridge leading from the processus metacarpalis III to the pisiform process contains a small foramen, similar to that in *Accipiter* (absent in Falconidae). The proximal width measures 6.6 mm, which is close to the dimensions recorded for the world's smallest known accipitrid species, namely the African *Accipiter minullus* (7.1 mm, male), and the South American *A. s. superciliosus* (7.2 mm, female) and *Gampsonyx swainsonii* (6.5 mm, male). The fossil is smaller than the corresponding bones of females of the smallest *Accipiter* species that occur on Flores today, i.e., *A. soloensis* (8.0 mm, Fig. 3E) and *A. virgatus* (8.35 mm). LB-Av-492 differs from *G. swainsonii* in that the processus alularis is set more distal with regard to the processus pisiformis. Unfortunately, specimens of *A. nanus* and *A. erythropus* were not available for comparison. LB-Av-496 shares with Accipitridae the long and pointed facies articularis digitalis minor, which is shorter and blunt in Falconidae. It differs from *G. swainsonii*, and agrees with *Accipiter*, in lacking a distinct depression on the ventral side between the facies articularis digitalis major and the facies articularis digitalis minor. It does, however, differ from *Accipiter* in having a shorter facies articularis digitalis minor and a more slender symphysis metacarpalis distalis. LB-Av-496 is too fragmentary for any useful measurements, but is in the smaller end of the range for *A. minullus* and *A. superciliosus*. As sexual size dimorphism can be significant in Accipitridae, the specimens could represent a small (male) individual of one of the smaller extant species recorded from Flores, *A. soloensis* or *A. virgatus* (Verhoeye and Holmes, 1998; Mees, 2006), or they might represent a small, unknown species no longer present on Flores.

AQUILA Brisson, 1760
AQUILA sp.
(Fig. 3F)

Referred Material—A distal left radius (LB-Av-305) and a proximal right carpometacarpus (LB-Av-182).

Horizon—Late Pleistocene (Spit 42) and Holocene (Spit 29).

Remarks—The dorsal ridge of the trochlea carpalis is damaged. The processus extensorius and the processus alularis are both large and the processus extensorius curves farther proximally than in *Milvus* and *Haliastur* to end subequal with the trochleae carpalis. It differs from *Hieraaetus* in that in proximal view, the processus extensorius extends ventrally to a lesser degree. LB-Av-182 agrees with *Aquila* (Fig. 3F) in that the fossa between the trochlea carpalis and the processus metacarpalis I as well as the fossa between the processus pisiformes and the processus metacarpalis I are distinct, but not as deeply excavated as in *Hieraaetus*, *Haliaeetus*, and *Milvus*. We therefore feel justified assigning this specimen to *Aquila*, but the preserved features do not allow for identification to species level.

The distal radius displays affinities with the genus *Aquila*, but differs from extant species. The specimen is larger than *Spilornis*, *Machaeramphus*, *Circus*, *Aviceda*, *Pernis*, *Haliastur*, and *Milvus*, and in the size range of *Haliaeetus* and *Aquila*. The radius is not pneumatized, which distinguishes it from most Aegypiinae. The facies articulare radiocarpale is strongly developed and consists of two articular facets separated by a distinct notch that distinguishes it from extant *Aquila* and *Haliaeetus*. The medial facet is the largest, is square-like in shape, and overhangs the depressio ligamentum on the ventral side. The lateral facet is elongated, oriented mediolaterally, and does not extend ventrally. The square shape of the medial facet resembles that of *Aquila*, whereas it is more elongated and extends farther down the shaft in *Haliaeetus*. However, the specimen is more constricted mediolaterally than in *Aquila* and *Haliaeetus*. The material represents at least one individual (MNI = 1).

GRUIFORMES Bonaparte, 1854
RALLIDAE Rafinesque, 1815
GALLIRALLUS Lafresnaye, 1841
GALLIRALLUS sp.
(Fig. 3G)

Referred Material—A right coracoid (LB-Av-357) missing a small part of the processus lateralis.

Horizon—Late Pleistocene (Spit 41).

Remarks—The processus acrocoracoideus does not extend beyond the anterior edge of the cotyla scapularis, and is pointed
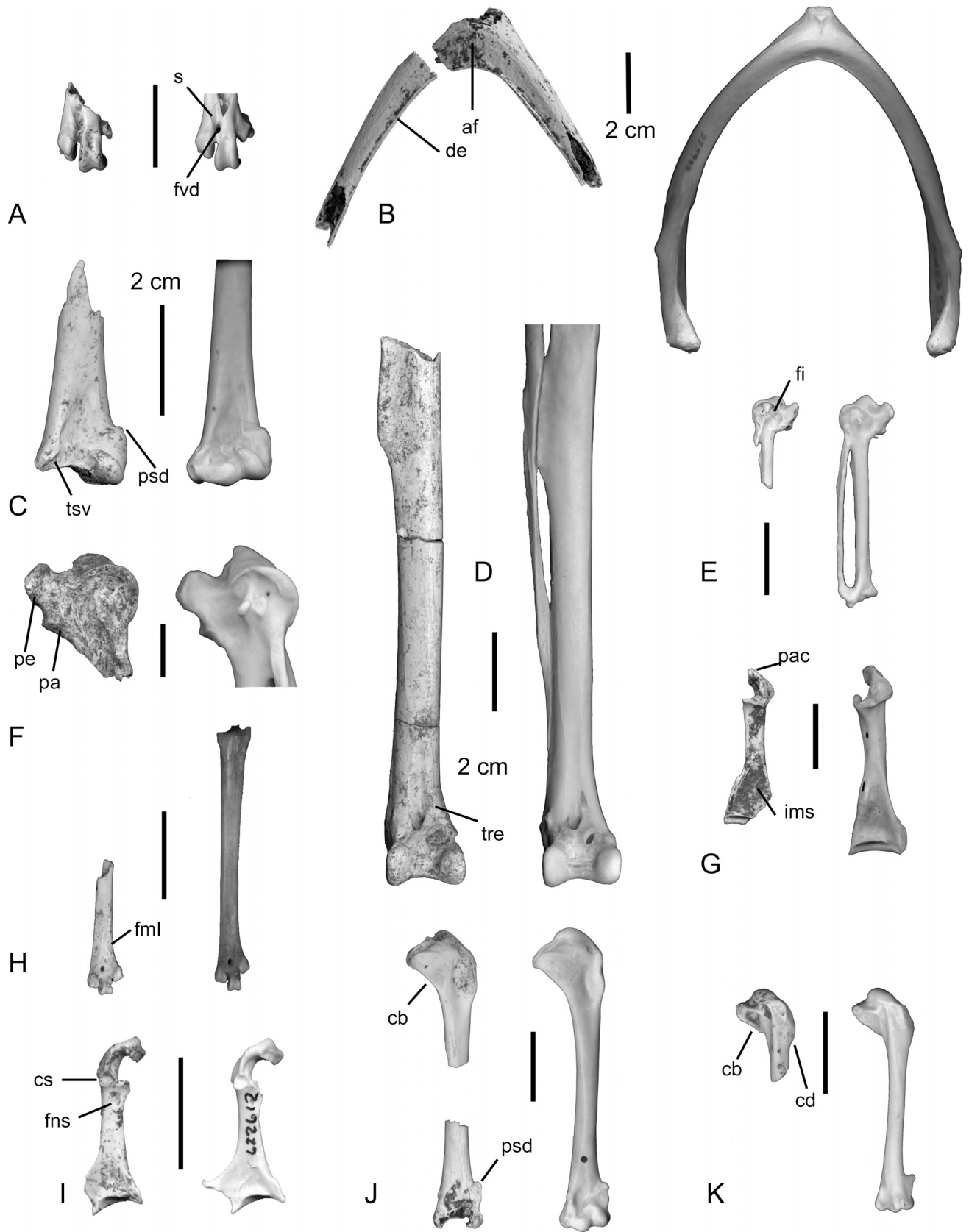
and slender as in *Gallirallus* and *Rallina*, and unlike *Amaurornis*, *Habroptila*, *Porzana*, *Crex*, and *Gallicrex*. The foramen n. supracoracoidei is elongated. The impressio m. sternocoracoidei is deeply excavated and extends far proximally, as in *Gallirallus* and unlike *Amaurornis*. Anteriorly, the impressio m. sternocoracoidei is bordered by a thickened edge that bears a small tubercle that is more distinct in *Amaurornis* than in *Gallirallus*. The specimen has a very deep sulcus m. supracoracoidei that is deeper than in *Amaurornis*. The bicipital attachment is rounded, as in *Amaurornis*, and unlike *Crex*, *Rallina*, *Rallus*, and some *Gallirallus*.

PORZANA Vieillot, 1816
PORZANA sp.
(Fig. 3H)

Referred Material—A left distal tarsometatarsus (LB-Av-466) and a proximal right ulna (LB-Av-620).

Horizon—Late Pleistocene (Spits 62 and 58).

Remarks—The distal tarsometatarsus has a pronounced fossa metatarsi I. The specimen shares with *Porzana* the position of the muscle scar on the facies caudalis, as well as the flattening of the facies caudalis. It differs from extant *Porzana* and agrees with the extinct flightless rail *Porzana keplerorum* from the Hawaiian Islands (Olson and James, 1991) in the more distal placement of the foramina vasculare distale and the relatively shorter trochlea III and IV. The proximal ulna has a short and blunt olecranon. The cotyla ventralis is rounded and cup-shaped, and is raised with respect to the cotyla dorsalis. The latter is flat and the pronounced processus cotylaris dorsalis extends dorsally further than in *Amaurornis*, similar to *Porzana*. In size, the specimen is smaller than *P. fusca* and closer to *P. pusilla*, but with a more slender shaft. The material represents at least one individual (MNI = 1).

CHARADRIIFORMES Huxley, 1867
CHARADRIIDAE Leach, 1820
PLUVIALIS Brisson, 1760
PLUVIALIS FULVA (Gmelin, 1789)
(Fig. 3I)

Referred Material—A left coracoid (LB-Av-335) and three left proximal carpometacarpi (LB-Av-46, LB-Av-376, and LB-Av-456).

Horizon—Late Pleistocene (Spits 50, 45, and 43).

Remarks—The presence of a foramen n. supracoracoidei in LB-Av-335 distinguishes the coracoid from those of Scolopacidae. The cotyla scapularis is relatively large and rounded, similar to *Pluvialis* but smaller than in *Charadrius*. The specimen is smaller than *Pluvialis squatarola* and similar in size and morphology to *Pluvialis fulva*. The carpometacarpi display a robust os metacarpale major (slender in Scolopacidae), a relatively short symphysis metacarpalis distalis (longer in Scolopacidae), and a short processus extensorius (elongated in Scolopacidae). The three left carpometacarpi represent three individuals (MNI = 3).

SCOLOPACIDAE Rafinesque, 1815
GALLINAGO Brisson, 1760
GALLINAGO sp.
(Fig. 3J)

Referred Material—Four left proximal humeri (LB-Av-316, LB-Av-398, LB-Av-405, and LB-Av-452), two left distal humeri (LB-Av-311 and LB-Av-406), a right distal humerus (LB-Av-312), a proximal right scapula (LB-Av-397), two right coracoids (LB-Av-334 and LB-Av-354), a proximal left ulna (LB-Av-555), a proximal right carpometacarpus (LB-Av-482), a left carpometacarpus (LB-Av-252), a left distal femur (LB-Av-578), and a right and a left distal tarsometatarsus (LB-Av-318 and 353).
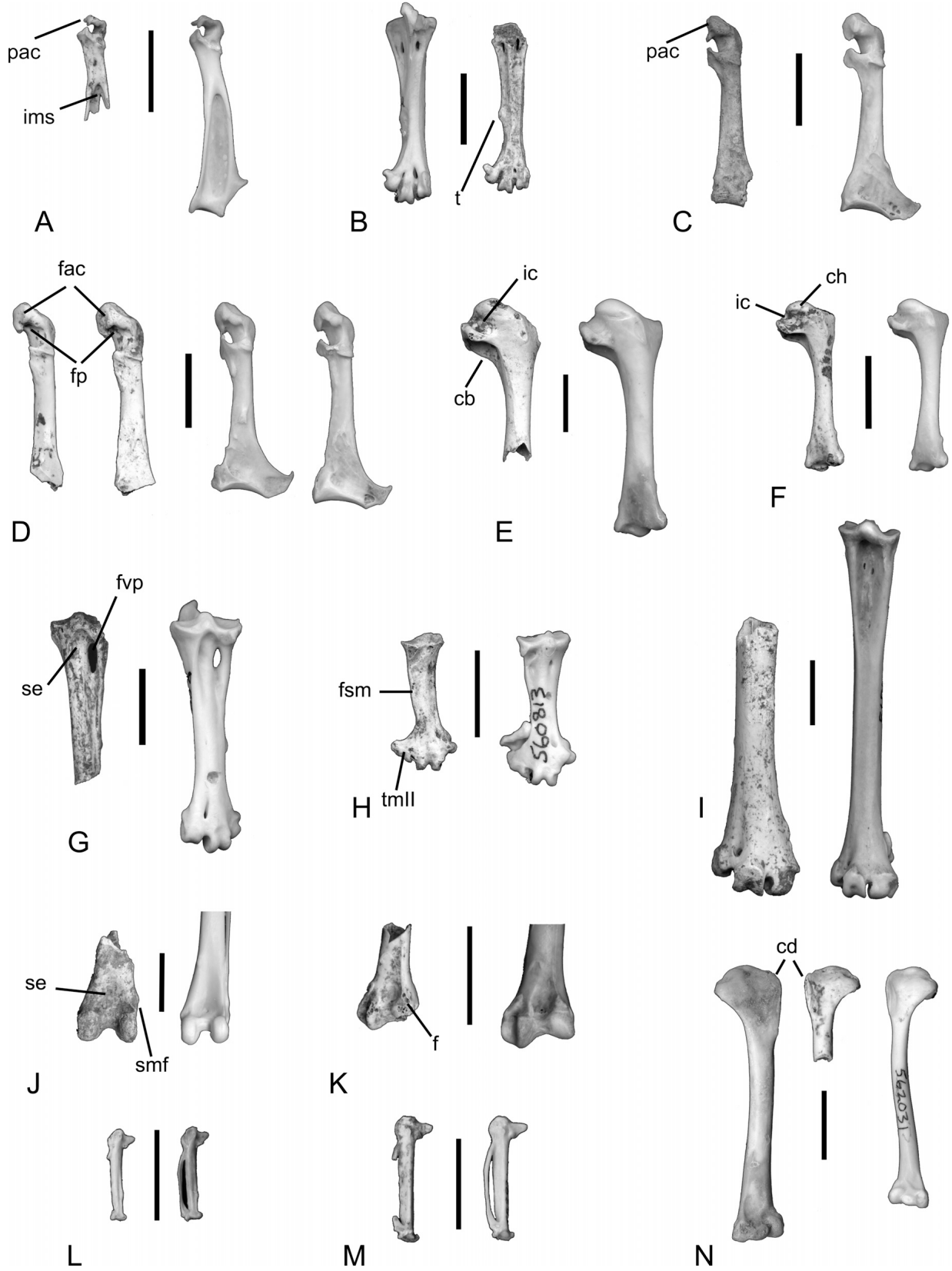
Horizon—Late Pleistocene (Spits 69, 67, 65, 62, 61, 56, 47, 46, 43, 39, and 37).

Remarks—The proximal humeri (Fig. 3J) have a low crista deltopectoralis (higher and triangular in Charadriidae) and a long and wide incisura capitis (short and narrow in Charadriidae). The fossa pneumotricipitalis is narrow and bordered medially by a distinct margo caudalis. The margo caudalis is much reduced in *Scolopax*, but present in *Gallinago*, *Arenaria*, *Heteroscelus*, and *Calidris*. The fossa pneumotricipitalis is wider in *Arenaria*, *Heteroscelus*, and *Calidris*. The bicipital crest merges smoothly with the shaft (Fig. 3J), a feature that distinguishes *Gallinago* from other Scolopacidae of similar size. The distal humeri share a small but pronounced processus supracondylaris dorsalis that extends at an oblique angle from the shaft (in Charadriidae, the processus supracondylaris dorsalis extends further from the shaft and is oriented more proximally). The coracoids lack foramina n. supracoracoidei, have a relatively large and round cotyla scapularis, and are rather robust. The carpometacarpi of Scolopacidae are slender, and have an elongated processus extensorius, and a long symphysis metacarpalis distalis. LB-Av-482 lacks the distal half and shows gnawing marks along its medial side (Fig. 6A). The elongated processus extensorius is preserved and the specimen is most similar in dimensions to *Gallinago*. The left distal carpometacarpus displays a long symphysis metacarpalis distalis and a slender os metacarpale major (more robust in Charadriidae), and agrees best with *Gallinago*, because the symphysis in this bone is longer and more slender than in *Arenaria*, *Calidris*, and *Heteroscelus*. In the distal femur, the epicondylus medialis is distinct and squarer in outline, as in Scolopacidae. The fossa poplitea contains a single centrally placed foramen and agrees in overall size and morphology with *Gallinago*. The tarsometatarsi (LB-Av-318 and LB-Av-353) display relatively long lateral and medial condyles, and with a narrow space between the medial and middle condyles (wider in Charadriidae). This material represents at least four individuals (MNI = 4).

ACTITIS Illiger, 1811
ACTITIS HYPOLEUCOS (Linnaeus, 1758)
(Fig. 3K)

← FIGURE 3. Anatidae through Charadriidae from Liang Bua. **A**, distal right tarsometatarsus of Anatidae, gen. et sp. indet. (left; LB-Av-388), and *Anas gibberifrons* (right), cranial view; **B**, furcula of *Leptoptilos robustus* (left; LB-Av-190) and *Leptoptilos dubius* (right), dorsal view; **C**, distal left humerus of *Haliastur* cf. *indus* (left; LB-Av-130) and *Haliastur indus* (right), dorsal view; **D**, right tibiotarsus of *Trigonoceps* sp. (left; LB-Av-104) and *Trigonoceps occipitalis* (right), cranial view; **E**, left carpometacarpus of *Accipiter* sp. (left; LB-Av-492) and *Accipiter soloensis* (right), ventral view; **F**, right carpometacarpus of *Aquila* sp. (left; LB-Av-182) and *Aquila audax* (right), ventral view; **G**, right coracoid of *Gallirallus* sp. (left; LB-Av-357), and *Gallirallus australis* (right), dorsal view; **H**, left tarsometatarsus of *Porzana* sp. (left; LB-Av-466) and *Porzana pusilla* (right), cranial view; **I**, left coracoid of *Pluvialis* cf. *fulva* (left; LB-Av-335) and *Pluvialis fulva* (right), cranial view; **J**, proximal left humerus (left; LB-Av-405) and distal left humerus (left; LB-Av-406) of *Gallinago* sp. and left humerus of *Gallinago stenura* (right), dorsal view; **K**, right humerus of *Actitis hypoleucos* (left; LB-Av-447) and *Actitis hypoleucos* (right), ventral view. **Abbreviations**: **af**, apophysis furculae; **cb**, crista bicipitalis; **cd**, crista deltopectoralis; **cs**, cotyla scapulae; **de**, distal edge; **fi**, fossa infratrochlearis; **fmI**, fossa metatarsi I; **fns**, foramen n. supracoracoidei; **fvd**, foramen vasculare distale; **ims**, impressio m. sternocoracoidei; **pa**, processus alularis; **pac**, processus acrocoracoideus; **pe**, processus extensorius; **psd**, processus supracondylaris dorsalis; **s**, sulcus; **tre**, tuberositas retinaculi extensori; **tsv**, tuberculum supracondylare ventrale. All scale bars equal 1 cm.

Referred Material—A right proximal humerus (LB-Av-57) and a proximal femur (LB-Av-382).

Horizon—Late Pleistocene (Spits 41 and 39).

Remarks—The fossil humerus is similar to *Actitis hypoleucos* in that the bicipital crest merges abruptly with the shaft (Fig. 3K), which distinguishes it from *Gallinago*, and displays a raised crus dorsale fossae, unlike *Calidris* and *Tringa* where it is flat, and a relatively short deltoid crest (longer in *Calidris* and *Tringa*). Furthermore, the fossil specimen differs from *Xenus cinereus* and *Heteroscelus brevipes* in having a proximally narrower dorsal fossa pneumotricipitalis, and in its smaller size. On the femur, the trochanter femoris is pronounced and curves slightly inward. The slope between the caput femoris and the trochanter femoris is straight, like *Actitis* and unlike *Calidris* where it is concave. The impressiones musculares iliotrochanteris extend along the shaft and form a ridge with the linea intermuscularis cranialis, which is more robust in *Xenus* and *Heteroscelus*. This material represents at least one individual (MNI = 1).

TURNICIDAE Gray, 1840
TURNIX Bonnaterre, 1791
TURNIX sp.
(Fig. 4A)

Referred Material—A right proximal coracoid (LB-Av-465), a left proximal femur (LB-Av-509), and a right proximal femur (LB-Av-619).

Horizon—Late Pleistocene (Spits 70, 65, and 58).

Remarks—The coracoid displays a very short and blunt processus acrocoracoideus and a deep impressio m. sternocoracoidei that extends well onto the proximal half of the bone, all of which are features that are characteristic of *Turnix*. The coracoid is smaller than *Turnix ocellata* and *T. sylvatica* and is in the size range of *T. suscitator*. The femora agree with Turnicidae in the presence of a well-pronounced trochanter femoris (higher than in Rallidae) that continues on the facies caudalis towards the medial side of the bone. The caput femoris is small and the facies articularis antitrochanterica is constricted laterally of the caput femoris. Although LB-Av-619 is more gracile than LB-Av-509, both femora are smaller than *T. sylvatica* and *T. occellata* and are in the size range of *T. suscitator*. This material represents at least two individuals (MNI = 2).

COLUMBIFORMES Latham, 1790
COLUMBIDAE Illiger, 1811
Gen. et sp. indet.
(Fig. 4B)

Referred Material—Two right tarsometatarsi (LB-Av-7 and LB-Av-532) and a proximal scapula (LB-Av-319).

Horizon—Late Pleistocene (Spits 32 and 69) and Holocene (Spit 6).

Remarks—The right tarsometatarsus LB-Av-7 (Fig. 4B) shows the enlarged trochlea metatarsi II characteristic of Columbidae, but differs from all species examined in the presence of a prominent tubercle proximal of the fossa metatarsi I. The length of the specimen is smaller than in *Columba*, *Ducula*, and *Caloenas*, and falls in the size range of *Treron* and *Macropygia*, but its proportions are different from those observed in *Treron*, *Macropygia*, *Streptopelia*, *Chalcohaps*, *Macropygia*, and *Ptilinopus*. Tarsometatarsus LB-Av-532 (Spit 6) is of a juvenile bird, because it lacks the proximal articulation and at the distal end the separate metatarsals are incompletely fused. The proximal scapula has a large, rounded facies articularis humeralis, and a well-developed, blunt acromion. The surface between the tip of the acromion and the facies articularis humeralis is straight and makes an almost 90° angle with the long axis of the bone. In size, the scapula is similar to *Treron*, but the proximal scapula is not diagnostic within Columbidae. This material represents at least two individuals (MNI = 2); however, stratigraphic details suggest at least three individuals (MNI = 3).

STREPTOPELIA Bonaparte, 1855
STREPTOPELIA cf. *BITORQUATA* (Temminck, 1809, in Knip de Courcelles and Temminck, 1808–1811)
(Fig. 4C)

Referred Material—A right coracoid (LB-Av-344), a right carpometacarpus (LB-Av-386), and a distal right tarsometatarsus (LB-Av-523).

Horizon—Holocene (Spits 5 and 4).

Remarks—The coracoid lacks the presence of pneumatic foramen under the processus acrocoracoideus (Worthy and Wragg, 2008), in which it differs from that in *Macropygia* and *Ptilinopus*. LB-Av-344 differs from *Treron* in having a less proximally projecting processus acrocoracoideus, and is in this respect more similar to *Streptopelia*. In size, the coracoid falls in the size range of *S. bitorquata*. The distal tarsometatarsus is most similar to *Streptopelia* in the distinct ridges on the plantar surface that run inwards from the medial edge of the trochlea metatarsi II and the lateral edge of the trochlea metatarsi IV. These ridges are most pronounced in *Streptopelia*. In size, the specimen is larger than in *S. chinensis* and most similar to *S. bitorquata*. The carpometacarpus has a less pronounced processus intermetacarpalis and the spatium intermetacarpale does not extend proximally into the fossa infratrochlearis, similar to *Streptopelia*. At least one individual is presented here (MNI = 1).

aff. *MACROPYGIA* Swainson, 1837/*PTILINOPUS* Swainson, 1825
(Fig. 4D)

Referred Material—Two right proximal coracoids (LB-Av-359 and LB-Av-360) and a distal right coracoid (LB-Av-355).

Horizon—Spits 69 and 46.

← FIGURE 4. Turnicidae through Alcedinidae from Liang Bua. **A**, right coracoid of *Turnix* sp. (left; LB-Av-465) and *Turnix suscitator* (right), dorsal view; **B**, right tarsometatarsus (right, LB-Av-7) of Columbidae, gen. et sp. indet., and *Treron pompadora*, caudal view; **C**, right coracoid of *Streptopelia* cf. *bitorquata* (left; LB-Av-344) and *Streptopelia bitorquata* (right), dorsal view; **D**, proximal coracoids of aff. *Macropygia/Ptilinopus* (far left, LB-Av-359; left, LB-Av-360), *Macropygia unchall* (right), and *Ptilinopus monacha* (far right), dorsal view; **E**, right humerus of *Macropygia* sp. (left; LB-Av-390) and *Macropygia unchall* (right), ventral view; **F**, right humerus of *Ptilinopus* sp. (left; LB-Av-396) and *Ptilinopus monacha* (right), ventral view; **G**, left tarsometatarsus of *Ducula* sp. (left; LB-Av-285) and *Ducula aenea* (right), cranial view; **H**, left tarsometatarsus of *Geoffroyus* cf. *geoffroyi* (left; LB-Av-347) and *Geoffroyus geoffroyi* (right), cranial view; **I**, right tarsometatarsus of *Tyto* sp. (left; LB-Av-183) and *Tyto alba* (right), cranial view; **J**, left tibiotarsus of Strigidae, gen. et sp. indet (left; LB-Av-184), and *Ninox novaeseelandiae* (right), cranial view; **K**, left femur of *Otus* sp. (left; LB-Av-608) and *Otus magicus* (right), caudal view; **L**, right carpometacarpus of *Collocalia esculenta* (left; LB-Av-25) and *Collocalia esculenta* (right), ventral view; **M**, left carpometacarpus of *Aerodramus* cf. *fuciphagus* (left; LB-Av-101) and *Aerodramus salangana* (right), ventral view; **N**, left humerus of Halcyoninae, gen. et sp. indet (left; LB-Av-296), right humerus of *Halcyon* sp. (middle; LB-Av-470), and right humerus of *Halcyon chloris* (right), dorsal view. **Abbreviations**: **cb**, crista bicipitalis; **cd**, crista deltopectoralis; **ch**, caput humeri; **f**, facet; **fac**, facies articularis clavicularis; **fp**, foramina pneumatica; **fsm**, facies subcutanea medialis; **fvp**, foramen vasculare proximale; **ic**, incisura capitis; **ims**, impressio m. sternocoracoidei; **pac**, processes acrocoroideus; **se**, sulcus extensorius; **smf**, sulcus m. fibularis; **t**, tuberculum; **tmII**, trochlea metatarsi II. Scale bars equal 1 cm.

Remarks—In both proximal coracoids, the tip of the processus procoracoideus is missing and they lack the distal part of the bone with the impressio m. sternocoracoidei and the facies articularis sternalis. They share with *Ptilinopus*, *Macropygia*, and the larger-bodied genera *Hemiphaga* (endemic to New Zealand) and *Goura* (endemic to New Guinea) the presence of large pneumatic foramina under the processus acrocoracoideus (Worthy and Wragg, 2008). The fossil specimens are most similar to *Ptilinopus* and *Macropygia* in their overall size and the large size of the pneumatic foramen. The facies articularis clavicularis is rounded, large, and almost concave, with a distinct notch ventrally. This differs from the condition observed in *Ptilinopus* and *Macropygia*, wherein the facies articularis clavicularis is smaller and not concave. Also, the notch is larger in *Ptilinopus* and *Macropygia*, and extends more dorsally in the latter. LB-Av-355 lacks the procoracoid and acrocoracoid and is less robust than in *Ducula*, *Treron*, and *Columba*. The impressio m. sternocoracoidei is distinct and deepens near the proximal side of the bone. In this it resembles *Macropygia* and *Ptilinopus*, and it lacks foramina vasculare, which are present in *Treron* and *Ducula*. This material represents at minimum two individuals (MNI = 2).

MACROPYGIA Swainson, 1837
MACROPYGIA sp.
(Fig. 4E)

Referred Material—Two right proximal humeri (LB-Av-389 and LB-Av-390), a left ulna (LB-Av-393), a right distal ulna (LB-Av-558), and a carpometacarpus (LB-Av-448).

Horizon—Late Pleistocene (Spits 69, 58, 44, and 40).

Remarks—The humeri differ from *Treron*, and agree more with *Macropygia* and *Ptilinopus* in that the bicipital crest merges more proximally with the shaft. Both specimens are larger than in *Ptilinopus* and fall in the size range of *Macropygia*. In addition, the incisura capitis is deeper in *Macropygia* and the Liang Bua specimens than in *Treron*. The carpometacarpus agrees with *Macropygia* and *Ptilinopus* in that the intermetacarpal space extends into the fossa supratrochlearis, whereas in *Treron*, *Chalcohaps*, and *Geopelia* the intermetacarpal space does not extend that far proximally. In addition, in *Macropygia* and *Ptilinopus*, the fossa infratrochlearis is deeper and the processus intermetacarpalis is more pronounced. LB-Av-448 differs from *Ptilinopus* in having a wider synostosis metacarpalis distalis, and in that respect agrees more with *Macropygia*. The complete ulna has a relatively short and blunt olecranon, which is more elongated and pointed in *Treron*, and more similar to *Macropygia* and *Streptopelia*. In both Liang Bua ulnae, the tuberculum carpale is more pointed inwards than in *Streptopelia*, and most similar to the condition observed in *Macropygia*. This material representing two individuals (MNI = 1).

PTILINOPUS Swainson, 1825
PTILINOPUS sp.
(Fig. 4F)

Referred Material—A right humerus (LB-Av-396).

Horizon—Late Pleistocene (Spit 67).

Remarks—The humerus shares with *Ptilinopus* the relatively low caput humeri, which is higher in *Treron*, *Streptopelia*, *Chalcophaps*, and *Macropygia*. The relatively wide incisura capitis is more similar to that in *Ptilinopus* than in *Geopelia*. The specimen is most similar in size to *P. monacha*, but more similar to *P. hyogastra* in the size of the muscle scar on the base of the crista deltopectoralis and the more elongate shape (less curved in anterior view) of the epicondylus ventralis and the processus flexorius.

DUCULA Hodgson, 1836
DUCULA sp.
(Fig. 4G)

Referred Material—A proximal left tarsometatarsus (LB-Av-285).

Horizon—Holocene (Spit 26).

Remarks—The tarsometatarsus is referred to *Ducula* because of the large foramina vasculare proximale on the medial half of the facies cranialis, the well-developed sulcus extensorius with a rounded proximal border, and the general robustness of the bone. In size, it is similar to both *D. aenea* and *D. bicolor*. Both species have been recorded on Flores (Coates and Bishop, 1997).

PSITTACIFORMES Wagler, 1830
PSITTACIDAE Rafinesque, 1815
GEOFFROYUS Bonaparte, 1850
GEOFFROYUS cf. *GEOFFROYI* (Bechstein, 1811)
(Fig. 4H)

Referred Material—A left proximal coracoid (LB-Av-587), a left proximal femur (LB-Av-609), three left tarsometatarsi (LB-Av-345–347), a right tarsometatarsus (LB-Av-350), and a distal left tibiotarsus (LB-Av-410).

Horizon—Late Pleistocene (Spits 41–39) and Holocene (Spits 28 and 26).

Remarks—At least three individuals (MNI = 3) of *Geoffroyus* cf. *geoffroyi* are represented here. On the proximal tarsometatarsi, the foramen vasculare mediale is greatly reduced and hardly visible. The hypotarsus is preserved in LB-Av-346 and LB-Av-347, and displays two enclosed canals, with the canal for the m. flexor digitorum longus being larger than the one for the flexor hallucis longus. The presence of two enclosed hypotarsal canals for the deep flexor tendons is considered the plesiomorphic hypotarsal condition (see Mayr, 2010; Worthy et al., 2011), and is shared by several groups including Strigopidae, Cacatuidae, Psittacidae, and certain Psittaculini group A (sensu Schweizer et al., 2010). Distally, the tarsometatarsi (Fig. 4H) show a large trochlea metatarsi II (missing in LB-Av-346) and the trochlea metatarsi IV bears a trochlea accessoria (Mayr, 2002), which is separated from the trochlea metatarsi IV by a groove. A large trochlea metatarsi II is characteristic of certain genera within Psittaculini, including *Psittacula*, *Tanygnathus*, *Geoffroyus*, and *Eclectus* (Mayr and Göhlich, 2004). The Liang Bua tarsometatarsi share with *Tanygnathus* and *Geoffroyus* a grooved ridge alongside the whole facies subcutanea medialis, which is shorter or even absent in *Psittacula*. The shaft is wide in *Tanygnathus*, whereas it is more slender in *Geoffroyus*, *Psittacula*, and the Liang Bua tarsometatarsi. The Liang Bua specimens are similar to *G. geoffroyi* in morphology, but no comparative material was available for *G. heteroclitus* and *G. simplex*, both of which are larger than *G. geoffroyi* (Forshaw, 1977). The proximal femur has a damaged crista trochanteris and caput femoris, but the onset of the trochanter femoris is curved inwards. The facies articularis antitrochanterica is not horizontal but sloped towards the top of the crista trochanteris. The impressiones iliotrochantericae are in line with the crista trochanteris and distally merge with the linea intermuscularis cranialis. Despite the damaged proximal end, the femur agrees in morphology with *G. geoffroyi*, but is slightly smaller in size.

STRIGIFORMES Wagler, 1830
TYTONIDAE Mathews, 1912
TYTO Billberg, 1828
TYTO sp.
(Fig. 4I)

Referred Material—A distal right tarsometatarsus (LB-Av-183), a left scapula (LB-Av-600), two proximal left coracoids (LB-Av-231 and LB-Av-294), and a distal right carpometacarpus (LB-Av-484).

Horizon—Late Pleistocene (Spits 47 and 45–42).

Remarks—Barn owls are represented by at least two individuals based on the two left coracoids. The tarsometatarsus (Fig. 4I) differs from Strigidae, and is similar to Tytonidae except for *Phodilus badius*, in that the trochlea metatarsi III is asymmetrical in distal view, with a plantarly extending lateral rim. Within Tytonidae, the fossil tarsometatarsus further differs from *P. badius*, and resembles *Tyto*, in the elongated and flat distal half of the shaft, which is more concave in *P. badius* as it carries the onset of the sulcus extensorius. The width across the distal condyles (14.0 mm) is larger than in extant *Tyto alba* (12.05 mm; n = 8) and *T. capensis* (10.6 mm). No leg elements of the Eastern Grass Owl *Tyto longimembris*, *T. delicatula*, *T. nigrobrunnea*, *T. sororcula*, *T. rosenbergii*, and *T. inexpectata* were available for comparison. For *T. longimembris*, Taylor (1994) notes that this species has long, bare legs but no data are available for the dimensions of the tarsometatarsus. The scapula is assigned to Tytonidae because of its short and blunt acromion, which is more elongated and pointed in strigid owls. It is, however, larger in size than *T. alba* but smaller than *T. longimembris*. The two coracoids are assigned to Tytonidae based on the foramina n. supracoracoidei, which attain a more proximal position in Strigidae. Both coracoids are larger than those of *T. alba*, but are smaller than in *T. longimembris*.

<div style="text-align:center">

STRIGIDAE Leach, 1820
Gen. et sp. indet.
(Fig. 4J)

</div>

Referred Material—A distal left tibiotarsus (LB-Av-184).
Horizon—Holocene (Spit 12).
Remarks—The distal tibiotarsus lacks a pons supratendineus, a feature characteristic of Strigiformes. The distal end is wider mediolaterally than anteroposteriorly, which distinguishes it from tytonid owls. The sulcus extensorius is wide and not as deep as in *Strix*, *Bubo*, and *Ketupa*, and is more similar to that in the smaller *Ninox* species. However, the sulcus m. fibularis is distinct and its anterior ridge meets the condylus lateralis at an angle, whereas it is in line with the condylus lateralis in *Ninox* and other strigid owls. In distal view, the anterior intercondylar space is deeper than the posterior one, a feature that is not observed in other Strigidae including *Ninox*. In size, the specimen falls within the range of the specimens of female *Asio flammeus* and *A. otus* measured.

<div style="text-align:center">

OTUS Pennant, 1769
OTUS sp.
(Fig. 4K)

</div>

Referred Material—A distal femur (LB-Av-608).
Horizon—Late Pleistocene (Spit 38).
Remarks—The femur is assigned to *Otus* sp. based on the presence of a small triangular facet proximal to the internal condyle (absent in *Ninox*) and the form of the crista lateralis sulci patellaris, which extends more proximally in *Otus* than in *Ninox* and *Glaucidium*. In size, it falls between *Otus* and *Glaucidium*.

Three species of scops owls have been recorded on Flores: the Moluccan scops owl *Otus magicus*, Wallace's scops owl *O. silvicola*, and the endemic Flores scops owl *O. alfredi* (Verhoeye and Holmes, 1998; Mees, 2006). Knowledge of the Flores scops owl (*O. alfredi*) was initially based on only three specimens collected in Western Flores in 1896 (Widodo et al., 1999). The validity of *O. alfredi* as a separate species was subsequently questioned and it was argued that *O. alfredi* rather constituted the red morph of the Moluccan scops owl (Sibley and Monroe, 1993; Mees, 2006). The rediscovery of the Flores scops owl in the Ruteng Mountains confirmed that *O. alfredi* is a separate species (Widodo et al., 1999). Both *O. alfredi* and *O. silvicola* have been recorded from the montane forests around Ruteng (Widodo et al., 1999), whereas the Moluccan scops owl appears to be a species that prefers deciduous, coastal forests (Butchart et al., 1996) and has never

been recorded in the Ruteng area. LB-Av-608 is smaller than extant *O. magicus*, but a lack of comparative material from *O. silvicola* and *O. alfredi* precludes a direct comparison at this time. The Liang Bua specimen is therefore most likely to represent either *O. alfredi* (which is the smallest of the three according to Coates and Bishop, 1997) or *O. silvicola*.

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APODIFORMES Peters, 1931–1951
APODIDAE (Hartert, 1897)

</div>

Swiftlets are the most abundant species throughout the Pleistocene and Holocene sediments, with a total of 105 specimens (50 carpometacarpi, 45 ulnae, seven coracoids, and three humeri; MNI = 28, see below). The swiftlet remains can be separated into a larger and a smaller species. The large species is most abundant (100 specimens) and occurs from Spit 84 throughout to Spit 6, whereas the smaller species (five specimens) occurs only in Spits 76, 54, 44, 40, and 6. Both large and small species occur together in Spit 6, but are otherwise found in separate spits. Measurements of complete carpometacarpi and ulnae were compared with relevant extant taxa of *Collocalia* and *Aerodramus*, and (for carpometacarpi only) with fossil swiftlets from the Great Cave of Niah on Borneo (kindly provided by C. Stimpson). The two forms are treated separately in the sections below according to their size.

<div style="text-align:center">

COLLOCALIA Gray, 1840
COLLOCALIA ESCULENTA (Linnaeus, 1758)
(Fig. 4L)

</div>

Referred Material—Two right carpometacarpi (LB-Av-25 and LB-Av-33), a left carpometacarpus (LB-Av-28), and two right coracoids (LB-Av-279 and LB-Av-281).
Horizon—Late Pleistocene (Spits 76, 54, 44, and 40) and Holocene (Spit 6).
Remarks—The five smaller specimens (MNI = 2) fall within the size range of *C. esculenta*, which is still present on Flores (Verhoeye and Holmes, 1998; Mees, 2006).

<div style="text-align:center">

AERODRAMUS Oberholser, 1906
AERODRAMUS cf. *FUCIPHAGUS* (Thunberg, 1812)
(Figs. 4M, 5D)

</div>

Referred Material—Twenty-one right carpometacarpi (LB-Av-11, LB-Av-13, LB-Av-17, LB-Av-20, LB-Av-26, LB-Av-38, LB-Av-44, LB-Av-50, LB-Av-64, LB-Av-69, LB-Av-70,
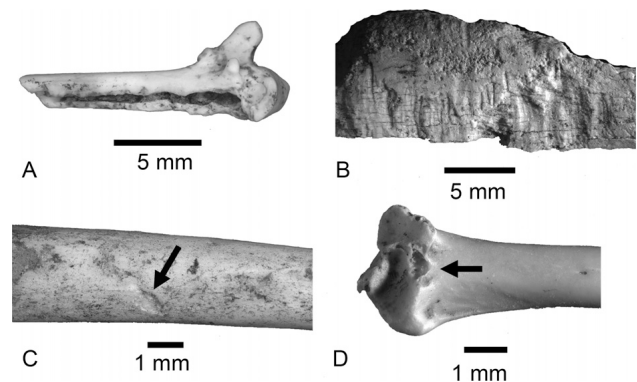

FIGURE 5. Examples of bone modification in the avian sample from Liang Bua's Sector XI. **A**, snipe (*Gallinago* sp.) right carpometacarpus (LB-Av-482) with gnawing marks alongside its medial side; **B**, fragment of a long bone (LB-Av-133) of a large bird with rodent (Muridae) gnawing marks; **C**, long bone fragment (LB-Av-538) of Aves indet. with bite mark possibly from a small varanid; **D**, swiftlet (*Aerodramus* cf. *fuciphagus*) left ulna (LB-Av-87) with signs of raptor digestion.

LB-Av-81, LB-Av-91, LB-Av-95, LB-Av-96, LB-Av-207, LB-Av-250, LB-Av-251, LB-Av-276, LB-Av-374, and LB-Av-575), 26 left carpometacarpi **(**LB-Av-10, LB-Av-12, LB-Av-22, LB-Av-24, LB-Av-27, LB-Av-35, LB-Av-37, LB-Av-39, LB-Av-42, LB-Av-43, LB-Av-45, LB-Av-47, LB-Av-54, LB-Av-68, LB-Av-72, LB-Av-74, LB-Av-90, LB-Av-97–101, LB-Av-247, LB-Av-435, LB-Av-480, and LB-Av-506), 17 right ulnae (LB-Av-9, LB-Av-16, LB-Av-18, LB-Av-21, LB-Av-40, LB-Av-48, LB-Av-49, LB-Av-53, LB-Av-71, LB-Av-75, LB-Av-86, LB-Av-94, LB-Av-245, LB-Av-263, LB-Av-264, LB-Av-277, and LB-Av-283), 28 left ulnae (LB-Av-14, LB-Av-19, LB-Av-23, LB-Av-30–32, LB-Av-34, LB-Av-36, LB-Av-41, LB-Av-52, LB-Av-65, LB-Av-66, LB-Av-76, LB-Av-78–80, LB-Av-84, LB-Av-87, LB-Av-89, LB-Av-93, LB-Av-102, LB-Av-191, LB-Av-246, LB-Av-253, LB-Av-284, LB-Av-352, LB-Av-370, and LB-Av-557), two right humeri (LB-Av-59 and LB-Av-60), one left humerus (LB-Av-61), two right coracoids (LB-Av-267 and LB-Av-278), and three left coracoids (LB-Av-232, LB-Av-268, and LB-Av-280).

Horizon—Late Pleistocene (Spits 84, 73, 67, 47, 43, 41–35, and 33–31) and Holocene (Spits 30–22, 19, 16, 15, 13, 12, 10, 8, and 6).

Remarks—The nine larger complete carpometacarpi fall within the size range of *Aerodramus salangana* and *A. maximus*; six group with *A. salangana* and three group with *A. maximus*. No specimens of *A. fuciphagus*, the only species of *Aerodramus* known from Flores (Coates and Bishop, 1997; Mees, 2006), were available for comparison. A normality test (Shapiro-Wilk) on the size distribution of the large Liang Bua carpometacarpi gives a P value of >0.05, supporting the interpretation that they represent a single population. Regression of wing-length data from regional conspecifics from Chantler and Driessens (2000) by C. Stimpson (pers. comm.) suggests that the carpometacarpi of *A. fuciphagus* would be smaller than the Liang Bua specimens. However, observations of the extant *A. fuciphagus* population on Flores suggest that this species is robust in size (M. Schellekens, pers. comm.). In addition, *A. fuciphagus* is very common on Flores and has recently been observed in Liang Bua (M. Schellekens, pers. comm.). It is therefore likely that the abundant swiftlet remains represent *A. fuciphagus* rather than a species that currently has a more northern range. At least 26 individuals of *Aerodramus* cf. *fuciphagus* are represented within the sediments of Sector XI.

CORACIIFORMES Forbes, 1884
ALCEDINIDAE Rafinesque, 1815
HALCYONINAE (Vigors, 1825)
Gen. et sp. indet.
(Fig. 4N)

Referred Material—A complete left humerus (LB-Av-296), two right proximal femora (LB-Av-508 and LB-Av-521), and a right distal tibiotarsus (LB-Av-524).

Horizon—Late Pleistocene (Spits 80, 70, 61, and 39).

Remarks—The humerus (Fig. 4N, left) has a large, laterally placed fossa m. brachialis, an elongated crista deltopectoralis, the wide fossa pneumotricipitalis, and a distinct tuberculum ventrale. It differs from Cerylinae (water kingfishers) in the absence of a pronounced margo caudalis that extends proximally to the caput humeri, and differs from the Alcedininae (river kingfishers) in its larger size and a much longer crista deltopectoralis. It shares with *Halcyon* and *Tanysiptera* the wide and excavated fossa pneumotricipitalis that undercuts the caput humeri, which is less distinct in *Pelargopsis* and *Dacelo*. It differs from *Halcyon* and *Tanysiptera* in the presence of longer crista deltopectoralis, a feature that is present in *Pelargopsis* and *Dacelo*. However, specimens of *Lacedo*, *Cittura*, *Melidora*, and *Syma* were not available for comparison.

The morphology of the femora (LB-Av-508 and LB-Av-521) is not very diagnostic. The femora resemble Halcyoninae (tree kingfishers) in having a trochanter femoris that does not project far proximally. In size, the Liang Bua specimens resemble *H.

lindsayi lindsayi, but LB-Av-508 appears slightly shorter. The tibiotarsus (LB-Av-524) has a very deep area intercondylaris, the canalis extensorius leads onto a broad sulcus extensorius, and the shaft is narrow and deep. It differs from Cerylinae and Alcedininae in being relatively wider at the distal articulation. Distal tibiotarsus morphology is quite variable within *Tanysiptera* and *Halcyon*, and the specimen falls within the observed variation. At least two individuals are represented by the two proximal femora (MNI = 2).

HALCYON Swainson, 1821
HALCYON sp.
(Fig. 4N)

Referred Material—Two left proximal coracoids (LB-Av-332 and LB-Av-582), a right proximal coracoid (LB-Av-356), three right proximal humeri (LB-Av-407, LB-Av-470, and LB-Av-545), one left proximal humerus (LB-Av-461), and a right (LB-Av-512) and a left (LB-Av-467) carpometacarpus.

Horizon—Late Pleistocene (Spits 75, 70, 68, 65, 63, 61, 57, 46, and 41).

Remarks—The four proximal humeri lack a pronounced margo caudalis that extends proximally to the caput humeri (present in Cerylinae), and differ from the Alcedininae in their larger size and a much longer crista deltopectoralis that extends well beyond the onset of the crus dorsale fossae (hardly extending past this point in Alcedininae). All four specimens differ from LB-Av-296 in having a shorter crista deltopectoralis (Fig. 4N). The distal edge of the caput humeri is curved as in *Halcyon* but is straighter in *Tanysiptera*. Also, the incisura capitis is bounded medially by a ridge between the caput humeri and a crus dorsale fossae that is more pronounced in *Halcyon* than in *Tanysiptera*. All four specimens are larger than in *Tanysiptera* and fall in the size range of the larger *Halcyon* species, including *H. funebris*, *H. chloris collaris*, and *H. smyrnensis fusca*. Although similar in size, *H. lindsayi* appears to have a longer crista deltopectoralis.

Three coracoids (LB-Av-356, LB-Av-582, and LB-Av-332) have a very slender shape and a much reduced processus acrocoracoideus. The processus procoracoideus is also not very pronounced. In both Cerylinae and Alcedininae, the facies articularis clavicularis is more pronounced than in Halcyoninae, and curves more ventrally. The reduction of the processus acrocoracoideus is most evident in *Halcyon*, and the Liang Bua specimens mostly resemble *Halcyon*. LB-Av-332 is a juvenile specimen, and slightly shorter and more slender than the other two specimens. In size, the specimens are smaller than *Pelagopsis* and *Dacelo* and are similar to that in *H. chloris collaris* and *H. lindsayi*. The carpometacarpi have a well-developed processus intermetacarpalis, facies articularis digitalis major and minor that are slightly set apart, and a sulcus tendineus that extends proximally until level with the onset of the processus intermetacarpalis. The facies articularis digitalis minor extends more distally in *Tanysiptera* than in *Halcyon*. The carpometacarpi are stout, especially the os metacarpale major, and are in this respect most similar to *H. funebris*. At least three individuals are represented here (MNI = 3)

Taphonomic Analysis

Despite the majority of the avian bone assemblage consisting of fragmentary remains, the bone surfaces are well preserved; very few bones are weathered (Fig. 5) or show signs of fluvial transportation (i.e., no 'rolling' of the bones), and small anatomical details are well preserved. A very small fraction of the whole assemblage (2%) displayed gnawing marks from rodents and the incidental small varanid (Fig. 5), but not a single cut mark was observed. The majority of the bones show little to no signs of weathering; respectively 72% and 12% of the bones were classified as Bone Weathering Stages 0 (bone shows no sign of

cracking or flaking) and 1 (bone shows cracking, normally parallel to the fiber structure) (Behrensmeyer, 1978). Signs of digestion (see Figure 5D) were evident on bones throughout the sequence (e.g., 95% of the swiftlet bones show signs of digestion with affected bones present in every level).

DISCUSSION

The Liang Bua sequence represents the first fossil record for birds on Flores, as well as for the whole of Wallacea. Within Southeast Asia, the Sector XI assemblage constitutes the longest fossil sequence for birds, because the age of the sediments extends well back into the late Pleistocene (Roberts et al., 2009), and further back in time than the fossil assemblages of Niah Cave on Borneo (~40,000 years; Stimpson, 2009) and Palawan on the Philippines (~11,000 years; Reis and Garong, 2001). At least two species (*L. robustus* and *Trigonoceps* sp.) disappear from the sequence toward the end of the Pleistocene. Their disappearance within these deposits corresponds with the disappearance of mammalian species such as *Stegodon florensis insularis* and *Homo floresiensis*, and may represent extinction events for these taxa. Although bird remains are less abundant than mammalian remains, avian diversity at Liang Bua is substantially greater than mammalian diversity, particularly during the late Pleistocene.

Bone accumulations in caves may result from fluvial transport, pitfalls, burrow deaths, hibernation/aestivation, and predation (Andrews, 1990). The absence of signs of transportation in the avian bone assemblage at Liang Bua indicates that the accumulation is unlikely to have resulted from transportation by the nearby Wae Racang River. Instead, species diversity, signs of digestion throughout the sequence, and the raptor diversity coinciding with the peak in avian bone abundance (Table 1) suggests that raptors were likely responsible for the accumulation of small bird bone material at Liang Bua. Birds of prey, particularly owls, are the major accumulators of small mammal and bird bone assemblages (Andrews, 1990; Boyer, 2010). In the Liang Bua late Pleistocene deposits, the majority of the non-predatory birds are much smaller than the barn owl (~400 g; Dunning, 2008) and fall within the size range of potential prey (<200 g; Andrews, 1990; Taylor, 1994). In addition to barn owls, other owl species, eagles, vultures, and giant storks may have been accumulators of bones in the assemblage. On Borneo, for instance, Brahminy Kites were observed to frequent the mouth of the large Niah Cave complex and prey on swiftlets (Smythies, 1968) and other small birds. Alternatively, predatory bats might have been responsible for the accumulation of small bird remains; avian prey remains of the Australian Ghost Bat *Macroderma gigas* are characterized by an abundance of distal wing elements of small birds (Boles, 1999). The abundance of distal wing elements of swiftlets in the Liang Bua sediments agrees with such a scenario. Although the presence of predatory bats in the Liang Bua sequence has yet to be confirmed, two extant species of bats from the Lesser Sundas, *Hipposideros diadema* (known from Flores) and *Megaderma spasma*, would at least occasionally eat birds (K. M. Helgen, pers. comm.).

Despite continued raptor or possible predatory bat activity during the Holocene, as evident from the digestion signs on swiftlet bones, the number of identified bird taxa from the Holocene sediments (0–300 cm, Units 1–3) is lower than that of the late Pleistocene (8 vs. 23 taxa, respectively; Fig. 2). This could signal a decline in the Liang Bua avian assemblage, because no major difference in taphonomy and avian bone preservation was observed between the late Pleistocene and Holocene assemblage. However, the Holocene sample size (number of identified specimens [NISP] = 46) is lower than Pleistocene sample size (NISP = 180). Qualified against avian NISP, the number of identified taxa from the Holocene equals 0.17, vs. 0.13 for the Pleistocene sediments (Units 8–6). The low number of Holocene taxa is thus related to the low sample size, and addition of new taxa with a larger sample size is likely.

Twenty-three taxa (in 13 families) were recorded within the Pleistocene units (8 and 7; see Table 1), representing a diverse avifauna. At least 80% of the Pleistocene taxa still occur on Flores today, but several are absent from the modern avifauna. The giant stork *Leptoptilos robustus* has not been found above Unit 7 and is now extinct (Meijer and Due, 2010). Vultures of the genus *Trigonoceps* are currently considered endemic to Africa (Mundy et al., 1992), but are present in Liang Bua from Units 8 through 6. Although Unit 6 may represent a mixture of Pleistocene and Holocene deposits, the absence of *Trigonoceps* sp. from younger layers points towards a late Pleistocene disappearance or extinction. The remains of a species of barn owl *Tyto* sp. consistently larger than *T. alba* were found only in Units 8 and 7. These remains might represent an extinct species, *T. longimembris*, or another of the Indonesian *Tyto* species. The crake *Porzana* sp. differs in morphology from all extant crakes and shows characteristics that are also observed in the flightless Small Maui Crake *P. keplerorum* from the Hawaiian island of Maui. Flightless rails are a common element in (sub)fossil insular avifaunas (Steadman, 2006), but without more pectoral elements it is not possible to determine whether the Liang Bua specimens indicate flightlessness or merely a change in hind-limb locomotion.

Paleoecological Implications

The late Pleistocene diverse avifauna suggests the presence of a range of habitats surrounding the cave. Wetland and forest habitats are well represented within the late Pleistocene assemblage (Fig. 6), as well as grassland and scrub habitats. Terrestrial-aquatic birds, such as snipes, sandpipers, plovers, and ducks, are abundant in the late Pleistocene assemblage (Table 1) and are indicative of the nearby presence of freshwater bodies such as rivers, lakes, and swamps. Charadriidae (plovers and allies) and Scolopacidae (snipes, sandpipers, and allies) are distributed in open country and preponderantly in habitats near water (semi-aquatic). Whereas plovers feed on small invertebrates on the exposed soil by sight, snipes and sandpipers use their bills and hunt by probing the mud. Overflow of the nearby Wae Racang River was likely an important geomorphological factor in the depositional history of the cave, with pooling events occurring multiple times during the late Pleistocene (Westaway et al., 2009a, 2009b). The presence of small freshwater pools nearby and inside the cave would have provided suitable habitats for birds that are not typically recovered in caves.

Forest-dwelling birds, such as *Macropygia*, *Ptilinopus*, *Geoffroyus* cf. *geoffroyi*, and swiftlets, indicate the nearby presence of tropical monsoonal forest with well-developed canopies. Swiftlets are common inhabitants of Southeast Asian caves (Smythies, 1968) and forage for insects on the wing immediately above the forest canopy or in forest breaks (Coates and Bishop, 1997). The Edible-nest Swiftlet *Aerodramus* cf. *fuciphagus* is the most common species in the assemblage (NISP = 100), whereas the Glossy Swiftlet *Collocalia esculenta* is less common (NISP = 5); however, both species are continuously present throughout the sequence and indicate that swiftlets have been part of the Flores avifauna for quite some time. Similarly, the Niah Caves on Borneo are well known for their large populations of swiftlets (Medway, 1962), and fossil evidence shows that swiftlets have been utilizing the cave complex for at least 40,000 years (Stimpson, 2009). Species in the assemblage that inhabit upper forest canopies include the frugivorous pigeons *Macropygia* and *Ptilinopus* and the Red-cheeked Parrot *Geoffroyus* cf. *geoffroyi*. Raptors can frequent a range of habitats, but eagles (genus *Aquila*) and goshawks (genus *Accipiter*) prefer forest cover (Coates and Bishop, 1997). Goshawks can often be found perching in the forest's midstorey or hunting along
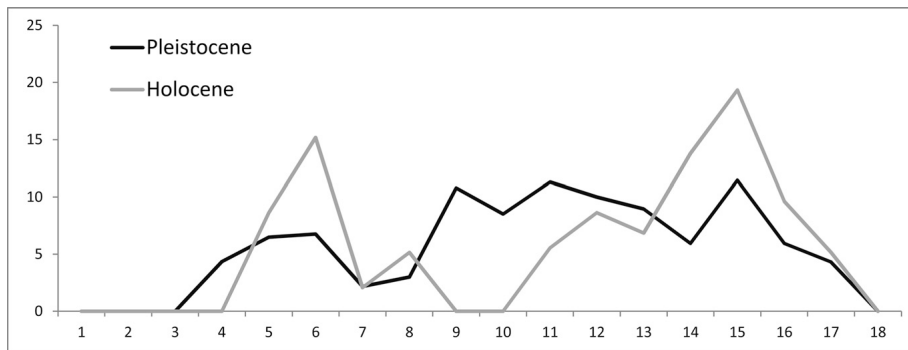
FIGURE 6. Habitat spectra for the Pleistocene and Holocene Liang Bua bird assemblages. All habitat affinities taken from Coates and Bishop (1997), except for *L. robustus* and *Trigonoceps* sp., which are based on their modern analogues in Mundy et al. (1992). 1, ocean; 2, inshore waters; 3, offshore islets; 4, seashore; 5, mangroves; 6, mittoral woodland; 7, coconut plantations; 8, swamp forest; 9, swamps, marshes and lakes; 10, rice fields; 11, grassland; 12, scrub; 13, savannah woodland; 14, lowland monsoon forest; 15, secondary forest and forest edge; 16, lowland rainforest; 17, montane forest; 18, alpine grassland. The vertical axis shows the habitat indices as percentages. Note that family-level identifications are excluded, and that the man-made habitats 'rice fields' and 'coconut plantations' did not exist in the Pleistocene.

the forest edge, whereas eagles hunt over the canopy and nearby open areas. The number of species in the Liang Bua assemblage that prefer forest habitats, and the different habitat levels within the forest that they represent, indicates that nearby tropical monsoonal forests were mature and floristically diverse. Such a forest would have provided ample food resources for *Homo floresiensis* (Westaway et al., 2009c).

A number of bird species in the late Pleistocene assemblage prefer more open habitats, such as the forest edges, grasslands, and scrub (Fig. 6), habitats that are also preferred by Komodo dragons. Such habitats probably existed in areas where the forest bordered on the river and gave way to marshes and grassland. Brahminy kites (*Haliastur* cf. *indus*) frequent waterways and forest openings, are often seen patrolling rivers for food (Coates and Bishop, 1997), and have been observed near Liang Bua (M. Schellekens, pers. comm.). Rails (*Porzana* sp. and *Gallirallus* sp.) generally prefer low, dense vegetation and forage at the edges of shallow water, and the tree kingfishers (Halcyoninae) inhabit thickly to lightly wooded country. Nearby wooded country and grasslands would have provided good hunting grounds for barn owls (*Tyto* sp.) that utilized the cave for roosting.

The Holocene layers document the first occurrences of the Island Collared Dove *Streptopelia* cf. *bitorquata* and Imperial pigeons (*Ducula* sp.). Whereas the Island Collared Dove is a species that prefers less densely wooded areas, Imperial pigeons are forest-dwelling birds (Coates and Bishop, 1997). Their presence along with swiftlets (*C. esculenta* and *A.* cf. *fuciphagus*), Red-cheeked parrots (*G.* cf. *geoffroyi*), and *Aquila* eagles suggests that the late Pleistocene forest cover persisted into the Holocene. However, wetland biotopes are less represented than in the Pleistocene, because many terrestrial-aquatic birds, such as the Charadriidae, Scolopacidae, and Halcyonidae, are absent. This might reflect the shift towards a drier climate that occurred around 39–17 ka (Westaway et al., 2009a), which might also have led to a change in the dominant vegetation from tropical monsoonal forests to less densely forested and open woodland. However, these taxa still occur on the island today (Coates and Bishop, 1997; Mees, 2006) and their absence from the Holocene sequence likely reflects the Wae Racang river changing its course and moving away from the entrance of the cave, thereby no longer attracting birds that prefer wetland habitats, rather than their extirpation from the island. Also, the persistence of forest birds into the Holocene is not consistent with a contraction of the forests immediately surrounding the cave. The disappearance of nearby wetland habitats, possibly amplified by the direct and indirect effects of the arrival of modern humans, more likely accounts for the absence of wetland bird species from Holocene assemblage.

A remarkable element in the late Pleistocene Liang Bua avifauna is the presence of large-bodied carnivorous birds, i.e., the vulture *Trigonoceps* sp. and the giant stork *Leptoptilos robustus*. Vultures at present are strikingly absent from insular Southeast Asia (Thiollay, 1998), and Liang Bua represents the first recorded Pleistocene occurrence of vultures in Wallacea. This indicates that the ranges of extant genera of vultures, even those with current distributions limited to Africa, may have been much larger in the past, a conclusion also supported by the presence of two African vulture genera in the middle Pleistocene of China (Zhang et al., 2012). In the absence of mammalian carnivores, large birds of prey often take over the major predator niche in insular faunal communities, taking advantage of the abundant small mammals and birds (Ballmann, 1973, 1976; Worthy and Holdaway, 2002). Analogous to the vultures and marabou storks of the African savannah, both *L. robustus* and *Trigonoceps* sp. are considered carrion eaters and may have been attracted to Liang Bua by the on-site butchering of *Stegodon* by *Homo floresiensis* (Morwood et al., 2004, 2005; van den Bergh et al., 2009). Vultures and marabou storks are fierce competitors for food. With their straight bill, marabou storks are unable to tear meat from a carcass, and much of their time at a carcass is spent intimidating vultures into dropping their chunks of meat (Mundy et al., 1992). White-headed vultures (*Trigonoceps occipitalis*) have been observed to usually remain on the fringes of activity at a carcass (Mundy et al., 1992), but they possess a powerful beak that allows them to feed on the tougher parts of a carcass, such as tendons and skin (Hertel, 1994). This would have enabled them to feed on discarded pieces of carcasses that were considered inedible by *H. floresiensis*. However, both white-headed vultures and marabou storks only partially rely on large carcasses (>40 kg) for food, and *L. robustus* and *Trigonoceps* sp. probably supplemented their diet by feeding on carcasses of small mammals or actively hunting smaller animals such as the abundant rats.

CONCLUSIONS

The bird remains from Liang Bua's Sector XI represent the first fossil record for birds on Flores, and in Wallacea generally. The Pleistocene assemblage constitutes a diverse avifauna that reflects an environment dominated by wetlands and forest, and to a lesser degree open woodland. The Holocene assemblage is different in species composition, and at least two taxa disappear

from the sequence toward the end of the Pleistocene. This is interpreted as evidence for an extinction event near the end of the Pleistocene, possibly resulting from a shift towards a drier local climate (although forest apparently persisted near the cave) and possibly amplified by the direct and indirect effects of the arrival of modern humans. Further analyses of bird remains from other excavated sectors within Liang Bua, as well as from other sites on the island, will shed more light on changes from the Pleistocene to Holocene and the impact of modern humans on the avifauna.

ACKNOWLEDGMENTS

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APPENDIX 1. List of species examined. † denotes extinct species.

Anseriformes—*Aythya australis* M 556840; *Nettapus pulchellus* F 347644; *Dendrocygna guttata* M 560773; *Dendrocygna arcuata* U 610657; *Anas gibberifrons* F 610561, M 226004.

Galliformes—*Megapodius freycinet* M 556996; *Bambusicola thoracica* U 318518; *Coturnix pectoralis* M 612659; *Gallus gallus* M 500286, F 560790; *Gallus varius* M 19729, M 319799, M 318496.

Ciconiiformes—*Leptoptilos crumeniferus* F 489395, M 489396; *Leptoptilos dubius* M 319788, F 225988, F 429220; *Leptoptilos javanicus* M 223897, U 430764.

Accipitriformes—*Accipiter fasciatus* M 620189, M 620190; *Accipiter haplochrous* F 561513; *Accipiter henicogrammus* F 554909, F556987; *Accipiter minullus* M 490283; *Accipiter novaehollandiae* F 613004; *Accipiter novaehollandiae obiensis* F 558307; *Accipiter novaehollandiae griseogularis* M 559036, M 559037, M 56077; *Accipiter soloensis* F 560782; *Accipiter superciliosus* M 431337, M 430926; *Accipiter superciliosus superciliosus* F 586298; *Accipiter virgatus confusus* F 488909; *Aegypius monachus* U 614152, F 428040; *Aquila audax* F 346461, U 344883, U 620191, M 620192, U 226901; *Aquila chrysaetos* M 500355; *Aquila gurneyi* U 554908; *Aquila rapax raptor* M 488148; *Aviceda subcristata rufa* F 558306; *Buteo buteo japonicus* F 318739; *Elanus caeruleus caeruleus* F 558446; *Elanus caeruleus leucurus* U 19603; *Falco moluccensis* F 560787; *Gypaetus barbatus* F 345684, U 17834; *Gyps africanus* F 431403, M 587405; *Gyps fulvus* F 227051; *Gyps fulvus coprotheres* U 561314; *Gyps himalayensis* M 19534; *Gyps rueppellii* U 430178; *Haliastur indus* F 556984, F 558304; *Haliastur sphenurus* M 610563; *Haliaeetus leucocephalis* U 288183; *Haliaeetus leucogaster* F 560785, M 560784; *Hieraaetus spilogaster* (= *Aquila fasciata*) F 490548, M 490783, M 430796; *Macheiramphus alcinus* U 559816; *Milvus migrans* U 318740, U 603402; *Neophron percnopterus* U 17835; *Pandion haliaetus* F 560783; *Pernis apivorus*

gurneyi F 343984, M 343983; *Pernis ptilorhynchus* U 620644; *Spizaetus cirrhatus limnaeetus* M 344616; *Spizaetus tyrannus* M 344051; *Stephanoaetus coronatus* M 346652; *Torgos tracheliotus* F 321827, M 320977, M 347597; *Torgos tracheliotus nubicus* U 19090; *Trigonoceps occipitalis* F 320859, M 347358.

Gruiformes—*Amaurornis phoenicurus* F 501102; *Amaurornis phoenicurus javanicus* F 562003; *Crex crex* M 490298; *Gallicrex cinerea* M 489266; *Gallirallus australis australis* F 18193; *Gallirallus dieffenbachii* U 559711; *Gallirallus owstoni* M 501068; *Gallirallus philippensis* M 632139; *Gallirallus philippensis swindellsi* U 561546; *Gymnocrex rosenbergii* M 225808; *Habroptila wallacii* F 557027; *Porzana pusilla* F 291705; *Porzana fusca bakeri* M 344361; *Porzana fusca erythrothorax* M 319482; *Gallirallus philippensis* F 560791; *Rallina eurizonoides minahassa* U 226005; *Porzana keplerorum*† 384600, 378233.

Charadriiformes—*Charadrius leschenaultii* F 621501; *Charadrius leschenaultii geoffroyi* M 292290; *Pluvialis dominica* U 498219; *Pluvialus fulva* M 622612; *Actitis hypoleucos* F 557032, F 613022; *Arenaria interpres* M 500787, F 500723; *Calidris alba* M 497901, M 610853; *Calidris acuminata* F 612669; *Calidris ruficollis* 488338; *Calidris ferruginea* F 558504; *Gallinago gallinago* M 603470, M 633452, M 633385; *Gallinago hardwickii* F 612667; *Gallinago megala* M 621521; *Gallinago stenura* M 557035; *Heteroscelus brevipes* M 500795; *Scolopax minor* M 502607, M 610887; *Scolopax rochussenii* F 558308; *Scolopax rusticola* F? 292760; *Turnix nigricollis* M 488643; *Turnix ocellata benguetensis* M 607266; *Turnix suscitator fasciata* F 562149, M 502147, M 562148; *Turnix suscitator interrumpenses* F 343204, F 343207; *Turnix sylvatica lepurana* M 430658, U 429078; *Turnix tanki blankfordii* M 344364; *Turnix varia* U 526322.

Columbiformes—*Caloenas nicobarica* F 557090; *Chalcophaps indica* F 557082, M 557059; *Columba vitiensis* U 290433; *Columba vitiensis griseogularis* U 560654; *Ducula aenea* F 432041, M 291373; *Ducula bicolor* M 560808, M557108; *Geopelia striata* M 292304; *Macropygia amboinensis* M 557039, M 557040; *Macropygia phasianella tenuirostris* F 562813; *Macropygia unchall* F 344626, F 344972; *Ptilinopus hyogastra* F 558298; *Ptilinopus melanospila melanospila* M 226177; *Ptilinopus monacha* M 557089; *Ptilinopus regina* M 620203; *Ptilinopus superbus* M 489040, M 557093; *Streptopelia bitorquata* M 576466, F 635307; *Streptopelia chinensis* F 558310; *Streptopelia chinensis tigrina* F 225814, 554910; *Streptopelia orientalis* M 633479; *Treron apicauda apicauda* F 343512 *Treron formosae* M 611769; *Treron formosae filipina* F 560659; *Treron pompadora* F 225810; *Treron pompadora axillaris* M 488904; *Treron vernans* M 559822.

Psittaciformes—*Aprosmictus erythropterus* M 620220; *Bolbopsittacus lunulatus lunulatus* M 613041; *Chalcopsitta atra* U 19885; *Charmosyna placentis intensior* M 558317; *Domicella garrula* M 557122; *Eos squamata* F 557117; *Geoffroyus geoffroyi* M 557133, M 557132; *Geoffroyus geoffroyi cyaniocollis* M 554907; *Glossopsitta concinna* F 612112; *Loriculus amabilis* M 557143; *Loriculus philippensis philippensis* M 613044; *Loriculus stigmatus* M 225818; *Micropsitta finschii* F 615016; *Oreopsittacus arfalu* M 610201; *Platycercus elegans* M 492465; *Psittaculirostris edwardsii* M 608091; *Psittacula krameri* 343238; *Tanygnathus lucionensis salvadori* F 562020; *Tanygnathus megalorhynchus* F 560814; *Tanygnathus megalorhynchus obiensis* M 558318; *Trichoglossus haematodus* F 612676, U 612679; *Trichoglossus haematodus intermedius* U 489032; *Vini kuhlii* F 498417; *Vini australis* U 319746.

Strigiformes—*Tyto alba* M 553887; *Tyto alba stertens* F 343261, M 343262; *Tyto alba lulu* F 561573, F 561574, F 612697, U 614954; *Tyto alba delicatula* F 492458; *Tyto capensis* U 560528; *Asio flammeus* U 19537, F 553265; *Asio otus* F 318562; *Bubo philippensis* F 489264; *Bubo sumatranus* U 559827; *Glaucidium brodiei* M 559829; *Ketupa ketupa* F 559828; *Ninox novaeseelandiae* F 492457, M 620226; *Ninox variegata* M 615018, F 615019; *Ninox scutulata* F 607324; *Ninox philippensis* F 613697; *Ninox strenua* F

632259; *Otus magicus* M 557174; *Phodilus badius* M 20310; *Strix varia* F 610975; *Strix uralensis* F 610403.

Apodiformes—*Aerodramus salangana* F 559831; *Aerodramus spodiopygia leucopygia* M 561579; *Aerodramus vanikorensis* F 557187, M 557186; *Aerodramus vanikorensis palawanensis* F 489010, U 489011, M 489009; *Collocalia esculenta* M 560820, M 560818, M 560822; *Collocalia marginata* F 635405; *Collocalia troglodytes* F 430517.

Coraciiformes—*Dacelo novaeguineae* F 612711; *Halcyon chloris collaris* M 560676, M 562031; *Halcyon funebris* F 557211; *Halcyon lindsayi lindsayi* F 613072; *Halcyon sancta* F 557198, M 557196; *Halcyon sancta sancta* F 489077; *Halcyon smyrnensis fusca* M 343265; *Tanysiptera galatea* F 557228, F 557230, F 557234, M 557216, M 557217; *Tanysiptera sylvia* F 614960; *Pelargopsis melanorhyncha* M 228198; *Pelargopsis capensis gouldi* M 562023; *Alcedo atthis* M? 557190, M 620468; *Alcedo atthis bengalensis* M 291713, M 292313; *Alcedo leucogaster* M 631689; *Ceyx rufidorsum rufidorsum* F 562034; *Ceyx cyanopectus cyanopectus* M 613065; *Ceyx lepidus* M 557191; *Ceryle lugubris guttulata* M 319068, U 318238; *Ceryle rudis leucomelanura* M 343520.

Passeriformes—*Corvus enca pusillus* F 562055; *Turdus obscurus* F 562863; *Passer montanus* F 559088.