



## RESEARCH ARTICLE

# Why did the chicken cross the Wallace Line? Archeological evidence suggests human-mediated dispersal of *Gallus* to Flores first occurred at least $\sim 2.25$ ka cal. BP

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## Abstract

Domesticated chickens (*Gallus gallus domesticus*) are a dominant part of the global human diet. Although the early domestication history of this species remains disputed, Mainland Southeast Asia (MSEA) is assumed to have been the initial domestication center. The eastward spread of chickens into Island Southeast Asia (ISEA) and the Pacific is typically attributed to human-mediated dispersals. Chicken remains are relatively common at Pacific Neolithic sites but are extremely rare in the archaeological records of MSEA and ISEA. Therefore, the exact routes and timing of the human-mediated spread of chickens from their native range in MSEA into the Pacific remain questions of interest. Here, we present the earliest evidence of *Gallus* on the Indonesian island of Flores at Liang Bua. This site has yielded an extensive stratigraphic sequence that spans from  $\sim 190,000$  calendar years (ka) ago until the present and includes dense accumulations of faunal remains. Twelve bones from the cave's Holocene deposits have been identified as *Gallus*. The oldest remains, a right and left coracoid, were each directly dated to  $\sim 2,250$  calibrated radiocarbon years before present (ka cal. BP), whereas the youngest *Gallus* elements are  $\sim 0.3$  ka old. Although wild Green Junglefowl (*Gallus varius*) and Red Junglefowl (*Gallus gallus*) are found on Flores today, the absence of either of these species in deposits at Liang Bua older than  $\sim 2.5$  ka as well as the size and shape of the oldest coracoids suggests that these remains likely represent domesticated *G. gallus*. This is the first evidence for domesticated chickens in the Neolithic of Flores and the first directly dated *Gallus*

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remains in Wallacea. The absence of chickens in the fossil record of ISEA suggests that Red Junglefowl (and perhaps Green Junglefowl also) reached Wallacea via human-mediated dispersal(s) at least  $\sim 2.25$  ka cal. BP.

#### KEYWORDS

farming, fowl, Liang Bua, Neolithic, Southeast Asia

## 1 | INTRODUCTION

Chickens<sup>1</sup> (*Gallus gallus domesticus*) are currently the most abundant domesticated animals in the world and a critically important part of the human diet (Serjeantson, 2009). Not surprisingly, the origin and timing of their domestication, and their subsequent spread across the world, remains a research topic of interest. Chickens were initially thought to have been domesticated from the Red Junglefowl (*G. gallus*), which is native to Mainland Southeast Asia (MSEA) and part of its extended continental shelf (Darwin, 1868; Fumihito et al., 1996), and a recent molecular analysis identified the subspecies *G. g. spadiceus* as the main wild ancestor of modern chickens (Wang et al., 2020). A widely accepted scenario posits that chickens were first domesticated in Southeast Asia and then taken north to China by  $\sim 8$  thousand calibrated years before present (ka cal. BP) from where they spread rapidly into western Eurasia (West & Zhou, 1988). However, this early Holocene scenario of chicken domestication has not received support from zooarchaeological evidence or paleoclimate data (Eda, 2021; Eda et al., 2016; Peters et al., 2016). The scarcity of chicken bones at archaeological sites in the region and the difficulties in distinguishing skeletal elements of *Gallus* from those of other Phasianidae species contributes to the challenges of pinpointing the origin(s) and early dispersal patterns of chicken domestication (Eda et al., 2016; Peters et al., 2016). Although the timing and location(s) of early chicken domestication thus remain unclear, it is most likely to have occurred first within their natural distribution in MSEA (Peters et al., 2022). This idea is supported by a recent re-assessment of reported archaeological occurrences of chickens from over 600 sites, which found that the first unambiguous skeletal evidence of chickens occurs  $\sim 3.6$ – $3.2$  thousand calendar years (ka) ago at Ban Non Wat, Thailand (Peters et al., 2022).

After initial domestication, human-mediated spread of chickens beyond Southeast Asia occurred westwards into Western Asia, Europe, and Africa by the first millennium BC (Best et al., 2022) and eastwards, which is less well documented. Chicken remains are common in Pacific archaeological assemblages after  $\sim 3$  ka, and genetic data indicate that distinct populations of chickens accompanied Lapita people as they dispersed eastwards and colonized Remote Oceania (Storey et al., 2008, 2012). The exact routes of chicken dispersal from MSEA into the Pacific region remain unknown because, in contrast to the Middle East, Europe, and the Pacific, remains of junglefowl and

chicken are rare in the archaeological records of MSEA and Island Southeast Asia (ISEA). Bones of *Lophura ignita*, *L. erythrothalma*, and *Arborophila* sp. from Niah Cave on Borneo (Stimpson, 2010) as well as potentially Red Junglefowl from Late Pleistocene deposits at Spirit Cave (Tham Phii Man) in Thailand (Conrad et al., 2016) indicate that wild Phasianidae were exploited by humans during the Late Pleistocene. Remains of *Gallus* sp. have been reported from Neolithic sites in MSEA (Conrad, 2015; Higham, 1989; Piper, 2017), but it is unclear if these represent wild jungle fowl or chickens.

Linguistic evidence suggests that chickens may have been imported into ISEA as early as 4.5 ka by Austronesian-speaking human populations together with dogs and pigs (Bellwood, 2005, 2017). However, genetic data point towards an ISEA origin of Polynesian chickens; the predominant chicken mitochondrial DNA lineage in the Pacific (haplotype D) is absent in Taiwan (Miao et al., 2013), and one of the ancestral single nucleotide polymorphism motifs found in ancient Polynesian chickens was also detected in the Philippines (Thomson et al., 2014). There is, however, little archeological evidence of chickens in this region to test this hypothesis. Bones attributed to *Gallus* from Gua Jimbe<sup>2</sup> on Java were directly radiocarbon dated to  $\sim 1.4$  ka cal. BP (Horn et al., 2019). Bautista (1991) reported on an unknown quantity of chicken remains from the site of Ambangan, the Philippines, dated to AD 800–1200. In Wallacea, Storey (2016) reported on chickens from Neolithic and historical contexts in the Banda Islands, but according to Peter Lape (Lape et al., 2018, and personal communication, September 2022), there are no definitive Neolithic *Gallus* remains from the Banda Islands. A human burial on Timor-Leste at Ira Ara yielded an intact clay pot that was dated to AD 1630–1690 and contained the remains of a small bird, probably an immature chicken (Lape et al., 2020). Given the scant record of *Gallus* in ISEA, the timing and routes of the initial dispersal of chickens into this region and subsequently into the Pacific as well as the roles that they played in early societies remain unclear. Here we report on remains of *Gallus* recovered during archaeological excavations at Liang Bua (Flores, Indonesia) that represent the earliest evidence for chickens in Wallacea.

## 2 | MATERIAL AND METHODS

The 12 skeletal elements described here were recovered during archeological excavations at Liang Bua (Table 1). These skeletal

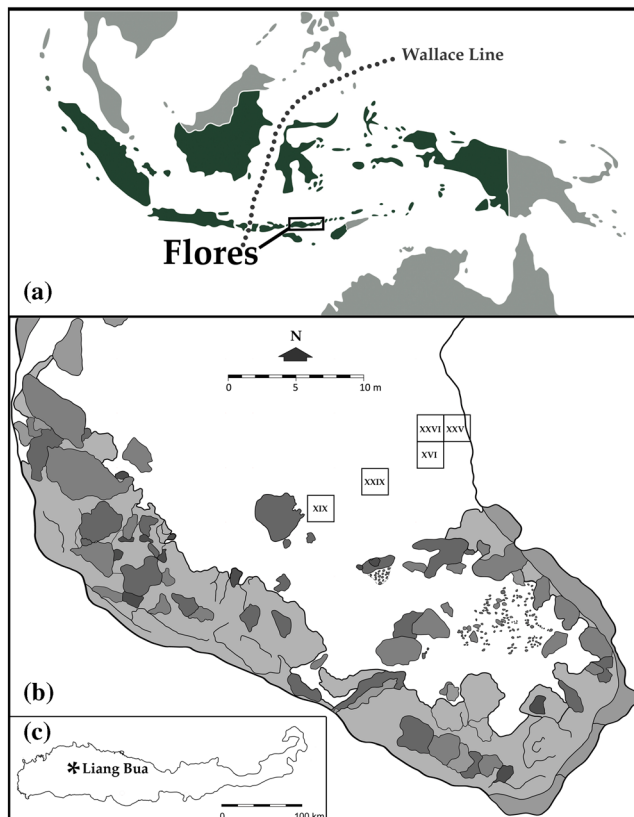
<sup>1</sup>In this paper, the word chicken specifically refers to domesticated *Gallus gallus*. Non-domesticated *G. gallus* and *G. varius* are referred to as Red Junglefowl and Green Junglefowl, respectively.

<sup>2</sup>Sometimes spelled “Goea Djimbe” as a left-over Dutch toponym.

elements derive from five excavated areas, Sectors XVI, XIX, XXV, XXVI, and XXIX, each of which was 2 × 2 m (Figure 1; Table 1) with excavations typically proceeding in 10-cm intervals (referred to as

**TABLE 1** Remains of *Gallus* and potential *Gallus*<sup>a</sup> specimens from Liang Bua (see text)

LB ID	Sector/spit	Element
LB-Av-1430	XVI/3	Left coracoid
LB-Av-1314	XVI/9	Shaft of a right coracoid
LB-Av-1916	XIX/9	Proximal left coracoid
LB-Av-2152	XXV/8	Right coracoid (in 2 pieces)
LB-Av-2151 <sup>a</sup>	XXV/12	Rostral premaxilla
LB-Av-2146	XXV/13	Fragment of a left proximal tibiotarsus
LB-Av-2148 <sup>a</sup>	XXVI/3	Rostral mandible
LB-Av-2150	XXVI/3	Distal right radius
LB-Av-2147	XXVI/3	Immature right ulna
LB-Av-2149	XXVI/3	Juvenile distal right radius
LB-Av-3446 <sup>a</sup>	XXIX/2	Pelvis fragment
LB-Av-3445 <sup>a</sup>	XXIX/5	Furcula



**FIGURE 1** Site location: (a) location of Flores and the Wallace Line in Southeast Asia; (b) plan of Liang Bua showing the excavated squares that have yielded the skeletal elements of chickens that are the focus of the present study; (c) the location of Liang Bua on Flores. Cave floor sediments are shaded white; exposed rocks, stalagmites, and other surfaces covered in speleothems are shaded in greys. [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

spits) while following observable stratigraphic layers. The bones were recovered during dry and wet sieving of the excavated sediments from stratigraphic Unit 8C, which represents the past ~3 ka and the uppermost layers in the Liang Bua depositional sequence (Sutikna et al., 2018). All of these bones have provisional registration numbers denoted as “LB-Av-##,” where “LB” refers to Liang Bua, “Av” to Aves, and “##” to a unique number. Measurements were taken according to von den Driesch (1976) using digital calipers to 0.1 mm. Skeletal elements from 22 extant specimens of *Gallus* were measured for comparison. These 22 specimens are curated at the Smithsonian Institution's National Museum of Natural History in Washington DC, USA (prefix USNM), and the Natural History Museum of Denmark in Copenhagen (prefix KUZM). Further details about these comparative specimens are provided in Table S1.

Five of the Liang Bua *Gallus* bones were sent for direct radiocarbon dating to DirectAMS Radiocarbon Dating Service in Bothell, Washington, USA. Each bone was chemically pretreated to extract its collagen, the <sup>14</sup>C content of which was measured using accelerator mass spectrometry. All radiocarbon ages were corrected for isotopic fractionation using the sample-specific  $\delta^{13}\text{C}$  values, which were measured on the prepared carbon by the accelerator, and calibrated using the IntCal20 calibration dataset for the Southern Hemisphere (SHCal20; Hogg et al., 2020) and the CALIB 8.2 program ([calib.org](https://calib.org)) (Stuiver & Reimer, 1993). The remaining bones were indirectly dated based on their stratigraphic positions in relation to previously published sets of radiocarbon ages from charcoal and other bone samples recovered from Unit 8C at Liang Bua (Evans et al., 2020; Julianto, 2022; Sutikna et al., 2018).

## 3 | RESULTS

### 3.1 | Referred material

Eight bones from Unit 8C at Liang Bua were referred to *Gallus* sp.: a complete left coracoid (LB-Av-1430) missing only the processus lateralis; a right coracoid in two pieces (LB-Av-2152); a proximal left coracoid (LB-Av-1916); the shaft of a right coracoid (LB-Av-1314); a distal right radius (LB-Av-2150); a juvenile distal right radius (LB-Av-2149); an immature right ulna (LB-Av-2147); and a fragment of a proximal left tibiotarsus (LB-Av-2146) consisting of the proximal part of the tibiotarsus without the proximal articulation. Additionally, the rostral part of a premaxilla (LB-Av-2151), the rostral half of a mandible (LB-Av-2148), a furcula (LB-Av-3445), and a pelvis fragment (LB-Av-3446) were identified as potential *Gallus* (Table 1).

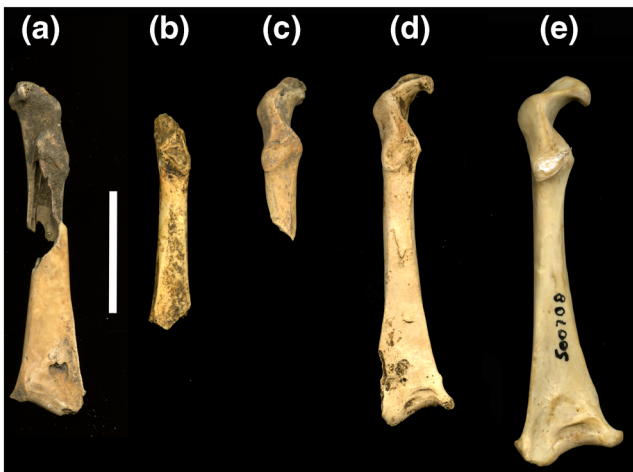
#### 3.1.1 | Description of the material and taxonomic affinities

##### *Coracoid*

The coracoids and coracoid fragments (LB-Av-1430, LB-Av-1314, LB-Av-1916, LB-Av-2152; Figure 2) are elongated and slender with a

short processus procoracoideus, a flat cotyla scapularis, and a facies articularis clavicularis that has a distinct hook at its dorsal side. The sternal end is narrow and LB-Av-2152 displays a distinct pneumatic foramen in the impressio m. sternocoracoidei, but only a depression is visible in LB-Av-1430. The Liang Bua coracoids are referred to Galliformes based on the flat cotyla scapularis, the short processus procoracoideus, a distinct impressio ligamentum acrocoracohumeralis, and the facies articularis clavicularis overhanging the sulcus m. supracoracoidei and displaying a hook on its dorsal side (Bocheński & Tomek, 2009; Mayr, 2006; Mourer-Chauviré, 1992). The galliform families Cracidae and Odontophoridae are limited to the New World, and Numinidae to Africa, and further comparisons here are limited to Phasianidae and Megapodiidae. The Liang Bua specimens agree with Phasianidae and can be distinguished from

Megapodiidae, by the facies articularis clavicularis, that (in proximal view) is notched in Phasianidae, but straight in Megapodiidae, the pronounced processus procoracoideus (less pronounced in Megapodiidae), and the distinct ridges on the ventral surface of the coracoid shafts that run from the medial edge of the sulcus m. supracoracoidei towards the lateral end of the facies articularis sternalis (pronounced in Phasianidae but only weakly developed in Megapodiidae). Extant Phasianidae on Flores are limited to four species in the genera *Synoicus* (*Synoicus ypsilophorus* and *S. chinensis*) and *Gallus* (*G. gallus* and *G. varius*), the only two phasianid genera present east of the Wallace Line (Eaton et al., 2016; Olson, 1978). *Synoicus* is a genus of small quails and easily distinguished from *Gallus* by its smaller size. The Liang Bua coracoids differ in size from those in *Synoicus*, and are similar to *Gallus* in that they display a facies articularis humeralis that is less pronounced on the ventral surface, and a notched facies articularis clavicularis (as the ventral lobe is set back with regard to the dorsal lobe), which is unnotched and more hooked in *Synoicus*. To our knowledge, there are no known osteological characteristics that separate Green Junglefowl (*G. varius*) from Red Junglefowl (*G. gallus*). Comparisons with a limited set of captive *G. varius* skeletons as well as *G. gallus domesticus* specimens show that the Liang Bua coracoids differ from both *G. varius* and *G. gallus domesticus* in the distal coracoid where the facies articularis sternalis is straighter in LB-Av-1430 and -2152, and the cotyla scapularis projects further from the shaft in both *G. gallus* and *G. varius* than in the Liang Bua specimens. In size (Table 2), the Liang Bua coracoids are larger than *Gallus sonneratii*, *G. varius*, *G. lafayettei* and *G. gallus*, and overlap in size with that of chickens.



**FIGURE 2** Coracoids of *Gallus* from Liang Bua and extant *Gallus* specimens in medial view. (a) Right coracoid (LB-Av-2152) in 2 pieces; (b) fragment of a right coracoid (LB-Av-1314); (c) a proximal left coracoid (LB-Av-1916); (d) a left coracoid (LB-Av-1430); (e) *Gallus gallus domesticus* (USNM 500708). Scale bar 2 cm [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

#### Ulna

The ulna (LB-Av-2147) is robust and curved with its shaft dorsoventrally compressed. The olecranon is short and blunt (Figure 3). Two parallel cutmarks, oblique to the long axis of the bone, are visible on the medial side of the proximal ulna (Figure 3d). Small, elongated pores, indicative of immature bone, are visible along this surface. Distally, the condylus ventralis is rounded and the tuberculum carpalis is

	GL	LM	Bb	Bf
LB-Av-1430	57.8	55.2		12
LB-Av-2152	55.5	52.3		11.5
<i>Gallus varius</i>	49.4	44.5	11.9	10.0
(n = 7/n = 3)	(40.7–53.3)	(38.9–48.1)	(11–13.3)	(9.8–10.2)
<i>Gallus sonneratii</i>	46.8	44.1	13.1	10.3
(n = 3/n = 2)	(44.1–50.3)	(41.3–46.9)	(12.2–14)	(9.1–11.6)
<i>Gallus lafayettei</i>	47.5	45.7	14.1	10.8
<i>Gallus gallus</i>	53			
<i>G. gallus domesticus</i>	62.2	47.1	13.8	10.8
(n = 9/n = 1)	(49.7–76.5)			
<i>G. gallus</i> (feral)	56.1			

Notes: Measurements were taken according to von den Driesch (1976). Note that n is higher for GL (first column) than for the other measurements.

**TABLE 2** Measurements in mm of the coracoid among species of *Gallus*

small and narrow. LB-Av-2147 exhibits the typical galliform shape with the distinct curved and dorsoventrally compressed shaft, the blunt olecranon aligned with the curvature of the shaft, and the distal



**FIGURE 3** Ulnae of *Gallus* from Liang Bua and extant *Gallus* specimens in ventral view. (a) Right ulna (LB-Av-2147); (b) *Gallus varius*, (USNM 19729); (c) *Gallus gallus domesticus* (USNM 500708); (d) close-up image showing cutmarks on the shaft of LB-Av-2147. Scale bar 2 cm, except for (d) (1 mm) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

part of the processus cotylaris dorsalis projecting further distally than the cotyla ventralis (Bocheński & Tomek, 2009). The specimen differs from Megapodiidae (except *Megapodius*) in the more distally projecting condylus ventrale ulnare, which is similar to the condition observed in Phasianidae and agrees most with Phasianidae in that the sulcus intercondylaris is deep (less deep in Megapodiidae). Within Phasianidae, the ulna is much larger than those of *Synoicus* and is similar in morphology to *Gallus*. In size (Table 3), it overlaps with *G. varius*, *G. sonneratii*, *G. lafayetti* and *G. gallus* for total length (GL) but is smaller than in chickens.

#### Radius

Both radii display a straight shaft with the ventrally curving distal articulation (Figure 4) typical of Galliformes. The juvenile radius (LB-Av-2149) is similar in shape as the adult radius (LB-Av-2150) but is smaller in size and shows the porous surface typical of immature bones. In comparison with extant Galliformes, the distal end of the radius in Phasianidae is relatively short and flares ventrally, whereas it flares less and projects further distally in Megapodiidae. In LB-Av-2150, the distal end flares out but is relatively short, and thus agrees most with Phasianidae. In size (Table 4), LB-Av-2150 overlaps with *G. varius*, *G. sonneratii*, *G. lafayetti*, and *G. gallus* but is smaller than in *G. gallus domesticus*.

#### Tibiotarsus

The tibiotarsus fragment (LB-Av-2146) preserves only the onset of the crista cnemialis lateralis and cranialis, which both extend distally down the shaft to a similar degree (Figure 5) as in *Gallus*. This morphology differs from that of the only other similar-sized Galliform genus on Flores, *Megapodius*, wherein the crista cnemialis cranialis extends further down the shaft than the crista cnemialis lateralis. Interestingly, the proximal end of LB-Av-2146 displays a clear flat surface that likely is the result of chopping.

#### Other potential *Gallus* remains

Two cranial fragments, the rostrum maxillae (LB-Av-2151) and the rostral mandibulae (LB-Av-2148) both display the general Galliform shape with a broad (~30°) and rounded tip (Figure 6). LB-Av-2151 preserves a small portion of the broad and flat maxillary processes of the premaxillae, and the processus frontalis premaxillare is narrow,

**TABLE 3** Measurements in mm of the ulna among species of *Gallus*

	GL	Dip	Bp	SC	Did
LB-Av-2147	61.5	11.75	7.86	4.1	8.5
<i>Gallus varius</i> (n = 7/n = 3)	61.9 (53.5–65.3)	10.6 (9.3–11.7)	7.1 (6.5–7.6)	3.2 (2.8–3.4)	8.1 (7–8.9)
<i>Gallus sonneratii</i> (n = 3/n = 2)	61.0 (58–66.4)	7.2 (9.3–12.3)	7.7 (7–8.5)	4.1 (3.8–4.5)	8.6 (8.1–9)
<i>Gallus lafayettii</i>	65.1	12.1	7.4	4.3	8.4
<i>Gallus gallus</i>	65.5				
<i>G. gallus domesticus</i> (n = 9/n = 1)	81.8(65.2–99.2)	12.0	7.5	3.9	8.5
<i>G. gallus</i> (feral)	75.5				

Notes: Measurements were taken according to von den Driesch (1976). Note that n is higher for GL (first column) than for the other measurements.

indicating a wide nasal opening. This is similar to Galliformes, and unlike Accipitriformes and Columbiformes. Within Galliformes, the wide nasal opening is shared in both Phasianidae and Megapodidae. LB-Av-2148 is curved downwards and elongated foramina neurovasculare can be seen along the lateral side. This morphology is similar in both Phasianidae and Megapodidae and does not allow for a

distinction between the two. The small size of both fragments (mandibular pars symphysialis measures ~8 mm) suggests they belong to *Gallus* rather than *Megapodius* (the only species of megapode on Flores) but they cannot be assigned with certainty. In addition, a furcula and pelvis fragment were preliminarily identified as *Gallus*, but have not been systematically compared to reference material. They have been included here in order to list all identified and putatively identified *Gallus* at Liang Bua.



**FIGURE 4** Radii of *Gallus* from Liang Bua and extant *Gallus* specimens in ventral view. (a) Right radius (LB-Av-2150); (b) fragment of a juvenile right radius (LB-Av-2149); (c) *Gallus varius* (USNM 19729); (d) *Gallus gallus domesticus* (USNM 500708). Scale bar 2 cm [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

### 3.2 | Ages of the Liang Bua *Gallus* remains

LB-Av-2146, LB-Av-2151, and LB-Av-2152 were recovered in spits 13 (125–135 cm depth), 12 (115–125 cm), and 8 (75–85 cm), respectively, of Sector XXV. The first two yielded direct calibrated radiocarbon ages of 2.23 (2.24–2.15) and 1.65 (1.71–1.61) ka cal. BP while LB-Av-2152 yielded an age of 0.96 (0.95–0.93) (Table 5). In contrast, LB-Av-2147, LB-Av-2148, LB-Av-2149, and LB-Av-2150, all of which derive from spit 3 (25–35 cm depth) in the immediately adjacent Sector XXVI, are likely younger than 0.49 (0.52–0.45) ka cal. BP based on charcoal recovered slightly deeper at 45 cm depth (Sutikna et al., 2018).

LB-Av-1430 and LB-Av-1314 were recovered in spits 3 (25–35 cm depth) and 9 (85–95 cm depth), respectively, of Sector XVI. Like the remains from spit 3 of Sector XXVI, LB-Av-1430 is probably not more than a few hundred years old. However, LB-Av-1314 yielded an age of 2.25 (2.32–2.22) ka cal. BP. Similarly, LB-Av-1916, from spit 9 (85–95 cm) of Sector XIX, yielded an age of 2.25 (2.33–2.19) ka cal. BP.

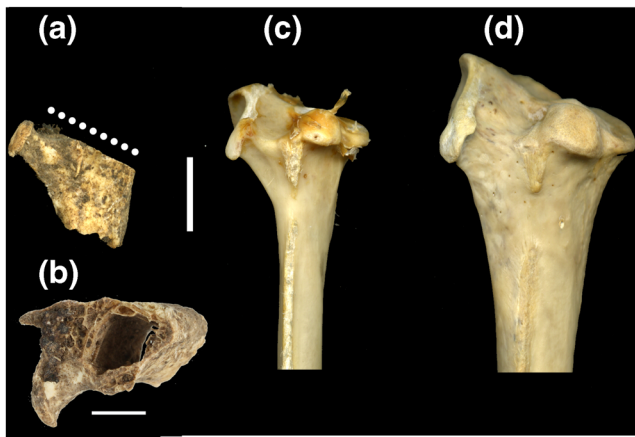
## 4 | DISCUSSION

The twelve bones from Liang Bua that were the focus of this study represent the first prehistoric record of *Gallus* on the oceanic island of Flores. Moreover, five of these bones yielded direct calibrated radiocarbon ages ranging between 2.25 and 0.96 (2.33–0.93) ka cal. BP and are thus the first securely dated bones of *Gallus* for Wallacea and ISEA (Table 5). Although we cannot exclude the possibility that some of these bones represent *G. varius*, the larger size of the coracoids

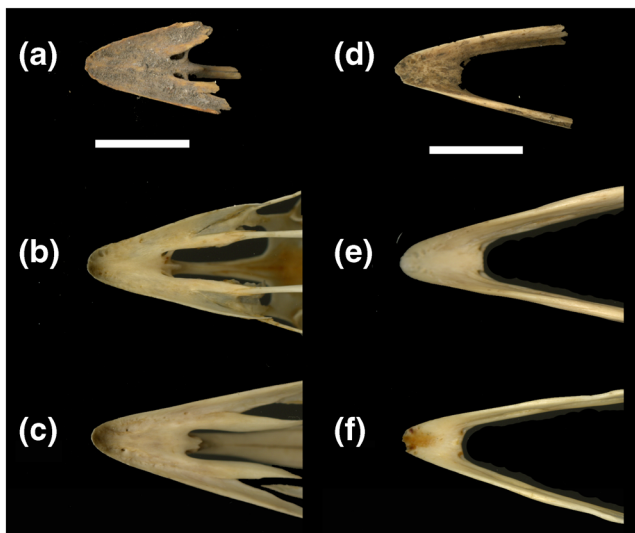
	GL	SC	Bd
LB-Av-2150	56.1	3.1	5.7
<i>Gallus varius</i> (n = 7/n = 3)	55.6 (47.2–60)	2.5 (2–3)	5.3 (4.4–5.9)
<i>Gallus sonneratii</i> (n = 3/n = 2)	54.2 (51.6–59.1)	2.9 (2.4–3.3)	6.4 (5.9–7)
<i>Gallus lafayettii</i>	59.9	2.7	6.3
<i>Gallus gallus</i>	58.8		
<i>G. gallus domesticus</i> (n = 9/n = 1)	74.1 (58.5–90.5)	2.8	6.6
<i>G. gallus</i> (feral)	69.2		

Notes: Measurements were taken according to von den Driesch (1976). Note that n is higher for GL (first column) than for the other measurements.

**TABLE 4** Measurements in mm of the radius among *Gallus* species



**FIGURE 5** Tibiotarsi of *Gallus* from Liang Bua and extant *Gallus* specimens in medial view. (a) Left proximal tibiotarsus fragment (LB-Av-2146); (b) view of the cut surface indicated by the dotted line in (a); (c) *Gallus varius* (USNM 19729); (d) *Gallus gallus domesticus* (USNM 500708). Scale bar 1 cm, except in B (5 mm) [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



**FIGURE 6** Cranial remains of potential *Gallus* from Liang Bua and extant *Gallus* specimens. (a) Rostrum maxillae (LB-Av-2151); (b) *Gallus gallus domesticus* (USNM 500708); (c) *Gallus varius* (USNM 19729); (d) rostral mandibulae (LB-Av-2148); (e) *G. gallus domesticus* (USNM 500708); (f) *G. varius* (USNM 19729). (a–c) Ventral view; (d–f) Dorsal view. Scale bar 1 cm [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

(two of which are the oldest bones in the sample), slight differences in morphology between the Liang Bua and captive *G. varius* specimens, and the context of the material suggests that these bones most likely belonged to *G. gallus*.

Modern chickens display significant variation in both size and morphology as a result of selective breeding (Foster, 2018), essentially extending beyond and/or accentuating particular variations present in

wild *G. gallus*. Morphological differences between wild and domesticated *G. gallus* might therefore be explained as a result of different phases in the domestication process. The effects of domestication on the osteology of *G. gallus*, especially for the earliest phases of domestication in any given place, remain poorly understood. The observed differences in morphology between the Liang Bua coracoids and those of both *G. varius* and *G. gallus domesticus* could be the result of the older Liang Bua specimens representing chickens in an early stage of the domestication process. A recent study on wild and captive Red Junglefowl suggested that body size in this species was reduced during the earliest stage of the domestication process (Eda, 2022). These findings are inconsistent with previous reports in which smaller domesticates, including chickens, show body size increases during the early stages of domestication (Serjeantson, 2009). At Liang Bua, the fact that the oldest bones are larger in size than is typical for captive *G. varius* and wild *G. gallus* (Table 2; see also data in Eda, 2022) suggests that they are indeed domesticated *G. gallus*. However, some of the younger bones overlap in size with both wild *G. gallus* and *G. varius*. Whether these bones represent hens or perhaps a smaller breed is unclear.

The overall faunal community composition and archaeology in Unit 8 at Liang Bua indicate clear changes in human subsistence behaviors beginning after ~5 ka ago (Alamsyah, 2021; Julianto, 2022; Sutikna et al., 2018). For example, in Unit 8B the proportion of aquatic vertebrates and invertebrates increases significantly, as does the proportion of introduced large mammals (e.g., pigs, porcupines, macaques, and civet cats) (Sutikna et al., 2018). The end of Unit 8B also documents the first occurrence of pottery as well as modern human burials with pottery, stone adzes, and pig tusks as grave goods (Morwood et al., 2009; Sutikna et al., 2018). The presence of pottery alone does not necessarily suggest that people at Liang Bua were farming, but Units 8B to 8C almost certainly mark the transition to a more sedentary lifestyle for human populations in this area. The first occurrence of *Gallus* at the site ~2.25 ka cal. BP suggests that these birds were either part of this new more sedentary lifestyle or accommodated within it soon afterwards, strengthening the interpretation that the remains described in this study indeed represent chickens.

The earliest chickens in the Middle East and Europe are thought to have been kept for ornamental and/or symbolic purposes rather than as a food source (Perry-Gal et al., 2015). Virtually nothing is known about the role(s) of chickens in early Southeast Asian societies. The chop mark on the tibiotarsus fragment, one of the oldest bones (~2.23 ka cal. BP), is through the proximal articulation just below the knee joint. Such chop marks are likely indicative of primary butchery to prepare the bird for cooking (Serjeantson, 2009). This suggests that the earliest chickens at Liang Bua were exploited for food. Transverse and oblique cut marks on the ulna shaft close to the quill knobs, such as those on the proximal ulna dated to ~0.3 ka (Figure 4), are often linked to the recovery of feathers (Romandini et al., 2016). Forth (2004) reported that the local Nage people on Flores use fowl feathers for headdresses and ceremonial clothing. Although little is known about the history of this tradition, the cutmarks on the ulna suggest that it might date back to at least several hundred years ago.

LB ID	<sup>14</sup> C age (yr BP)	Median calibrated age(yr cal. BP)	95% CI <sup>a</sup> (ka cal. BP)
LB-Av-1314	2,226 ± 20	2,250	2.32–2.22
LB-Av-1916	2,242 ± 20	2,249	2.33–2.19
LB-Av-2152	1,110 ± 19	958	0.95–0.93
LB-Av-2151	1,792 ± 20	1,650	1.71–1.61
LB-Av-2146	2,342 ± 21	2,226	2.24–2.15

**TABLE 5** <sup>14</sup>C ages for Liang Bua *Gallus* remains

<sup>a</sup>The 95% CIs given here are for the largest relative area under the probability distribution, which does not always include the median probability. In the case of LB-Av-2152, for 1,110 ± 19 ka, there are three age ranges at 2-sigma, and the largest relative area (0.491) does not include the median probability.

As indicated by the presence of a juvenile bone in the same layer, chickens were likely reared nearby at that time and probably were well established as an important part of local diets and traditions.

Red and Green Junglefowl are considered native to Southeast Asia including Wallacea (Birdlife International, 2022). However, chicken remains in this region are limited to recent archaeological contexts and *Gallus* is absent from the region's fossil record (Hawkins et al., 2017; Meijer, 2014; Meijer et al., 2015, 2019). Even sites with abundant bird material and extended faunal sequences, such as Niah Caves on Borneo (Stimpson, 2010) and Laili Cave on Timor (Hawkins et al., 2017), have not reported any junglefowl remains (although other Phasianidae species were recovered from Niah Caves, see Stimpson, 2010).

Liang Bua preserves a rich faunal sequence with over 400,000 vertebrate elements recovered to date. Among this large assemblage, over 4,000 elements have been identified as avian representing more than 40 taxa, and birds are present throughout the entire stratigraphic sequence (Meijer & Due, 2010; Meijer et al., 2010, 2013, 2017, 2022; Sutikna et al., 2018). Despite this richness in avian taxa, no bones of *Gallus* have been recorded from the ~190-ka sequence except those described in this study. Their conspicuous absence prior to ~2.5 ka ago is particularly striking given the omnipresence of chickens throughout Flores today. Junglefowl are forest birds and both *G. gallus* and *G. varius* are found in forests, forest edges, and scrubland (Coates & Bishop, 1997). For large portions of the late Middle Pleistocene until ~3 ka ago, the area surrounding Liang Bua would likely have been suitable habitat for wild junglefowl (Sutikna et al., 2018; Veatch et al., 2019; Westaway et al., 2009). The variety of avian taxa recorded at Liang Bua ranges from very small (e.g., swiftlets) to very large (e.g., giant marabou storks) birds, and includes forest, grassland, and aquatic adapted species (Meijer et al., 2013, 2017). The absence of *Gallus* is thus not reasonably explained by either taphonomic biases or habitat preferences. In addition, remains of the only other Phasianid in the region, *Synoicus*, are present in the Late Pleistocene sequence (Meijer et al., 2015). Similarly, in the So'a Basin of central Flores, junglefowl are also absent from multiple late Early to early Middle Pleistocene localities, which have otherwise yielded at least nine avian species of varying body sizes (Meijer et al., 2015). Based on the fossil records at Liang Bua and the So'a Basin, *Gallus* was either absent entirely or so rare that they have yet to be identified at these sites.

Why are such ubiquitous, and presumably native, birds absent on Flores? One explanation, previously pointed out by others (Olson, 1978), would be that Red Junglefowl, which are notoriously bad fliers, were introduced to Wallacea by humans. This suggests that the present distribution of Red Junglefowl is likely much larger than in the past, when its distribution was almost certainly limited to the Sunda Shelf. Perhaps the dispersal of Green Junglefowl east of the Wallace Line was also human-mediated. *Gallus varius* has a limited distribution that includes Java, Bali, Lombok, and Flores (BirdLife International, 2022) and molecular evidence suggests that it diverged from the other three species of *Gallus* ~4 million years ago (Hosner et al., 2016; Lawal et al., 2020; Wang et al., 2020). Since *G. varius* originated from west of the Wallace Line, it is unclear when it dispersed eastwards. Beebe's (1921) account of *G. varius* describes its ability to cross open water barriers to roost on islets off the coast of Java but crossing the Wallace Line would have required flying considerably greater distances. Nonetheless, perhaps the wild populations of *G. varius* found on Flores and Lombok today may represent the descendants of an early, independent dispersal of *Gallus* across the Wallace Line. If true, then its reported preference for drier and coastal habitats (Beebe, 1921) might explain its absence from the inland sites of Liang Bua and the So'a Basin.

Based on current distributions of Red Junglefowl, natural dispersals to some islands on the continental shelf, such as Sumatra and Java might have happened during times of low sea level. However, islands east of the Wallace Line would have been beyond reach until *G. gallus* was managed (Conrad, 2022; Zeder, 2015) by humans as part of a new more sedentary lifestyle that was sweeping the region. The subsequent eastward dispersals of these human populations (Bellwood, 2017) most likely enabled chickens to cross the Wallace Line. Such a scenario explains the absence of chickens in the avian fossil record of Wallacea more generally. Of interest here is that feral *G. gallus* populations in the Philippines and Sulawesi are not considered natural (Parkes, 1962). The conspicuous absence of junglefowl in the Liang Bua stratigraphic sequence up until relatively recently (i.e., within the past 2,300 years) supports the idea that domesticated or managed *G. gallus* was introduced to Flores by humans as part of a suite of animals that facilitated a more sedentary way of life. Where these chickens came from, and if they formed a source population for chickens further east, remains questions of interest for further study.



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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

## DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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## REFERENCES

- Alamsyah, N. (2021). Nitrogen and carbon stable isotope analysis of Holocene pigs from Liang Bua (Flores, Indonesia). M.Sc. Thesis, Lakehead University.
- Bautista, A. P. (1991). A zooarchaeological perspective on the Ambangan Site, a prehistoric settlement in Butuan, Agusan del Norte, Southern Philippines. *Indo-Pacific Prehistory Association Bulletin*, 10, 161–170.
- Beebe, W. (1921). *A monograph of the pheasants* (Vol. 2). Witherby & Co.
- Bellwood, P. (2005). *First farmers: The origins of agricultural societies*. Blackwell Publishing.
- Bellwood, P. (2017). *First islanders: Prehistory and human migration in island Southeast Asia*. Wiley Blackwell. <https://doi.org/10.1002/9781119251583>
- Best, J., Doherty, S., Armit, I., Boev, Z., Büster, L., Cunliffe, B., Foster, A., Frimet, B., Hamilton-Dyer, S., Higham, T., Lebrasseur, O., Miller, H., Peters, J., Seigle, M., Skelton, C., Symmons, R., Thomas, R., Trentacoste, A., Maltby, M., ... Sykes, N. (2022). Redefining the timing and circumstances of the chicken's introduction to Europe and north-west Africa. *Antiquity*, 96, 868–882. <https://doi.org/10.15184/aqy.2021.90>
- BirdLife International. (2022). IUCN Red List for birds. Downloaded from [birdlife.org](http://birdlife.org) on 03/05/2022.
- Bocheński, Z. M., & Tomek, T. (2009). *A key for the identification of domestic bird bones in Europe: Preliminary determination*. Institute of Systematics and Evolution of Animals, Polish Academy of Sciences.
- Coates, B. J., & Bishop, K. D. (1997). *A guide to the birds of Wallacea. Sulawesi, the Moluccas and lesser Sunda Islands, Indonesia*. Dove Publications.
- Conrad, C. (2015). Archaeozoology in mainland Southeast Asia: Changing methodology and Pleistocene to Holocene forager subsistence patterns in Thailand and peninsular Malaysia. *Open Quaternary*, 1, 1–23.
- Conrad, C. (2022). Contextualizing Ancestral Pueblo Turkey (*Meleagris gallopavo* spp.) management. *Journal of Archaeological Method and Theory*, 29, 624–665. <https://doi.org/10.1007/s10816-021-09531-9>
- Conrad, C., Higham, C., Eda, M., & Marwick, B. (2016). Palaeoecology and forager subsistence strategies during the Pleistocene–Holocene transition: A reinvestigation of the zooarchaeological assemblage from Spirit cave, Mae Hong Son Province, Thailand. *Asian Perspectives*, 55, 2–27. <https://doi.org/10.1353/asi.2016.0013>
- Darwin, C. R. (1868). *The variation of animals and plants under domestication*. John Murray.
- Eaton, J. A., van Balen, B., Brickle, N. W., & Rheindt, F. E. (2016). *Birds of the Indonesian archipelago. Greater Sundas and Wallacea*. Lynx Edicions.
- Eda, M. (2021). Origin of the domestic chicken from modern biological and zooarchaeological approaches. *Animal Frontiers*, 11, 52–61. <https://doi.org/10.1093/af/vfab016>
- Eda, M. (2022). The osteological microevolution of Red Junglefowl and domestic fowl under the domestication process. *Quaternary International*, 626–627, 14–21. <https://doi.org/10.1016/j.quaint.2020.10.001>
- Eda, M., Lu, P., Kikuchi, H., Li, Z., Li, F., & Yuan, J. (2016). Reevaluation of early Holocene chicken domestication in northern China. *Journal of Archaeological Science*, 67, 25–31. <https://doi.org/10.1016/j.jas.2016.01.012>
- Evans, B. J., Gansauge, M.-T., Tocheri, M. W., Schillaci, M. A., Sutikna, T., Jatmiko, Klegarth, A., Tosi, A. J., Melnick, D. J., & Meyer, M. (2020). Mitogenomics of macaques (*Macaca*) across Wallace's line in the context of modern human dispersals. *Journal of Human Evolution*, 146, 102852. <https://doi.org/10.1016/j.jhevol.2020.102852>
- Forth, G. (2004). *Nage birds. Classification and symbolism among an eastern Indonesian people*. London and New York.
- Foster, A. (2018). Identifying chicken breeds in the archaeological record: a geometric and linear morphometric approach. Ph.D. thesis, University of Leicester.
- Fumihito, A., Miyake, T., Takada, M., Shingu, R., Endo, T., Gojbori, T., Kondo, N., & Ohno, S. (1996). Monophyletic origin and unique dispersal patterns of domestic fowls. *Proceedings of the National Academy of Science of the United States of America*, 93, 6792–6795. <https://doi.org/10.1073/pnas.93.13.6792>
- Hawkins, S., O'Connor, S., & Louys, J. (2017). Taphonomy of bird (Aves) remains at Laili cave, Timor-Leste, and implications for human-bird interactions during the Pleistocene. *Archaeological and Anthropological Sciences*, 11, 6325–6337.
- Higham, C. (1989). *The archaeology of mainland Southeast Asia: From 10,000 B.C. to the fall of Angkor*. Cambridge University Press.
- Hogg, A. G., Heaton, T. J., Hua, Q., Palmer, J. G., Turney, C. S. M., Southon, J., Bayliss, A., Blackwe Boswijk, G., Bronk Ramsey, C., Pearson, C., Petchey, F., Reimer, P., Reimer, R., & Wacker, L. (2020). SHCal20 Southern Hemisphere calibration, 0–55,000 years cal BP. *Radiocarbon*, 62, 759–778. <https://doi.org/10.1017/RDC.2020.59>
- Horn, I. R., Kenens, Y., Palmblad, N. M., Dalebout, H., Langeveld, B., Meijer, H. J. M., Fischer, A., Florens, F. B. V., Gilbert, M. P. T., Niemann, J., van der Plas-Duijvestein, S. J., Rijdsdijk, K. F., & Gravendeel, B. (2019). Palaeoproteomics of fossil bird bones for

- taxonomic classification. *Zoological Journal of the Linnean Society*, 186, 650–665. <https://doi.org/10.1093/zoolinnean/zlz012>
- Hosner, P. A., Faircloth, B. C., Glenn, T. C., Braun, E. L., & Kimball, R. T. (2016). Avoiding missing data biases in phylogenomic inference: An empirical study in the landfowl (Aves: Galliformes). *Molecular Biology and Evolution*, 33, 1110–1125. <https://doi.org/10.1093/molbev/msv347>
- Julianto, I. M. A. (2022). New insights into modern human behaviour at Liang Bua (Flores, Indonesia) based on the temporal distribution of pottery and mollusks during the past 5,000 years. M.Sc. Thesis, Lakehead University.
- Lape, P. V., Krigbaum, J., Futch, J., Jordan, A., & Peterson, E. (2020). The Ira Ara site: A fortified settlement and burial complex in Timor-Leste. *Terra Australis*, 53, 49–66. <https://doi.org/10.2307/j.ctv1bvnd1j.8>
- Lape, P. V., Peterson, E., Tanudirjo, D., Shiung, C., Lee, G., Field, J., & Coster, A. (2018). New data from an open neolithic site in eastern Indonesia. *Asian Perspectives*, 57, 222–243. <https://doi.org/10.1353/asi.2018.0015>
- Lawal, R. A., Martin, S. H., Vanmechelen, K., Vereijken, A., Silva, P., Al-Atiyat, R. M., Aljumaah, R. S., Mwacharo, J. M., Wu, D.-D., Zhang, Y.-P., Hocking, P. M., Smith, J., Wragg, D., & Hanotte, O. (2020). The wild species genome ancestry of domestic chickens. *BMC Biology*, 18, 13. <https://doi.org/10.1186/s12915-020-0738-1>
- Mayr, G. (2006). New specimens of the early Eocene stem group galliform *Paraortygoides* (Gallinuloididae), with comments on the evolution of a crop in the stem lineage of Galliformes. *Journal of Ornithology*, 147, 31–37. <https://doi.org/10.1007/s10336-005-0006-8>
- Meijer, H. J. M. (2014). The avian fossil record in Insular Southeast Asia and its implications for avian biogeography and palaeoecology. *PeerJ*, 2, e295. <https://doi.org/10.7717/peerj.295>
- Meijer, H. J. M., & Due, R. A. (2010). A new species of giant marabou stork (Aves: Ciconiiformes) from the Pleistocene of Liang Bua, Flores (Indonesia). *Zoological Journal of the Linnean Society*, 160, 707–724. <https://doi.org/10.1111/j.1096-3642.2010.00616.x>
- Meijer, H. J. M., Due, R. A., Sutikna, T., Wahyu Saptomo, E., Jatmiko, Tocheri, M. W., & Mayr, G. (2017). Late Pleistocene songbirds of Liang Bua (Flores, Indonesia); the first fossil passerine fauna described from Wallacea. *PeerJ*, 5, e3676. <https://doi.org/10.7717/peerj.3676>
- Meijer, H. J. M., Louys, J., & O'Connor, S. (2019). First record of avian extinctions from the Late Pleistocene and Holocene of Timor Leste. *Quaternary Science Reviews*, 203, 170–184. <https://doi.org/10.1016/j.quascirev.2018.11.005>
- Meijer, H. J. M., Sutikna, T., Wahyu Saptomo, E., Due, R. A., Wasisto, S., James, H. F., Morwood, M. J., & Tocheri, M. W. (2013). Late Pleistocene-Holocene non-passerine avifauna of Liang Bua (Flores, Indonesia). *Journal of Vertebrate Paleontology*, 33, 877–894. <https://doi.org/10.1080/02724634.2013.746941>
- Meijer, H. J. M., Sutikna, T., Wahyu Saptomo, E., & Tocheri, M. W. (2022). More bones of *Leptoptilos robustus* from Flores reveal new insights into giant marabou stork paleobiology and biogeography. *Royal Society Open Science*, 9, 220435. <https://doi.org/10.1098/rsos.220435>
- Meijer, H. J. M., Tocheri, M. W., Due, R. A., Sutikna, T., Wahyu Saptomo, E., & James, H. F. (2015). Continental-style avian extinctions on an oceanic island. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 429, 163–170.
- Meijer, H. J. M., van den Hoek Ostende, L. W., van den Bergh, G. D., & de Vos, J. (2010). The fellowship of the hobbit: The fauna surrounding *Homo floresiensis*. *Journal of Biogeography*, 37, 995–1006. <https://doi.org/10.1111/j.1365-2699.2010.02308.x>
- Miao, Y.-W., Peng, M.-S., Wu, G.-S., Ouyang, W.-N., Yang, Z.-Y., Yu, N., Liang, J.-P., Pianchou, G., Beja-Pereira, A., Mitra, B., Palanichamy, M. G., Baig, M., Chaudhuri, T. K., Shen, Y.-Y., Kong, Q.-P., Murphy, R. W., Yao, Y.-G., & Zhang, Y.-P. (2013). Chicken domestication: An updated perspective based on mitochondrial genomes. *Heredity*, 110, 277–282. <https://doi.org/10.1038/hdy.2012.83>
- Morwood, M. J., Sutikna, T., Saptomo, E. W., Jatmiko, & Westaway, K. E. (2009). Preface: Research at Liang Bua, Flores, Indonesia. *Journal of Human Evolution*, 57, 407–449.
- Mourer-Chauviré, C. (1992). The Galliformes (Aves) from the phosphorites du Quercy (France): Systematics and biostratigraphy. In K. E. Campbell (Ed.), *Papers in avian paleontology honoring Pierce Brodkorb* (Vol. 36, pp. 67–95). National History Museum of Los Angeles County Science Series.
- Olson, S. L. (1978). The significance of the distribution of the Megapodiidae. *Emu*, 80, 21–24. <https://doi.org/10.1071/MU9800021>
- Parkes, K. C. (1962). The Red Junglefowl of the Philippines: Native or introduced? *The Auk*, 79, 479–481. <https://doi.org/10.2307/4082830>
- Perry-Gal, L., Erlich, A., Gilboa, A., & Bar-Oz, G. (2015). Earliest economic exploitation of chicken outside East Asia: Evidence from the Hellenistic southern Levant. *Proceedings of the National Academy of Science of the United States of America*, 112, 9849–9854. <https://doi.org/10.1073/pnas.1504236112>
- Peters, J., Lebrasseur, O., Deng, H., & Larson, G. (2016). Holocene cultural history of red Junglefowl (*Gallus gallus*) and its domestic descendant in East Asia. *Quaternary Science Reviews*, 142, 102–119. <https://doi.org/10.1016/j.quascirev.2016.04.004>
- Peters, J., Lebrasseur, O., Irving-Pease, E. K., Paxinos, P. D., Best, J., Smallman, R., Callou, C., Gardeisen, A., Tritel, S., Frantz, L., Sykes, N., Fuller, D. Q., & Larson, G. (2022). The biocultural origins and dispersal of domestic chickens. *Proceedings of the National Academy of Science of the United States of America*, 119, e2121978119. <https://doi.org/10.1073/pnas.2121978119>
- Piper, P. J. (2017). The origins and arrival of the earliest domestic animals in mainland and island Southeast Asia: A developing story of complexity. *Terra Australis*, 45, 251–273.
- Romandini, M., Fiore, I., Gala, M., Cestari, M., Guida, G., Tagliacozzo, A., & Peresani, M. (2016). Neanderthal scraping and manual handling of raptors wing bones: Evidence from Fumane cave. Experimental activities and comparison. *Quaternary International*, 421, 154–172.
- Serjeantson, D. (2009). Birds. In *Cambridge manuals in archaeology*. Cambridge University Press.
- Stimpson, C. M. (2010). Late Quaternary environments and human impact in Northern Borneo: the evidence from the bird (Aves) and bat (Mammalia: Chiroptera) faunas from the archaeological of the Great Cave of Niah, Sarawak. Ph.D. thesis, University of Cambridge.
- Storey, A. A. (2016). Scratching out a living. Chickens in ancient Pacific economies. In M. Oxenham & H. Buckley (Eds.), *The Routledge Handbook of Bioarchaeology in Southeast Asia and the Pacific Islands* (pp. 483–501). Routledge.
- Storey, A. A., Athens, J. S., Bryant, D., Carson, M., Emery, K., deFrance, S., Higham, C., Huynen, L., Intoh, M., Jones, S., Kirch, P. V., Ladefoged, T., McCoy, P., Morales-Muñiz, A., Quiroz, D., Reitz, E., Robins, J., Walter, R., & Matisoo-Smith, E. (2012). Investigating the global dispersal of chickens in prehistory using ancient mitochondrial DNA signatures. *PLoS ONE*, 7, e39171. <https://doi.org/10.1371/journal.pone.0039171>
- Storey, A. A., Ladefoged, T., & Matisoo-Smith, E. A. (2008). Counting your chickens: Density and distribution of chicken remains in archaeological sites of Oceania. *International Journal of Osteoarchaeology*, 18, 240–261. <https://doi.org/10.1002/oa.947>
- Stuiver, M., & Reimer, P. J. (1993). CALIB rev. 8. *Radiocarbon*, 35, 215–230. <https://doi.org/10.1017/S0033822200013904>
- Sutikna, T., Tocheri, M. W., Faith, T., Jatmiko, Meijer, H. J. M., Wahyu Saptomo, E., & Roberts, R. G. (2018). The spatio-temporal distribution of archaeological and faunal finds at Liang Bua (Flores, Indonesia) in light of the revised chronology for *Homo floresiensis*. *Journal of Human Evolution*, 124, 52–74. <https://doi.org/10.1016/j.jhevol.2018.07.001>

- Veatch, E. G., Tocheri, M. W., Sutikna, T., McGrath, K., Wahyu Saptomo, E., & Jatmiko. (2019). Temporal shifts in the distribution of murine rodent body size classes at Liang Bua (Flores, Indonesia) reveal new insights into the paleoecology of *Homo floresiensis* and associated fauna. *Journal of Human Evolution*, 130, 45–60. <https://doi.org/10.1016/j.jhevol.2019.02.002>
- von den Driesch, A. (1976). *A guide to the measurement of animal bone from archaeological sites*. Peabody Museum Bulletin 1. Peabody Museum of Archaeology and Ethnology.
- Wang, M. S., Thakur, M., Peng, M. S., Jiang, Y., Frantz, L. A. F., Li, M., Zhang, J. J., Wang, S., Peters, J., Otecko, N. O., Suwannapoom, C., Guo, X., Zheng, Z. Q., Esmailizadeh, A., Hirimuthugoda, N. Y., Ashari, H., Suladari, S., Zein, M. S. A., Kusza, S., ... Zhang, Y. P. (2020). 863 genomes reveal the origin and domestication of chicken. *Cell Research*, 30, 693–701. <https://doi.org/10.1038/s41422-020-0349-y>
- West, B., & Zhou, B.-X. (1988). Did chickens go west? New evidence for domestication. *Journal of Archaeological Science*, 15, 515–533. [https://doi.org/10.1016/0305-4403\(88\)90080-5](https://doi.org/10.1016/0305-4403(88)90080-5)
- Westaway, K. E., Roberts, R. G., Sutikna, T., Morwood, M. J., Drysdale, R., Zhao, J.-x., & Chivas, A. R. (2009). The evolving landscape and climate of western Flores: An environmental context for the archaeological site of Liang Bua. *Journal of Human Evolution*, 57, 450–464.
- Zeder, M. (2015). Core questions in domestication research. *Proceedings of the National Academy of Science of the United States of America*, 112, 3191–3198. <https://doi.org/10.1073/pnas.1501711112>

## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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