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The biocultural origins and dispersal of domestic chickens

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Though chickens are the most numerous and ubiquitous domestic bird, their origins, the circumstances of their initial association with people, and the routes along which they dispersed across the world remain controversial. In order to establish a robust spatial and temporal framework for their origins and dispersal, we assessed archaeological occurrences and the domestic status of chickens from ∼600 sites in 89 countries by combining zoogeographic, morphological, osteometric, stratigraphic, contextual, iconographic, and textual data. Our results suggest that the first unambiguous domestic chicken bones are found at Neolithic Ban Non Wat in central Thailand dated to ∼1650 to 1250 BCE, and that chickens were not domesticated in the Indian Subcontinent. Chickens did not arrive in Central China, South Asia, or Mesopotamia until the late second millennium BCE, and in Ethiopia and Mediterranean Europe by ∼800 BCE. To investigate the circumstances of their initial domestication, we correlated the temporal spread of rice and millet cultivation with the first appearance of chickens within the range of red junglefowl species. Our results suggest that agricultural practices focused on the production and storage of cereal staples served to draw arboreal red junglefowl into the human niche. Thus, the arrival of rice agriculture may have first facilitated the initiation of the chicken domestication process, and then, following their integration within human communities, allowed for their dispersal across the globe.

domestication | chickens | dispersal | human niche

Significance

Chickens are the world's most numerous domestic animal. In order to understand when, where, and how they first became associated with human societies, we critically assessed the domestic status of chicken remains described in >600 sites in 89 countries, and evaluated zoogeographic, morphological, osteometric, stratigraphic, contextual, iconographic, and textual data. Although previous studies have made claims for an early origin of chickens, our results suggest that unambiguous chickens were not present until ∼1650 to 1250 BCE in central Thailand. A correlation between early chickens and the first appearance of rice and millet cultivation suggests that the production and storage of these cereals may have acted as a magnet, thus initiating the chicken domestication process.

Despite the global ubiquity and cultural importance of chickens (*Gallus gallus domesticus* L., 1758), the timing and circumstances of their domestication and subsequent dispersal remain both obscure and controversial (1). Although the spatiotemporal patterns of chicken dispersal following their domestication have been addressed by several studies (2–4), two key publications (5, 6) pertaining to the early history of chicken domestication are almost always cited but rarely challenged (*SI Appendix*, Table S1). In brief, the first argues for a Southeast Asian and possible South Indian origin for chickens (5), and the second claims that domestic chickens first appeared in northern China before following a northern trajectory toward Europe (6). Both of these oft-cited syntheses summarized, but did not critically assess either the original osteological and stratigraphic data or the cultural implications for the presence of chickens across the Old World.

Inferring chicken origins and dispersal have primarily been hampered by a paucity of archaeological remains, and more specifically, issues related to excavation and recovery biases, faunal identification, and dating (7). Excavations that do not consistently employ fine sieving, for example, are unlikely to systematically retrieve chicken bones. When bird remains are recovered, confident identification can be problematic in the absence of reference collections, since chicken bones are difficult to distinguish from other related galliform species. Although early Holocene bird remains from northern China were initially claimed to be chickens (8), a reanalysis of those bones based upon discrete osteomorphological criteria demonstrated that the specimens were derived from pheasants (1, 9). More generally, ongoing hybridization between wild red junglefowl (*G. gallus*) populations and those birds living in human settlements (10) complicates the task of identifying early poultry husbandry in the archaeological record.

The low density of excavated archaeological sites, specifically within the distribution of red junglefowl, means that the earliest shifts in the relationship between people and these birds remain opaque. Additionally, chicken bones are prone to taphonomic loss through scavenger activity (11) and stratigraphic displacement (12). The latter can lead to invalid claims regarding their dating and cultural context, and a recent program of radiocarbon dating demonstrated that numerous early claims for the first appearance of chickens in Europe were spurious (13).

Regarding their geographic origin, genetic studies have demonstrated that of the four extant junglefowl species, chickens were primarily derived from the red junglefowl (14, 15). A more recent study analyzed 863 genomes from modern *Gallus* specimens, including all five subspecies of red junglefowl, and identified the subspecies *Gallus gallus*

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spadiceus as the most likely progenitor of domestic chickens (16). This result suggests that the chicken domestication process began within the distribution of this subspecies in Southeast Asia (Fig. 1 and *SI Appendix*, Fig S1). Genomic analyses further suggested that the divergence between the ancestral population of modern domestic chickens and *G. gallus spadiceus* occurred between 12,800 and 6,200 y ago. Importantly, this range cannot be equated with the initiation of a domestication process. Instead, this timeframe represents the divergence between *G. gallus spadiceus* and the lineage from which domestic chickens were derived (17), and thus represents an upper bound on the chicken domestication timeframe.

Here, in order to establish a robust spatial and temporal framework for the early occurrence of chickens both within and beyond the range of red junglefowl, including Africa and Oceania, we reevaluated reports of chicken remains from >600 archaeological sites in 89 countries. We did so by assessing the claims for chickens in their chrono-cultural and geographic contexts, and wherever possible, by reassessing the taxonomic determination of existing specimens by measuring either published photographs or the actual bones. We then combined zoogeographic, contextual, and osteometric data to confirm or question the domestic status of the birds. We also critically reviewed the stratigraphic position of each of the remains and assessed their intrusive potential. We complemented these efforts by investigating iconographic, written, and linguistic records pertaining to chickens. In addition, we interpreted these records within the context of the ecological characteristics and distributions of all the jungle fowl subspecies.

These analyses allowed us to generate two datasets: a comprehensive table of archaeological remains consisting of chickens that were confidently assigned as domestic using conservative measures (*SI Appendix*, Table S2), and a list of remains whose identification or stratigraphic position was ambiguous (*SI Appendix*, Table S3). We then correlated the resulting spatiotemporal pattern of archaeological chickens with human societies and their subsistence strategies. This correlation allowed us to address the process, circumstances, and cultural context in which the initial shift in the human–chicken relationship that led to domestication took place, and the contexts of their subsequent translocations.

Results

Early Domestic Chickens within the Distribution of Red Junglefowl. Chicken bones are rare in prehistoric archaeofaunal assemblages from mainland Southeast Asia. One exception is the Neolithic moated site of Ban Non Wat (~1650 to 1250 BCE) in northeast Thailand, where >95% of the avifauna has been ascribed to *Gallus*. Given the presence of other domesticates, including pigs and dogs, and the fact that people would have had access to a highly diverse avifauna in this ecological setting, the

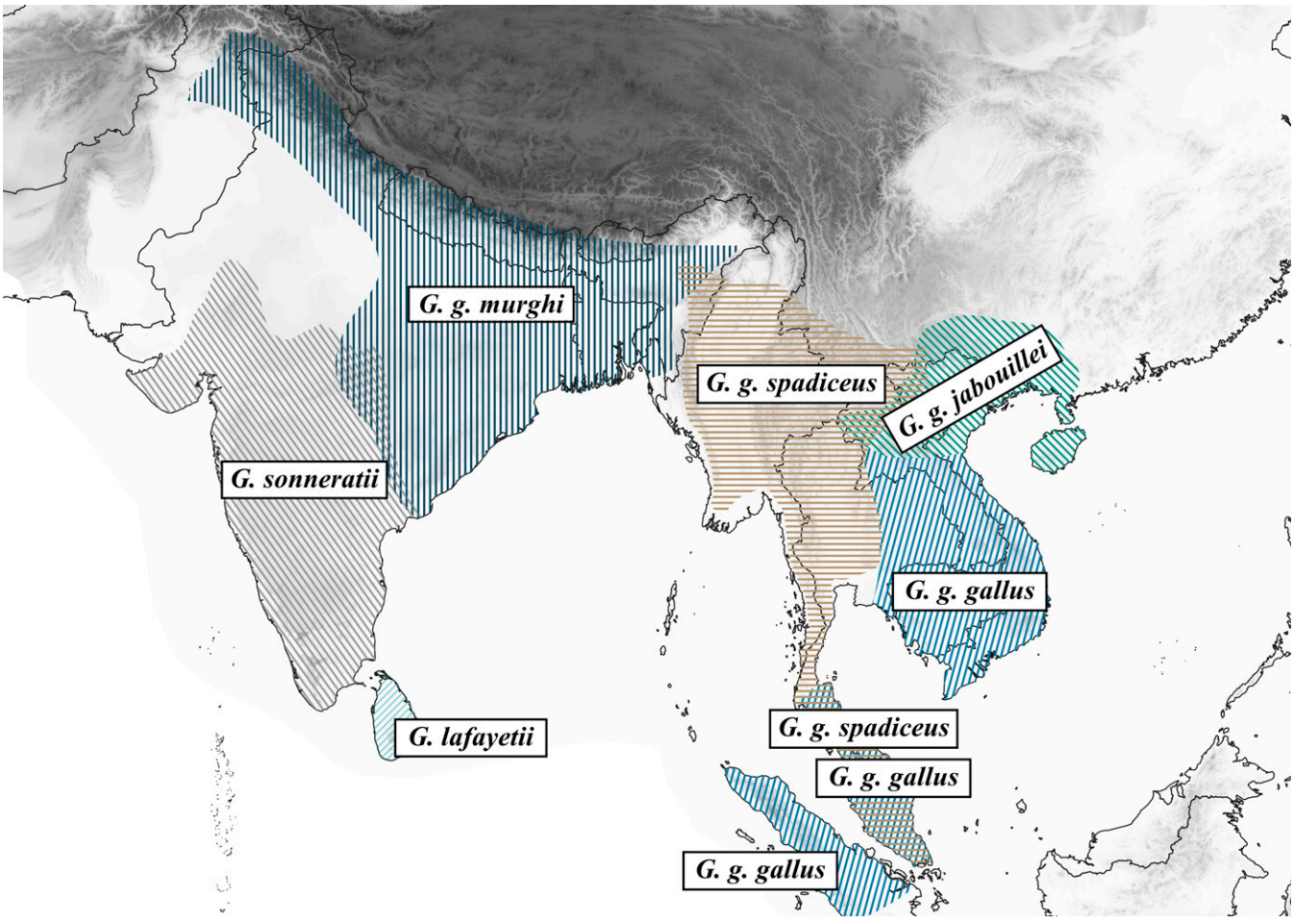

Fig. 1. A map depicting the distribution of both the gray and Ceylon junglefowl species and three subspecies of red junglefowl: *G. gallus murghi*, *G. gallus spadiceus*, and *G. gallus jabouillei*. The distribution of *G. gallus gallus* is depicted as the remainder of mainland southeast Asia and Sumatra following the general distribution in ref. 16. The *G. gallus murghi* distribution follows that of *SI Appendix*, Fig. S1, which draws on published maps in ornithological sources and the Global Biodiversity Information Facility (GBIF) records (119–121). For *G. gallus spadiceus* and *G. gallus jabouillei*, the GBIF records were augmented by specimens with genetic data reported by refs. 16 and 122.

abundance of *Gallus* remains has been interpreted as evidence that they may represent a domestic population (18, 19). Although their domestic status remains unresolved (20), two other factors lend weight to the initial assessment. First, an exceedingly high proportion of juvenile bones are present in the assemblage. Second, these birds were deposited as grave goods alongside domestic pigs, dogs, and bovines in human burials at Bronze Age Ban Non Wat (~1038 to 950 BCE) (18) and Ban Na Di (~800 to 500 BCE) (21) (*SI Appendix*, Table S2).

In the Indian subcontinent, the identification of *Gallus* remains is problematic due to the co-occurrence of both an endemic red junglefowl subspecies (*Gallus gallus murghi*) and the gray junglefowl (*Gallus sonneratii*). (Fig. 1 and *SI Appendix*, Fig. S1). *Gallus* remains from forager dumps on the Middle Ganges ~4500 to 2000 BCE likely belong to wild birds (22), and domestic chickens have been claimed to feature in the assemblages associated with farming communities of the Mature Harappan culture ~2600 to 1900 BCE in the Indus River basin (5, 22, 23). Our analysis demonstrates that key specimens from sites belonging to this cultural phase including Mohenjo-daro (24) and Harappa (25), have either been misidentified, or are too large to be confidently categorized as prehistoric domestic birds (*SI Appendix*, Table S3). Extensive excavations at Harappa have also failed to identify any new *Gallus* bones (26).

Our reappraisal of published chicken bone specimens in Chalcolithic and Bronze Age sites across India and Pakistan dating ~3500 to 1000 BCE undermines both the species identification (since they are located in the distribution range of gray junglefowl) (*SI Appendix*, Fig. S2) and the domestication status of these remains (*SI Appendix*, Table S3). At the site of Daimabad, India, *Gallus* is absent from earlier Savalda and Harappan levels, but prominent in the subsequent early Jorwe levels dating from ~1500 to 1200 BCE (27). *Gallus* bones have been reported from several other sites of the Jorwe period (Nevasa, Inamgaon, Tuljapur Garhi, Walki), as well as contemporaneous sites farther south (Southern Neolithic Period III) (22). This period appears to coincide with historical linguistic reconstructions for the Dravidian languages in South India, since each of three linguistic subphyla have distinct etyma, thus indicating that chickens became widespread after these languages diverged ~1200 BCE (1500 to 500 BCE) (28, 29). This timing is also consistent with Vedic texts in which chickens are unattested prior to ~1200 BCE (30). Collectively, these lines of evidence suggest that poultry farming in South Asia was a post-Harappan development.

Early Domestic Chickens Beyond the Distribution of Red Junglefowl.

East and Northeast Asia. Previous claims for the presence of chickens in the Yellow River basin 11,000 to 8,000 y ago (8) are not supported by either the climatic, palynological, or archaeofaunal records, all of which suggest the environmental conditions in the region were not conducive to the thermophilic *Gallus* (1, 31). In addition, a reanalysis of the archaeological bones determined the remains did not belong to chickens (1, 9). In fact, the earliest remains that can confidently be attributed to domestic chickens in East Asia date to the late Shang Dynasty, which spanned ~1350 to 1046 BCE (*SI Appendix*, Table S2). In Japan, chickens did not arrive until the Middle Yayoi ~100 BCE to 100 CE, a timing consistent with their first appearance in the Korean Peninsula (1).

Central Asia. In Central Asia, the earliest evidence of chickens thus far consists of depictions of cockerels in the Pazyryk kurgans of the Altai Mountains dated to ~500 to 300 BCE (32), and chicken remains have been identified in the late fourth century BCE fortress of Kurgansol (Uzbekistan) built by Alexander's troops (33). The absence of chickens in this region prior to the late Iron Age ~800 to 600 BCE (34, 35) contradicts the long-standing hypothesis that poultry farming spread west and north from the Yellow River basin during the Neolithic across Asia to Europe (6).

Island Southeast Asia and the Pacific. The earliest confidently dated chicken remains from archaeological sites in the Solomon Islands, Vanuatu, and Tonga in Near Oceania have been directly dated to the early first millennium BCE (36). Their appearance at these sites so far East suggests they must have been present in Island Southeast Asia prior to this date. And although historical linguistic studies have suggested that chickens were first introduced beyond continental Peninsular East Asia ~2000 BCE (37), the earliest zooarchaeological appearance in the Indonesian Banda Islands is only ~700 CE (38) (*SI Appendix*, Table S2). In Remote Oceania, chickens arrived with people in Hawaii ~1200 CE (36), about 500 y prior to the earliest records of the European introduction of poultry in Australia (1788 CE) (39) and New Zealand (1773 CE) (40).

Southwest Asia. The zooarchaeological record in Southwest Asia is difficult to interpret. Although isolated chicken remains have been claimed on Bronze Age settlements, radiocarbon dating has revealed that specimens excavated at Korucutepe, Turkey (12) and Jerusalem, Israel were intrusive (*SI Appendix*, Table S3). The linguistic and iconographic records in this region are also problematic. The term *dar meluḫḫa* ("francolins from *meluḫḫa*") mentioned on mid-third millennium BCE cuneiform tablets, has been interpreted to refer to chickens, since *meluḫḫa* meant Indus Valley (41). Our reassessment of the zooarchaeological evidence from the Indian subcontinent implies that domestic fowl first appeared after the Harappan civilization, and that these translations may therefore be inaccurate. The bird's Akkadian name, *su-la-mu*, describes it as dark-colored (42), which could correspond instead to black francolins (*Francolinus francolinus*) (43). Dark plumage could also imply gray junglefowl, a species common in the Indian subcontinent generally and in the Indus region specifically (44) (*SI Appendix*, Fig. S1).

Toward the end of the Bronze Age ~1,200 BCE, a depiction of *Gallus* from the temple area of Ishtar, Iraq (an ancient Mesopotamian deity) suggests a religious motive for its introduction. Scattered bone finds across Mesopotamia and the Levant postdating the Late Bronze Age collapse (45), however, imply the adoption of chicken husbandry during Iron Age I (~1150 to 965 BCE). Their increasing numbers at Neo-Assyrian, Urartian, Phrygian (*SI Appendix*, Table S2), and Levantine sites (46) indicate growing economic interest in the species' exploitation during the Iron Age II period (~965 to 530 BCE). The zooarchaeological record corroborates an increased visibility of *Gallus* in the iconographic record, including a depiction on the orthostat of Tell Halaf (present day Syria) dated to ~900 BCE (47), and on numerous cylinder seals between ~800 to 600 BCE (41, 48). A "land of the chickens" (probably Media, located in modern northwest Iran) (49) is mentioned in the royal inscriptions of Tiglath-Pileser III (745 to 723 BCE), and the phrase "chickens being seen in the city" appears in the seventh century BCE omen series *Šumma ālu* (50).

Northeast Africa. Zooarchaeology, historical texts, historical linguistics, and iconography suggest that chickens followed multiple routes into Africa. Since the Annals of Pharaoh Tuthmose III (1479 to 1425 BCE) mention a tribute from Mesopotamia of four birds that "do bear every day" (51), it has been suggested that these birds were chickens and that they were first introduced into North Africa via the Nile Valley. This interpretation seems

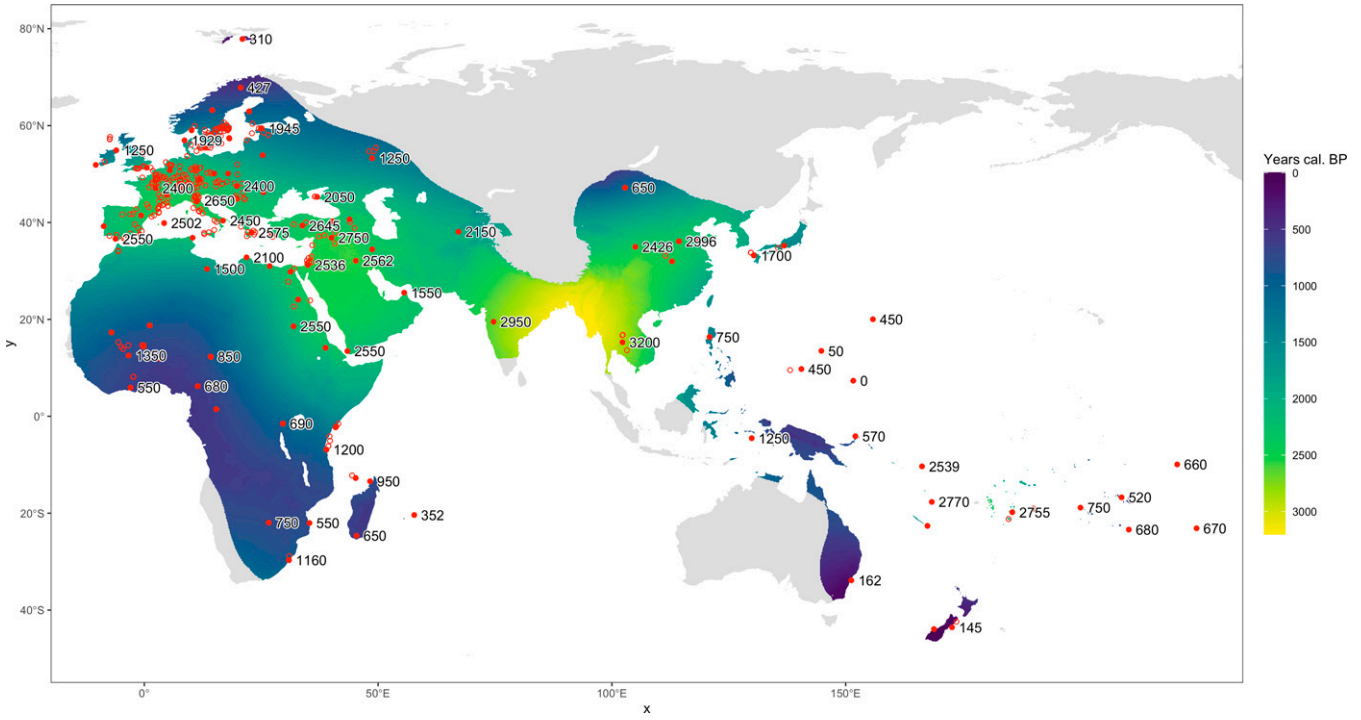

Fig. 2. A map depicting the earliest confidently assigned chicken remains across Eurasia, Africa, and Oceania alongside a spatial kriging interpolation of the timing of the arrival of chickens. The inference was performed using 100 independent, confidently assigned, and dated chicken remains listed in *SI Appendix*, Table S2. Each data point was placed on a spatial grid with resolution 10 min of a degree. Solid dots represent samples used in the spatial kriging, and hollow dots represent additional sample locations not incorporated into the interpolation. The colored shading indicates the inferred age for the introduction of chickens across the map. Gray areas indicate locations with a SE above the maximum threshold (see *SI Appendix* for a full description of the methods used to produce the map).

unlikely since the zooarchaeological record indicates that chickens were not present in contemporaneous Mesopotamia. This quotation more likely refers to either geese or ducks (41), especially since the "earliest chicken" reported from a contemporaneous New Kingdom Theban tomb dating to 1550 to 1070 BCE (52) is a misidentified duck (*SI Appendix*, Table S3). The determination of late second millennium BCE *Gallus* depictions as a domestic chicken on a 19th Dynasty (1292 to 1189 BCE) ostracon and a 20th Dynasty (1189 to 1077 BCE) silver bowl (53) are also problematic, since these depictions could represent wild junglefowl species. It was not until the Achaemenid period, at least 600 y later (~550 to 330 BCE), that chicken remains have been identified in lower Egypt (54, 55). Under Ptolemaic rule (305 to 30 BCE), fowl husbandry intensified and spread from the Nile delta upstream to the region of the first cataract (56, 57).

Direct radiocarbon-dated chicken bones from Pre-Aksumite northern Ethiopia (~800 to 600 BCE) demonstrate that, prior to their presence in Achaemenid Egypt, chickens had been translocated, likely across the Red Sea, to the Horn of Africa (58). South of the Horn, however, the earliest evidence for *Gallus* appears more than a millennium later (59), and arrived alongside the black rat, rice and mungbean that originated from the Indian subcontinent (60, 61). From coastal southeastern Africa, poultry farming dispersed both into the interior of Africa (Fig. 2), and to the Comoro Islands and Madagascar by ~750 to 900 CE.

The chicken's name in Malagasy has no roots in any of the western Austronesian languages. Instead, linguistic elements in neighboring Comorian indicate a connection to Bantu, and hence an introduction from coastal Africa (62), which is supported by the close genetic affinity of Malagasy and East African chickens (63). Austronesians were present in Madagascar by 500 CE and may have arrived with chickens. If so, those founder flocks did not survive, and the bird's Austronesian name was lost. In Mauritius, chickens were only introduced in 1598 CE by the Dutch East India Company (64).

North and West Africa. In North and West Africa, linguistic studies have suggested that chickens possibly dispersed from East Africa through the Sahara (65). The zooarchaeological record, however, demonstrates that chickens were present in West African Mande-speaking territory prior to their arrival in the northern Sahel (66, 67) (*SI Appendix*, Table S2). Given that fifth century BCE Phoenician seafarers (68) and Roman merchants both established trading posts on the Moroccan Atlantic coast (69) or somewhat inland (70), it is possible that chickens were introduced from Berber-speaking Northwest Africa to West Africa primarily by maritime trade. The subsequent dispersal from coastal West Africa upstream along the drainage basins of Senegal, Gambia, and other rivers could then explain the mid-first millennium BCE occurrence of chicken bones in Mande-speaking territory.

Europe. In Europe, numerous claims have been made for the presence of chickens in Neolithic and Bronze Age sites (71–74). A recent study reevaluated key specimens used to postulate early chicken husbandry, but direct radiocarbon dating of the remains revealed that all the presumed Neolithic to Bronze Age chicken remains in Bulgaria, Greece, and France were intrusive, and that of these, the earliest sample dated to only 137 to 327 CE (13). This study also established the spatiotemporal pattern of the dispersal of chickens across Europe. Greek seafarers transported chickens across the northern Mediterranean and the earliest directly dated chickens in southern Europe have been excavated in Italy from two Greek colonies dated to 776 to 540 BCE. Phoenician merchants introduced chickens to the southern Mediterranean, including the Balearic Islands and the southern Iberian Peninsula during this period (75) (*SI Appendix*, Table S2). Trade between

western Mediterranean craft centers and early Celtic communities promoted the chicken's northward expansion. By the late sixth/early fifth century BCE, chickens were present in the Upper Rhine and Danube River basins (76) (Fig. 2), and in southeast England (13). By that time, chickens had also been introduced to the coastal Black Sea region through Greek trade networks, suggesting that the chicken's initial dispersal in Europe was primarily through maritime routes.

Chicken farming became firmly established in western continental Europe during the late Iron Age and under Roman cultural influence in the Low Countries (*SI Appendix*, Table S2). Chickens arrived in coastal southwest Sweden at the onset of the first millennium CE or slightly earlier, before dispersing during the Migration period (~400 to 550 CE). The chicken's first appearance in the eastern Baltic region dates to the late Pre-Roman Iron Age, where these remains may have been associated with a burial (77). The presence of this bird may represent a trade import, however, since chickens were clearly exploited across the Baltic States and in Finland by the late Iron Age (~600 to 800 CE) (Fig. 2 and *SI Appendix*, Table S2). Throughout much of early medieval Europe, poultry farming likely benefited from the spread of Christianity (78), and chickens were also associated with early monastic contexts in Ireland (*SI Appendix*, Table S2).

Discussion

Assessing the Spatiotemporal Pattern of Chicken Domestication. Two initial hypotheses proposed separate temporal and geographic origins of domestic chickens. Zeuner (5) argued that domestic chickens were present in the Indus Valley during the mature Harappan period (~2600 to 1900 BCE) and subsequently introduced to Mesopotamia. Based upon the presumption that archaeological bird remains dated to the sixth millennium BCE in Neolithic northern China were chickens, West and Zhou (6) claimed that chicken domestication must have taken place in Southeast Asia prior to this before being translocated into China, and then farther west following a northern route. A more recent study concluded that red junglefowl were domesticated in the Yellow River basin shortly after the onset of the Holocene (8) (*SI Appendix*, Table S1).

With respect to South Asia, the claim that chickens were present within the Indus Valley Civilization was based upon two bone remains from Harappa (25) and four from Mohenjo-daro (24), as well as an incomplete "hen" figurine from Mohenjo-daro (23, 79). Our reanalysis of the two Harappan bones shows that one is morphologically inconsistent with *Gallus*, and the other's taxonomic classification is ambiguous. The taxonomic classification of three of the four fragmentary bird bones from Mohenjo-daro is also questionable. In addition, all of these bones, including a completely preserved femur, pertain to individuals that significantly exceed the size of prehistoric chickens. Finally, all four specimens have been collected in upper strata. Given the propensity for chicken bones to move between stratigraphic boundaries (13), it's possible these remains are recent intrusions. These lines of evidence call into question the assumption that poultry farming was present in Bronze Age Mohenjo-daro (*SI Appendix*, Table S3).

Excavations conducted in other Indus Valley Civilization sites and contemporaneous settlements produced additional chicken bones, especially in Saraushtra (*SI Appendix*, Fig. S2). These specimens were classified as domestic fowl based on the absence of modern wild jungle fowl populations in the region (22) and the aforementioned incorrect claim for fowl husbandry in the Indus Valley. Although currently located beyond the present-day natural distribution of both red and gray junglefowl (Fig. 1 and *SI Appendix*, Fig. S1), this region shares similar ecological characteristics and borders the region where gray junglefowl is extant (80). It is therefore likely that the natural range of gray junglefowl extended into the Indus River basin during the Mid-Holocene, and that these remains derive instead from local wild populations. This conclusion is supported by the presence of other fauna present in zooarchaeological assemblages, or in Harappan art (including Indian Hog Deer: *Axis porcinus*; Swamp Deer: *Cervus duvauceli*; and the Indian Rhinoceros: *Rhinoceros unicornis*), indicating relatively larger distributions of several fauna in the past (81). The combined weight of this evidence suggests that, contrary to the long-standing hypothesis, chickens were not domesticated in the Indus Valley.

Regarding northern China, subsequent reevaluations of the galliform remains (1, 9), as well as photographs and drawings, demonstrate that they are pheasant bones (2, 82). In addition, high-resolution climate and precipitation records from temperate Holocene East Asia, and the habitat requirements of the vertebrate taxa associated with the pheasants, suggest that the subtropical forest habitat conducive to thermophilic red junglefowl did not extend into northern China during the Holocene climatic optimum (1). Finally, mitochondrial analyses of modern breeds support a late dispersal scenario of chickens into northern China (83). Our analysis thus supports a much later arrival in this region consistent with the first appearance of chickens in Japan in the early first millennium CE, and in Mongolia during the early second millennium CE.

Our combined reanalyses of zooarchaeological, linguistic, genetic, and iconographic evidence suggests the following scenario. The first chickens were likely derived from a population of the subspecies *G. gallus spadiceus*, whose current range spans southwestern China, northern Thailand, and Myanmar (16) (Fig.1). The first unambiguous chicken bones in the archaeological record are present within the faunal assemblage at Neolithic Ban Non Wat in central Thailand, and date to ~1650 to 1250 BCE. Once incorporated into human societies, chickens dispersed into and beyond the range of other *Gallus* subspecies and species. The evidence presented here demonstrates that chickens did not appear in archaeological contexts within Central China, South Asia, or Mesopotamia until the late second millennium BCE, just before their initial presence in Melanesia. By ~700 BCE, chickens had arrived in Ethiopia and Mediterranean Europe (Fig. 2). This western dispersal was substantially more rapid than the establishment of chicken populations in temperate regions present in higher latitudes (Fig. 2). Overall, our analyses indicate a temporal origin and spread of chickens that substantially postdates many of those suggested by previous studies (6, 8).

A Hypothesis for the Process of Chicken Domestication. Within the native range of red junglefowl, many Southeast Asian languages refer to chickens as "bamboo fowl," given how readily they take advantage of cyclical bamboo mass flowering and seeding events (10). Red junglefowl are also known to consume rice grains (*Oryza* sp.) (44, 84), a staple dietary component of Southeast Asian domestic chickens (85). Rice and millet (*Setaria italica*) were cultivated by mixed foraging and cereal producing Neolithic communities in mainland Southeast Asia (86–88). An analysis of the material culture (including pottery decoration) associated with these agriculturalists suggests that rice and millet cultivating communities dispersed from the Yangtze valley (89–92) into southern China, where they arrived by the mid-third millennium BCE (90, 93). From there, they continued into peninsular

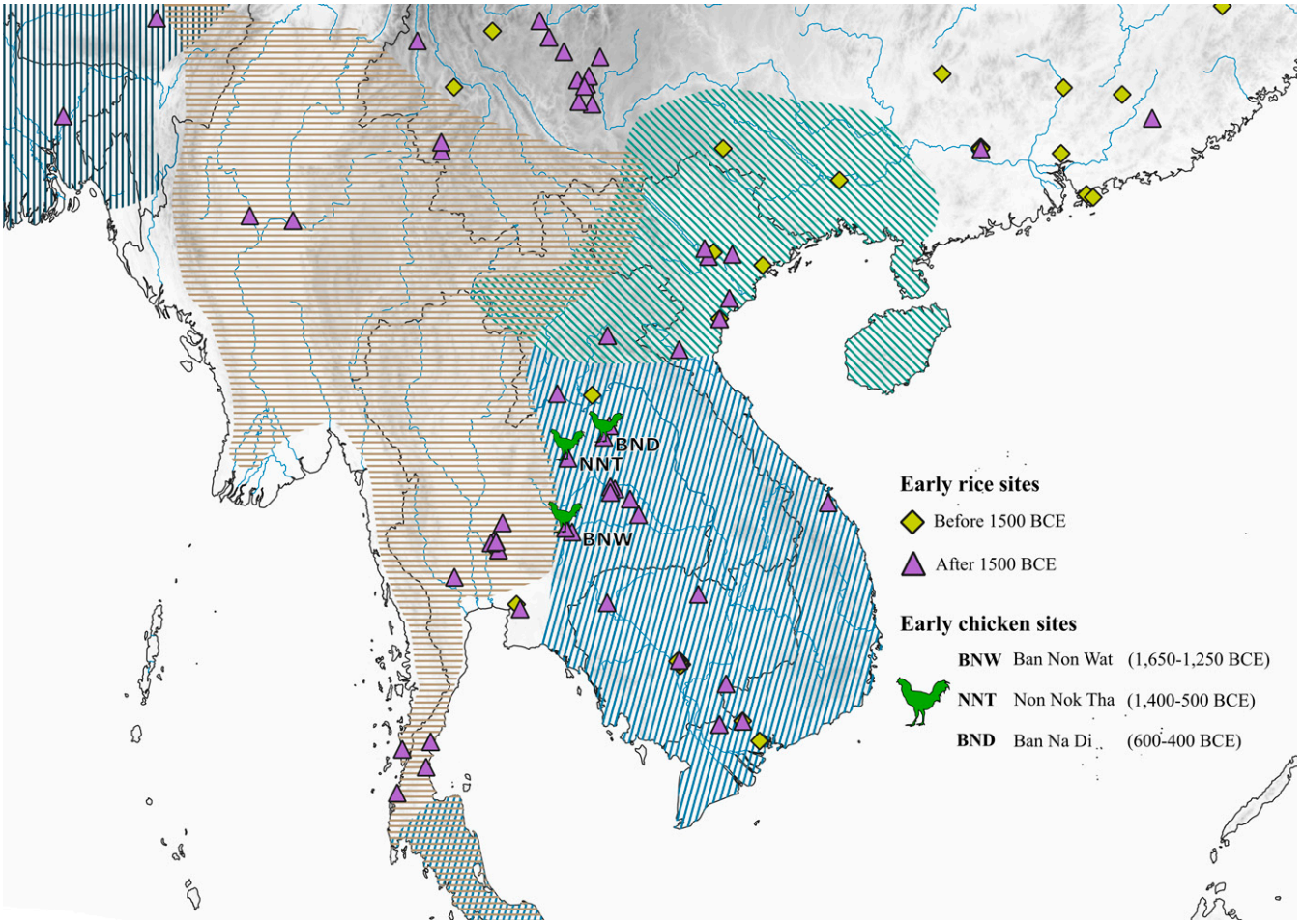

Fig. 3. A map depicting the distribution of dated archaeological rice finds taken from the revised Rice Archaeological Database compiled by D.Q.F. and colleagues, RAD 2.0 (90), with newly added archaeological records and cleaned reports with associated dates that appear too early based on current understanding of archaeological chronology. This is especially the case in mainland Southeast Asia where most of the arrival of cereal agriculture is now thought to be ~2500 BC for northern Vietnam and southernmost China only and ~2000 BC for the rest of the region (94, 123).

Southeast Asia, where people following distinct dispersal pathways emphasized either rice or millet (94).

Land reclamation for cereal cultivation led to the replacement of primary forest by secondary vegetation, a habitat more suitable for red junglefowl. Outside of bamboo thickets, red junglefowl are known to thrive in slash-and-burn agricultural systems (10). The novel presence of cultivated fields, fallow fields (necessary for either millet or rainfed rice), cereal harvest residues, remainders of human food preparation and consumption, invertebrates associated with keeping pigs and cattle, and other aspects of the human niche may have attracted red junglefowl to human settlements and their immediate catchment.

The long-term abundance of cereals within the human niche would have led to dramatic shifts in selective pressure that lasted multiple generations, including a relaxation of selection against larger clutch size, as well as increased selection against territoriality in cocks (10). These conditions likely also facilitated larger bird population densities near farming communities, followed by subsequent "accommodation" of birds within the village. The availability of cultivated cereals may have therefore catalyzed a shift in the relationship between people and red junglefowl consistent with the commensal pathway (95, 96).

The current archaeobotanical evidence indicates that sites with rice cultivation appeared within the distribution of *G. gallus spadiceus* [the subspecies recently identified as the most likely progenitor of chickens (16)] from about 2000 BCE in two regions: southern Yunnan and northeast Thailand (Fig. 3 and *SI Appendix*, Table S4). Although cereal farming was also present at this time within the inferred distributions of *Gallus gallus jabouillei* and *G. gallus gallus*, there is as yet no evidence for the early presence of domestic chicken populations. Although there is confirmation of early rice farming near coastal areas and in low-lying wetlands (86, 94), the zooarchaeological records in Neolithic Vietnam, for example, show evidence for the hunting of wetland birds, but lack remains of *Gallus* (97). In more interior zones, early rainfed rice/millet cultivation likely spurred a tighter relationship between people and *G. gallus spadiceus*, as attested by the earliest confirmed chicken bones at Ban Non Wat and Non Nok Tha (*SI Appendix*, Table S2) (98). Because the rice was rainfed, it would have required more land area and fallow cycles relative to later, more productive irrigated rice (87), and these conditions would have created large areas of secondary thicket vegetation. In the northern region of the *G. gallus spadiceus* distribution, similar processes were likely possible, but detailed avifaunal studies at prehistoric archaeological sites in Yunnan have not yet been carried out.

In regions north of Yunnan, wet rice agriculture, characterized by small-scale, intensive wetland fields in the Yangtze (87, 99), is present as early as 4000 to 3000 BCE, and these wet paddyfield systems spread throughout central China during the Neolithic. Chickens, however, were absent in the Neolithic (100) and only appear ~1000 BCE (Fig. 3). Relative to wet rice, dry rice and millet cultivation that predominate in the tropical south is

characterized by more extensive mosaics of field and fallow, a niche more suited to wild and commensal red junglefowl.

A Combined Chicken–Rice Dispersal Across Asia and Africa. Following the integration of chickens and human agricultural societies, the correlated spatiotemporal patterns of rice and chicken dispersal across Asia is striking. In South Asia for example, sedentism became widespread in the Ganges plains in the second millennium BCE (22, 101), and domesticated rice, wheat, barley, and other grain crops began to dominate the economy (102, 103). At this time, agriculture in the Deccan focused on small millets, beans, and occasionally wheat and barley (22, 101). It is during this period, perhaps from the later second millennium BCE, that the subsistence context would have been ideal for chickens or commensal jungle fowl, and this timing corresponds with the arrival of bird remains unambiguously identified as chickens in the Indian subcontinent.

While there is evidence for proto-indica rice management by hunter–fisher–gatherers in the middle Ganges plains predating ∼2000 BCE (102, 104, 105), proto-indica rice was managed in natural, seasonal wetlands that were unlikely to attract *Gallus* in large numbers. This is illustrated by a dearth of *Gallus* remains and a low level of both cereal production and livestock husbandry in the archaeological record (22). The domesticated indica rice introduced ∼1600 to 1500 BCE in the Upper and Middle Ganges (104, 105) was typically rainfed in more extensive systems with periods of fallow (102, 106), and thus more attractive to fowl. Recent genomic evidence derived from modern populations suggested that although modern domestic chickens in South Asia possess signatures associated with the local subspecies *G. gallus murghi*, these ancestral affinities are the result not of a local, independent domestication process, but the result of admixture with introduced domestic chickens derived from *G. gallus spadiceus* (16).

In Iron Age Mesopotamia, rice and millet cultivation may also have been linked to the initiation and intensification of poultry farming. For example, the cultivation of Chinese millets (*Panicum miliaceum*, *Setaria italica*) began in the later second millennium BCE (107–109) and intensified after ∼1000 BCE (110, 111), precisely when poultry husbandry becomes visible archaeologically (Fig. 2 and *SI Appendix*, Table S2). Middle Assyrian texts also confirm that irrigated rice became established in Syria by ∼1100 BCE, and references to this practice increased from the eighth century BCE (112). Thus, alongside the diversification of grain crops, chickens may represent an additional element of the broadening of Near Eastern subsistence practices after the late Bronze Age collapse (45).

There is also a correlation in Africa between the appearance of chickens and rice agriculture. The translocation of chickens to coastal Southeast Africa and the Indian Ocean islands in the eighth/ninth centuries CE coincides with the introduction of Asian crops, such as rice, tree cotton, and mung bean (113). In addition, archaeobotanical evidence in the Niger Basin illustrates the prominent role of cereal diversification, including more widespread rice cultivation and increasing urbanism ∼300 to 900 CE (114), a temporal window that coincides with the first appearance of chickens.

Conclusion

Our reassessment of archaeological, iconographic and textual evidence indicates first that the origins and dispersal of domestic chickens both within and beyond the native range of red junglefowl was, relative to many farm animals, a relatively late phenomenon (Fig. 2). Our conservative approach suggests that chickens were incorporated into human societies as domestic birds by 1500 BCE in peninsular Southeast Asia, and that they then rapidly spread south into Island Southeast Asia and west across South Asia and Mesopotamia to Europe and Africa. Additional archaeological investigations are necessary to test this chronology, and new excavations may reveal not only an earlier association between humans and red junglefowl, but also earlier human-mediated translocations of chickens across the globe.

The attractiveness of rice and millet agriculture to red junglefowl may have facilitated both the initiation of the domestication process, and the subsequent dispersal of domestic chickens. Initially, the more extensive cultivation systems that created mosaics of secondary tropical scrub (fallows) alongside cereal fields may have been important, whereas later, more intensive rice agriculture would have provided grain surpluses to support larger populations of domestic birds. The year-long availability of grains and associated foodstuffs may thus have served to draw these arboreal birds into a human niche. Archaeologically, the first appearance in peninsular Southeast Asia of both rice and unambiguous domestic chickens is also consistent with the recent conclusion that domestic chickens were derived from the subspecies *G. gallus spadiceus* (16).

Grain production within a human niche has been shown to also attract other birds. For example, a recent genetic and isotopic study (115) of pheasant (*Phasianus colchicus*) bone remains (originally presumed to be chickens) from the site of Dadiwan in northern China demonstrated that the birds subsisted on cultivated millet, thus suggesting that this grain attracted different gallinaceous birds into village settings. By providing predictable feeding opportunities across the region for distinct bird species (including red junglefowl), grain cultivation may have acted as a magnet for seed-eating birds, thereby kickstarting a shift in the commensal relationship with people that eventually led to domestication.

Future efforts to integrate newly excavated sites and the application of direct radiocarbon dating will modify the picture presented here, while providing insights into the climatic, economic, and socio-cultural characteristics that influenced the dispersal of chickens across the globe. From a biological perspective, although rice and millet cultivation may have facilitated chicken husbandry in subtropical regions, it was the species' adaptability and granivorous diet that led to its adoption by agriculturalists cultivating barley, wheat, and other cereals in arid and temperate environments. In addition, the delayed integration of fowl into human settlements at higher latitudes in Eurasia (Fig. 2 and *SI Appendix*, Table S2) suggests that the generally thermophilic species adapted more slowly to colder climates.

Culturally, the presence of early iconography and chicken bones in Mesopotamian and western European palatial architecture, noble households, elite burials, sanctuaries, and other divine contexts, suggests that chickens were initially associated with elites in numerous locations (116). A recent study (13) demonstrated that early chickens in European archaeological contexts appear as complete skeletons. Cut marks on individual chicken bones found as refuse are not present until several centuries later, suggesting that the first chickens were initially revered rather than consumed. Since the regular keeping of chickens for food did not take place until centuries after their arrival in Europe, this also undermines the hypothesis that meat consumption drove the chicken's transition to a domestic bird.

To test the scenario outlined above, it is necessary to carefully document and directly date additional *Gallus* finds. In addition, the establishment of osteological identification criteria separating wild junglefowl from their domestic relatives, and the

simultaneous generation and analysis of morphological, isotopic, and ancient genetic datasets is essential to refine the origins and dispersal of the world's most ubiquitous domestic bird.

Materials and Methods

Evaluation of Archaeological Chicken Remains. To critically assess and establish the early appearance of domestic chicken remains across Eurasia, Africa, and Oceania, this study analyzed the remains described in faunal databases and publications. We did so by revisiting and critiquing the species identification, the determination of domestic status, the integrity of the site's stratigraphy, and the overall zooarchaeological and cultural context of the sites. This conservative approach allowed us to generate two tables: one which includes the earliest recorded archaeological remains that we could confidently assign as domestic chickens (*SI Appendix*, Table S2), and a list of remains whose identification, dating, and stratigraphic position was ambiguous (*SI Appendix*, Table S3) (117, 118). This latter table also described the rationale for the exclusion of the individual remains from *SI Appendix*, Table S2. The challenges of compiling this global dataset included issues related to preservation, identification, recovery, and dating. More detailed descriptions of each of these topics and how they influenced the compilation of the tables are included in *SI Appendix*.

Data Availability. Data have been deposited in GitHub (https://github.com/ekirving/chickens). All other study data are included in the main text and *SI Appendix*.

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