

Domestication and the comparative embryology of birds

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Abstract

Studies of domesticated animals have greatly contributed to our understanding of avian embryology. Foundational questions in developmental biology were motivated by Aristotle's observations of chicken embryos. By the 19th century, the chicken embryo was at the center stage of developmental biology, but how closely does this model species mirror the ample taxonomic diversity that characterizes the avian tree of life? Here, we provide a brief overview of the taxonomic breadth of comparative embryological studies in birds. We particularly focused on staging tables and papers that attempted to document the timing of developmental transformations. We show that most of the current knowledge of avian embryology is based on Galliformes (chicken and quail) and Anseriformes (duck and goose). Nonetheless, data are available for some ecologically diverse avian subclades, including Struthioniformes (e.g., ostrich, emu) and Sphenisciformes (penguins). Thus far, there has only been a handful of descriptive embryological studies in the most speciose subclade of Aves, that is, the songbirds (Passeriformes). Furthermore, we found that temporal variances for developmental events are generally uniform across a consensus chronological sequence for birds. Based on the available data, developmental trajectories for chicken and other model species appear to be highly similar. We discuss future avenues of research in comparative avian embryology in light of the currently available wealth of data on domesticated species and beyond.

KEYWORDS

avian embryology, chicken, developmental variance, domesticated birds

1 | INTRODUCTION

The selective breeding of plants and animals for human use and consumption (domestication) has enabled human civilization to flourish (Larson & Fuller, 2014; Sánchez-Villagra, 2022). From a scientific perspective, the intricate relationship between humans and domesticated animals can be traced to Aristotle's fascination with the embryology of chicken (*Gallus gallus*) in the 4th century BC (Leroi, 2014). Aristotle is regarded as the first developmental

biologist because he described morphological changes in chick embryos, thereby establishing that organisms are not “preconstructed” but are rather the sum of progressive tissue transformations (Leroi, 2014). Many of such transformations were well documented with the advent of staining and enhanced microscopy technologies of the 19th century (Mason, 2009; Wolpert, 2004). By the 20th century, embryos of the domesticated chicken were among the best described, particularly among tetrapod animals (Duval, 1889; Hamburger & Hamilton, 1951;

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Keibel & Abraham, 1900; Künzel et al., 1962; Lillie, 1908; Stern, 2005, 2018).

Descriptive embryological studies in chicken supported several groundbreaking experiments that validated key principles in modern developmental biology (Huxley & de Beer, 1934; Mason, 2009; Stern, 2005, 2018; Wolpert, 2004). For example, critical insights into the mechanisms of pattern formation and morphogenesis were gained via experiments on limb bud development (Saunders, 1948; Zwilling & Hansborough, 1956). Chicken embryos were attractive models to experimental embryologists owing to practical reasons (Tzika et al., 2008). Eggs can be readily obtained year-round and are laid with embryos that do not yet feature a primitive streak, thus most developmental events can be observed (Hamburger & Hamilton, 1951; Künzel et al., 1962). Furthermore, eggs are rather large and can be manipulated in the laboratory with relative ease (Mason, 2009). Interest in chicken embryology motivated the enhancement of criteria to describe the timing of developmental events (Arnaout et al., 2021; Hamburger & Hamilton, 1951; Künzel et al., 1962; Toledo Fonseca et al., 2013), including those that unfold before oviposition (Eyal-Giladi & Kochav, 1976). There was also interest in using chicken embryology as a reference to guide studies on wild avian species (Herbert, 1969; Price, 1938; Schumacher & Wolff, 1966).

Beyond chicken, embryology in other domesticated species of Galliformes was also described in the 20th century (Clark, 1960; Fant, 1957; Hendrickx & Hanzlik, 1965; Labisky & Opsahl, 1958; Mun & Kosin, 1960; Smith Padgett & Ivey, 1960; Wilhelm & Robertson, 1941; Williams & Phillips, 1944). Although domesticated lineages outside of Galliformes were also studied (duck and goose; Cooper & Batt, 1972; Koecke, 1958; Montgomery et al., 1978), the diversity of species in which embryonic development has been studied in detail remains low compared to mammals (Cordero et al., 2020; Hopwood, 2007; Werneburg & Geiger, 2016). As such, Butler and Juurlink's (1987) *Atlas for Staging Mammalian and Chick Embryos* included 14 representative mammalian species and prioritized chicken as the comparative reference for birds, which continues to be the case today (Bellairs & Osmond, 2014; Bronner-Fraser, 2008; Stern, 2018).

There are nearly 10,000 bird species (Tobias et al., 2020). This diversity has served as an outstanding model to study the evolution of growth rates, incubation time, and other life-history traits (Austin et al., 2020; Cooney et al., 2020; Starck & Ricklefs, 1998). However, similar macroevolutionary comparisons of sequential transformations in the embryonic development of birds remain rare and the taxonomic breadth of sampled species is biased towards domesticated species. This is sensible because many avian species cannot be sampled because they are protected or are otherwise of conservation concern (Jetz et al., 2014). Moreover, birds lay eggs in a sequential fashion, such that collecting an entire clutch in the wild would require much interference from the mother (Deeming & Reynolds, 2015). Also, locating natural nests can be a challenging and time-consuming endeavor (Deeming & Reynolds, 2015). Thus, the study of domesticated species has been highly useful to researchers aiming to trace

the ontogenetic origins of morphological diversity in birds (Schneider, 2018).

The objective of the present study was to provide a brief overview of the available data on the timing of developmental events in avian embryos. In birds, changes in the timing of development may sometimes reflect interspecific differences in life history (Starck & Ricklefs, 1998), but also key changes in the growth rate of functionally relevant traits (Dobrova et al., 2021; Faux & Field, 2017). We aimed to characterize the taxonomic breadth of published studies that focused on describing avian embryology and its chronology. This enabled us to explore trends in the timing of developmental characters across ontogeny. Lastly, to address whether observations in a particular taxon can be generalized to others, we explore similarities in developmental trajectories of chicken and other well-studied (i.e., model) bird species, including common commercial breeds. We defined model species as those that can be easily bred or reared in the laboratory and have therefore been the subject of research across multiple biological subdisciplines.

2 | STUDIES OF DEVELOPMENTAL CHARACTERS IN BIRDS

We adopted Starck's (1993) definition of "physical" and "morphological" measures in incubation days and ranked stages of avian species, respectively. However, rather than measuring morphological changes in embryos as a ranked sequence of developmental stages (Starck, 1993), we ranked the median for incubation days during which we observed developmental events across species. Owing to the sample small sizes, the median was used. Developmental events were described by scoring characters from the Standard System to Study Vertebrate Embryos, that is, SES (Werneburg, 2009). The SES characters were initially designed to compare homologous traits in embryos of diverse vertebrate species, though avian-specific characters were later added to this system (Nuñez-León et al., 2021). We extracted temporal data for the appearance of characters that were available in the primary literature (see online supplementary file). Our search yielded 51 studies. However, several studies could not be included because they lacked data for absolute incubation time, as only relative stages were indicated. Converting absolute timing data from hours to days optimized the total number of species that could be sampled. If values were available from multiple studies for the same species, redundant data were combined by taking the median of values. After filtering, the timing (in days) of 122 characters in 24 species, see Table 1, was mapped onto a pruned topology of Aves based on the phylogenetic studies of Jetz et al. (2014) and Prum et al. (2015) (Figure 1).

Anseriformes and Galliformes were overrepresented (11 out of 24 species) in our dataset. Only three members of the most speciose avian clade, the songbirds (Passeriformes), were represented in the data. However, character sequences for two of the three species were well sampled (>62% scored characters). By contrast, the three species of shorebirds (Charadiiformes: *Uria*

TABLE 1 List of avian species sampled in this study.

Species	Data source	% Characters scored
<i>Gallus gallus</i>	Hamburger and Hamilton (1951); Künzel et al. (1962); Li et al. (2019); Lumsangkul et al. (2018); Sellier et al. (2006)	80
<i>Anas platyrhynchos</i>	Caldwell and Snart (1974) Li et al. (2019); Lumsangkul et al. (2018); Sellier et al. (2006)	74
<i>Taeniopygia guttata</i>	Murray et al. (2013)	64
<i>Lonchura striata</i>	Yamasaki and Tonosaki (1988)	62
<i>Anser cygnoides</i>	Li et al. (2019); Sellier et al. (2006)	63
<i>Coturnix chinensis</i>	Nakamura et al. (2019)	61
<i>Columba livia</i>	Olea and Sandoval (2012)	54
<i>Coturnix coturnix</i>	Ainsworth et al. (2010); Sellier et al. (2006)	54
<i>Meleagris gallopavo</i>	Sellier et al., 2006; Wilhelm and Robertson (1941); Williams and Phillips (1944)	47
<i>Nannopterum auritus</i>	Powell et al. (1998)	45
<i>Phasianus colchicus</i>	Fant (1957); Labisky and Opsahl (1958)	45
<i>Numida meleagris</i>	Ancel et al. (1994); Conrado Sousa de Araujo et al. (2019); Sellier et al. (2006)	43
<i>Falco sparverius</i>	Bird et al. (1984); Pisenti and Santolo (2001)	40
<i>Struthio camelus</i>	Brand et al. (2014, 2017); Gefen and Ar (2001)	39
<i>Colinus virginianus</i>	Hendrickx and Hanzlik (1965)	35
<i>Dromaius novaehollandiae</i>	Nagai et al. (2011)	32
<i>Pygoscelis adeliae</i>	Herbert (1967, 1969)	25
<i>Branta canadensis</i>	J. A. Cooper and Batt (1972)	25
<i>Sterna hirundo</i>	Hays and LeCroy (1971)	21
<i>Aix sponsa</i>	Montgomery et al. (1978)	20
<i>Uria aalge</i>	Mahoney and Threlfall (1981)	16
<i>Agelaius phoeniceus</i>	Daniel (1957)	13
<i>Larus delawarensis</i>	Ryder and Somppi (1977)	12
<i>Milvus migrans</i>	Desai and Malhotra (1980)	10

Note: Species are ranked according to the percentage of characters (out of 122) that could be scored based on descriptions that were available in the literature (see Supporting Information data file).

Developmental characters

Hatching
 Sharp egg tooth recognizable
 Urogenital papilla bud inconspicuous
 Beak keratinized
 Eyelid covers eye (at least half of it)
 Cervical flexure disappeared
 Hind limb feathers distal
 Throat feathers
 Eyelid ventral to lens
 Forelimb feathers distal
 Forelimb feathers proximal
 First claw hind limb
 Neck feathers
 Lower eyelid feathers
 Cornification: Beak has a keratinized tip
 Alar pterygia papillae
 Capital pterygia papillae
 Separate phalanges are visible in the toes
 Separate phalanges are visible in the fingers
 First claw forelimb
 Head projection disappeared
 Humeral pterygia papillae
 Tail feathers
 Head feathers
 Urogenital papilla bud
 Hind limb feathers proximal
 Caudal pterygia papillae
 Femoral pterygia papillae
 Toe
 Scleral papillae inconspicuous
 Spinal/dorsal pterygia papillae
 Lower part reaches tip of beak
 Nostrils formed
 Membranes between the toes are completely gone
 Back feathers
 Eyelid at level of scleral papillae
 Caruncle appears
 Thoracic bulbus disappeared
 Mandibular arch bud occlusion point = jaw closure
 Membrana nictitans
 Finger
 Egg tooth apparent
 Mandibular arch bud level frontonasal groove
 Hind limb sporn
 Scleral papillae
 Maxillary process fused to upper part of the beak
 Membranes between the fingers are completely gone
 Eyelid begun overgrow
 Digital serration hind limb
 Maxillary process fuses with frontonasal process
 Digital serration forelimb
 Digital grooves forelimb
 Knob-like beak recognizable
 Lower lid appears
 Mandibular arch bud anterior eye
 Digital grooves hind limb
 Ptiliforms
 Hind limb knee
 Pharyngeal slits closed
 Forelimb elbow
 Maxillary process anterior to eye
 Hind limb digital plate
 Forelimb digital plate
 Contour lensiris
 Optic fissure
 Mandibular arch bud anterior lens
 Forelimb paddle
 External nares
 Mandibular arch bud posterior lens
 Mandibular arch bud midline eye
 Maxillary process anterior to lens
 Hind limb elongated
 Forelimb elongated
 Hind limb paddle
 Hyoid flap
 46-50 somite pairs
 Maxillary process midline of eye
 Hindlimb AER
 Forelimb bud
 Otic capsule inconspicuous
 Nuchal fold
 Cervical flexure 90°
 Hind limb bud
 Otic vesicle
 Somites hard to count
 Mandibular arch bud
 Maxillary process posterior to eye
 Hind limb ridge
 Mandibular process of the mandibular arch posterior eye
 Maxillary bud
 Otic placode
 Olfactory placode
 41-45 somite pairs
 Fifth arch bud
 Ventricle S-shaped
 36-40 somite pairs
 Tail bud
 Fourth pharyngeal slit
 Lens placode
 Fourth arch bud
 Forelimb ridge
 Anterior cephalic projection
 31-35 somite pairs
 Posterior neuropore closed
 Third pharyngeal slit
 Second arch bud
 Ventricle bulbus
 Optic vesicle
 Second pharyngeal slit
 First pharyngeal slit
 26-30 somite pairs
 Third arch bud
 21-25 somite pairs
 Anterior neuropore closed
 16-20 somite pairs
 Head bulbus
 11-15 somite pairs
 6-10 somite pairs
 Neural folds begin to close
 1-5 somite pairs
 Primitive streak present
 Blastoporus



FIGURE 1 Phylogenetic distribution for the timing of 122 developmental characters in avian species. Phylogeny after Prum et al. (2015) and Jetz et al. (2014). Empty cells denote characters for which data were unavailable and the heatmap color gradient depicts the incubation days at which developmental characters were scored. Data sources and the proportion of characters scored per species are shown in Table 1. Silhouettes representing avian taxonomic orders are from phyloPic (www.PhyloPic.org; Public domain dedication 1.0 license).

aalge, *Larus delawarensis*, and *Sterna hirundo*) were sparsely sampled (< 30% scored characters), as was the sole representative of the birds of prey (Accipitriformes: *Milvus migrans*). As expected, *Gallus gallus* featured the most complete character sequence (Figure 1; Table 1). The earliest-branching subclade in the topology, Struthioniformes, was represented by the ostrich (*Struthio carnelus*) and emu (*Dromaius novaehollandiae*), which featured the longest incubation periods in our data set (Figure 1). Examinations in other members of avian subclades that were highlighted in our analyses were sometimes restricted to a specific set of stages. As such, data for the passerines *Turdus pilaris*, see Blom and Lilja (2005), as well as the blue tit (*Cyanistes caeruleus*) and great tit (*Parus major*) (Hemmings & Birkhead, 2016), were excluded. Although we only included data for *Pygoscelis adeliae* as the sole representative of Sphenisciformes (penguins), embryos of closely related species (*P. antarctica* and *P. papua*) have been studied (Herbert, 1967). Embryos of the emperor penguin (*Aptenodytes forsteri*) were also described but chronological information on these specimens was limited (Glenister, 1953), thus we excluded this species.

It is worth noting that several subclades could not be included in our survey because timing data (measured in days or hours) were unavailable or incomplete, e.g., Psittaciformes (Abraham, 1901; Carril & Tambussi, 2015, 2017; Carril et al., 2016; Tokita et al., 2013). Embryonic development in taxa with highly derived craniofacial traits, such as Strigiformes (*Tyto alba*), was documented but estimates for incubation time were incomplete (Köppl et al., 2005). The exclusion of these and other studies that did not meet our sampling criteria should not diminish their importance. In fact, perhaps the best anatomical descriptions of avian embryos in nondomesticated species are available in the classical embryological literature, including accounts on enigmatic species such as the kiwi (Apterygiformes: *Apteryx* spp.) (Parker, 1891, 1892). An exhaustive description of a Charadiiformes species (*Vanellus vanellus*) was also published in Keibel's outstanding *Normentafeln* series (Grosser & Tandler, 1909).

3 | VARIATIONAL TRENDS IN ONTOGENY

Differences that characterize the morphology of species may originate or become apparent during the growth period that precedes the end of embryonic development, as this is when ontogenetic sequences are more likely to undergo evolutionary change (Alberch & Blanco, 1996; Duboule, 1994). As embryonic development ensues, inductive tissue interactions decrease because traits gain greater structural independence, and energy is prioritized for growth (Galís & Metz, 2001). It has, therefore, been hypothesized that this growth-dominated period might coincide with elevated levels of phenotypic variation among individuals of a species or among species (De Jong et al., 2009; Irmiler et al., 2004; Werneburg et al., 2021). This hypothesis has been supported in mammals (Cordero et al., 2020), as well as by a recent study that concluded that interspecific variation in the duration of the growth period (Hamburger and Hamilton

Stages 33–45) was most variable in embryos of 20 bird species (Cooney et al., 2020). We took the opportunity to address this expectation by comparing variances for the timing of developmental characters in most species studied by Cooney et al. (2020).

For characters that could be scored in more than five species, we computed and compared a robust coefficient of variation (RCV) based on the standardized median absolute deviation, that is, RCV_M (Arachchige et al., 2020). Temporal variances for characters might be affected by different developmental periods of species (Laurin & Germain, 2011). To account for this, data were divided by the total duration of egg incubation before computing RCV_M . In general, variances were uniformly distributed across the consensus median-ranked character sequence for the bird species sampled (Figure 2). Notably, the most temporally variable developmental event was described by the “blastoporous” character, which was ranked first in the median-ranked sequence (Figure 2). Note that our “blastoporous” character is synonymous with the pre-primitive streak terminology used to describe the onset of gastrulation in chicken embryos, which may begin before oviposition (Eyal-Giladi & Kochav, 1976; Lee et al., 2020). Otherwise, the large yolk of avian eggs obscures the observation of a proper blastopore (Dye, 2012).

The elevated variance for the “blastoporous” character might have been related to the delayed appearance, i.e., three days after oviposition, of the pre-primitive streak in penguin embryos (Herbert, 1967). This was supported by histological sections that confirmed that the neural tube and associated characters mature about three days later in penguins relative to chickens (Herbert, 1969). This shift is attributed to an overall slower rate of development in penguins, which was possibly caused by exposure to cold temperatures during the collection of eggs in the field (Herbert, 1967, 1969). Similar slowdowns in the emergence of traits that are generally expected to be highly canalized are perhaps not uncommon in vertebrate animals exposed to extreme environmental fluctuations. Experimental exposure to hypoxia caused the delayed development of the eye in zebrafish embryos (Schmidt & Starck, 2010). Even so, how the environment influences the pace of avian embryonic development is still unclear. An experiment on eight tropical songbirds found that embryonic development was prolonged, rather than accelerated, by increasing incubation temperature (Robinson et al., 2013). Furthermore, whether eggs are incubated artificially or naturally (with parental care) did not affect incubation duration in the zebra finch (*Taeniopygia guttata*) (Hemmings & Birkhead, 2016).

As in comparisons of ossification sequences that also included model domesticated species (Koyabu et al., 2014; Maxwell, 2008; Mitgutsch et al., 2011), our ranked sequences of developmental events were highly conserved with the exception of a few characters (Figure 3). These analyses did not show a progressive increase in temporal variances of characters, as one may predict based on the findings of Cooney et al. (2020). This may be explained by the fact that most of our characters described the organogenic phase of development that is expected to be highly evolutionarily conserved in vertebrates (Cooney et al., 2020; Cordero, 2021; Cordero et al., 2020).

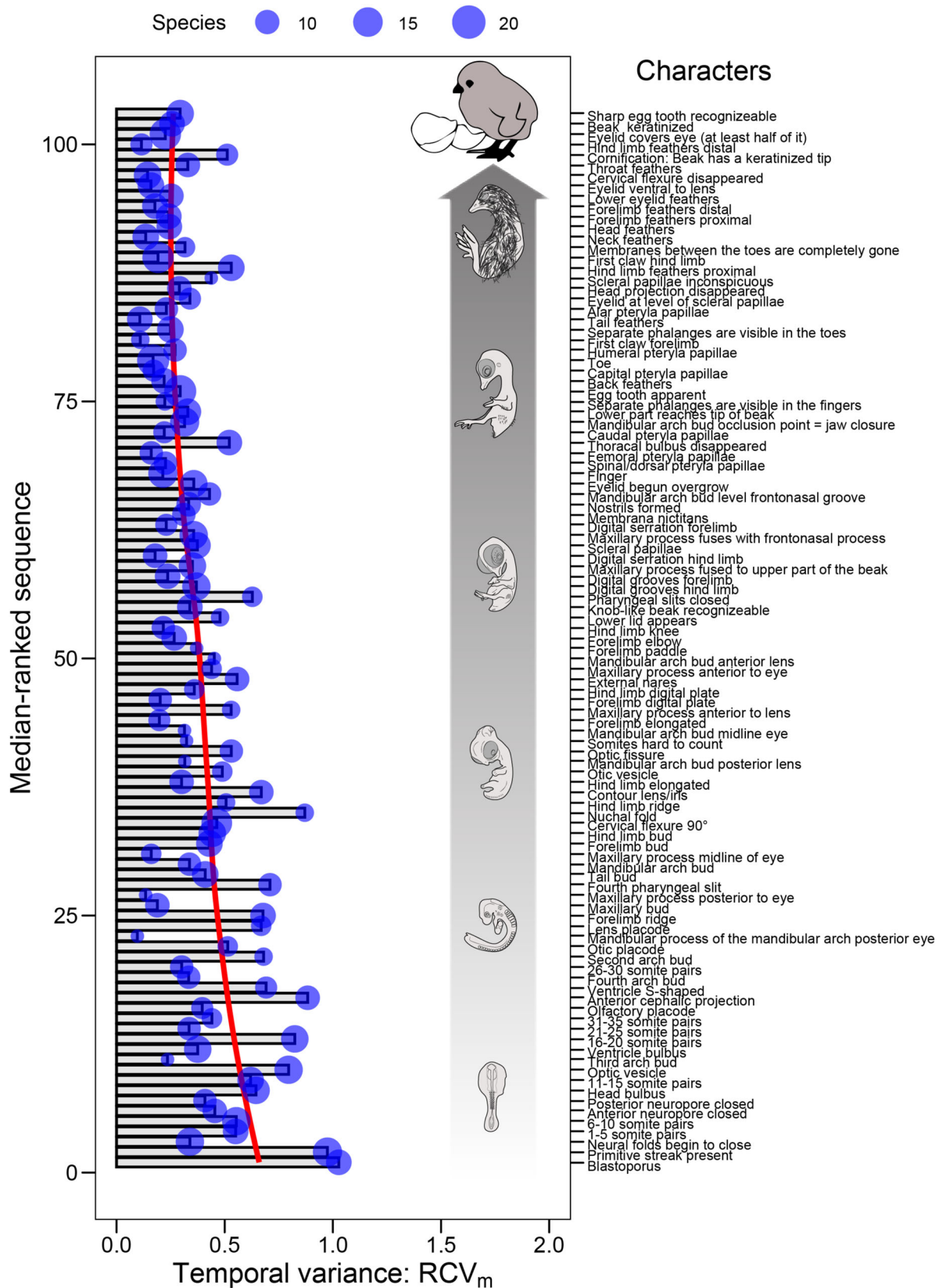


FIGURE 2 Variation in the timing of developmental characters in 24 avian species. The RCV_m (standardized median absolute deviation) values for characters were ranked by the median (see y-axis) and fitted with locally estimated scatterplot smoothing (red line). RCV, robust coefficient of variation.

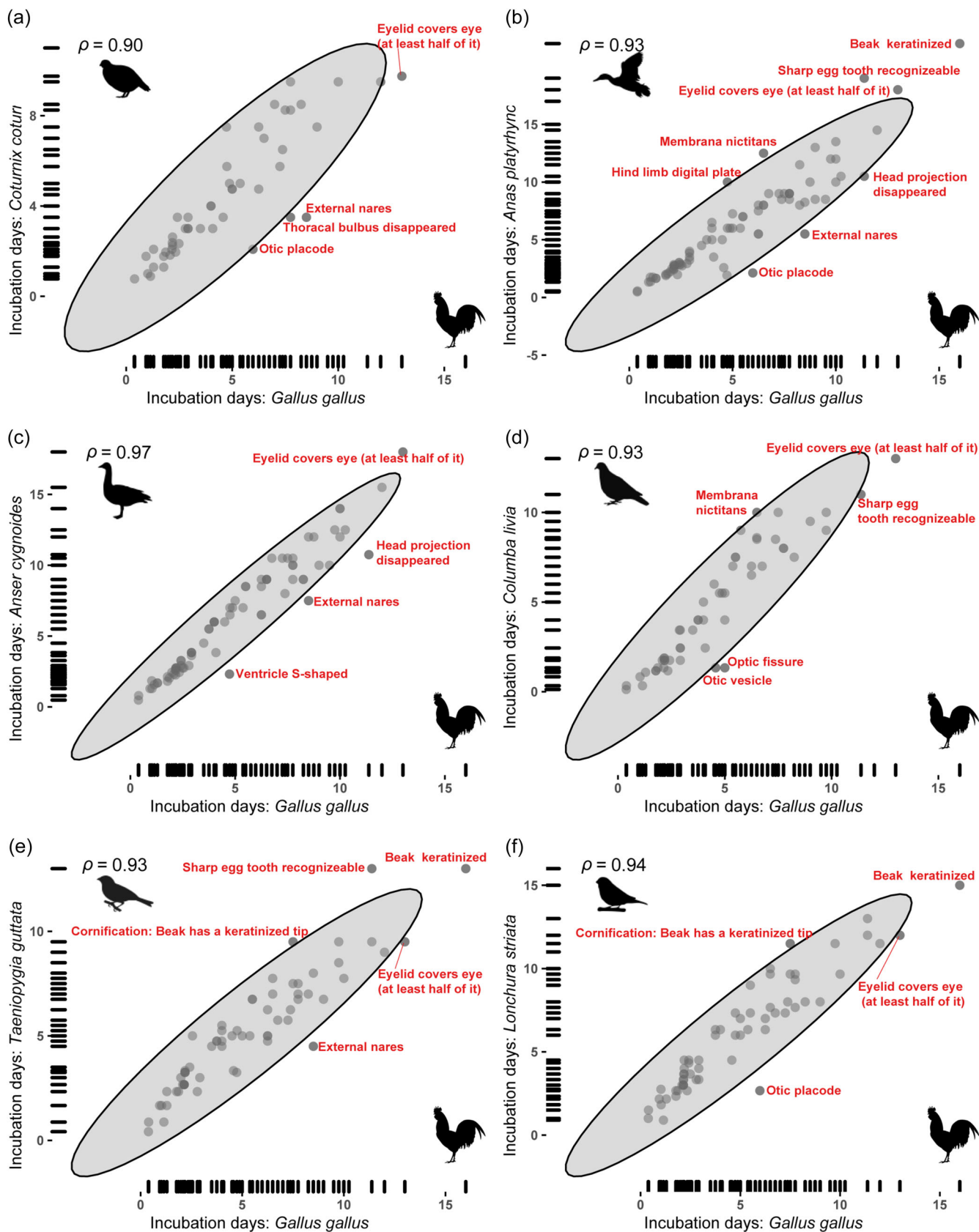


FIGURE 3 Spearman rank correlations (ρ) on the timing of developmental characters for chicken (*Gallus gallus*; see x-axis) against select avian species (y-axis) that are considered models for the study of development. (a) *Coturnix coturnix*; (b) *Anas platyrhynchos*; (c) *Anser cygnoides*; (d) *Columba livia*; (e) *Taeniopygia guttata*; and (f) *Lonchura striata*. Characters outside the 95% confidence intervals for correlations (grey ellipses) are highlighted in red. Species silhouettes are from PhyloPic (www.PhyloPic.org; public domain dedication 1.0 license).

To comprehensively address this hypothesis, additional bird species will need to be studied. Also, scoring the timing of developmental transformations is one of several means by which the origins of phenotypic differences among species may be observed. Describing the relative growth of the beak and limb has proven effective in demonstrating divergence at the interspecific level (Faux & Field, 2017)2014, as well as within species (Nuñez-León et al., 2021).

4 | A COMPARISON OF MODEL SPECIES IN AVIAN EMBRYOLOGY

Our pairwise analyses of model species focused on the timing of appearance for a set of developmental events that can be externally scored without clearing or dissecting embryos. The observed temporal differences may not necessarily translate to tissue-level changes that ultimately produce discrete morphological differences among species (Werneburg & Sánchez-Villagra, 2009). In addition, heterochronies may be detected across distinct levels of biological organization (Dobrevá et al., 2021). Species-specific phenotypes may emerge via changes in growth processes that span both embryonic and post-embryonic life stages, as in beak shape development in Darwin's finches (Abzhanov et al., 2004; Grant, 1981). Nonetheless, identifying temporal differences in embryonic development remains valuable to studies seeking to identify the origin of phenotypic diversification in birds (Dobrevá et al., 2021). An understanding of embryonic development is also informative to research on life history characteristics of avian species. Descriptive embryology has been used to evaluate hatching failure (Hemmings & Birkhead, 2016).

Most characters that potentially represent heterochronic shifts in our pairwise comparisons of model species were related to beak keratinization, egg tooth differentiation, or eyelid structural changes (Figure 3). It is worth noting that some of these potential heterochronies may be the result of technical error and potential biases in character interpretation. We, therefore, welcome researchers to further explore these data and cross-reference the source studies (Table 1). In addition, our survey was restricted to studies wherein absolute timing data was unambiguously listed and we present these data in day units, rather than standardized units, to clearly expose variation in egg incubation duration (Figure 1). It is possible to expand upon this study by using proxies for developmental time (ranks or relative timing) if absolute time data is not available for some species. For instance, a subset of characters could be compared by standardizing the onset of trait development by the total duration of trait formation in different species, that is, the "continuous analysis" of Laurin and Germain (2011). Also, the timing of cranial ossification modules has been studied using this approach in domestic mammals (Koyabu et al., 2014).

It was hypothesized that early-occurring events in the developmental sequence of birds are highly evolutionarily conserved (Starck, 1993), though we showed that early development might be

delayed in species that are exposed to extreme environmental conditions. Also, it was reported that differences in the growth rates of some traits, including the blastoderm, might already be discernable at the onset of avian embryogenesis (Nagai et al., 2011; Sellier et al., 2006). Beyond these exceptions, the use of model species, such as chicken and quail, as proxy references for early development in distantly related species is well justified. As supported by our comparisons of developmental sequences of chicken against other model avian species. Even so, there are slight differences in developmental rates of quail, chicken, and goose (Sellier et al., 2006). Thus, further clarifying spatial and temporal differences in avian morphogenesis, even in closely related species, remains crucial to experiments in developmental biology (Dobrevá et al., 2021). For example, quail features an unusually shaped nucleolus that permits differential staining of cells when transplanted to chick tissue, i.e. quail-chick chimeras (Lwigale & Schneider, 2008). In quail-duck chimeras, mechanisms that underlie morphological differences between these species are perhaps easier to discern, because these species differ in growth rate and incubation duration (Lwigale & Schneider, 2008). As a result, the use of the quail-duck chimera system has proven valuable in exposing the mechanisms that determine craniofacial variation in these lineages (Schneider, 2018). It would be intriguing to discover additional temporal and structural differences as more species are sampled across the avian tree of life. An open question concerns the degree to which diverse species distributed across the altricial-precocial spectrum vary in the timing of organogenesis (Blom & Lilja, 2005; Olea et al., 2016; Starck & Ricklefs, 1998). Such analyses are beyond the scope of the present paper, but we encourage researchers to incorporate embryological data described herein with comparative phylogenetic analyses on the evolution of the altricial-precocial spectrum. Already, it was shown that the total duration of embryogenesis is truncated in the altricial zebra finch (*Taeniopygia guttata*), though the sequence of developmental events is seemingly conserved relative to the precocial chicken (Hemmings & Birkhead, 2016). In agreement, the developmental character sequences of zebra finch and chicken were highly concordant in our study.

Model avian species have proven highly useful in the design of assays aimed at exposing the molecular mechanisms that guide tissue construction and pattern formation in embryos (Bronner-Fraser, 2008; Mason, 2009; Schoenwolf, 1999; Wolpert, 2004). In a landmark study, chicken embryos were used to optimize *in situ* hybridization assays that were subsequently used to trace gene expression changes associated with beak morphological differences among Darwin's finches (Abzhanov et al., 2004). Morphogenetic events observed during beak development in Darwin's finches were further validated in chicken and duck embryos (Abzhanov et al., 2004; Wu et al., 2004). Similarly, chicken embryos were used as a reference in experiments that revealed the cellular mechanisms of limb reduction in the emu (Young et al., 2019). This study followed comparative embryological assays that previously hinted at a slowdown in the outgrowth of the forelimb buds in emu embryos (Nagai et al., 2011).

5 | DEVELOPMENT UNDER DOMESTICATION

Pinpointing heterochronic shifts in ontogeny could yield additional insights into the potential for domesticated organisms to undergo an evolutionary change in human-controlled environments. It was recently shown that, within *Gallus gallus*, the initial processes by which embryos are assembled remain canalized, and thus parameters that later control relative trait dimensions are probably more likely to undergo change during the evolution of domesticated breeds (Nuñez-León et al., 2021). Because changes to early tissue differentiation processes would most likely induce lethal phenotypes, early development in vertebrate embryos tends to be conserved (discussed in Galis & Metz, 2001). Thus, universally shared developmental constraints also apply to avian evolution in human-controlled environments, even if human-assisted breeding favors viable offspring with potentially maladaptive traits (Nuñez-León et al., 2019; Nuñez-León et al., 2021). Maladaptive forms can be clearly observed in domesticated forms. For example, selective breeding for rapid growth may generate ascites and skeletal deformities in broiler chickens (Julian, 1998). In this sense, domestication can be viewed as an experiment that provides insights into selective processes that may not be fully appreciated in nature, particularly in vertebrate animals. As such, domestication as a whole can be thought of as a model system for the extended evolutionary synthesis (Zeder, 2017). In support of this framework, poultry scientists have made key contributions by describing the chronology of developmental events that are otherwise challenging to document in wild species (Brand et al., 2014, 2017; Dupuy et al., 2002; Gefen & Ar, 2001; Lumsangkul et al., 2018; Malecki et al., 2005; Sellier et al., 2006; Toledo Fonseca et al., 2013). These studies are highly informative in understanding how development may vary at the intraspecific level and are valuable to future research on natural populations (e.g., Hemmings & Birkhead, 2016).

Domesticated species are well suited for future studies that disrupt inductive tissue interactions via, for example, gene-editing technologies. By examining the resulting phenotypic variances and number of viable offspring, gene editing may permit biologists to robustly test the hypothesis that early embryonic development is under strong stabilizing selection and thus late-occurring developmental events are more amenable to undergoing adaptive change. Along these lines, the growth-dominated period of development can be considered a critical window for the phenotypic diversification of birds. It is now well understood that limb morphological differences that define avian diversity are best appreciated during this period (Cubo & Arthur, 2001; Faux & Field, 2017; Feduccia & Nowicki, 2002; Wang & Clarke, 2014). In domesticated species, exaggerated forms arise via altered growth processes (late in development) that are not necessarily accompanied by major rearrangements in the sequence of morphological characters (Alberch & Blanco, 1996). Crucially, molecular assays are of critical importance because they may reveal changes in cell proliferation processes that cannot be discerned by examining external morphological differences between species, for example, limb growth deceleration in emu relative to chicken (Young et al., 2019).

6 | DOMESTIC SPECIES AND THE FUTURE OF COMPARATIVE AVIAN EMBRYOLOGY

The taxonomic breadth of avian species sampled in comparative embryological studies warrants expansion (Flores-Santin et al., 2021), though this may prove challenging owing to conservation concerns and variable life history characteristics of species. Nonetheless, the stages for chicken embryos of Hamburger and Hamilton (1951) were recently used as reference points to statistically predict (using regression models) the duration of developmental phases in diverse species in which data for the corresponding developmental characters were missing (Cooney et al., 2020). A similar approach was employed to estimate ages in a rare series of kiwi embryos (Prier et al., 2013). Future studies may need to rely on such creative approaches, as well as emerging technologies that may permit the efficient and noninvasive (*in ovo*) characterization of embryonic features in natural and laboratory settings (Freemeyer et al., 2018; Henning et al., 2011; Winkens et al., 2021). We recommend the employment of modern visualization and quantitative tools coupled with the targeted sampling of late developmental stages that display lineage-specific morphological traits. This approach has already proven fruitful in illuminating the genetic underpinnings of beak morphology during the development of various finch lineages (Abzhanov et al., 2004; Fritz et al., 2014; Mallarino et al., 2012).

Similar to mammals (Parsons et al., 2020), should we expect mechanisms that generate species-specific morphological differences at the macroevolutionary level to be mirrored intraspecifically? This may be the case under chicken domestication (Nuñez-León et al., 2021). Using the chicken embryo as a model, it would be worth examining the extent to which genetic costs of domestication (see Makino et al., 2018; Moyers et al., 2018), or even the transgenerational epigenetic inheritance of traits (see Guerrero-Bosagna et al., 2018), have influenced the evolution of avian ontogenies. Comparing the tolerance to environmental fluctuation in domesticated versus wild species is also another promising line of research. Recent broad-scale macroevolutionary comparisons have shown that ecological adaptation has influenced the timing of key developmental phases in avian evolution (Cooney et al., 2020). In addition, whether temperature-sensitive plasticity in the onset of gastrulation and subsequent growth incurs fitness consequences remains unclear (Malecki et al., 2005; Olson et al., 2006). How intraspecific geographic variation in life-history traits relates to embryology could also be further investigated (Cooper et al., 2011). These and many other questions could be addressed by using domesticated species as a reference to guide field and laboratory experiments and thus move knowledge of avian phenotypic evolution forward. As such, we hope that our discussion of the presently available comparative embryological data stimulates further exploration of the developmental processes that underlie patterns of morphological diversity in birds.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

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Data are available as Supporting Information.

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SUPPORTING INFORMATION

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

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