

Chapter 7

Tooth vs. Beak:

The Evolutionary Developmental Control of the Avian Feeding Apparatus

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ABSTRACT

Recent discoveries of exquisitely preserved nonavian and avian theropod dinosaurs have not only prompted studies of theropod tooth morphologies, but have also provided information about the origin and early evolution of avian beaks. Recent studies on beak morphologies and morphogenesis in Darwin's finches have greatly improved our understanding of how avian beaks adapt to various ecological niches, but the question of how birds lost their teeth during the course of evolution has long been debated. Evolutionary developmental experiments performed on extant bird embryos bridge the gap between paleontological and neontological evidence, suggesting that the avian beak could have originated through heterochronic truncation of odontogenesis over evolutionary time. Here, we systematically review independently evolved regional and complete edentulism present in nonavian and avian theropod dinosaurs, and suggest that the tooth-reduction processes of different jaw bones are likely to be independently controlled. Through reviewing the recent advances of molecular regulations involved in tooth and avian beak morphogenic processes, we suggest that several molecules regulating the development of the avian beak also mediate the growth of keratinous rhamphothecae, and the divergence of odontogenic signalling pathways are likely to have accounted for both of these processes.

INTRODUCTION

Food is the main source of energy for the survival of animals. Therefore, the mechanisms by which food is ingested (feeding modes) play important roles in shaping animals' developmental patterns, morphogenetic processes, behaviors, and reproduction through their effects on metabolism (Temeles et al., 2010). Despite various feeding modes, the feeding apparatuses are relatively conserved among different clades of animals: most jawed vertebrates feed through teeth or beaks (Louchart and

Viriot, 2011), while other mechanisms for feeding account for less than 1% of the diversity of feeding apparatuses of extant jawed vertebrates (Davit-Béal et al., 2009; Louchart and Viriot, 2011), including baleen (e.g., mysticete whales), sticky tongues (e.g., toads), and mouthparts designed for suction (e.g., seahorses). Note that throughout this review, we define "beak" as the edentulous, rigid bony mouthpart of all vertebrates that is used for eating, preening, fighting, etc., and the term "rhamphotheca" refers to the keratinous sheath that covers the bony beak.

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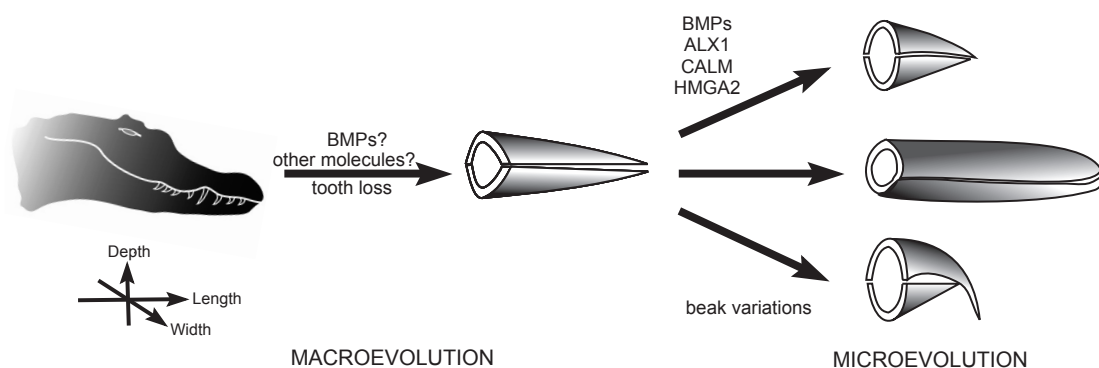


FIG. 1. Macroevolution and microevolution of avian beak from toothed ancestor's snout. The avian beak is inferred to have evolved from the snout of toothed nonavian dinosaurian ancestors through alterations to the signaling pathways involving bone morphogenetic proteins (BMPs) and other molecules. BMP, ALX homeobox protein 1 (ALX1), calcium-modulated protein (CALM) and high-mobility group AT-hook 2 (HMGA2) are all important molecules that regulate the diversity of beak shapes. Not to scale.

Birds account for almost 99.9% of extant beaked vertebrates (Meredith et al., 2014), and the remaining 0.1% are chelonians (Rhodin et al., 2017) and a few mammals (Thomas, 1889; Green, 1937; Manger et al., 1998; Musser and Archer, 1998; Davit-Béal et al., 2009). Avian beaks have many functions including preening, fighting, and courtship, in addition to feeding (Gill, 2006). Although they vary significantly in size, shape, curvature, and color, avian beaks share similar architectures: a thin keratinized epidermal layer, known as the rhamphotheca, covers the underlying bony bases in both upper and lower jaws (Gill, 2006). This prototype is highly adaptable as evidenced by a high degree of variation in beak function and morphology (Gill, 2006). The adaptability of the beak has been a major contributing factor in birds' successful adoption of various dietary and ecological niches (Mallarino et al., 2011; Bhullar et al., 2015).

In 1859, Darwin inferred the rapid evolution of avian beaks in response to environmental changes in *The Origin of Species* (Darwin, 1859). Only two years later, the discovery of *Archaeopteryx* skeletons (especially the London and Berlin specimens) demonstrated that the ancestor of modern birds was toothed (Owen, 1863a; 1863b; Evans, 1865; Dames, 1884; Howgate, 1984), raising the question of how the avian

beak originated. Since then, the evolution and morphogenesis of the avian beak has attracted many biologists (Abzhanov et al., 2004; Podos and Nowicki, 2004; Wu et al., 2004a; Abzhanov et al., 2006; Wu et al., 2006; Genbrugge et al., 2011; Mallarino et al., 2011; Lamichhaney et al., 2015; Lamichhaney et al., 2016). While the diversity of extant birds provides an opportunity to understand the morphogenesis and microevolution of the beak (Abzhanov et al., 2004; Wu et al., 2004b; Wu et al., 2006; de Leon et al., 2010), the question of how beaked extant birds evolved from toothed ancestors has been poorly understood (Heilmann, 1927; Dilger, 1957; Zhou et al., 2009; Meredith et al., 2014). The recently discovered ontogenetic transition from tooth to beak in a Jurassic ceratosaurian theropod *Limusaurus inextricabilis* has shed new light on this question and transformed our understanding of the evolutionary origins of beaks (fig. 1; Wang et al., 2017b).

Here, we review the debate over the evolutionary origin of avian beaks, and comment on recent research advances that combine paleontological evidence with neontological experimental results. In the following two sections, we will review the molecular basis of tooth and beak development, respectively. In the fourth and the fifth sections, we will review the independently

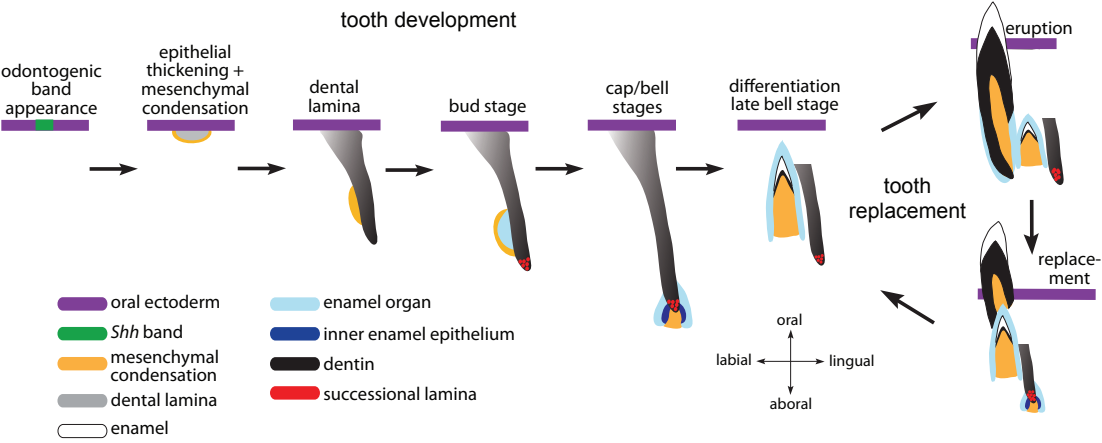


FIG. 2. Schematic drawing showing tooth developmental and replacement processes of archosaurs (modified from Richman and Handrigan, 2011; and Wu et al., 2013). Not to scale.

evolved instances of regional and complete edentulism in nonavian and avian theropod dinosaurs, respectively. The hypotheses of the evolutionary origin of avian beaks will then be briefly surveyed, from the classic paleontological hypotheses to recent evidences derived from the evolutionary developmental biology experiments. In the last section, we will briefly discuss the evolutionary significance of the avian beak, and comment on some recent advances clarifying the relationships between the emergence of the beak and craniofacial evolution in birds.

BIOLOGY OF TOOTH DEVELOPMENT AND REPLACEMENT

As an ectodermal organ, the development of teeth is regulated by sequential and reciprocal interactions between the epithelium and underlying mesenchyme (Thesleff, 2003). Although size, shape, and tooth count may vary among different taxa, the basic molecules and early signaling pathways of odontogenesis are essentially conserved across vertebrate phylogeny (Huysseune and Sire, 1998; Chen et al., 2000; Berkovitz and Shellis, 2016).

Knowledge of the molecular basis of tooth development comes primarily from the mouse (Thesleff, 2003). Prior to the initiation of tooth

formation, the tooth-forming region is marked by a band expressing *Shh* (sonic hedgehog) and *Pitx2* (paired-like homeodomain transcription factor 2) (Jernvall et al., 2000; Cobourne et al., 2004; Fraser et al., 2006; Buchtová et al., 2008; Fraser et al., 2009; Smith et al., 2009; Richman and Handrigan, 2011), which are required for tooth formation (fig. 2; Chen et al., 2000). When tooth formation is initiated, the oral epithelium thickens and expresses BMPs (bone morphogenetic proteins) and FGFs (fibroblast growth factors) that lead to condensation of the oral mesenchyme (fig. 1), which activate a set of mesenchymal signals that then act on the epithelium and mediate the formation of placodes at each future tooth position (Thesleff, 2003; Jussila and Thesleff, 2012). During the tooth bud stage, the epithelium folds and invaginates into the underlying mesenchyme. This is followed by the cap stage during which the epithelium extends further into the condensing mesenchyme and wraps itself around the mesenchyme. The enamel knot, another signaling center that expresses multiple signaling molecules including BMPs, FGFs, WNT, and SHH that induce reciprocal signals from the mesenchyme, appears (Thesleff, 2003; Jernvall and Thesleff, 2012). Subsequently, the inner enamel epithelium and the mesenchyme differentiate into ameloblasts and odontoblasts at

the epithelial-mesenchymal interface, secreting enamel and dentin matrices, respectively (Thesleff, 2003; Jernvall and Thesleff, 2012; Jussila and Thesleff, 2012).

Like other ectodermal organs such as hair, scales, and feathers, teeth undergo cyclic regeneration through which a new tooth is produced with possible phenotypic changes occurring during regeneration (Streelman et al., 2003; Jernvall and Thesleff, 2012; Wu et al., 2013). The maintenance of dental regeneration is made possible by a cluster of odontogenic stem cells (Huyseune and Thesleff, 2004; Whitlock and Richman, 2013; Wu et al., 2013; Tsai et al., 2016). Although cells with stem-cell properties were also identified in mouse molar dental pulp, follicle, and epithelium, they are used for continual tooth growth, and are not able to regenerate a new tooth after a tooth is lost. This results in a single generation of molars (Huang et al., 2009). For example, mouse incisors can grow continuously, as they are maintained by stem cells enriched at the labial incisor cervical loop (Harada et al., 1999; Renvoisé and Michon, 2014; Whitlock and Richman, 2013), but cannot regenerate the incisor if it is lost. Therefore, the mouse is not an ideal model for studying the cyclical tooth replacements in polyphyodonty vertebrates such as dinosaurs.

The dental lamina is an invagination of the oral epithelium into underlying mesenchyme, and its free aboral end is enriched in odontogenic stem cells that are highly proliferative (Smith et al., 2009; Wu et al., 2013). These stem cells form the successional lamina where the subsequent generations of teeth are differentiated (Huyseune, 2006; Jussila and Thesleff, 2012; Jussila et al., 2014). Therefore, the ability of the dental lamina to continuously differentiate into successional laminae is essential for the maintenance of tooth replacement (fig. 2). In taxa whose teeth can be replaced for many generations throughout life (polyphyodonty), such as reptiles and fishes, the successional lamina exists throughout life (Huyseune, 2006; Zahradnick et al., 2012; Wu et al., 2013). Most

mammals are diphyodont, they only replace their teeth once (Luo et al., 2004), and the successional lamina degenerates following the first tooth replacement (Järvinen et al., 2009; Richman and Handrigan, 2011; Buchtová et al., 2012; Buchtová et al., 2013; Whitlock and Richman, 2013; Dosedělová et al., 2015). Taken together, the existence of the successional lamina is directly related to the maintenance of tooth replacement (Jussila et al., 2014).

The frequency of tooth replacement depends on the division cycles of the odontogenic stem cells (Wu et al., 2013), which can be different among various vertebrate taxa and different ontogenetic stages of the same species. For instance, the primary teeth of mammals may be replaced at an interval of several months to decades (Berkovitz and Shellis, 2018), and in most cases their tooth family units consist of only one functional tooth. In contrast, some taxa (e.g., Chondrichthyes and Actinopterygii) can replace a whole set of teeth within a few days such that several replacement teeth can be found in the tooth family units (Peyer, 1968; Mochizuki and Fujui, 1983; Berkovitz and Shellis, 2016). Therefore, the replacement frequency of a given tooth position can be discerned from the exact tooth count of that tooth family unit (Wu et al., 2013).

The pattern of tooth replacement along the tooth row also varies among vertebrate taxa, which is more obvious in vertebrates with thecodonty as opposed to pleurodonty or acrodonity. In mammals, tooth replacement is highly regionally specific, with incisors (mesial teeth) replaced earlier than other antemolars (Berkovitz and Shellis, 2018). Much attention has been paid to mammal premolar replacement. Teeth are alternatively replaced in mammallike cynodonts with indeterminate cranial growth patterns (e.g., *Pachygenelus*) (Luo et al., 2004). The early-diverging clades of crown mammals have a rostrocaudally sequential replacement of premolars, which is the reverse alternate pattern of some, if not all, early-diverging trechnotherians (Luo et al., 2004). The replacement of premolars in most

extant placentals is also sequential, either rostro-caudally (e.g., ungulates and carnivores) or caudo-rostrally (e.g., some insectivores) (Luo et al., 2004). In extant metatherians, only the ultimate premolar on each jaw quadrant is replaced (Cifelli and Muizon, 1998; Rougier et al., 1998; Luo et al., 2004). Therefore, the tooth replacement pattern has undergone several reversals and changes across the evolutionary history of mammals.

Most nonmammalian vertebrates are polyphyodont (Edmund, 1960), with early studies that address tooth replacement in these vertebrates dating to near the turn of the 19th century (Röse, 1893a; 1893b; Harrison, 1901; Woerdeman, 1919a; 1919b; 1921a; 1921b). These works identified an alternating tooth replacement pattern in nonmammalian vertebrates such that teeth arise and replace alternately at odd and even positions to form a wave. This pattern was defined as *Zahnreihen*, or “replacement waves,” by Woerdeman (1921b; Edmund, 1960). A *Zahnreihen* consists of a series of adjacent teeth from different tooth family units that are roughly at the same developmental stage.

Two theories have been proposed to explain the alternating pattern of tooth replacement: one is the “wave-stimulation theory” and the other refers to a “zone of inhibition” (Richman and Handrigan, 2011). The “wave-stimulation theory” is based primarily on observations and is thus somewhat speculative, emphasizing that tooth growth and replacement are controlled by periodically expressed stimuli in the dental mesenchyme that pass distally from the mesial end of the tooth row (Edmund, 1960; 1962). Accordingly, new teeth are formed along the tooth rows in the same direction that the stimuli pass through, and the alternating tooth-replacement patterns are produced by the time intervals between multiple successive *Zahnreihen*s coexisting at a given time (Edmund, 1960). While this theory is consistent with observations of replacement in some taxa (Cooper et al., 1970; Ziegler, 1971; Bolt and Demar, 1975; Hanai and Tsuihiji, 2019; He et al., 2018), it must be acknowledged that not all animals replace teeth

in anteroposterior or posteroanterior orders and intraspecific order reversal is not rare (Miller and Radnor, 1970). The validity of this theory has been tested in both alligators and lizards through surgeries removing teeth and paradentium, and the results suggest that the recovery of teeth is not required for subsequent tooth initiation (Osborn, 1970; 1977; Westergaard and Ferguson, 1987, 1990; Buchtová et al., 2013; Brink et al., 2018). In some taxa, *Zahnreihen* may exist in immature individuals, but it has been suggested they are gradually broken down with increasing maturity (Miller and Radnor, 1970; Buchtová et al., 2013). This is probably related to cranial growth patterns as tooth replacement patterns are necessarily modified by cranial growth.

The theory of a “zone of inhibition” asserts that a developing tooth secretes some inhibitors into the surrounding paradentium, depressing the odontogenic process in neighboring tooth positions, and the growth of the neighboring teeth can start only after the predecessor between them stops growing (Osborn, 1971). The potential inhibitors have not been identified (Whitlock and Richman, 2013), yet surgical experiments in reptiles have demonstrated that tooth replacement is independently controlled by tooth family units rather than a global signal transmitting along the tooth rows (Brink et al., 2018). This is consistent with the observable variability in dental replacement patterns. Taken together, the available evidence suggests there is no clear common rule of vertebrate tooth-replacement patterns. The independent control of tooth replacement could be a prerequisite for regional tooth variation, replacement, and reduction in many vertebrates (Brink et al., 2018).

MOLECULAR BASIS FOR AVIAN BEAK MORPHOGENESIS

Avian beaks are formed from multiple facial prominences, each of which has a neural crest-derived mesenchymal core that is covered externally by an epithelial layer of ectoderm (Francis-West et al., 1998; Helms and Schneider,

2003; Richman and Lee, 2003). The upper beak comprises five prominences, including a fused frontonasal mass and paired maxillary and lateral nasal prominences (Romanoff, 1960; Wu et al., 2006). The lower beak is formed from two highly proliferating sites (one on each side) that are later fused into a single mandibular prominence (Romanoff, 1960; Wu et al., 2006). All prominences are coordinated with proportional sizes to produce a species-specific beak morphology (Abzhanov et al., 2004; Wu et al., 2004a; Wu et al., 2006). Transplantations of presumptive neural crest cells between quail and duck produced chimeric beak phenotypes, demonstrating that interspecific variations of beak morphogenesis can be guided by these cells (Schneider and Helms, 2003).

Beak morphogenesis consists of three major processes: the outgrowth of beak primordial mesenchyme (skeletal basis), the development of integument inside the oral cavity (oral mucosa) and the growth of the external keratinous sheath covering the snout (rhamphothecae). In chickens, beak growth starts by the end of embryonic day 5 (E5) and is marked by the initiation of the fused mandibular processes elongation (Romanoff, 1960). Later, the mesenchymal cell proliferation increases in the frontonasal mass, resulting in relatively faster growth of the upper beak than that of the lower beak (Romanoff, 1960). The mesenchymal cell proliferation centers are species specific, which constitute the structural basis of the species-specific beak morphotypes. Both chicken and duck have two mesenchymal cell proliferation centers in the frontal mass by E5, but they are fused at the subsequent developmental stages in chicken while they remain separated in duck (Wu et al., 2004a, 2006). It is unclear how this difference would give rise to the interspecific differences of beak morphologies.

Beak morphogenesis is regulated at both genomic and gene expression levels. At the genomic level, *ALX1* (ALX homeobox protein 1) encodes a transcription factor affecting craniofacial development demonstrated to be associated with beak shape diversity in Darwin's finches,

while beak size is primarily controlled by a genomic region containing *HMGA2* (High-mobility group AT-hook 2) (fig. 1; (Lamichhaney et al., 2015, 2016). At the gene expression level, a recent study suggests that increased spatiotemporal activity of FGF and WNT could produce a completely fused premaxilla-dominated avian beak in contrast to the ancestral archosaurian forms that are characterized by paired abbreviated and rounded premaxillae (Bhullar et al., 2015). The interspecific morphological differences of avian beaks can also be modulated by BMP4, CALM (calcium-modulated protein, or calmodulin), FGF8, and WNT, which affect the proliferation activity of facial prominences (Abzhanov et al., 2004; Wu et al., 2004a, 2006). The information collectively suggests the emergence of a morphological novelty can be produced through manipulating the expression patterns of existing signals in addition to creating new regulatory networks (Wu et al., 2006; Bhullar et al., 2015).

Development of the rhamphotheca in extant birds is initiated by keratinization of epithelium from the anterior tips of both the premaxillae and dentaries at embryonic day 7 (E7) (Romanoff, 1960; Wu et al., 2006; Wang et al., 2017a), which then proceeds posteriorly to form complete horny sheaths covering the jaws (Wu et al., 2006; Hieronymus and Witmer, 2010). Avian rhamphothecae contain both alpha and beta keratins. Experiments show proper interactions between these keratins are necessary for normal formation of keratinous epidermal appendages (Wu et al., 2015). Variation in the spatial organization and interaction of alpha and beta keratins likely contribute to the morphological and structural diversity of avian beaks, but our current knowledge is limited to the chicken.

A recent study shows several molecules that regulate the morphogenesis of the beak, such as BMP4 and Noggin, are also involved in the growth of rhamphotheca (Wang et al., 2017a), and the overexpression of BMP4 in chicken embryos can produce rhamphotheca hypertrophy and/or ectopic beak keratin growth (Wang et al., 2017a). Although this has been suggested as a possible

cause of odontogenic truncation (Wang et al., 2017a), the detailed signaling transductions that mediate the early truncation of odontogenesis, beak morphogenesis, and development of the keratinous rhamphotheca remain unclear.

TRACKING BEAK EVOLUTION IN NONAVIALAN DINOSAURS

Extant birds are toothless, but most of their nonavian and avian ancestors were toothed, suggesting the origin of rhamphotheca and tooth reduction are coupled (Wang et al., 2017a). Beaks evolved independently in ornithischians, sauropodomorph, and theropod dinosaurs, and appeared in many theropod clades in parallel with their appearance in birds (Wang et al., 2017a), with each independent evolution of a beak accompanied by some form of tooth reduction. In this section, we primarily document the presence of rhamphothecae with tooth reductions in theropod dinosaurs (fig. 3). Three types of tooth reduction are considered: (1) reduction of tooth number due either to the simplified shortening of the tooth row or that of the tooth-bearing elements; (2) reduction of tooth generations and the decrease of tooth replacement rate; and (3), reduction of tooth size compared to close relatives. Each form of reduction often occurs in conjunction with one or both of the others. We emphasize that all conditions discussed in this review are based on known specimens, and other conditions cannot be ruled out given the fact that new specimens continue to be discovered.

CERATOSAURIA: Though ontogenetic tooth reduction is common in extant vertebrates (Wang et al., 2017b), it is very rarely preserved in the fossil record. Ontogenetic reduction leading to edentulous adults has been reported in *Limusaurus* (Wang et al., 2017b), representing the only known example of edentulism in ceratosaurs. The youngest *Limusaurus* (presumed hatchlings) have one premaxillary, eight maxillary, and 12 dentary teeth on each side, whereas all teeth have been gradually lost, accompanied by a remodeling of the alveoli during the first

two years of postnatal growth (Wang et al., 2017b). The presence of a single posteriorly positioned premaxillary tooth and an anteriorly edentulous dentary in some of the youngest *Limusaurus* suggests the tooth reduction of the upper jaw started from the anterior tip of the premaxilla (Wang et al., 2017b). The presence of only a single replacement tooth in the largest *Limusaurus* hatchlings suggests the cessation of normal tooth replacement is probably an indicator of tooth reduction (Wang et al., 2017a).

ORNITHOMIMOSAURIA: The evolution of ornithomimosaurians is characterized by the loss of dentition (Makovicky et al., 2004). Early-diverging ornithomimosaurians have teeth (Perez-Moreno et al., 1994; Ji et al., 2003; Kobayashi and Barsbold, 2005; Choiniere et al., 2012), but regional edentulism is present in all known toothed ornithomimosaurians (Wang et al., 2017a). Teeth are present in all known dentigerous elements of *Nqwebasaurus* and all elements of *Pelecanimimus* (Perez-Moreno et al., 1994), but the maxillary tooth row is shorter than that of the dentary in both taxa, and in *Nqwebasaurus* the maxillary tooth row ends anterior to the antorbital fenestra (Choiniere et al., 2012). In *Harpymimus* and *Shenzhousaurus*, teeth are restricted to the anterior end of the dentary and neither the premaxilla nor maxilla bear teeth (Ji et al., 2003; Kobayashi and Barsbold, 2005). A series of impressed neurovascular grooves characterizes the medial aspect of the anterior end of the dentary in *Harpymimus* suggesting this region may have also been covered by a rhamphotheca (Kobayashi and Barsbold, 2005). Besides the Early Cretaceous ornithomimosaurians, all known Late Cretaceous ornithomimosaurians have beaks that were covered with rhamphothecae (Kobayashi et al., 1999; Norell et al., 2001a; Kobayashi and Lü, 2003; Lee et al., 2014a). These data suggest the loss of dentition in ornithomimosaurians proceeds from posterior to anterior (Choiniere et al., 2012) and the edentulism of the upper jaw was achieved prior to that of the lower jaw. Microtomographic data of immature ornithomimosaurians are neces-

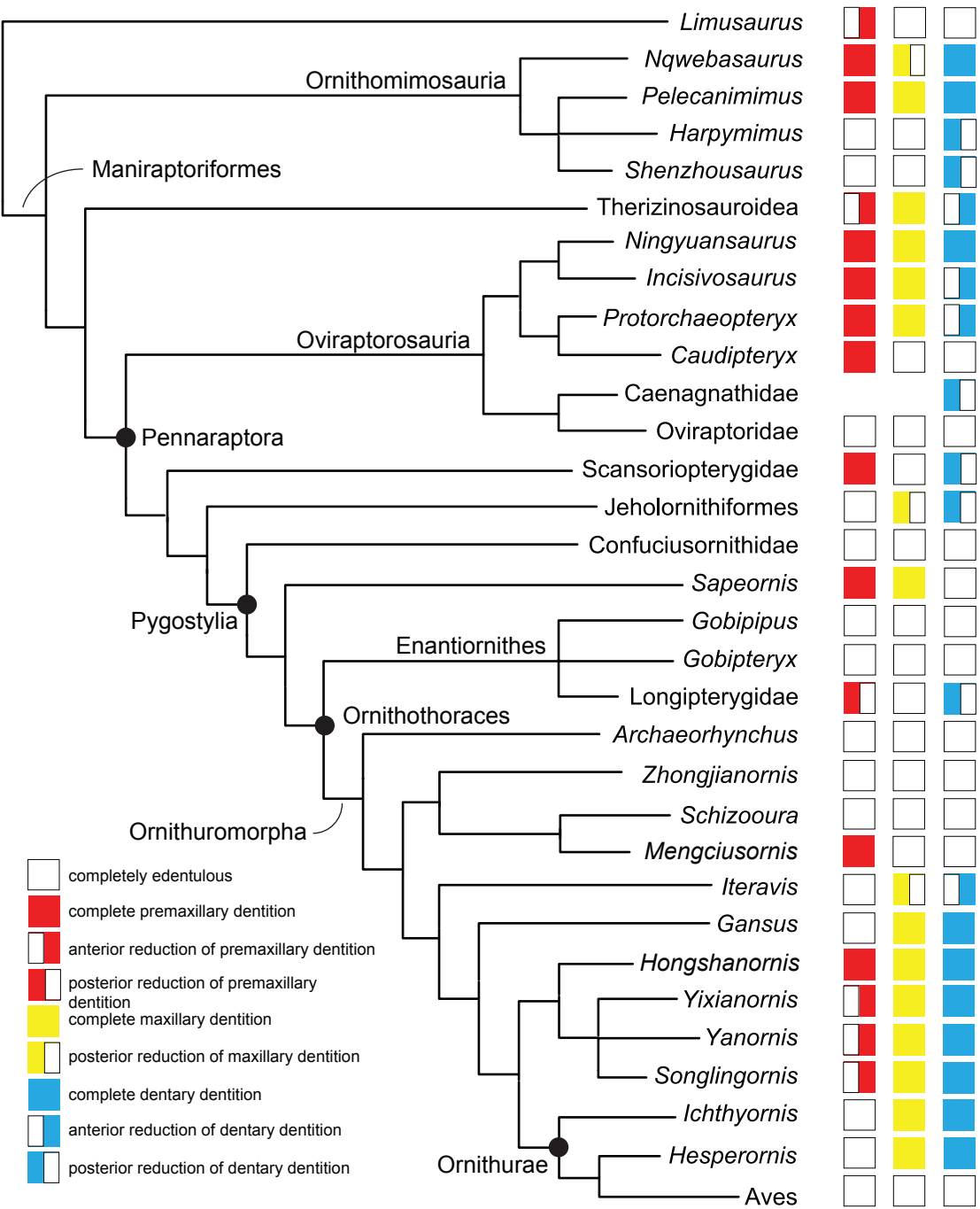


FIG. 3. Simplified phylogenetic hypothesis of theropod dinosaurs showing the tooth-reduction patterns in different clades (modified from Wang et al., 2014a, 2017a, 2019; and Zheng et al., 2018).

sary to investigate whether the evolutionary tooth reduction in this clade is heterochronically controlled.

THERIZINOSAURIA: The early-diverging therizinosaurians *Falcarius* and *Eshanosaurus* have fully toothed dentaries (Xu et al., 2001; Zanno, 2010). *Falcarius* also has maxillary teeth, but whether teeth are present in premaxillae is unknown (Zanno, 2010). The premaxillae and the anterior end of the dentaries are edentulous in all known therizinosauroids including embryos (Clark et al., 2004; Kunderát et al., 2008; Lautenschlager et al., 2013), but the dentary's edentulous region is shorter in *Jianchangosaurus* than that in other therizinosauroids (Pu et al., 2013a).

OVIRAPTOROSAURIA: Similar to ornithomimosaurians, oviraptorosaurians are also characterized by a progressive loss of teeth throughout their evolutionary history (Osmólska et al., 2004; Wang et al., 2017a; Wang et al., 2018). All known noncaenagnathoid oviraptorosaurians are toothed. Early-diverging oviraptorosaurians including *Ningyuansaurus* (Ji et al., 2012), *Protarchaeopteryx* (Ji et al., 1998), and *Incisivosaurus* (Xu et al., 2002) have teeth in all dentigerous elements, but *Incisivosaurus* and *Protarchaeopteryx* start losing teeth from the anterior end of dentaries, and their maxillary and dentary teeth are remarkably reduced both in size and number relative to those in *Ningyuansaurus* (Xu et al., 2002; Balanoff et al., 2009). *Caudipteryx* has four premaxillary teeth, but its maxilla and dentary are edentulous (Ji et al., 1998; Zhou et al., 2000), indicating the dentary teeth would have been lost first in early-diverging oviraptorosaurians followed by maxillary teeth (fig. 3).

Small premaxillary teeth were reported in an as of yet undescribed specimen of the caenagnathid *Avimimus* (Watabe et al., 2000), and remain the only report of upper dentition in Caenagnathoidea, though some have cast doubt on this observation (Gregory Funston, personal commun., 2019). Structures that have been interpreted (Wang et al., 2018) as vestigial alveoli are present in dentaries in almost all known specimens of caenagnathids (Currie et al., 1993; Xu et

al., 2007; Longrich et al., 2013; Funston and Currie, 2014; Lamanna et al., 2014; Bell et al., 2015; Tsuihiji et al., 2015; Yao et al., 2015; Tsuihiji et al., 2016). This suggests that dentary teeth were present at some point during the ontogeny of caenagnathids, and an ontogenetic tooth reduction comparable to that in *Limusaurus* is also present in caenagnathid oviraptorosaurians (Wang et al., 2017a, 2018). In small specimens of caenagnathids, posterior vestigial alveoli are smaller than the anterior ones (Wang et al., 2018), and the anterior tip of the dentary is edentulous as in *Incisivosaurus* and *Protarchaeopteryx*. This suggests the ontogenetic tooth reduction occurred from both the anterior and posterior ends of the dentary in caenagnathid oviraptorosaurians.

Through investigating histological sections of dentaries from a growth series of Caenagnathidae and prior studies of the ontogeny of interdental tissues, Funston et al. (2020) argued that the lingual grooves and ridges of caenagnathid dentaries that were interpreted as vestigial alveoli and interdental septa respectively (Wang et al., 2018) cannot have previously housed teeth during caenagnathid ontogeny. We agree with the histological observations of Funston et al. (2020), but we disagree that they negate a hypothesis of ontogenetic edentulism in Caenagnathidae and will respond to their critiques elsewhere.

All known oviraptorid dinosaurs are completely edentulous, including embryos (Norell et al., 1994, 2001b; Wang et al., 2016), and none bear any dentary structures suggestive of ontogenetic edentulism (fig. 3).

SCANSORIOPTERYGIDAE: Teeth are restricted to the premaxillae and anterior dentary in all known Scansoriopterygidae including *Epidendrosaurus* (Zhang et al., 2002) and *Yi* (Xu et al., 2015), but *Epidexipteryx* probably has maxillary teeth as well (Zhang et al., 2008a). The presence of more complete dentitions in Early Cretaceous oviraptorosaurians, Jurassic avialans, and deinonychosaurians indicates the condition in Scansoriopterygidae is an apomorphic reduction of the posterior dentition (Wang et al., 2017a).

TRACKING BEAK EVOLUTION IN THE EARLY EVOLUTION OF BIRDS

JEHOLORNITHIFORMES: All known specimens of *Jeholornis* lack premaxillary teeth (Zhou and Zhang, 2002; O'Connor et al., 2012; Zhou, 2015). Although teeth were initially described as absent from the upper jaws in *J. prima* (Zhou and Zhang, 2002; 2003a; O'Connor et al., 2012), a single tooth and an empty alveolus are present in the maxilla of *J. palmapenis* (O'Connor et al., 2012). An undescribed specimen of *Jeholornis* preserves a single maxillary tooth (Wang et al., 2017a), while another specimen (STM 3-32) has two maxillary teeth (Zhou, 2015). All known maxillary teeth of *Jeholornis* are restricted to the anterior portion of the maxilla below the ascending process. Teeth in the lower jaw are restricted to the anterior extent of the dentaries. Three small teeth were reported in the dentary of the holotype of *J. prima* (IVPP V13274) (Zhou and Zhang, 2002; 2003a), whereas only two are present in IVPP V13350 (Zhou and Zhang, 2003a). The dentaries of *J. palmapenis* and a possible *J. prima* are edentulous (Ji et al., 2002; O'Connor et al., 2012; Zhou, 2015). The dentition of *Jeholornis* has been significantly reduced in comparison to all known Jurassic paravians such as *Archaeopteryx* (Zhou and Zhang, 2003a; O'Connor et al., 2012), with complete edentulism occurring first in the premaxilla, while the maxilla and dentary experienced reductions proceeding from posterior to anterior.

The variability in the dentition of *Jeholornis* suggests the possibility of an ontogenetic reduction of the dentition in this taxon (Wang et al., 2017a), but this hypothesis cannot be tested at the present time since it is not clear whether available specimens of *Jeholornis* represent a growth series of a single species, and currently no high-resolution CT images are available to verify whether alveolar vestiges are present in these specimens.

CONFUCIUSORNITHIDAE: All known confuciusornithids are completely edentulous and show clear osteological correlations of rham-

photheca, and CT images have revealed no sign of a vestigial tooth or alveolus in *Confuciusornis* (Ji et al., 1999; Zhang et al., 2008b; Wang et al., 2017a; Wang and Zhou, 2018).

SAPEORNITHIFORMES: All known *Sapeornis* specimens have premaxillary and maxillary teeth when these dentigerous element are preserved, but dentary teeth are present only in some small specimens (Zhou and Zhang, 2003b). A recent study suggests the variation of dental formula in *Sapeornithiformes* is taphonomic (Wang et al., 2017c), however no hypothesis is offered to explain the relative tendency for dentary teeth to be lost while the upper dentition is retained within alveoli. All known specimens of *Sapeornis* from the Jiufotang Formation are hypothesized to represent a growth series of a single species *Sapeornis chaoyangensis* (Gao et al., 2012; Pu et al., 2013b), and the absence of dentary teeth in some specimens suggests that teeth have been lost from this taxon through ontogenetic truncation of odontogenesis as in *Limusaurus* and caenagnathids (Wang et al., 2017a).

Currently known specimens suggest edentulism first took place in the dentary, where dentition is reduced, followed by the posterior portion of the maxilla, and the premaxilla is the area from which teeth are least likely to be lost (Wang et al., 2017c). The dentary teeth, if present, are usually accompanied by two or three empty alveolar homologs anterior to these teeth (Wang et al., 2017a). Posterior to the last dentary tooth or alveolar homologs, a series of regularly distributed foramina are present on the lingula aspect of the dentary, which internally communicate with a canal that is hypothesized to represent a closed alveolar canal (Wang et al., 2017a). These lines of evidence collectively suggest dentary teeth of *Sapeornis* are reduced from both the posterior and anterior ends of the tooth row (fig. 3). The anterior end of the lower jaw is likely to have been covered by a horny rhamphotheca, and how the remaining few dentary teeth functioned in feeding is unclear.

ENANTIORNITHES: Pengornithids have numerous small teeth preserved in all dentigerous

bones (Wang et al., 2014a; Hu et al., 2015; O'Connor et al., 2016), representing the primitive condition of Enantiornithes. Dental reductions begin in the maxilla and dentary in several enantiornithines such as *Cathayornis*, Bohaiornithidae, and Longipterygidae (Martin and Zhou, 1997; O'Connor and Dyke, 2010; Wang and Liu, 2016). Bohaiornithids can be distinguished from other enantiornithines in having anteriorly located large and robust subconical teeth (Wang et al., 2014b; Peteya et al., 2017), which probably represent functional compensation for the reduced tooth count in addition to the presence of gastroliths (Li et al., 2014). The teeth of Longipterygidae are further reduced compared to those seen in Bohaiornithidae. Large posteriorly recurved teeth are present only in the premaxilla and the anterior end of the dentary, while the maxillae are edentulous (Zhang et al., 2001; O'Connor et al., 2009; Li et al., 2012; Wang et al., 2017a). However, it is unclear whether the jaw bones of longipterygids were covered by rhamphothecae posteriorly.

Teeth are completely absent in *Gobipipus* and *Gobipteryx* (Elzanowski, 1976; Elzanowski, 1977; 1981; Chiappe et al., 2001; Kurochkin et al., 2013), representing the only known examples of edentulous enantiornithines (Zhou, 2015). *Gobipipus* is known only from embryonic specimens with edentulous jaw bones (Elzanowski, 1981; Kurochkin et al., 2013), but whether teeth are also absent in adults is unknown given the possibility of delayed tooth eruption (Wang et al., 2017d). *Gobipteryx* is known from postjuvenile specimens, and the presence of the acuminate occlusal margins of the beak and neurovascular foramina on the external surfaces of premaxilla and dentary all indicate the presence of horny rhamphothecae (Elzanowski, 1976; Chiappe et al., 2001; Wang et al., 2017a).

Teeth are also present in embryonic and neonatal enantiornithines (Sanz et al., 1997; Zhou and Zhang, 2004; Xing et al., 2017; Kaye et al., 2019). A Spanish Early Cretaceous neonatal enantiornithine bears four premaxillary teeth, at least five maxillary teeth, and eight dentary teeth (Sanz et

al., 1997). An Early Cretaceous embryonic enantiornithine from China that has been only preliminarily described bears maxillary teeth, though the tooth count in each element is unclear (Zhou and Zhang, 2004). A single premaxillary tooth has been reported in an amber embedded enantiornithine hatchling (Xing et al., 2017), though the taxonomic affinities of this specimen are impossible to determine based only on the presence of the premaxillary tooth, because all known enantiornithines have at least three premaxillary teeth except *Gobipipus* and *Gobipteryx*, as has been mentioned above. The reason for the absence of maxillary and dentary teeth in this specimen may be taphonomic, since embryonic teeth are common for both extinct and extant toothed archosaurs (Westergaard and Ferguson, 1987; Westergaard and Ferguson, 1990; Sanz et al., 1997; Wang and Zhou, 2004; Zhou and Zhang, 2004; Kunderát et al., 2008), though an independent reduction of dentition is possible.

ORNITHUROMORPHA (INCLUDING AVES): Tooth reduction patterns are fairly complicated among Ornithuromorpha. *Archaeorhynchus*, *Schizoura*, and *Zhongjianornis* are completely edentulous in known specimens (Zhou and Zhang, 2006; Zhou et al., 2009, 2012, 2013; Wang and Zhou, 2016), and their beaks are inferred to have been covered with rhamphothecae. The condition in younger ontogenetic stages of these taxa is unknown. The Early Cretaceous *Yanornis*, *Yixianornis*, and *Songlingornis* all have dentigerous premaxillae, maxillae, and dentaries (Zhou and Zhang, 2001), but premaxillary teeth of these taxa are posteriorly located and the edentulous anterior tip of their upper jaws are thus inferred to be covered by rhamphothecae (Zhou and Zhang, 2001; Zhou, 2015). In *Gansus zheni* (Liu et al., 2014), *Iteravis* (Zhou et al., 2014), *Ichthyornis*, and *Hesperornis* (Marsh, 1875), the premaxillae are edentulous while the maxillary teeth are reduced to various degrees, and a rhamphotheca is therefore inferred to have covered at least the premaxilla in these taxa. Despite the apparent absence of dentition in hongshanornithids, the identification of teeth and alveoli in both the upper and lower

jaws suggest this group is also toothed (O'Connor et al., 2010; Chiappe et al., 2014). The recently described *Mengciusornis* has four premaxillary teeth and an edentulous maxilla and dentary (Wang et al., 2019). This implies that the way ornithuromorphs reduced their dentition was more complicated than expected.

In addition to the various states of tooth reduction in premaxillae, maxillae, and dentaries, an edentulous “prementary” is present in some Ornithuromorpha (fig. 3). This intersymphyseal ossification is topologically similar to the prementary of ornithischian dinosaurs but is unlikely to be homologous with that element (O'Connor et al., 2010). Its presence is relatively common in extinct ornithurines and a likely homolog is present in Pelagornithidae (Mayr and Rubilar-Rogers, 2010), but it has been lost in all extant crown birds (Zhou and Martin, 2011; Bailleul et al., 2019). It is interesting that among ornithurines, the presence of the prementary always corresponds to the presence of anterior edentulism of the premaxillae (Zhou and Martin, 2011), and similar correspondence is also present in ornithischians. This indicates that the small triangular element anterior to the left dentary of *Mengciusornis* may not be the prementary given there are four premaxillary teeth present in this taxon (Wang et al., 2019).

All known Aves are completely edentulous throughout postnatal ontogeny, but epithelial thickenings presumably homologous to the dental lamina are temporarily present during embryonic stages in at least some taxa (Chen et al., 2000).

EVOLUTIONARY ORIGIN OF AVIAN BEAK

EARLY UNDERSTANDING OF AVIAN TOOTH LOSS

Scientific study of rudimentary avian dental structures can be traced back to the early 19th century when transiently present papillae were found in bird embryos that were suggested to be homologs of reptilian teeth (Cuvier, 1821; St. Hilaire, 1821). However, these were later discounted as dermal papillae, which are common

for integumentary derivatives and therefore were ignored by academia for quite a while (Blanchard, 1860; Gardiner, 1884; Heilmann, 1927; Harris et al., 2006).

Before the mid-nineteenth century, the public understanding of the toothlessness of birds was so ingrained that the avian affinities of the first *Archaeopteryx* skeleton (London specimen) was questioned by many in academia (Wellnhofer, 2010). Hermann von Meyer, the German paleontologist who reported the isolated feather of *Archaeopteryx* (von Meyer, 1861; von Meyer, 1862), described the London specimen as “a feathered animal which differs from our birds essentially” (Wellnhofer, 2010). Richard Owen described *Archaeopteryx* as a bird despite many features that are reminiscent of reptiles, including the clawed wings and the elongate tail (Owen, 1863a). Owen dismissed the importance of a premaxilla with teeth preserved next to the pelvis, suggesting that it came from an unknown fish (Owen, 1863a).

It was not until the discoveries of *Hesperornis*, *Ichthyornis*, and the iconic Berlin *Archaeopteryx* in 1870s that most were convinced that early birds were toothed (Marsh, 1872a; 1872b; Dames, 1884). The presence of teeth in early birds unquestionably linked the beaked extant bird to a toothed reptilian ancestor (Gegenbaur, 1863; Cope, 1867). The question of how birds originated soon became a topic of contention in the natural sciences by the end of the 19th century. Thomas Huxley extensively compared *Archaeopteryx* with other reptiles and suggested that it was much closer to dinosaurs than to any other groups of reptiles (the dinosaur hypothesis) (Huxley, 1868; 1870). Indeed, the presence of teeth in *Archaeopteryx* gave Huxley and his followers high confidence that birds evolved from dinosaurs (Seeley, 1901; Nopcsa, 1907), but none of them published on the question of how birds lost their teeth during the course of evolution.

Gerhard Heilmann was the first person who dealt with this question, but only briefly in his book *The Origin of Birds*: “the oldest birds had

teeth, but these, being no longer needed, were gradually lost, and the jaws were recovered with horny sheaths...the teeth that were lost, it would no more have been able to recover" (Heilmann, 1927: 139).

Heilmann did not answer the question of how birds lost their teeth, but crucially hypothesized that the degradation of avian teeth and the formation of beaks were coupled. In 1957, William Dilger further developed Heilmann's idea, and hypothesized that avian tooth loss was a response to weight-saving demands for the evolution of flight (Dilger, 1957). This explanation was influential for more than four decades, and influenced numerous studies of avian locomotion and/or diet (Feduccia, 1999; Zhou and Zhang, 2006; Zhou et al., 2009; Louchart and Viriot, 2011; Zanno and Makovicky, 2011; Zheng et al., 2011; Zheng et al., 2014; Wang et al., 2017c; O'Connor et al., 2018; Zheng et al., 2018). However, recent studies suggest the selection pressure favoring body mass reduction is unlikely to be a factor in the tooth reduction of early birds (Lautenschlager et al., 2013; Zhou et al., 2019).

NEO-DARWINIAN INTERPRETATIONS OF THE MACROEVOLUTION OF AVIAN BEAKS

A recent comparative genomics study consisting of extant representatives of nearly all avian orders suggested that inactivation mutations of odontogenic genes may account for the evolution of avian tooth reduction (Meredith et al., 2014). In contrast, a series of investigations suggested that early odontogenic signals are conserved in embryonic chicken (Kollar and Fisher, 1980; Chen et al., 2000; Mitsiadis et al., 2003), and a classic experiment even induced enameled dental structures through the recombination of chicken oral epithelium and mouse molar mesenchyme (Kollar and Fisher, 1980). Although this result was probably altered via contamination by mouse dental epithelium (Chen et al., 2000), rudimentary dental structures including local epithelial thickenings can be induced by replacing chick oral mesenchyme with skin mesen-

chyme or even mouse mesenchyme (Chen et al., 2000; Mitsiadis et al., 2003). These lines of evidence suggest avian oral epithelium can still respond to signals from oral mesenchyme in toothed amniotes, and mutations of odontogenic genes in extant birds alone cannot account for the evolution of avian tooth reduction. A separate study hypothesized that the arrest of tooth development in modern birds is probably due to loss of mesenchymal odontogenic signals in modern birds (Mitsiadis et al., 2003), and as reviewed above, avian evolution is marked by partial tooth reductions, demonstrating that other factors contributed to avian tooth loss prior to any inactivation of the necessary genetic architecture.

EPIGENETIC EVIDENCE

Interactions between oral epithelium and mesenchyme are prerequisites for the initiation of odontogenic processes in vertebrates (Thesleff, 2003). The morphogenic processes of many chicken organs can be affected by an autosomal recessive mutation *talpid*² (Abbott et al., 1959; Dvorak and Fallon, 1991). However, conical dental rudiments occur at the anterior tips of both the premaxillae and dentaries of embryonic *talpid*² chicken mutants, which morphologically resemble the null-generation teeth of *Alligator* in topology and morphology (Harris et al., 2006). By comparing the odontogenic tissues of *talpid*² mutant and wild-type chicken embryos, it has been suggested that the absence of avian teeth was due primarily to the loss of direct contact between oral epithelium and the underlying mesenchyme in modern birds, making the avian epithelium unable to induce odontogenic processes (Harris et al., 2006).

In addition to the epithelium-mesenchyme apposition, another phenomenon present in *talpid*² chicken mutants is that their keratinization of epithelium is only restricted to the aboral aspect of the mouth (Harris et al., 2006; Louchart and Viriot, 2011). Because a non-keratinized oral epithelium is required for interaction with mesenchyme when initiating odontogenesis, the

presence of dental rudiments in *talpid*² mutants was suggested to be related to the absence of keratinized oral epithelium (Louchart and Viriot, 2011). In wild type chicken embryos, oral epithelium keratinization initiates penecontemporaneously with the cessation of the oral epithelial thickening (Wang et al., 2017a), further support this assertion. While these experiments demonstrate the expression of keratin in oral epithelium may have truncated odontogenic signals in embryonic birds, the absence of keratinization of oral epithelium still cannot maintain the growth of the tooth rudiments and no mineralized teeth have been successfully induced de novo in extant birds (Sire et al., 2008).

The ontogenetic tooth reduction present in *Limusaurus* and hypothesized for *Sapeornis* illustrates the importance of secondary tool and ontogenetic dietary changes in the evolution of edentulism, as tooth loss without secondary tools and corresponding dietary changes would likely be lethal. Secondary tools such as rhamphothecae, gizzard, or both, appear before the loss of teeth and take on functions normally served by the dentition such as food acquisition and mechanical digestion (Wang et al., 2017a).

Several molecules involved in the odontogenic signaling pathways, such as BMP4 (Bone morphogenesis protein 4) and its antagonist Noggin, also regulate the growth of rhamphotheca (Abzhinov et al., 2004; Wu et al., 2004a; Wu et al., 2006; Wang et al., 2017a). The overexpression of BMP4 could not only produce hypertrophic rhamphotheca and/or ectopic beak keratin growth (Wang et al., 2017a), but could also truncate normal odontogenic signaling pathways, resulting in a tooth agenesis (Hu et al., 2012; Vogel et al., 2014). Acceleration of postnatal growth of rhamphothecae could overgrow alveoli and would likely induce alveolar remodeling (Wang et al., 2017a). A single replacement tooth present inside a completely enclosed dentary alveolus in a hatching *Limusaurus* suggests the remodeling of the alveolus must have been accomplished after the initiation of the development of the replacement tooth, and the normal epithelial-mesenchymal

contact would have been cut off by occlusal enclosure of the alveolus, explaining why the growth of the replacement tooth was truncated. Taken together, the truncation of odontogenesis is a result, rather than the cause, of the growth of rhamphotheca, which is a process combining the divergence of odontogenic signaling pathways and the loss of epithelial-mesenchymal interactions (Wang et al., 2017a).

Based on these discoveries, a four-step scenario of avian beak evolution has been depicted based on the current evolutionary developmental evidence, which emphasizes the correlation between tooth reduction and rhamphotheca expansion (Wang et al., 2017a). This epigenetic interpretation explains the various tooth reduction patterns could be aroused by the random growth of ectopic beak keratin. During the evolution of birds, a postnatal expansion of rhamphotheca can be achieved progressively earlier in ontogeny through heterochrony (Wang et al., 2017a; Yang and Sander, 2018), resulting in the embryonic truncation of odontogenesis in extant birds.

DISCUSSION

Since the ancestors of all beaked tetrapods were toothed (Li et al., 2008; Davit-Béal et al., 2009; Zhou et al., 2009; Louchart and Viriot, 2011; Fraser et al., 2012; Meredith et al., 2014; Li et al., 2018), tooth reduction patterns must have directly impacted the independent origins and evolution of beaks.

Among various instances of regional edentulism occurring in theropods, the evolutionary tooth reductions are proceeded from the posterior ends of the maxillae and dentaries toward the rostrum (rostral reduction) in some lineages of theropods (e.g. Ornithomimosauria and Scansoriopterygidae) as well as enantiornithine birds and the recently reported ornithuromorph *Mengciusornis*, whereas in *Limusaurus*, Therizinosaoria, Oviraptorosauria, and Ornithuromorpha, tooth reduction proceeded from the rostral tips of the premaxillae and dentaries toward the pharynx (oral reduction). This suggests the

tooth reduction seen in theropods was dominated by at least two different patterns (Louchart and Viriot, 2011). Other patterns, such as the centrally contracted tooth row present in early-diverging birds may combine the two (Wang et al., 2017a, 2017c). The orad tooth reduction pattern is likely to have played an important role in the origin of beaked crown birds. The replacement of teeth with a beak at the anterior portion of the rostrum reduces the functional primacy of teeth for food acquisition and enhances the potential for secondary tools such as beaks, gastric mills, crops, tongue specializations, etc. to take over other functions of teeth. In addition, a progressively earlier appearance of rhamphotheca through heterochronic development would have prompted the evolution of a beak (Wang et al., 2017a). In contrast, the enlarged anterior teeth present in many taxa that have experienced a rostrad tooth reduction pattern (e.g. Scansoriopterygidae, enantiornithine) suggest the remaining teeth are still functionally important for food acquisition.

It should be noted that in comparison to the condition of ancestral archosaurs and most non-avian theropods, tooth replacement in theropods on the stem to birds is fairly diminished. Extant alligators have tooth family units each consisting of three teeth: one is the functional tooth, a second is the replacement tooth, and the third is a developing tooth bud connecting with the dental lamina (Wu et al., 2013). Tooth replacement in non-avian theropod dinosaurs appears similar to most other archosaurs, but it can be observed only in a few taxa of Mesozoic birds (e.g. *Archaeopteryx* (Wellnhofer, 2009), *Ichthyornis* and *Hesperornis* (Martin and Stewart, 1977; Dumont et al., 2016)) and appears to be absent in most toothed avian taxa, especially those with various tooth reductions. This suggests that reductions in frequency of tooth replacement and number of generations could be a prelude to regional and complete edentulism.

Although current evidence suggests teeth can be lost independently from different jaw bones, the correspondent edentulism of prederatives

and premaxillae (at least the anterior tips) suggests the tooth reductions in the upper jaw are linked by some unknown mechanisms with those in the lower jaw. The independent regional tooth loss is not difficult to understand, given jaw bones are differentiated from different groups of neural crest cells (Helms and Schneider, 2003; Schneider and Helms, 2003). However, the question of how odontogenic signals in the upper jaws are connected with those in the lower jaws is worthy to investigate in the near future.

Tooth loss in early birds has long been regarded as a phenomenon driven by the evolution of flight and/or adaptation of herbivorous diet (Dilger, 1957; Feduccia, 1999; Zhou et al., 2009; Zanno and Makovicky, 2011; Larson et al., 2016; Wang et al., 2017c; Zheng et al., 2018). However, some other studies demonstrated the body mass effect of tooth reduction is negligible in Mesozoic birds and suggested the edentulism is just in favor of the skull mechanics in addition to adapt herbivorous diet (Zanno and Makovicky, 2011; Lautenschlager et al., 2013; Zhou et al., 2019). The evolutionary success of crown birds is clearly unlikely to have been caused by a single factor, and various authors have suggested pedomorphic evolutionary developmental patterns (Bhullar et al., 2012), miniaturized body sizes (Lee et al., 2014b), improved flapping flight (Heers et al., 2018), a transition from omnivorous to herbivorous diet (Zanno and Makovicky, 2011) and a collapse of global forest and/or other environmental catastrophes (Larson et al., 2016; Field et al., 2018). Body miniaturization, various flight capabilities and dietary transitions are potential internal factors favoring crown-bird survivorship over other contemporaneous small theropods (Field et al., 2018). They constitute the raw materials that were selected by external elements such as regional and global climate and environmental changes.

Natural selection is not the only determinant of the direction of evolutionary change (Psujek and Beer, 2008). The premise for the presence of a new feature is that it must be created by existing developmental mechanisms or through mod-

ifications of existing developmental mechanisms, and its adaptation to a particular environmental niche is the result of natural selection (Psujek and Beer, 2008). The regional upregulation of BMP4 could not only create the modern form of avian beaks and prompt the growth of rhamphotheca (Bhullar et al., 2015; Wang et al., 2017a), but also likely mediates the truncation of odontogenic processes (Wang et al., 2017a). This suggests the cranial evolution of modern birds would have been regulated by common signaling pathways through which variations of different cranial elements are coordinated, and the various tooth reduction patterns seen in early birds may have linked with different beak and/or cranial growth strategies. During growth of dentigerous elements, the normal functions of tooth rows are maintained through enlargement and/or increase of replacement teeth, and the frequency of tooth replacement is usually high in the region where jaw bones grow rapidly. The loss of teeth apparently did not prevent the evolution of the avian skull, which in turn may have led to the avian craniofacial diversity. From this perspective, the slow and finite tooth replacement prior to the regional or complete edentulism in theropod dinosaurs on the line to birds could probably result from the unbalance of some signaling pathways involved in the cranial developmental processes. Investigations into the relationships between allometric craniofacial development, tooth replacement and growth of beak keratin would be worthwhile in the near future.

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