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P R E S S

From snout to beak: the loss of teeth in birds

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All living birds are toothless, constituting by far the most diverse toothless vertebrate clade, and are striking examples of evolutionary success following tooth loss. In recent years, an unprecedented number of Mesozoic birds have been described, illustrating the evolution of dentition reductions. Simultaneously, major advances in experimental embryology have yielded new results concerning avian edentulism. Reviewing these lines of evidence, we propose hypotheses for its causes, with a prominent role for the horny beak during development. A horny beak and a muscular gizzard functionally 'replaced' dentition for food acquisition and processing, respectively. Together with edentulism itself, these features and others contributed to the later success of birds, as a result of their high performance or additional functionality working in concert in these complex organisms.

Tracking the roots of bird beak success

Food acquisition and processing are fundamental in all heterotrophs because they control the availability of energy required for maintenance, growth and reproduction. Therefore, the mechanism by which food is brought from the environment into the organism is of the most basic biological importance. In this context, it is interesting that, in tetrapods, essentially just two basic mechanisms have evolved to achieve this: dentition and a horny beak (rhamphotheca; see Glossary) together account for almost 100% of the modern diversity in food acquisition apparatus among the 30 000 living tetrapods. Of these, two-thirds are toothed reptiles, amphibians or mammals. Most of the remaining third bear elements of rhamphotheca, and are essentially the circa 9900 bird species, and also chelonians and monotreme mammals. Finally, toothless and beakless tetrapods include toads and a few mammals [1].

Although all modern birds are toothless, most of the Mesozoic representatives were toothed, with various tooth shapes associated with diverse diets, showing that dentition reduction occurred after the differentiation of birds [2–4]. Hence, the evolution of birds clearly represents a key model with which to understand how, in general, the loss of *a priori* crucial structures, such as a dentition, can be overcome during evolution. Here, we discuss two groups of causes of such evolutionary processes: the determinants of development, and the adaptive characteristics of the resulting phenotypes directly under the influence of natural selection. First, we synthesize the latest results in

Glossary

Arcilineal: simple movement of the lower jaw relative to the upper jaw in which it closes or opens following an arc, and without longitudinal or transverse movements. This is the basal type of jaw movement in tetrapods, characteristic of Diapsida among reptiles, and the only one known in Aves. By contrast other tetrapods exhibit propalineal (caudo-rostral; e.g. turtles and tortoises) or transverse jaw movements, or both (e.g. mammals) [11].

Caruncle (also called the 'egg tooth'): keratinous tip of the rostrum present on embryos of many oviparous vertebrates, which helps to open the egg, and which disappears after hatching.

Caudal–rostral: anatomical direction from the side of the tail (posterior) to that of the rostrum (anterior).

Dollo's law: the quasi-impossibility for a developmentally lost complex structure to reappear homologously later in evolution.

Epithelium–mesenchyme interactions: the whole set of influences of epithelial cells on cells of the underlying mesenchyme at specific locations during development, and which progressively shape organs such as teeth. Enamel derives from the epithelium and dentine from the mesenchyme. Epithelium and mesenchyme successively and reciprocally interact with each other via several signal molecules, which induce reactions on competent cells. The nature, dosage, sequential timing and precise location of action of these signal molecules are crucial parameters that regulate precise tooth morphogenesis, differentiation and mineralization of the dental tissues. The networks of odontogenetic signalling pathways are complex, and involve mechanisms of modulation, inhibition, coexpression and others, between molecules.

Edentulism: total absence of teeth in an organism (essentially in jaws, and also other locations for some more basal groups of vertebrates).

First-generation teeth: incompletely formed teeth that erupt first in the development, for instance in alligators, where they are rapidly resorbed during embryonic development and replaced by the following generation of teeth. As in most other reptiles, every tooth is then replaced after some time by a newly formed underlying tooth, and again repeatedly during the whole life of the organism (i.e. continuous dental replacement) [15].

Homeothermy: the ability of an organism to maintain a constant body temperature regardless of the external conditions. The opposite is poikilothermy, in which the body temperature of an organism varies considerably, essentially as a consequence of variation in external conditions.

Kinesis: in skulls, the ability of bone parts to move relative to others, generally without an articulation and, in birds, often through a flexible plate of bone (synostosis). Kinetic skulls are the most widespread forms in vertebrates, and occur in all modern birds. In the latter, kinesis often exists at several levels of the rostrum and mandible.

Mouse mesenchyme–chicken epithelium recombinations: in dental development, these are experiments hybridizing oral epithelium and mesenchyme of these two taxa to examine how teeth develop. They enable researchers to decipher the role of each of these tissues at various developmental stages, and their interaction steps.

Muscular gizzard: a powerful organ containing and processing food, predominantly in birds, and unknown in other extant tetrapods. The rare, disputed occurrences of ingested grit (also called gastroliths, or gizzard stones) in some lizards and crocodiles are ambiguous [41]. Also called gastric mill, the gizzard is situated after the crop and the true stomach. It grinds food with the help of ingested grit. Secondary losses of this function have occurred, for instance, in nectarivores and meat-eaters [10].

Neornithes: the monophyletic group constituting all modern birds within the class Aves (birds). They are all toothless. By contrast, many Mesozoic birds had teeth in at least parts of their jaws [2,3]. Based on current evidence, the last birds bearing teeth became extinct close to the Cretaceous–Paleogene (K–P) boundary, 65.5 Ma [4]. Only toothless Neornithes survived the K–P crisis, and later became exceptionally diverse during the Cenozoic. As Neornithes comprises 94% of the approximately 10 500 toothless extant tetrapods, they are the best example of successful diversification following tooth loss among all vertebrates.

avian dental development (odontogenesis), which has seen considerable recent progress [5,6]. We then review the fossil record of dentition diversity and dentition reductions in birds, using the Mesozoic fossil record. The latter has expanded tremendously during the past decade, especially in China [3,7–9]. We extend our investigations to other tetrapods to assess the genuine association of traits and correlates of tooth loss in birds, such as the appearance of a rhamphotheca, the generalization of a muscular gizzard with gastroliths, and others [1,10,11]. Confronting developmental and evolutionary evidence, and expanding comparisons beyond birds, reveals new patterns and suggests new hypotheses to explain them.

Evo-devo insights

Three types of developmental event, which are not mutually exclusive, might have led to repeated dentition reduction and loss in birds. Here, we examine the evidence for each of these in turn.

Inactivation of odontogenetic genes

Odontogenesis in vertebrates comprises oral epithelium–mesenchyme interactions during which the tooth germ passes through successive morphological stages (i.e. lamina, bud, cap and bell stages) before tooth mineralization. In the classic avian developmental model, the chick embryo (*Gallus*), the earliest steps of odontogenesis still occur but the sequence of development stops at embryonic day E5 (i.e. the fifth day of embryo development) before the tooth bud stage has been reached [12]. This arrest of avian odontogenesis is probably the result of gene inactivation within odontogenetic pathways [12]. Support for this comes from studies using chick epithelium–mouse mesenchyme recombinant embryos, in which the presence of mouse mesenchyme would be expected to provide missing reactivity to epithelial signaling that still exists in the chicken. Disputed early recombinations were reported to have produced teeth [13], but these are now suspected of contamination and have never been reproduced [5,14]. However, recently produced chimeras yielded tooth rudiments, without contamination by mouse epithelium [14]. These results suggested that epithelium–mesenchyme interactions that are no longer expressed could be artificially reactivated.

Epithelium–mesenchyme shift

As further evidence, tooth rudiments were observed in embryos of *talpid²* (*ta²*) mutant chickens, in which several genes necessary for odontogenesis are expressed [5]. These rudiments only occur at the rostral tip of dentaries and premaxillaries [5]. They are simple in form, conical in shape, composed of dental mesenchyme and epithelium, and show a putative dentine matrix, but lack dentine and enamel secretion. Interestingly, they look similar in development, morphology and position to the first-generation teeth of crocodilians and other reptiles [15]. Because the *ta²* mutation is lethal at E17 at the latest, it is impossible to observe later dental development or succession. By comparing *ta²* and wild-type chick embryos, it was proposed that the arrest of dental development in wild type resulted from a loss of contact, in the course of avian evolution, between the epithelial signaling centre and the underlying competent mesenchyme [5]. This loss of apposition would have occurred through a lateral shift of the epithelium relative to the mesenchyme, at the level of the oral–aboral transition. This loss of embryologic contact during evolution would have made it impossible for the epithelium to induce the first odontogenic interactions with the mesenchyme, despite the partial conservation of signaling molecules, because contact is necessary for these interactions. The genetic processes responsible for this hypothetical shift are unknown.

Diversion of gene function

Interestingly, the rhamphotheca, keratinized on the aboral side only, had to be removed to uncover *ta²* dental rudiments [5]. The initiation of odontogenesis, located at the oral–aboral limit, is made possible by the presence of non-keratinized, living epithelium, which is necessary for interactions with mesenchyme. Keratinization of the epithelium in wild-type chicks starts at E9 [16], much earlier than the initiation of tooth rudiments in *ta²* (ca. E15–E17). The absence of early keratinization of the oral side of the rhamphotheca observed in *ta²* probably made possible the odontogenic interactions at this level. Hence, local epithelial keratinization appears to be a possible cause for the local arrest of odontogenesis. Several signaling pathways are common to tooth and rhamphotheca development [17,18]. For some of these pathways, a mutation inducing a diversion from odontogenesis to formation of the rhamphotheca might have been a possible cause for the arrest of odontogenesis in birds, for these reasons.

Further changes following tooth loss

Following tooth loss in Neornithes, mutations have accumulated, resulting in the inactivation of genes encoding one specific dentine protein and all three specific enamel proteins; these genes are now pseudogenes in the chicken [6,19]. Therefore, the true teeth obtained through recent mouse mesenchyme–chicken epithelium recombinations [20] are likely to result from contamination by mouse epithelium, because chick epithelium is definitely unable to produce enamel. However, the shape of some teeth obtained by these authors surprisingly resembles *Archaeopteryx* or alligator teeth [20]. This might result from conserved dental morphogenetic determinants in the chick epithelium.

It is unlikely that the developmental aspects of the different hypotheses for arrest of odontogenesis could be fossilized, because they are expressed at very early

developmental stages and they concern soft tissues. However, some implications might be reflected in adult fossils. The ta^2 mutants show that the arrest of odontogenesis could have arisen locally on the jaws [5]. Therefore, some fossil birds could be expected to show only local absence of teeth in jaw bones. In addition, the proposed close relationship between odontogenesis arrest and rhamphotheca development could be expected to result in a close association of toothless parts of jaws with elements of rhamphotheca, in some fossil birds.

Tooth loss in avian evolution

The developmental processes discussed above suggest probable mechanisms for tooth loss. However, to find out how tooth loss actually happened, how many times and with what phenotypes produced as a result of the underlying genetic changes, it is necessary to trace the evolution of bird dentitions through time, using the fossil record.

Patterns of tooth loss

The Cenozoic bird fossil record [65.5 million years ago (Ma) to present] only contains toothless Neornithes (Figure 1). A single questionable, probably non-neornithine taxon is reported from the Paleocene (ca. 62 Ma), but lacks cranial material [21]. By contrast, most of the Mesozoic birds bear teeth, from 146 to 65.5 Ma. The class Aves (all birds) is defined as the monophyletic group comprising all the descendants of the most recent common ancestor of *Archaeopteryx* and the Neornithes [22]. The prevailing hypothesis places Aves within theropod dinosaurs, generally the closest to the Scansoriopterygidae, followed by the Troodontidae, Dromaeosauridae and Oviraptorosauria [23–26]. We follow this framework here, although plausible alternatives exist [22,27–31] (Figure 1). Members of the first three of these theropod clades and the Archaeopterygidae bear one row of marginal, simple, pointed teeth on jaw bones [25,26], as do the extant Crocodilia, the living sister group of birds. Hence, regardless of the hypothesis of avian ancestry, a complete dentition is the basal condition preceding avian dentition reductions.

More than 60 Mesozoic bird species, and additional unnamed specimens, preserve enough cranial elements to allow observations on jaws (see the supplementary material online). We propose a consensus phylogenetic framework (references in the supplementary material online), on which we place these taxa and their dentition patterns (Figure 1). We define dentition reduction as tooth loss in at least one of the three tooth-bearing paired jaw bones; namely the maxillary, premaxillary and dentary. Our determination of independent dentition reductions is helped in that jaw bones where teeth are lost in a lineage are highly unlikely to become toothed again. Among vertebrates, only a single frog species is interpreted as having re-evolved teeth in a previously toothless jaw bone, other jaw bones having been toothed continuously [32]. Even more unlikely is the reappearance of teeth after total edentulism in a lineage. This has never been observed among vertebrates, and conforms to Dollo's law [32,33].

During the late Jurassic or Cretaceous, dentition reduction occurred at least six times independently in birds, among which edentulism was reached at least four times

independently. Three of these independent partial reductions probably represent intermediate stages between complete dentition and cases of edentulism (Figure 1).

In basal birds (*sensu* [9]; i.e. more basal than Ornithothoraces) as well as in Enantiornithes, evolution proceeded through partial tooth losses starting in the maxillaries and at the caudal ends of the premaxillaries or dentaries, or both (Figure 2). By contrast, among the Ornithuromorpha, evolution proceeded with tooth loss starting from the rostral-most part of the premaxillaries, and with conserved maxillary and dentary teeth. Taxa more derived toward Neornithes then show increased toothlessness, affecting whole premaxillaries only. Paradoxically, the restriction of dental rudiments to the rostral end of the jaws of ta^2 chicken mutants is reminiscent of the evolutionary patterns of dentition reduction in the Enantiornithes and basal birds, rather than in the Ornithuromorpha, to which chickens belong. This is not surprising, however, because features of such strongly affected mutants cannot be considered as real atavisms of Neornithes.

Incidentally, there are striking occurrences in the Pterosauria (other flying archosaurs; Figure 3) of diverse intermediate patterns of dentition reduction [34,35] similar to the diversity observed in Aves. Pterosaurs could be an important model for the study of convergence with birds in dentition reductions, subject to various possible morphofunctional constraints (M. Fastnacht, PhD thesis, Gutenberg University, 2005).

Timing of tooth loss

Previous rough estimates have suggested that edentulism in Neornithes was reached within a narrow possible time interval, generally between 100 and 80 Ma [5,6,12,20]. By contrast, we notice that the available data allow a wider possible interval between circa 125 Ma and 65.5 Ma. Neornithes are subdivided into two monophyletic clades: the Palaeognathae (tinamous, ostrich and other ratites) and Neognathae (all other extant birds) [36]. These two clades diverged at the latest between 95 and 80 Ma [36]. However, in the Cretaceous, there are no fossil Neornithes characteristic of the Palaeognathae or the Neognathae and bearing complete jaw elements. Therefore, this precludes any attempt to specify whether tooth loss occurred once, before the Palaeognathae–Neognathae divergence, or twice, after the divergence. As for the birds more basal than the Neornithes, their dentition reductions are all confined between circa 150 Ma and 110 Ma, except perhaps in the *Gobipteryx* lineage. Iterations in dentition reductions at the beginning of avian history reveal that the genetic bases of odontogenesis were already altered, and only minimal mutations would have caused dentition reductions several times.

The fossil record reveals that dentition reductions occurred many times within the Aves, and reached edentulism several times independently. These repeated events early in avian history indicate that the odontogenetic program had already been altered previously. Dentition reductions followed various patterns according to the different clades and lineages. In the line to toothlessness in
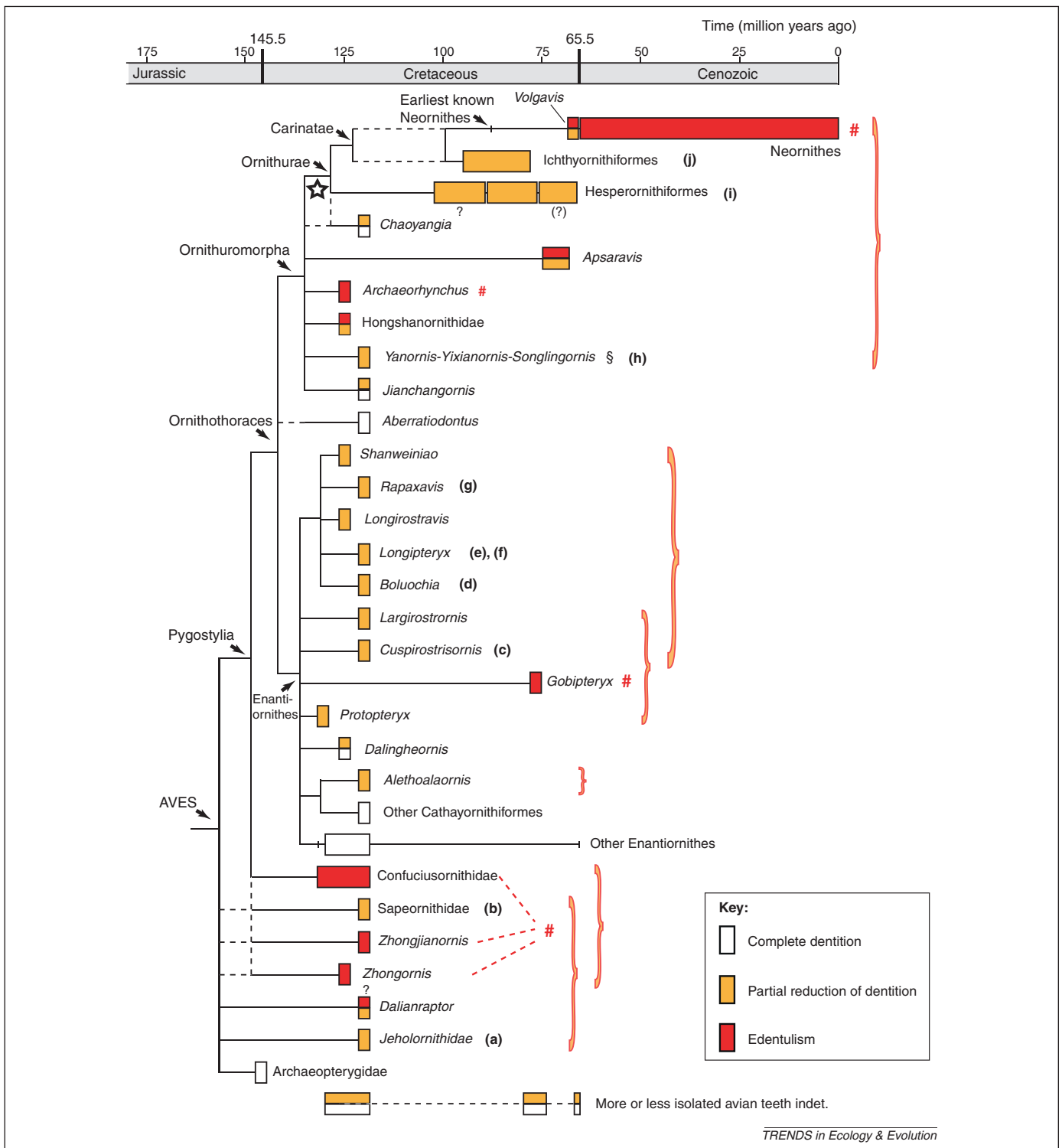
Figure 1. Occurrences of tooth loss and dentition reduction in Aves in a phylogenetic and temporally constrained framework. The white bars shows taxa with complete dentition; the orange bars, taxa with partially reduced dentition, and the red bars, toothless taxa. Two superimposed bars indicate that the two conditions are currently possible alternative hypotheses. The phylogenetic framework, and the dentition and temporal data follow the references in the supplementary material online. Isolated avian teeth: lower Barremian of Spain [ca. 128 million years ago (Ma)]; lower Aptian of China (125–120 Ma); Campanian of Alberta, Canada (between 83 Ma and 71 Ma); late Maastrichtian of Belgium (65.8 Ma; Ornithuromorpha). # indicates the minimal number of independent cases of edentulism; and the orange parentheses indicate the minimal number of independent groups, or continuums, of partial dentition reductions. The independent cases of partial reduction are identified using phylogeny combined with the recognition of different patterns that cannot be earlier stages of others (Figure 2). § In this lineage, the partial reduction is only incipient (teeth remain in premaxillaries). Parentheses can overlap, because the position of some taxa is not sufficiently well resolved. In the Enantiornithes, the inclusion of taxa in parentheses is speculative for the same reasons. Partial dentition reductions are either independent or branched at the base of lineages later evolving edentulism. The four cases of edentulism probably originated within three of the independent continuums of partial reductions, including two cases of edentulism from the single group of partial reduction in the Ornithuromorpha, most parsimoniously. The star indicates the approximate shift from a lower to higher degree of metabolism (Box 1). In alternative phylogenies, the Scansoriopterygidae, Troodontidae, Dromaeosauridae and Oviraptorosauria would be placed within and at the base of Aves after the divergence of Archaeopterygidae [22,27–30]. Incidentally, a recent analysis places *Archaeopteryx* more distant from basal birds such as *Jeholornis*, than the Scansoriopterygidae, but with 'only tentative statistical support' [31]. In this hypothesis, the Aves as defined in the main text [22] would contain at least part of the Scansoriopterygidae, Troodontidae, Dromaeosauridae and Oviraptorosauria, rather than exclude *Archaeopteryx* from Aves, as the authors suggest [31]. However, we follow the most widely accepted hypothesis for Aves here (see main text). The legend to Figure 2 contains details of **(a–j)**.
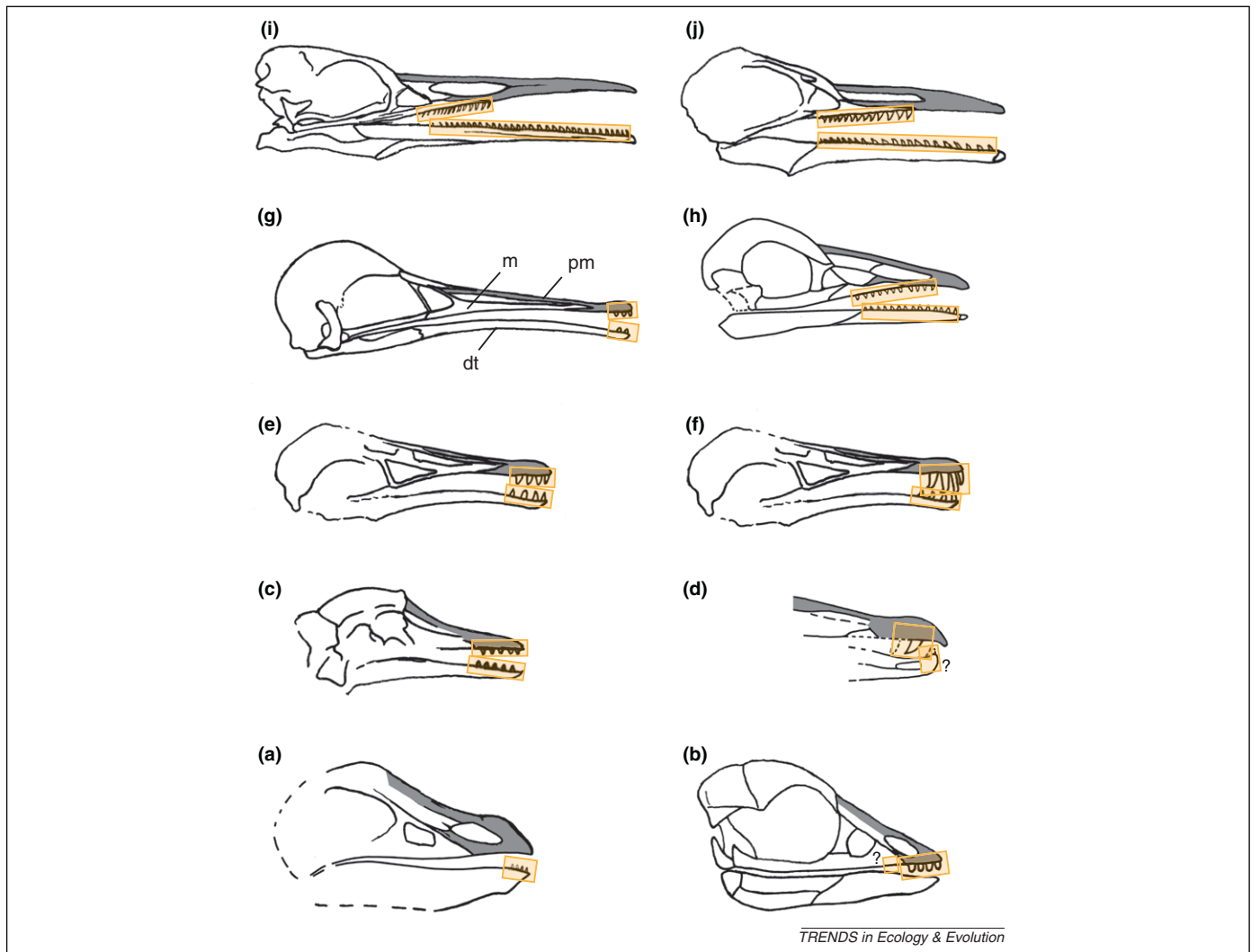
Figure 2. Examples of patterns of partial dentition reduction in birds, illustrated by different Cretaceous species (showing right side only). Toothed parts of jaws are highlighted in orange and the premaxillary in grey. Lettering refers to Figure 1. **(a)** *Jeholornis prima*, **(b)** *Sapeornis chaoyangensis*, **(c)** *Cuspirostrisornis houi*, **(d)** *Boluochia zhengi*, **(e)** *Longipteryx chaoyangensis*, **(f)** *Longipteryx* sp. [3], **(g)** *Rapaxavis pani*, **(h)** *Yanornis martini*, **(i)** *Hesperornis regalis*, **(j)** *Ichthyornis dispar*. Abbreviations: d, dentary; m, maxillary; pm, premaxillary. Other patterns are known (see the supplementary material online). Based on data and references in the supplementary material online.

the Neornithes, teeth first disappeared from the premaxillaries.

Crucial innovations for edentulism

Among the anatomical, physiological or behavioral innovations thought to have favored the viability of edentulism in birds [1,10,11], we examine first the evolution of the rhamphotheca (which also played a major role developmentally) in relation to dentition reduction. We then address the role of the muscular gizzard and, more indirectly, that of homeothermy and sustained active flight.

Rhamphotheca

Being composed essentially of keratin [37], elements of rhamphotheca are only rarely fossilized as incrustations of organic matter on fine sedimentary slabs (e.g. in several Confuciusornithidae). However, in several cases, the former presence of a rhamphotheca in fossils can be deduced from the presence of densely distributed neurovascular foramina on the smooth surface of a jaw bone [38]. Among Mesozoic birds (see the supplementary material online),

a complete rhamphotheca is observed in the toothless Confuciusornithidae and *Archaeorhynchus*. In *Ichthyornis* and the Hesperornithiformes, which both lack only the premaxillary teeth, the presence of former elements of rhamphotheca manifests on all toothless parts of the jaws [38]. On the line to the Neornithes, the expansion of the rhamphotheca that progressively replaced the dentition starting from the rostral end of the premaxillaries is congruent with hypotheses of an early development of the rhamphotheca in living Neornithes starting from the caruncle, at rostral tip [38,39]. In a few cases, it seems that, although teeth were absent in parts of the jaws, these parts were not covered by a rhamphotheca. Conversely, a rhamphotheca might have covered rostrolateral parts of the jaws while the dentition was still complete, in a few taxa [3,40]. Establishing the earliest occurrences of a rhamphotheca in various lineages will allow a precise understanding of the diverse sequences of rhamphothecal appearance versus dentition reduction, an important axis of investigation now also initiated in pterosaurs [34]. It will also allow the hypothesis to be tested in several lineages [1] that, in avian
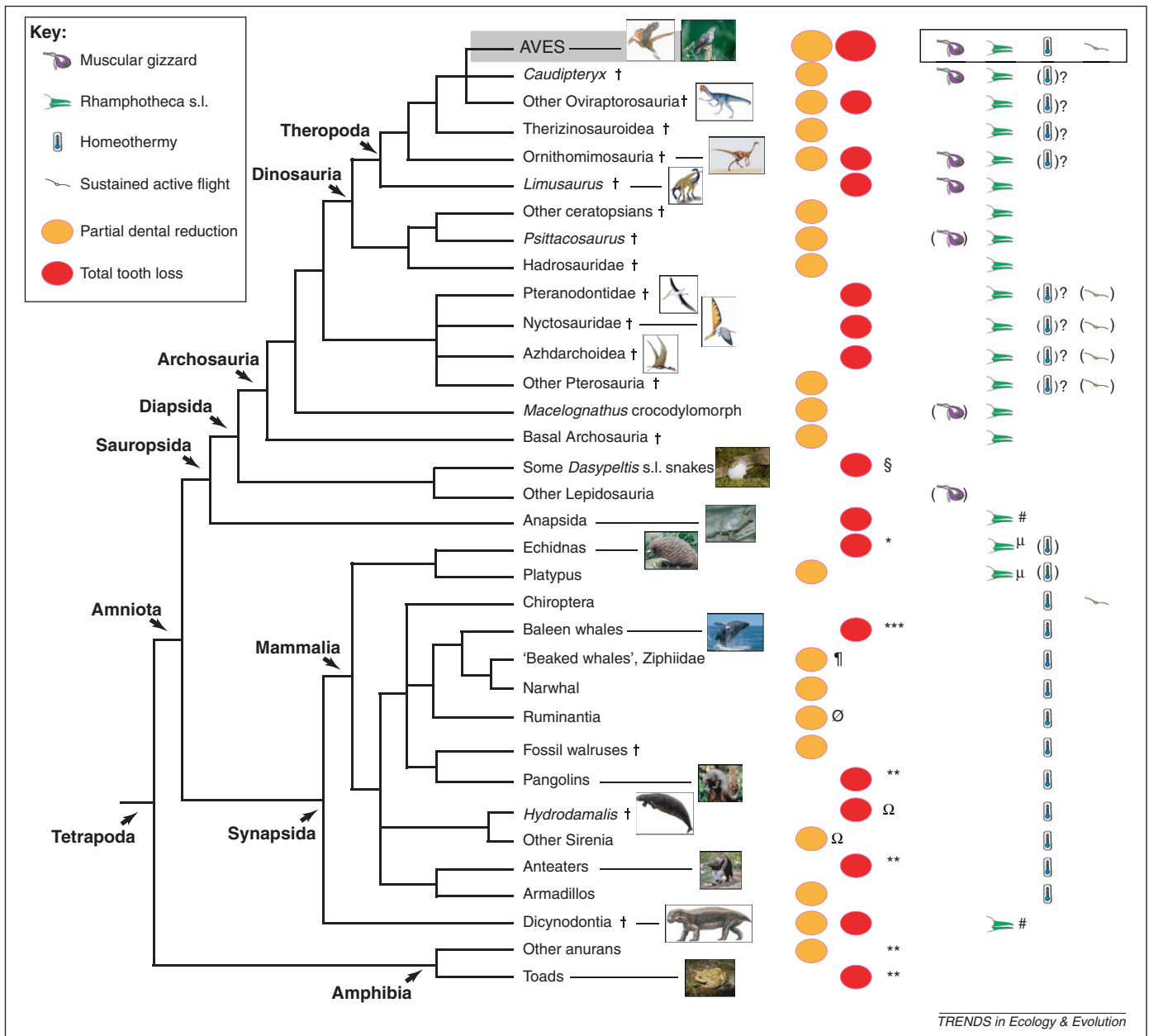
Figure 3. Occurrences of tooth loss, partial dentition reduction and potential correlates in tetrapods, in a phylogenetic framework. Attributes are indicated for taxa in which they apply to at least one lineage. Larger ellipses in the Aves indicate a higher frequency of independent events (Figure 1). A cross (†) indicates an extinct group. A 'gizzard' icon between parentheses indicates that the characteristic is unconfirmed for this taxon. A 'metabolism' icon between parentheses means that homeothermy is incomplete, and a question mark is added to indicate hypothetical cases. A 'flight' icon between parentheses indicates that flight was probably not as sustained and active as in the Neornithes. The following are features thought to help overcome tooth loss: §, internal tracheal bony spines, which help to crush eggs; *, specialized tongue; **, elongated protractile sticky tongue; ***, baleen; ¶, all but one species, with total edentulism in females; Ø, callous pad of hardened gum on premaxillaries; Ω, keratinous grinding plates; #, rhamphotheca associated with propalineal jaw movements. Other rhamphothecae are associated *a priori* with arcilineal jaw movements; μ, keratinized beak and palatal or tongue spines (with horny grinding plates in the platypus and elongated tongue in echidnas; the platypus has teeth when juvenile, and a beak when adult [1]). Incidentally, rhamphotheca-like elements in mammals are not homologous with the rhamphotheca in archosaurs. They are composed of α-keratin in mammals as opposed to β-keratin in birds. The consensus phylogenetic framework follows the following sources: for mammals [89]; for theropods, the framework adopted in the main text (Figure 1) and, for other tetrapods, that used in [1,38], as well as references below. Dentition reductions, rhamphothecae sensu lato and other feeding-apparatus features are taken from [1,38], and additional sources for theropods [46,90,91], pterosaurs [35,92–94], crocodylomorphs [95], snakes [96] and mammals [97–99]; gizzards from [11,41,42,46,90]; homeothermy from Box 1 and [75]; and sustained active flight, see main text. Representatives of edentulous taxa are illustrated.

evolution, the presence of a rhamphotheca (or parts of it) was necessary prior to edentulism for the latter to be adaptively viable.

Gizzard
A muscular gizzard containing ingested grit used for food processing is a unique attribute of birds among modern tetrapods [41,42]. The gizzard processes food at least as efficiently as toothed jaws [10,11], and it is used for food processing in most extant birds [10,41,43], not only in vegetarians (granivores, frugivores and other plant eaters; contra [44]), but also in omnivores, insectivores, most carnivores sensu lato and others [43,45]. Fossil evidence of a functional muscular gizzard in the Mesozoic, based on gastroliths, exists for *Sapeornis*, one of the first birds with dentition reduction, and the ornithuromorphs *Yanornis* and *Archaeorhynchus*. However, it is most probable that, once acquired, this trait existed in all birds since at least

Box 1. The metabolic quest: were dinosaurs and pterosaurs warm blooded?

Characterizing metabolism in dinosaurs and pterosaurs has been a challenge for decades. Tools used as proxies have included bone structure, growth rates inferred from histological sections, isotopic ratios, and more indirect parameters, such as predator–prey ratios, posture and gait, respiratory, cardiovascular, pelvic and gastrointestinal structures, presence of nasal turbinates, skeletal pneumaticity, inferred presence of feathers or fur, and 'polar dinosaurs'.

However, the different studies are discordant and all have their particular shortcoming. Some interpretations present dinosaurs as rather 'ectothermic' [61–64], others as rather 'endothermic' [65–67]. Incidentally, basal or resting metabolic rates, or endothermy versus ectothermy, refer to chemical physiological processes in living organisms, which are unknown in extinct taxa. The more pertinent parameter is the degree of homeothermy versus poikilothermy, whatever the cause (i.e. higher metabolic rates and true endothermy, special ectothermic intake or mass endothermy). Many arguments are still speculative, with a complex interplay of parameters, such that firm conclusions are difficult to reach. In the current state of the controversy, it is reasonable to consider that most dinosaurs were basically poikilothermic (i.e. their body temperature was not maintained at a high level and varied according to the environment), with varying degrees of regulation in some groups. Such regulation could have arisen from enhanced ectothermic intake or, for large taxa, from gigantothermy (i.e. mass endothermy) [62,68]. A particular group, the coelurosaurs, appears to have been more homeothermic than others and, their small size suggests that they had some degree of true endothermy [68,69]. However, this possible degree of endothermy would not have reached the levels known in modern birds and mammals.

The case of pterosaurs remains unresolved, and equivocal [63], with some arguing for near homeothermic metabolism [70,71] at least in larger taxa [71], and others favoring more poikilothermic metabolism [72–74]. Homeothermy should only be considered to have potentially evolved in some pterosaur lineages.

Today, only birds and eutherian mammals [68,75] are truly homeothermic and endothermic. Their high metabolism allows them to make sustained efforts, including active sustained walking, running, swimming, and flying, and to live in all climates. Among Mesozoic birds, there is a clear evolution in metabolism between the more basal groups and the Enantiornithes on the one hand, and the Ornithurae, including the Neornithes on the other hand. Basal birds were apparently poikilothermic, whereas growth rates indicate a shift toward modern homeothermy at the base of the Ornithurae, most probably with endothermy [64,76,77] (Figure 2).

the last common ancestor of *Sapeornis* and all more-derived birds.

Tooth loss, rhamphothecae and gizzards in other tetrapods

Dentition reductions occurred in a limited number of tetrapod clades outside Aves, including total edentulism in 15 independent clades of extant or extinct groups (Figure 3). These reductions, partial or total, are relatively more common in archosaurs than in other tetrapods. The closer to Aves, the more frequent they are, and always concomitant with the acquisition of elements of rhamphotheca. Evidence of a muscular gizzard, intrinsically rare, is known at least in several clades of dinosaurs considered the closest to Aves, and is always concomitant with elements of rhamphotheca and edentulism or important partial dentition reduction. The gizzard in the Aves could either be inherited from non-avian theropods, down to basal ones such as *Limusaurus* [46], or have reappeared independently. The advent of elements of a rhamphotheca, a gizzard, homeothermy or sustained active flight (see below) occurred in several groups other than birds, although never all together, as is seen in the birds.

Towards a model

We suggest that, despite the loss of dentition, a network of related innovations in complex interplay through natural selection has favored avian evolutionary diversification, in particular in the Neornithes. The acquisition of a muscular gizzard and of a rhamphotheca appear to have been crucial in allowing edentulism and making it viable. Food is stored in the crop, and hence continuously available even outside feeding activities. The muscular gizzard with ingested gastroliths efficiently processes this food, allowing the continuous provision of abundant nutrients necessary for the high metabolic demands of flight [10,11]. Together with many morphological changes, such as lightening of the skeleton, skeletal structure reinforcements and fusions, and displacement of the center of gravity [47,48]), higher

metabolism allowed the improvement and diversification of sustained powered flight [48,49]. Homeothermy and sustained powered flight arose in an indirect link with the whole process of tooth loss in birds, and with other innovations. These two particular attributes probably participated in the successful diversification of henceforward edentulous birds, unrivalled among edentulous vertebrates. Homeothermy was probably acquired near the base of the Ornithurae (Box 1, Figure 1), which concurs approximately with the acquisition of modern-like sustained powered flight in the lineages leading to *Apsaravis*, *Ichthyornis* and the Neornithes [47–50].

Based on the biological impact of such innovations, and their distribution in other tetrapods, we propose a tentative framework for the ecomorphological diversification of birds (Figure 4). The main characteristics that are proposed to have allowed or favored viability and greater evolutionary success after tooth loss occur together exclusively in the Aves (Figure 3). Pterosaurs apparently lacked a gizzard, true homeothermy (Box 1) and, hence, possibly sustained active flight. Their quadrupedality [35] perhaps also impeded the colonization of as many ecological niches as birds. Chelonians all have a rhamphotheca, but lack a gizzard, and process food with their jaws by propalineal movements. By contrast, birds do not process food with jaw movements, these being simply arcilineal [11]. In addition, chelonians are poikilothermic and ectothermic. Another interesting combination occurs in bats, which have sustained powered flight and true homeothermy. However, bats did not undergo any dentition reduction, neither do they bear any concomitant incipient rhamphotheca; furthermore, they lack a gizzard and process food with their teeth. Their near-exclusively nocturnal activity might have been an impediment to further ecomorphological diversification. As in pterosaurs, quadrupedality perhaps participated in this relative evolutionary confinement.

Meanwhile, the loss of teeth in birds allowed for the unprecedented magnitude of diversification of rhamphothecae, in terms of size and shape. Neornithine birds
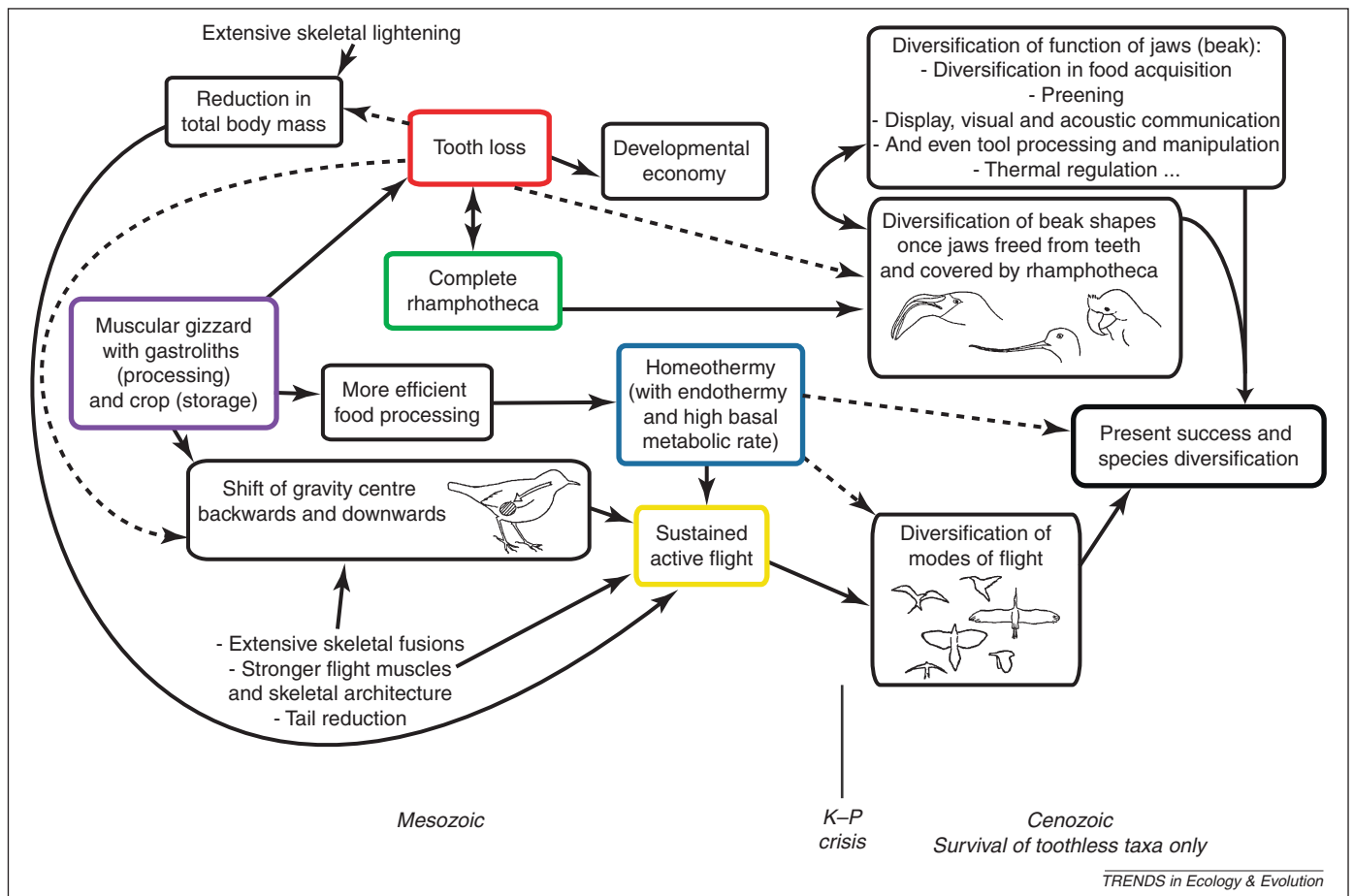
Figure 4. Proposed evolutionary interactions related to the loss of teeth in birds. Several major morphological, physiological and behavioral innovations favored or made possible (arrows) the evolution of other innovations in a complex way: some facilitated edentulism in birds, whereas others led to avian evolutionary success following, and despite, tooth loss, as the Aves are the most speciose class of extant tetrapods. Dashed arrows represent less obvious influences. The horizontal distribution of events reflects approximately their relative temporal occurrences, when known, although some cannot be assigned to a well-defined relative placement; for example, tooth loss occurred several different times during the Mesozoic (see main text for details and references). The extinction of toothed birds close to the Cretaceous–Paleogene (K–P) crisis might derive from contingent effects of the sudden asteroid collision [100]. It could also derive in part from physiological characteristics, such as incomplete homeothermy and endothermy, which might have made non-Neornithes less resilient to the deep and rapid climatic and food-web changes that characterized the crisis [100]. The model might, in part, not only apply to tooth loss on the line to Neornithes, as a few of the innovations depicted here are observed in association with tooth loss in other lineages (e.g. that of *Confuciusornis* or *Gobipteryx* [3]).

and pterosaurs are the only archosaurs in which the jaws reach lengths above 70% of the total skull length [3,51]. Tooth loss probably also favored jaw slenderness in pterosaurs (M. Fastnacht, PhD thesis, Gutenberg University, 2005). The diversity in beak shapes and functions in extant birds exceeds by far that observed in the jaws, or snout of all other tetrapods, and involves slender or light architectures, extremely varied shapes and curvatures, and specialized kineses [47,48,52,53] that would have been impossible with a dentition. This dramatic diversification mostly involved the rostral parts of jaws, and is thought to have largely participated in neornithine adaptive radiation [54]. By contrast, Mesozoic birds that retained teeth show only a limited diversity of shapes of the snout or incipient beak (e.g. Figure 2), and even the few edentulous and beaked Mesozoic species show relatively short or conical beaks [3]. The evolution of diverse extreme beak shapes was completed during the first half of the Cenozoic, following tooth loss: in pelicans, stork-like birds, duck-like and flamingo-like taxa, birds of prey, wide-gaped and short-beaked aerial insectivores, and even hummingbirds [21,48,55,56]. The rhamphotheca proves at least as

efficient as teeth for food acquisition, whether it is smooth, serrated, or even covering pseudo-teeth (Box 2). Beaks took on additional functions secondarily, such as feeding young, preening, grooming, courtship and display, communication, and even tool manufacture and manipulation [52,57,58] (Figure 4). Such functions added to food acquisition, and associated beak morphologies probably participated in the success of the Neornithes.

This simplistic model emphasizes only a few of the many characteristics that birds acquired at different times, and that could have widely compensated for the non-adaptive effects of tooth loss, in balance in such complex, integrated organisms. Such characteristics include the rhamphotheca and muscular gizzard and, more distantly, homeothermy and sustained powered flight.

Concluding remarks

The concentration of independent dentition reductions, including edentulism, in early birds is unrivalled and attests to an early fragility in their odontogenetic program. Patterns of intermediate, partial stages of dentition reduction were diverse, as seen in the pterosaurs. The pattern

Box 2. False 'teeth' in modern birds: analogy or atavism?

In many Neornithes, although toothless, serrations of various scales exist on the beak tomia (sharp edges). They generally shape only the outer rhamphothecal surface, but not the underlying bone. The smallest serrations, called scopate tomia, occur in approximately 30 bird families [78]. Roughly 0.3–0.7 mm high, they form brush-like ridges that increase the coefficient of friction and allow better adherence, especially when grasping and holding hard-shelled food items [78]. Some hummingbirds have serrate tomia (denticles ca. 0.2 mm) that they use for catching insects or piercing the base of flowers [79]. Piscivorous kingfishers have lacerate beak tomia, with wider, more irregularly incised serrations [78]. Larger, millimetric saw-shaped serrations occur in piscivorous mergansers, and geese bear similar serrations, used for cutting herbs [48]. Specialized baleen-like projections used in filter-feeding occur in flamingos, several ducks and others [48]. Toucans (Ramphastidae) have forward-facing rhamphothecal serrations sometimes reaching the centimetric scale [80] and faintly shaping the underlying bone (AL pers. obs.). Falcons, shrikes, two barbet genera (Capitonidae) [81–83] and many other birds, have one or two paired rostral or mandibular serrations, or 'tomial teeth', sometimes also markedly shaping the underlying bone.

Pseudo-teeth characterize the extinct Cenozoic clade Odontopterygiformes, the pelagic 'pseudo-toothed' or 'bony-toothed' birds, which existed for more than 50 million years [84,85]. The numerous centimetric bony projections distributed like teeth along the beak bone tomia were probably covered by the rhamphotheca [84,85]. Presumably fragile, they might have helped catching soft prey [85]. Recently extinct Moa-Nalo of the Hawaiian Islands comprised three species with numerous bony odontoids of smaller size that were more saw-like [86]. It is unclear how these highly modified terrestrial, giant and flightless folivorous ducks [87,88] used these odontoids, which were also probably covered by rhamphotheca [86].

Serrations represent very small, functional 'teeth analogs', efficient for grasping and holding, in numerous different lineages. Pseudo-teeth and odontoids are more enigmatic teeth analogs. All these types of structure in the Neornithes evolved subsequent to edentulism. It has been suggested that pseudo-teeth in Odontopterygiformes might derive from conserved dental-specific developmental bases [85], based on shape similarity with teeth rudiments of the ta^2 mutant chicken [5]. However, developmental and histological evidence is still missing in support of such a hypothesis of partial homology. Specifically, ta^2 teeth rudiments cannot be cited as such evidence, as their shape similarity with pseudo-teeth is not obvious, and their nature differs radically from that of pseudo-teeth, which are bony projections of the jaw bones.

occurring on the line to neornithine edentulism is congruent with recent developmental models of the rhamphotheca. The appearance of rhamphothecal elements probably had a crucial role in the arrest of odontogenesis. At least in the Ornithurae, the rhamphotheca covered jaw bones simultaneously with local edentulism, illustrating transformation from a snout to a beak. Once genetically programmed, edentulism appears to have been allowed or favored through natural selection by the unique combination of avian features, which are in balance in the complex organisms that they constitute. These key characteristics, acquired at different times during the Mesozoic, include the rhamphotheca, the muscular gizzard with ingested grit, and the crop. Homeothermy and sustained active flight also arose in birds in an indirect link with edentulism. A horny beak and a gizzard did more than compensate for edentulism in terms of food acquisition and processing. They contributed, with their high performances or additional functions, to the later success of neornithine birds, the most diverse group of tetrapods.

Prospects

There is a need to investigate the presence and extent of the rhamphotheca in different lineages of Mesozoic birds, and the evolution of its spatial relation with dentition. Comparisons at different levels with pterosaurs are required, as this group appears to share many characteristics with birds regarding dentition. Concerning avian dental evolution, preceding tooth losses, tooth size (generally millimetric) and shape appear to be very diverse across the different lineages [3]. These aspects still need to be better characterized, as do dental microstructures [59], implantation and replacement, the latter two being controversial in comparison with other tetrapods [3,22,60].

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.tree.2011.09.004.

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