Chapter 7
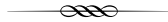
Sparrows with Teeth and Claws?

Reconstructing the Cretaceous Enantiornithes (Aves: Ornithothoraces)

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Introduction

Palaeontology – the study of ancient life – is a unique scientific discipline in that a strong dose of imagination and creativity is present, expressing itself through the creation of *in vivo* reconstructions of extinct creatures. Such reconstructions are important for engaging public interest in palae-ontology. Although a trained scientist or devoted amateur may study a skeleton and be able to visualize what it would have looked like *in vivo* (alive), this requires a comprehensive knowledge of skeletal anatomy that can only be acquired through extensive training. Reconstructions are especially important visual tools if the fossil taxon is known from only a small portion of the skeleton. Fossils are notoriously rare and incomplete, and species have been named from a single bone or even less. As such, recon-structions are constantly transforming with discoveries of new material and data.

Many palaeontologists were set on their career path at an early age, stimulated by a childhood interest in prehistoric animals brought on by vivid reconstructions seen in books or on television. A number were in-spired by the Jurassic Park movies, in which not only the visual appear-ance of Mesozoic reptiles was reconstructed, but also their movements and behaviours. Perhaps unsurprisingly, many palaeontologists dabble in art, a necessity for creating scientific figures, sometimes bringing their discov-eries to life by creating their own reconstructions. Similarly, palaeoartists,

artists who have dedicated themselves to the reconstruction of ancient life, are typically avid amateur palaeontologists whose work is often detail oriented, strongly rooted in fossil evidence and the latest discoveries. Artists often work closely with palaeontologists to ensure their work is of the upmost accuracy. Others disregard the work of scientists and offer their own interpretations – these pseudoscientists are often widely recognized on the internet, but are detrimental to the general public's understanding of extinct life.

In recent decades, both exceptional new discoveries and the development of new methodologies have revolutionized the field of palaeontology, and provided rich new details that contribute to the increasingly life-like aspect of recent palaeo reconstructions. New methods include both the use of advanced technology, such as synchrotron-based computed tomographic (CT) scanning (three-dimensional X-ray images, for example),[1] and the novel application of methods typically utilized by other disciplines, such as Raman spectroscopy (which reveals chemical signatures) and the histochemical staining (a technique used by doctors and biologists to differentiate the structural elements of tissues by their colour or the intensity of staining by chemical dyes) of fossils.[2] The exceptional discovery of feathers (or protofeathers in some cases) preserved on various groups of dinosaur fossils uncovered primarily in Late Jurassic – Early Cretaceous deposits in north-eastern China[3] have revealed – to the dismay of many – that even *T. rex* might have been covered in 'dino fuzz' (protofeathers) during at least part of its lifetime,[4] and that oviraptorosaurs had small 'proto-wings' on their forelimbs,[5] while many deinonychosaurs had 'proto-wings' on their forelimbs and hindlimbs.[6] Raman spectroscopy has revealed the colour of dinosaur eggs,[7] and CT scans have provided unprecedented anatomical details, especially concerning internal structures like the semi-circular canals[8] and enigmatic structures like the avian predentary (a bone at the tip of the lower jaw in some Cretaceous birds that is absent in neornithines, the clade that includes all modern birds).[9]

These same deposits in north-eastern China that revealed that the ancestors to *T. rex* were covered in dino-fuzz have produced an enormous diversity of early bird fossils.[10] More than half of all known species of Mesozoic birds come from three formations and a period of the Early Cretaceous spanning approximately 10 million years (from 130 to 120 Ma).[11] These deposits reveal a diverse biota living in a system of ancient lakes and forests, punctuated by volcanic activity. This celebrated Jehol Biota has revealed more about the diversity and biology of Mesozoic birds than all other known avian-bearing strata combined.[12] The Jehol deposits represent Lagerstätten, meaning they are characterized by exceptional preservation, exemplified by the preservation of soft tissues such as feathers.[13]

Bird fossils are especially rare for two reasons: birds are small, their body size being constrained by flight; and their bones are hollow, a feature that is aerodynamically advantageous because of reduced body mass. As such, the Mesozoic fossil record of birds in most places is poor and fragmentary. Lacustrine (lake) deposits in particular represent taphonomic windows for the preservation of delicate fossils like birds. In contrast to most other Cretaceous avian bearing strata, fossils from the volcano-lacustrine Jehol Biota are typically nearly complete and fully articulated.[14] These spectacular fossils often preserve typically rare traces such as stomach contents and soft tissues most commonly in the form of feathers, but also including rare traces of organs such as lungs and ovaries. Embryos and juveniles have also been recovered.

One group of birds – the Enantiornithes[15] – dominated the Jehol Biota as well as nearly every known Cretaceous avifauna, with the exception of those from marine deposits.[16] Enantiornithines were the dominant clade of continental birds in the Cretaceous and are considered the first major avian radiation.[17] They account for approximately half of all the diversity of Mesozoic birds currently recognized. The Enantiornithes are a fairly derived Cretaceous clade. Their sister-taxon, the Ornithuromorpha, is the clade that modern birds (Neornithes) nest within. Together, these two clades are called the Ornithothoraces. Non-ornithothoracine birds (birds more primitive than the enantiornithines and ornithuromorphs such as *Jeholornis* and *Sapeornis*) are only definitively known in the Upper Jurassic Solnhofen Limestones in southern Germany, which produce *Archaeopteryx*, and the Lower Cretaceous deposits that record the Jehol Biota.[18]

Most data pertaining to the Enantiornithes is from the Early Cretaceous, where hundreds (if not thousands) of exceptional specimens from the Jehol Biota have revealed an enormous wealth of information. As a result, our understanding of this clade is strongly skewed to a single region over a relatively short period. Additional Early Cretaceous Lagerstätten in north-western China (the Xiagou Formation at Changma)[19] and Spain (Las Hoyas)[20] have also contributed important data, although the specimens from these deposits are far fewer and less complete.

By contrast, most Late Cretaceous enantiornithines are recognized from very incomplete specimens. Although a few partial skeletons have been found (e.g. *Mirarce*, *Neuquenornis*, *Elsornis*, *Yuornis*),[21] a majority of Late Cretaceous species are known from a few associated bones or even less than a single complete element.[22] However, these specimens are almost always preserved in three dimensions, revealing minute details such as muscle scars, whereas specimens from Early Cretaceous Lagerstätten are almost always crushed flat and do not preserve such details. As such, reconstructions of Early Cretaceous taxa are based on actual specimen

data, whereas Late Cretaceous reconstructions must heavily borrow from skeletal and soft tissue details preserved in older fossils that can be phylogenetically inferred to have been present (as scientists infer the Late Cretaceous *T. rex* was likely feathered at some point in its life, based on basal tyrannosauroids from the Early Cretaceous).

Recently, ~100 Ma (early Late Cretaceous) amber from Myanmar has proved to be an unlikely new source of information regarding enantiornithines. A handful of birds have been recovered.[23] These are typically fragmentary, consisting of an isolated wing or a leg, although one nearly complete hatchling is known. These specimens are exceptionally well preserved in three-dimensions, and in most cases the skeletal remains are associated with soft tissues. Numerous isolated feathers have also been recovered, which are most likely referable to Enantiornithes – the only group of birds recovered with certainty from these deposits so far.

The Basic Bauplan

Avian lineages basal to enantiornithines possessed distinct characteristics that made them strikingly different from neornithines. Among these differences, *Archaeopteryx* and *Jeholornis* possessed elongate reptilian tails formed by over twenty free caudal vertebrae;[24] confuciusornithiforms (a group of Early Cretaceous birds from the Jehol Biota) had hands with three digits with large claws, and unusual long and narrow remiges (the flight feathers of the wing);[25] and *Archaeopteryx* and *Sapeornis* lacked an ossified sternum, suggesting that the breast muscle (the m. *pectoralis*) would have been small.[26] In Ornithothoraces the basic avian skeletal morphology was in place: the tail is abbreviated and ends in a distally fused element, the pygostyle, which is the bone that would have supported the tail feathers (rectrices) and associated musculature; the coracoid (a bone that connects the cranial edge to the sternum to the shoulder joint that supports the forelimb) is elongate and separate from the scapula; the furcula (wishbone) demarcates a narrow interclavicular angle; and the sternum is keeled with caudal trabeculae (bony processes that extend out from the caudolateral margins of the bone).[27] As such, enantiornithines would have strongly resembled living birds, with a few important differences, the most obvious being the presence of teeth and small manual (hand) claws in most taxa. Compared to ornithuromorphs, enantiornithine skeletal structure is notably more primitive. While both have a narrow furcula, that of Cretaceous ornithuromorphs was U-shaped and resembles that of living birds, whereas that of enantiornithines was Y-shaped, a morphology unique to this clade.[28] Similarly, the pygostyle of ornithuromorphs resembles that

of living birds being small and ploughshare shaped, whereas that of en-antiornithines was proportionately longer and more robust than that of neornithines.[29]

Compared to neornithines, cranial disparity was very limited in the Enantiornithes – all taxa were mesorostrine (the rostrum, the portion of the skull that in living birds forms the beak, accounts for 50–70 per cent the total skull length) whereas neornithines include brevirostral (30–50 per cent skull length) and longirostral (70–90 per cent) forms. Within the mesorostral range, the longipterygids (a diverse group of enantiornithines from the Jehol Biota), with their rostrum accounting for 60–65 per cent of the total skull length, represent a distinct departure from other enantiorni-thines, in which the rostrum is close to 50 per cent skull length.[30]

Most enantiornithines retain teeth, although at least some Late Creta-ceous species, like *Gobipteryx* and *Yuornis*, were edentulous (teeth absent) like all living birds, and presumably had a rostrum covered in a keratinous sheath – the rhamphotheca.[31] Most commonly, teeth were fairly low in number (6–8 in each dentary), and simple and conical. However, pengorni-thids (a basal family of enantiornithines from the Jehol Biota) had higher tooth counts (~11 dentary teeth) and low-crowned teeth. The longiptery-gids, with their proportionately elongate rostra, had dentition restricted to the tip of their rostrum. Their tooth morphology varied from small peg-like in *Longirostravis* and *Rapaxavis*, to large and strongly recurved in *Longipteryx*. Bohaiornithids (the most diverse family of enantiornithines in the Jehol Biota) had proportionately robust teeth compared to other enantiornithines, which may suggest a more durophagous diet. Some en-antiornithines (e.g. *Monoenantiornis*, *Sulcavis*) reveal enamel wrinkles that may have served to strengthen the teeth.[32]

Cranial morphology further indicates that cranial kinesis (relative movement between the upper jaw and braincase) was likely absent, in-dicating that certain feeding behaviours such as probing were absent in these birds.[33] The skull was robust compared to that of living birds, re-taining a postorbital bone and free squamosal bone.[34] In neornithines, the premaxilla (the bone forming the tip of the rostrum) is expanded, while the maxilla (the bone forming the sides of the rostrum) is reduced. This results in the external nares (nostrils) being retracted (the exception being the Kiwi bird). The external nares in enantiornithines would have been more rostrally located, as the premaxilla was unexpanded in all known taxa except *Gobipteryx*.

In the postcranial skeleton, the morphology of the cervical vertebrae suggests the neck of enantiornithines would have lacked the mobility pres-ent in extant birds, because the articular surfaces were only incipiently heterocoelic. Heterocoeleous vertebrae, which have saddle-shaped articu-

lar surfaces, provide greater flexibility and are characteristic of the neck in living birds. They also lack the diversity of neck proportions observed in extant birds. The enantiornithine neck consisted of only 10–12 vertebrae, compared to 11–25 in neornithines. The sternum was much smaller in enantiornithines, and the keel (the ventrally projecting process of the sternum that provides expanded surface area for the attachment of the large flight muscles) was low and caudally limited in Early Cretaceous taxa, such that the m. *pectoralis* would have been smaller and less powerful in enantiornithines compared to most neornithines. The enantiornithine synsacrum (formed by fusion of the sacral vertebrae) was shorter than that of ornithuromorphs, formed by fewer vertebrae (usually 7 or 8, whereas in neornithines the number can exceed 19), and the pelvis was unfused – both to the synsacrum and, in most cases, at the level of the acetabulum (the hip socket for the femur). The ilium (one of the three bones that forms each side of the pelvis) was proportionately smaller than that of neornithines, and the pubes were not fully retroverted.[35] Although some taxa had proportionately long wings (e.g. *Longipteryx*), no enantiornithines with elongate hindlimbs are definitively known.[36] In most taxa the ratio of the forelimb to hindlimb is close to one.

Most enantiornithines were small birds similar to extant passerines (the large group of extant perching birds that includes all songbirds). Compared to species in the Early Cretaceous, Late Cretaceous taxa occupy a greater size range, ranging from very small forms the size of hummingbirds and up to the largest-known enantiornithines, roughly the size of Turkey vultures.[37] A vast majority of known enantiornithines preserve morphologies that suggest they were arboreal, including an elongate, reversed and distally located hallux (the first pedal digit, which is 'reversed' so that it opposes the rest of the digits in all perching birds) and large, curved pedal claws.[38] All known Early Cretaceous species are interpreted as primarily arboreal, whereas in the Late Cretaceous there appears to be a greater ecological diversity – although because specimens are much more incomplete, habitat is more difficult to ascertain. The Late Cretaceous *Elsornis* was probably flightless based on the shape and proportions of its humerus.[39]

The skeletal morphology of enantiornithines indicates they were clearly capable of powered flight, although skeletal diversity is more limited compared to neornithines indicating they had not achieved the diversity of flight styles observed in modern birds. Early Cretaceous species appear to be mostly intermittent fliers using bounding or flap-gliding flight,[40] although the Bohaiornithidae may have utilized brief continuous flapping.[41] Large Late Cretaceous taxa almost certainly utilized different flight styles, as intermittent flight is restricted to small taxa, although aerodynamic capabilities in Late Cretaceous taxa have yet to be explored, probably because

they are mostly so incomplete. The appearance of advanced skeletal morphologies in the Late Cretaceous, such as an expanded sternal keel and increased pneumaticity (air-filled spaces within bones), indicate improved flight performance, which probably facilitated the increase in body size.

Plumage and Other Soft Tissues

Enantiornithine plumage is fairly well known due primarily to the numerous specimens from Early Cretaceous Lagerstätten preserving a halo of feathers and other soft tissues, resembling fresh roadkill.[42] This extends mostly to general wing shape, the extent of hindlimb feathering, and tail morphology (Illustration 7.1). Body feathers in other regions are poorly known due to overlap. Melanosomes are preserved allowing coloration to be at least partially determined through destructive sampling.

No Late Cretaceous specimen has well-preserved feathers, with the exception of Burmese amber specimens. These three-dimensional amber mummies have revealed that interpretations regarding the structure of the unusual so-called rachis-dominated tail feathers (the rachis is the central shaft of a feather) based on two-dimensional lithic specimens from Early Cretaceous Lagerstätten were completely wrong,[43] and exposed the presence of unusual scales with filamentous projections on the feet,[44] which owing to their extremely delicate morphology and lack of coloration, are unlikely to preserve in other depositional environments. The purpose of these scale-filaments is unknown, although a tactile function has been proposed.[45] These specimens also provide the best information regarding large-scale plumage patterns in the wing.[46]

Early Cretaceous enantiornithines had fairly short broad wings, hindlimb feathers that typically extended to the ankle, and most commonly a complete absence of rectrices (the larger feathers in the tail that are commonly used for steering), with only short contour feathers (feathers that cover the body) around the pygostyle.[47] Body feathers had a wispy appearance and are often described as rachis-less, although it is more likely that a short, thin rachis was present, but obscured by overlap between feathers. Body feathers on the dorsal surface of the body are generally longer than those on the ventral surface. Hindlimb feathers typically decrease in length distal in the limb, ending at the ankle, although fairly long crural feathers (feathers that cover the tibial portion of the leg) are documented in one specimen,[48] and short feathers extending down the tarsometatarsus (the bone of the foot that bears the toes) are present in another.[49] In one Burmese amber specimen, short feathers extend all the way down the toes,[50] as in some extant owls.

Illustration 7.1 Three male *Feitianius paradisi* from the Xiagou Formation displaying for two females in a forest dominated by *Torreya* sp. Acrylic painting, reconstructing *Feitianius* from life, by Michael Rothman. Image © M. Rothman.

The final appearance of some living birds is strongly linked to the orientation of the feathers (e.g. owls). It is possible that such structural morphologies cannot be detected in the fossil record. However, the limited morphological variation observed among enantiornithines compared to that in neornithines suggests such specialized feather morphologies were probably absent in this clade. Due to compression, the body feathers in specimens from lithic Lagerstätten are usually oriented at right angles to the bony surface, and it is nearly impossible to determine their original *in vivo* orientation.[51] As such, the feathers along the dorsal margin of the head project from the skull like a mohawk. In *Protopteryx*, these feathers were described as a cranial crest, interpreted as an *in vivo* feature.[52] However, experiments on extant birds strongly suggest that this is a taphonomic artefact.[53] Similarly, the hindlimb feathers projecting from the tibiotarsus (a compound leg bone formed by fusion of the tibia to the astragalus and calcaneum, the two proximal tarsal bones) have been described as small hindwings, although it is more likely that *in vivo* these feathers hung down, giving the legs a shaggy appearance.[54]

Elongate tail feathers, when present, most commonly consist of a pair of elongate rachis-dominated feathers (RDFs).[55] These unusual feathers consist of an extremely thin C-shaped rachis that, when preserved, flattened in lithic specimens appears proportionately wide, earning these feathers the name 'rachis-dominated'.[56] The feathers are most commonly racket-plumes, feathers in which the pennaceous, vaned portion is distally restricted so that the feather visually resembles a badminton racket, although fully pennaceous RDFs are present in some pengornithids. These tail feathers typically exceed the total body length of the bird. Most often these feathers occur as a single pair, although *Paraprotopteryx* preserves two pairs. These tail feathers have been interpreted as sexually dimorphic ornaments present only in males, which has been supported by their absence in specimens that are identified as female based on the preservation of female reproductive tissues[57] (Illustration 7.2).

A potentially aerodynamic tail shape is only documented in *Chiappeavis*, which preserves a short fan-shaped array of rectrices.[58] UV light photos illuminating the soft tissue surrounding the skeleton indicate an absence of rectricial bulbs – soft tissue structures that include the muscles responsible for tail fanning in extant birds.[59] Without rectricial bulbs to open and close the tail fan, the aerodynamic benefit of this tail shape would be limited.[60] The holotype and only known specimen of *Feitianius paradisi* from the Changma avifauna reveals an elaborate tail morphology consisting of several different feather morphotypes[61] (Illustration 7.1). In living birds, tails with such complex morphologies are most commonly associated with sexual dimorphism and polygamy, indicating the holotype of *Feitianius* is most likely male.

The main aerodynamic surface of the wing is formed by the remiges. Lift in the wing is augmented by patagia, flaps of skin that extend off the forelimb. The propatagium, the flap that extends between the shoulder and wrist, and the postpatagium, the skin flap that extends across the proximal portions of the remiges, evolved outside enantiornithines, being documented in more primitive non-ornithothoracine birds like confuciusornithiforms.[62] In addition to these two patagia, enantiornithines had another skin flap shared with modern birds but not present in more basal lineages. This skin flap, the alular patagium, extends between the alular digit (the bird equivalent of a thumb) and major digit (the longest digit of the avian hand).[63] This feature complemented the alula (also called the 'bastard wing'), a feathered structure only found in ornithothoracines, which extends off the alular digit and is important during take-off and landing.[64]

In the past, it was thought impossible to understand certain aspects of an extinct animal's biology, such as colour. However, in the twenty-first century, it has become possible to at least partially understand colour in extinct feathered organisms through the presence of preserved melanosomes, melanin containing mono-organelles (organelles are subunits within cells).[65] This has resulted in a distinct decrease in the variety of colours employed by artists to reconstruct these animals, and resulted in a rather dreary palette of browns, reddish browns, white, black, and grey (illustrations 7.1 and 7.2). However, this is most likely due to the fact that melanosome-based coloration only accounts for a narrow range of colours, and thus colour reconstructions based entirely on these structures are not providing the complete picture.

Structural colours are responsible for the spectacular range of hues observed in peacock plumage. These colours are imparted by the microstructure of the keratin matrix of the feather, and have yet to be reported in enantiornithines.[66] In most Cretaceous feathers all that is preserved is the decay-resistant melanosomes, while the keratin matrix is heavily degraded or completely lost, preventing identification of structural colour. However, in exceptional conditions structural colour can preserve, as it has been reported in one Late Jurassic non-avian paravian[67] and an Eocene feather,[68] leaving the potential for structural colour to be identified in exceptionally well-preserved enantiornithines in the future. Bright colours are also sometimes produced by pigments, such as carotenoids, which have yet to be found preserved in fossil feathers.[69]

Melanosome-based coloration has only been studied in a few enantiornithines: one specimen of *Protopteryx*,[70] the pengornithid *Yuanchuavis*,[71] and an indeterminant bohaiornithid.[72] These studies reveal the presence of elongate eumelanosomes (elongate melanosomes responsible

for black colour) indicating the plumage was at least partially black. Melanosome-based coloration can vary enormously within a single feather, limiting the utility of this method, which requires a sample of the preserved feather to be extracted so it can be viewed using scanning electron microscopy.[73] Although spots and spangles are rarely preserved in Jehol fossils, such patterns have yet to be documented in any enantiornithine. These spots, usually on the distal tip of the feather, correspond to regions of increased melanization and not necessarily differences in coloration.[74] The tips of feathers are often heavily melanized to reduce feather wear. A juvenile enantiornithine from the Early Cretaceous of Brazil preserves unusual spots on the rachis of its paired RDFs, which have been interpreted as indicative of *in vivo* coloration.[75] However, the rachis is not commonly melanized and no analyses have been conducted to support the interpretation that these spots represent a true feature.

As such, the greatest wealth of information regarding plumage colour and patterning comes from specimens in Burmese amber, which include among their number several partial and complete wings, revealing overall patterns of light and dark coloration.[76] In these specimens the feathers are preserved in various shades of brown, ornamented with pale spots and bands. The brown appearance may be at least partially a product of the yellow of the amber, and might also be due to chemical alterations unique to this preservational medium. However, the large-scale patterns of light and dark areas are considered to reflect *in vivo* morphologies based on the overall consistency of the spots and stripes, whereas if light spots were inferred to be due to degradation their morphology would be expected to be more sporadic. The patterns revealed by these amber specimens suggest crypsis (patterns evolved to avoid detection by other animals), but this may be partially due to the young ontogenetic stage inferred for many of these specimens.[77] Juvenile neornithines are typically more drably coloured compared to their adult counterparts.[78]

Behaviour

Numerous behavioural aspects can be inferred from the fossil record. Tail plumage in at least one enantiornithine suggests polygamy, with males competing to mate with numerous females.[79] This interpretation is supported by the structure of the pygostyle, which suggests the presence of musculature for raising and depressing the ornamental tail feathers.[80] This suggests that male enantiornithines may have engaged in some form of display behaviour like that observed in pheasants (Illustration 7.1). Similarly, the lack of rectricial bulbs indicates that enantiornithines would not

have actively fanned and contracted their tails during flight.[81] The rigid skull morphology, which suggests cranial kinesis was absent,[82] also indicates feeding strategies were limited, because behaviours like mud-probing require a specific form of cranial kinesis called distal rhynchokinesis.[83] The presence of teeth in most taxa also indicates that seed or nut-cracking was also unlikely to have been possible.[84]

A few morphologies are only found in enantiornithines – without extant analogues it is difficult to interpret what these morphologies indicate about behaviour. Two Burmese amber enantiornithines preserve pedal morphologies that are not utilized by the ten thousand (or more) species of living birds. Pedal morphology is a good indicator of ecology and this highlights the unique aspects of the enantiornithine radiation – although many specializations utilized by modern birds did not evolve in enantiornithines, this group evolved to utilize unique morphospace (morphospace refers to representations of the possible form, shape or structure an organism can assume) and may have occupied ecological niches not utilized by birds today, or utilized these ecological niches through different behaviours. For example, one Burmese enantiornithine, *Elektorornis*, preserves a hyperelongated third pedal digit.[85] This has been interpreted as indicative of a probing feeding adaptation. Some living birds also feed by probing but through the use of tools or an elongate tongue. The Burmese enantiornithine *Fortipesavis* preserves soft tissue traces that indicate the presence of an unusually wide fourth pedal digit,[86] which may have increased stability while utilizing mobile purchases similar to the syndactyl foot in alcedinids (kingfishers).[87]

Soft tissue traces indicate that enantiornithines, like modern birds, laid a single egg at a time.[88] Preserved eggs and nests suggest at least some enantiornithines utilized breeding colonies that were situated near a source of water.[89] A humid nesting environment is supported by the microstructure of the eggshell cuticle preserved in *Avimaia*[90] (Illustration 7.2). Eggs were inserted half buried into soft, muddy or sandy substrates, indicating that enantiornithines did not engage in egg turning.[91] This in turn suggest the chalaza, a membrane that keeps the developing embryo in place, was absent. Egg colour, which can now be determined in exceptional specimens using Raman spectroscopy to identify traces of the original pigments, supports inferences that the nests were open.[92] The single Mongolian enantiornithine egg studied so far reveals a pattern of brown speckles. The presence of adult bones together with perinatal bones suggests some amount of parental care, although this may be limited to nest attendance. The discovery of fledged late-stage embryos and hatchlings,[93] highly ossified embryonic remains,[94] and the large number of recovered ju-

Illustration 7.2 Enantiornithine *Avimaia schweitzerae* from the Xiagou Formation, colonially nesting near Poaceae-related plants. Acrylic painting by Michael Rothman. Image © Jingmai O'Connor.

veniles,[95] all together indicate that enantiornithines were highly precocial, capable of flight from the moment they hatched and their feathers dried. This is supported by osteohistological studies of specimens from various ontogenetic stages ranging from late-stage embryo to adult, that indicate enantiornithines mostly grew slowly, taking many years to reach adult size, and achieving reproductive maturity before skeletal maturity.[96] As small arboreal birds, this level of precociality goes beyond even that observed in the so-called super-precocial extant megapodes from Australia, which – although capable of flight from the day they are free from their mound nests – rarely engage in such behaviour, being primarily ground-dwelling birds.[97]

Although traces of diet are abundantly preserved in the Jehol Biota, none that are unequivocal pertain to enantiornithines.[98] This suggests that most enantiornithines from this avifauna fed on soft food items unlikely to preserve. No specimen preserves gastroliths (small stones swallowed to aid digestion) forming a gastric mill further supporting inferences their diet was soft. However, this does somewhat conflict with the apparently durophagous (durophagous predators consume hard-shelled bearing organisms) tooth morphology observed in bohaiornithids. The only enantiornithine that preserves traces of diet is *Eoalulavis* from the Early Cretaceous of Spain, in which traces of aquatic invertebrates are present in the abdominal cavity.[99] This suggests aquatic feeding habits in at least some enantiornithines, which are also suggested by preserved colonial nesting sites, as such colonies are only utilized today by aquatic and semi-aquatic birds.

Habitat

Because enantiornithines are restricted to the Cretaceous, this limits the types of plants that would have coexisted with these birds. Although ferns and gymnosperms (plants with unenclosed seeds such as conifers) would have dominated in the Early Cretaceous, this period documents the sudden appearance of flowering plants (angiosperms) as well as the appearance of grasses.[100] Most enantiornithines are arboreal, meaning they would mostly have inhabited forested environments.[101] The palaeoenvironment of different geologic units can be reconstructed from the type of rock they consist of (which indicates the depositional environment), fossils they contain, and geochemical analyses that hint at temperature and seasonality. The Jehol has produced a rich flora including early flowering plants, and a diverse fauna of insects, mammals, pterosaurs, dinosaurs and other animals that together can be used to create a rich and detailed backdrop for recon-

structions of enantiornithines from this biota in a region of lakes and temperate forest punctuated with volcanic activity.[102] The stomach contents of *Eoalulavis* from Spain suggest this taxon foraged near water, and the Las Hoyas locality is interpreted as an ancient wetland based on fossils and lithology.[103] In addition to feeding on other organisms, enantiornithines would have been preyed upon by others. One *Microraptor* (the so-called tetrapteryx dinosaur) preserves the remains of an enantiornithine in the stomach, indicating that this volant dromaeosaurid (a group of feathered dinosaurs closely related to birds) represented at least one of the many predators faced by Jehol enantiornithines.[104] Enantiornithine remains have also been found in the stomach of an ichthyosaur, although this occurrence is considered to have resulted from scavenging.[105] Notably, this association suggests that some Early Cretaceous enantiornithines lived in near marine habitats. The 100 My forests that produced Burmese amber were also near marine, as evidenced from preserved ammonites.

Conclusions

The enantiornithines have a short scientific history, discovered only forty years ago, and our understanding of this clade has grown enormously over the last three decades. Currently there is ample evidence to accurately reconstruct enantiornithines from their mode of flight, to the overall shape of their plumage, to their life cycle. A vast majority of available data is from the Early Cretaceous Jehol avifauna, with relatively little being known about enantiornithines from other localities. Diet and colour remain poorly known – diet from the lack of preserved evidence and colour from limited investigation. Only three melanosome-based studies have been published so far, and recent discoveries of Burmese amber enantiornithines have only been studied superficially at this time. Due to the high rate of discovery that continues in north-eastern China and to the application of new techniques, our scientific understanding of enantiornithines will continue to grow rapidly, providing rich new biological details with which to reconstruct these birds that dominated the Cretaceous aviary.

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11. Pan et al., 'The Jehol Biota'; Yang et al., 'The Appearance and Duration of the Jehol Biota'.
12. Chiappe and Meng, *Birds of Stone*.
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14. Ibid.
15. Walker, 'New Subclass of Birds'.
16. Zhou and Zhang, 'Mesozoic Birds of China'.
17. O'Connor, Chiappe and Bell, 'Pre-Modern Birds'.
18. Ibid.
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20. Sanz et al., 'The Birds from the Lower Cretaceous of Las Hoyas'.
21. Chiappe and Calvo, '*Neuquenornis volans*'; Chiappe et al., 'A New Enantiornithine Bird'; Atterholt, Hutchison and O'Connor, 'The Most Complete Enantiornithine'; Xu et al., 'A New, Remarkably Preserved, Enantiornithine Bird'.
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28. Ibid.
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59. Chiappe and Meng, *Birds of Stone*.
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68. Vinther et al., 'Structural Coloration'.
69. Thomas et al., 'Seeking Carotenoid Pigments'.
70. O'Connor et al., 'New Information on the Plumage of *Protopteryx*'.
71. Wang et al. 'An Early Cretaceous Enantiornithine Bird'.
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74. Zheng et al., 'Exceptional Preservation of Soft Tissue'.
75. De Souza Carvalho et al., 'A Mesozoic Bird'.
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100. Chang et al., *The Jehol Fossils*; Wu, You and Li, 'Dinosaur-Associated Poaceae Epidermis'.
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105. Kear, Boles and Smith, 'Unusual Gut Contents'.

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