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Fossil Focus: Oviraptorosauria

by Waisum Ma

Introduction:

Oviraptorosauria is a group of theropod dinosaurs that first appeared around 125 million years ago, during the early Cretaceous period. They evolved into diverse forms before being wiped out 66 million years ago in the extinction at the end of the Cretaceous, an event that killed all the non-avian dinosaurs. The first known oviraptorosaurian — called *Oviraptor* — was unearthed in 1923 by the American Museum of Natural History expedition team in the Gobi Desert of Mongolia. It was found near some eggs assumed to be from the dinosaur *Protoceratops*, which led researchers to infer that *Oviraptor* stole the eggs of other species — the name means 'egg thief'. This interpretation was refuted after researchers discovered oviraptorosaurian fossils brooding nests of their own eggs, but this iconic name remains. This is perhaps one of the most well-known incidents in the history of dinosaur research. However, oviraptorosaurians are more than just the main character of this story — they are anatomically and ecologically diverse, and key to the understanding of dinosaur–bird evolution.

Figure 1 —Skull of Incisivosaurus, one of the earliest oviraptorosaurians (IVPP V13326). Image credit: Xing Xu and Waisum Ma.

Definite oviraptorosaurian fossils are known from Asia and North America, comprising more than 40 named genera. Although some fragments found in Argentina and Australia were once classed as oviraptorosaurians, this was later refuted. The earliest known oviraptorosaurian was *Incisivosaurus*, from Jehol Group in northeastern China (Fig. 1). It is a small dinosaur with a skull around 10 centimetres long. However, some oviraptorosaurians became enormous. *Anzu* from Hell Creek Formation in Montana represents the largest known oviraptorosaurian from North American, estimated to be about 3.5 metres long. *Gigantoraptor*, the largest of all oviraptorosaurians (and probably of all bird-like dinosaurs), reached a body length of about 8 metres (Fig. 2A). Both *Anzu* and *Gigantoraptor* belong to a subgroup of oviraptorosaurs called Caenagnathidae, which is one of the two major lineages of later-diverging oviraptorosaurians (the other is Oviraptoridae). Caenagnathids have been discovered in North America and Asia, whereas oviraptorids are only known from Asia. Nemegt Basin of Mongolia is one of the most prolific regions for oviraptorosaurians, yielding *Avimimus*, one caenagnathid and several oviraptorids.

Dinosaurs without teeth

Caenagnathids and oviraptorids are some of the most peculiar dinosaurs. Unlike most of their theropod relatives, they are completely toothless (Fig. 2). Theropods that have lost their teeth are thought to have had a rhamphotheca — a beak made of keratin, as seen in living birds and turtles. Researchers think this because they have found some fossils with exceptionally preserved beaks (including a specimen of the ornithomimosaur *Gallimimus*). Other fossils have numerous holes called foramina at the front of their upper and lower jaws. In modern beaked animals, foramina provide nutrients to the beak, so in extinct dinosaurs they probably had a similar function.

The earliest oviraptorosaurian, *Incisivosaurus*, had teeth in its upper and lower jaws (Fig. 1), although it had fewer teeth than more ancestral theropods. *Caudipteryx*, another oviraptorosaurian that diverged from other species early on, had teeth only at the very front of its upper jaw. Later-diverging groups, such as *Avimimus*, caenagnathids and oviraptorids, are all toothless. However, their skulls were different in other ways. For example, the general shape of caenagnathid and oviraptorid lower jaws, or mandibles, are very different. Caenagnathid mandibles are usually slender with an upturned tip at the front, whereas those of oviraptorids are turned down at the front and more robust in general. Caenagnathids also have a special protrusion in their mandibles called a lingual triturating shelf, which probably helped them to pick up food. This structure is absent in *Avimimus* and oviraptorids, except for a small Mongolian oviraptorid called *Gobiraptor*, which has a weakly developed shelf.

Figure 2 — A, Mandible of caenagnathid Gigantoraptor, the largest known oviraptorosaurian. Image credit: Xing Xu and Waisum Ma. B, Life reconstruction of Corythoraptor, a crested oviraptorid from Ganzhou, southern China. Image credit: Lü et al. (2017).

Some later-diverging oviraptorosaurians have a tall crest on their skulls, similar to that of a cassowary (Fig. 2B), made up of several individual bones. Among the caenagnathids, only one species has been found with a substantial portion of the cranium preserved: *Anzu*, which has a prominent crest. More oviraptorids have been found with a complete cranium, and a number of these are crested. *Rinchenia* and *Corythoraptor* are the best examples of crested oviraptorids (Fig. 2B): their crania are as high as their skulls are long, and sometimes even higher. Given that we can't study the behaviour of extinct animals directly, it remains unclear why some oviraptorosaurians evolved a cranial crest. But by comparing the crests of *Corythoraptor* and cassowaries, researchers have suggested that oviraptorosaurians might have used their crests to attract mates.

Diets of oviraptorosaurians

It is unclear what oviraptorosaurians ate, because their skeletons lack obvious adaptations to a particular diet. The diets of extinct dinosaurs can be inferred using a variety of approaches, one of the most common being looking at their teeth. For example, hadrosaurs had numerous teeth specialized for grinding vegetation, whereas the curved, serrated teeth of dromaeosaurids suggest a carnivorous diet. Some early-diverging oviraptorosaurians that had teeth were preserved with stones in their stomachs, something often seen in herbivorous dinosaurs, implying that they ate vegetation to some extent.

However, there is no direct evidence for the diets of later-diverging oviraptorosaurians, so they have to be inferred by other means. So far, there are two major hypotheses. The first suggests that both caenagnathids and oviraptorids were herbivorous, but that oviraptorids, with their more robust jaws, ate tougher plants. The second hypothesis proposes that oviraptorids were herbivorous, whereas some caenagnathids were omnivorous or even carnivorous. Caenagnathid hindlimbs were adapted for running, and these, along with the upturned tips of their lower jaws, have been considered adaptations for predation. Functional analysis of how their jaws would have moved has also reinforced this hypothesis. Although the diets of caenagnathids are still uncertain, it seems generally accepted that most oviraptorids were adapted to herbivory.

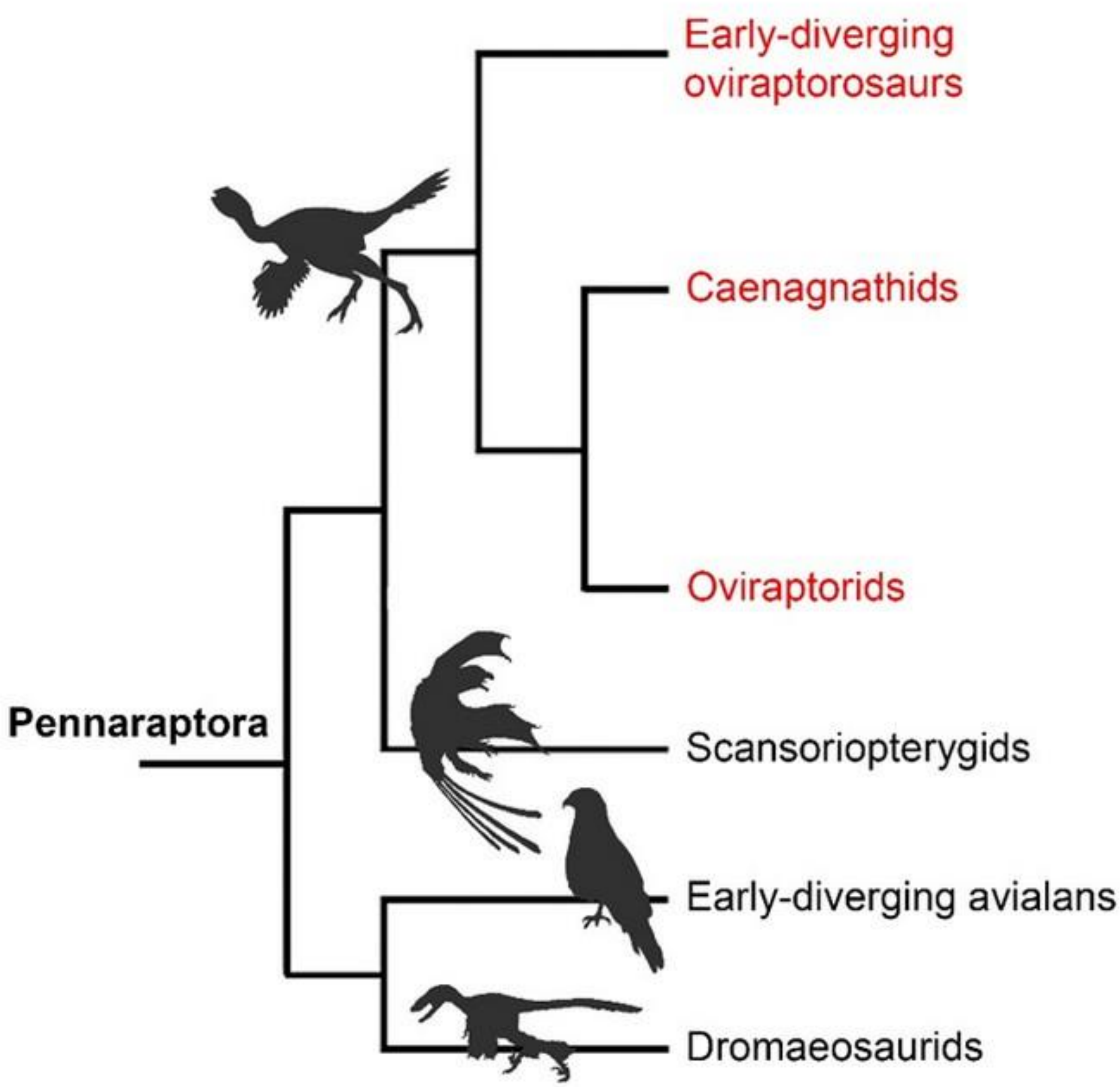

Figure 3 — A phylogenetic tree showing major pennaraptoran groups. Tree topology follows Pei et al. (2020). Silhouette modified from PhyloPic.

Implications for dinosaur evolution

Oviraptorosaurians are always described as bird-like dinosaurs, but they are not birds. Analyses of their evolutionary relationships suggest that Oviraptorosauria are part of Pennaraptora (Fig. 3), a group including the birds and non-avian theropods that possess bird-like feathers with a central quill. Given the close relationship with birds, studying oviraptorosaurians is essential to understanding the ancestral condition of various aspects in early bird evolution, one of which is reproductive biology. Studies of oviraptorosaurian eggs demonstrate that several reproductive features found in birds are also shared by non-avian dinosaurs; these include coloured eggs, ovulation of a single egg per oviduct per time, and egg-brooding behaviour. Oviraptorosaurians have also been used as models for studying the loss of teeth in theropods, a significant macroevolutionary change accompanying the rise of modern birds. Oviraptorosaurians are not the most iconic dinosaurs, but the knowledge stemming from their fossils should not be underestimated.

Suggestions for further reading

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