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Abigail Karparis

University of New Hampshire, Durham

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College of Liberal Arts

Department of Anthropology



The Evolution of Flightless Ratite Birds

by Abigail Karparris

May, 2018

Introduction

Birds are well known for their unique (other than bats) ability among vertebrates of flight. Through millions of years of evolution, before they were even classified as such, and for reasons and methods still largely unknown, birds evolved the ability to fly. However, like all evolution, there is no end goal or final product. Because of this, traits and adaptations evolve and then can disappear if they are no longer beneficial to the organism or would better serve the organism's fitness in a different way. Flight is no exception, and several groups of birds have lost their ability to fly in recent geological time.

An example of flightless birds are the ratites, of the infraclass Palaeognathae. This group includes the extinct moas (Dinornithiformes) and elephant birds (Aepyornithidae) and the living kiwis (Apterygidae), emus (Dromaiidae), cassowaries (Casuariidae), rheas (Rheidae), and ostriches (Struthionidae) (Table 1). It also includes the tinamous (Tinamidae) which are the only family in the Palaeognathae that can fly, if only for short distances (Baker, Pereira, 2009; Mitchell et al, 2014). Because these birds can fly but are still Palaeognathae, they are critical in understanding the evolution of flightlessness and how tinamous fits into the cladistics in this infraclass. These birds are predominately found in the continents and islands of the southern hemisphere, other than some species of extinct Asian ostrich and some tinamous that are found in Mexico (Mitchell et al, 2014; Baker, Pereira, 2009). Other flightless birds like the kakapo, rails, and penguins, have lost their ability to fly much more recently, and their ecology and history can serve as a potential model for the transition back to the ground.

Table 1: The families in the infraclass Palaeognathae

| Common Name | Family | Number of Species | Location |
|----------------|------------------|-------------------|---------------|
| Elephant Birds | Aepyornithidae | 7 (all extinct) | Madagascar |
| Moas | Dinornithiformes | 9 (all extinct) | New Zealand |
| Emus | Dromaiidae | 1 | Australia |
| Cassowaries | Casuariidae | 3 | Australia |
| Rheas | Rheidae | 2 | South America |

| | | | |
|-----------|---------------|----------------|-----------------------------------|
| Ostriches | Struthionidae | 10 (8 extinct) | Southern Asia and Mainland Africa |
| Kiwis | Apterygidae | 5 | New Zealand |
| Tinamou | Tinamidae | 47 | Mexico, Central/South America |

Unique Physical Features

The evolutionary process of returning to the ground and losing the ability to fly, is more extensive than just the shrinking of wings. Ratite are unique in many other ways and have special characteristics that set them apart from other birds. Their wings have become small and vestigial, unable to support the often times proportionally larger bodies of the birds in this group (McNak 1994). In most ratite, they are nearly invisible through human eye sight alone (Maxwell, Larsson, 2007). Ostriches are the exception, and as can be seen in Figure 1, they diverged first from the rest of the Palaeognathae (Baker, Pereira, 2009; Mitchell et al, 2014). Although they still cannot fly, ostriches have large wings that are used in mating rituals and in defensive displays (Baker Pereira, 2009). All birds that fly have a keeled sternum, which is a large chest bone that anchors the strong muscles required for flight (Maxwell, Larsson, 2007). Ratite lack this keel because they do not need the strong muscles to support wings that do not exist. Tinamou are the only group in the Palaeognathae that have retained this keel, because they continue to fly, albeit not very well (Baker, Pereira, 2009).

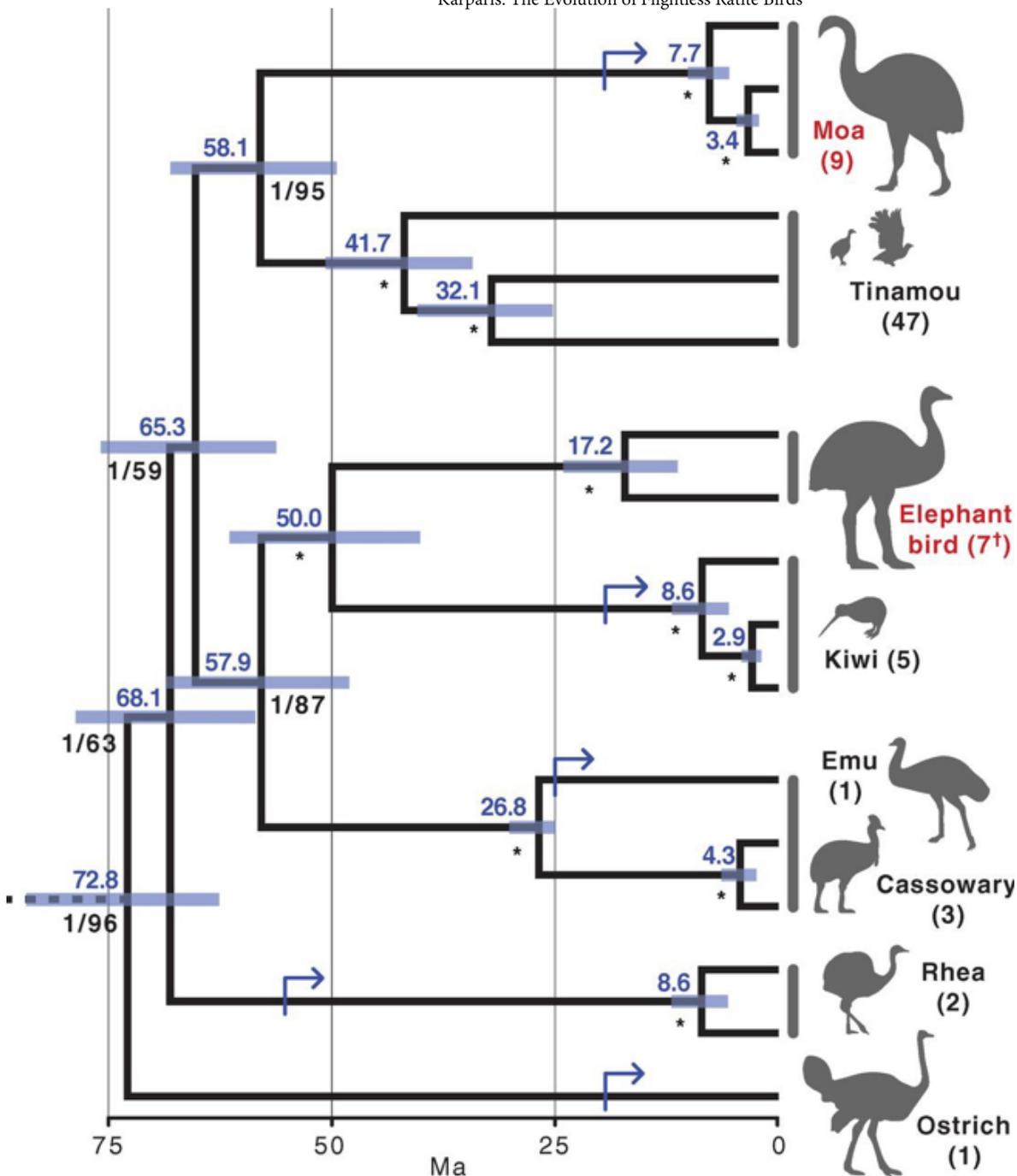


Figure 1: A cladogram for the infraclass Palaeognathae (Mitchell et al, 2014)

Because ratite do not need the hollow, light bones to fly that other birds have, their bones have become thicker. This is most apparent in their legs, which lack the traditional air chambers that other birds have (Alexander, 1983). This is an adaptation that resulted after increased dependence on the legs for transportation and defense as opposed to the wings for transportation and evasion. An organism that breaks its leg but relies on its legs for transportation and thus survival will likely result in death. Thicker stronger legs break less easily, are more adequate as a defense mechanism through kicking and clawing, which most ratite employ, and are stronger for running and walking on land (Cubo, Arthur, 2001). Their dependence on walking as a form of mobility is also apparent in their young, who are born far more developed than their aerial counterparts, and can run shortly after birth. An organism that is closer to the ground is at greater risk of predation early on in its life. It does not have the security of being high up in the trees and thus ratite also have a thicker egg shell to protect their unhatched offspring from predators. These birds tend to

have smaller clutch sizes as well, and protect their offspring more. In 2006, McNab and Ellis found that flightless rails had clutch sizes half the size of flighted rails due to the tremendous energy it takes to produce eggs. Laying less eggs, and then protecting those eggs increases fitness for life on the ground (McNab, Ellis, 2006).

Perhaps the most universally distinctive characteristic among Palaeognathae is their palate and nasal cavity structure. It is very complex, and not fused together, unlike other birds, and is more akin to that of reptiles and dinosaurs (Gussekkloo, 2000). This is associated with a better sense of smell; which most other birds do not have. Like reptiles, Palaeognathae are mostly ground dwelling and when they diverged from the same common ancestor that all reptiles and birds diverged from, they also retained their sense of smell that other birds lost (Gussekkloo, 2000). A strong sense of smell is not a necessary trait for animals that live in the air, because they can rely on sight and sound more, as they are often above most things. Organisms that live on the ground need smell to detect predators and prey that they cannot necessarily see.

Reasons for the Loss of Flight

It seems strange that evolution would abandon a trait like flight that provides an organism with a distinct advantage in attaining resources and fulfilling its niche. There are several theories on why this occurred, and it also depends on the location where they are found. The most dominant and widespread theory is that after the Cretaceous-Paleogene Extinction 66 million years ago, where three quarters of the earth's species went extinct, opening up many new niches in the absence of species. Proportionally, more species of birds survived, enabling them to fill those niches over time (Feduccia, 1995). The time shortly after the K-Pg extinction also correlates with an increased diversification of ratite, which can be seen in Figure 1 (Mitchell et al, 2014). This further supports this theory, because organisms would diversify to fill the vacant niches. These niches would have previously been occupied, predominantly by large reptiles, which could not fly. This meant the ratite that filled them, lost their ability to fly, and became more reliant on their feet for transportation (Feduccia, 1995). It also correlates with an increase in overall size, as ratite are and were some of the largest birds.

After the birds began to fill those niches, their reliance on flight would have decreased. It is inefficient to supply a part of the body that is not being used with energy for tissue. Limited resources cannot be wasted on wings that are not used, they have to be allocated for other things that are necessary for life. Eventually, birds with smaller wings would have had a higher efficiency of resource use and thus fitness, resulting in the population's overall wing size to decrease over time until their wings were functionally non-existent. This theory is supported by McNab's research in 1994, where he looked at the basal rate of metabolism and compared them to both the loss of flight and the loss of pectoral muscles connected to the keel. He found that birds that lost the ability to fly, but continue to use their wings, so they still have the developed pectoral muscles, are not more energy efficient. This would include birds like penguins, that can no longer fly, but use their wings for swimming, so they retained their keel and strong chest muscles. Conversely, he found that energy conservation does contribute to the evolution of birds that do not use their wings for anything and therefore do not have developed pectoral muscles or a keel, like in the ratite (McNab, 1994). Another study showed similar results, that starlings that foraged on the ground were more energy efficient than those that did in the air, expressing that when the niche is available, it is more efficient to live on the ground than in the air (Bautista, et al, 2000).

How it Happened

There is no shortage of disagreement as to when the loss of flight occurred in the ratite. Some believe that last common ancestor could fly and several different losses of flight occurred in several different places leading to convergent evolution while others believe the last common ancestor could not fly, which is the prevailing belief (Harshman et al. 2008). Still others believe that the Palaeognathae ancestors never actually had the ability to competently fly, meaning ratite never actually lost flight at all. It is

unknown if they lost flight before Gondwana broke up, or after, and there is evidence supporting both arguments, suggesting both may be true to some extent.

Cooper et al. (1992) suggests that common ancestors could fly, and this allowed them to colonize the parts of Gondwana after they had separated. This is supported by the kiwis and moa of New Zealand. Because of New Zealand's isolation (Figure 2), one would expect that kiwi and moa would have a more recent common ancestor than that of other ratite, and therefore be more closely related. However, Cooper et al. sequenced DNA from both families and found that this was not the case. Instead, kiwis are more closely related to emus and cassowaries of Australia, and the extinct elephant birds of Madagascar. Mitchell et al (2014) also found similar results. This may suggest two colonizations of New Zealand by ratites. They suggest that, due to fossil records, moa were there first, isolated by continental drift, and that kiwi later moved to New Zealand, perhaps by flying. This would conflict with the theory that all ratite derived from a common flightless ancestor, and instead support that flight has been a part of the ratite evolution since the least common ancestor.

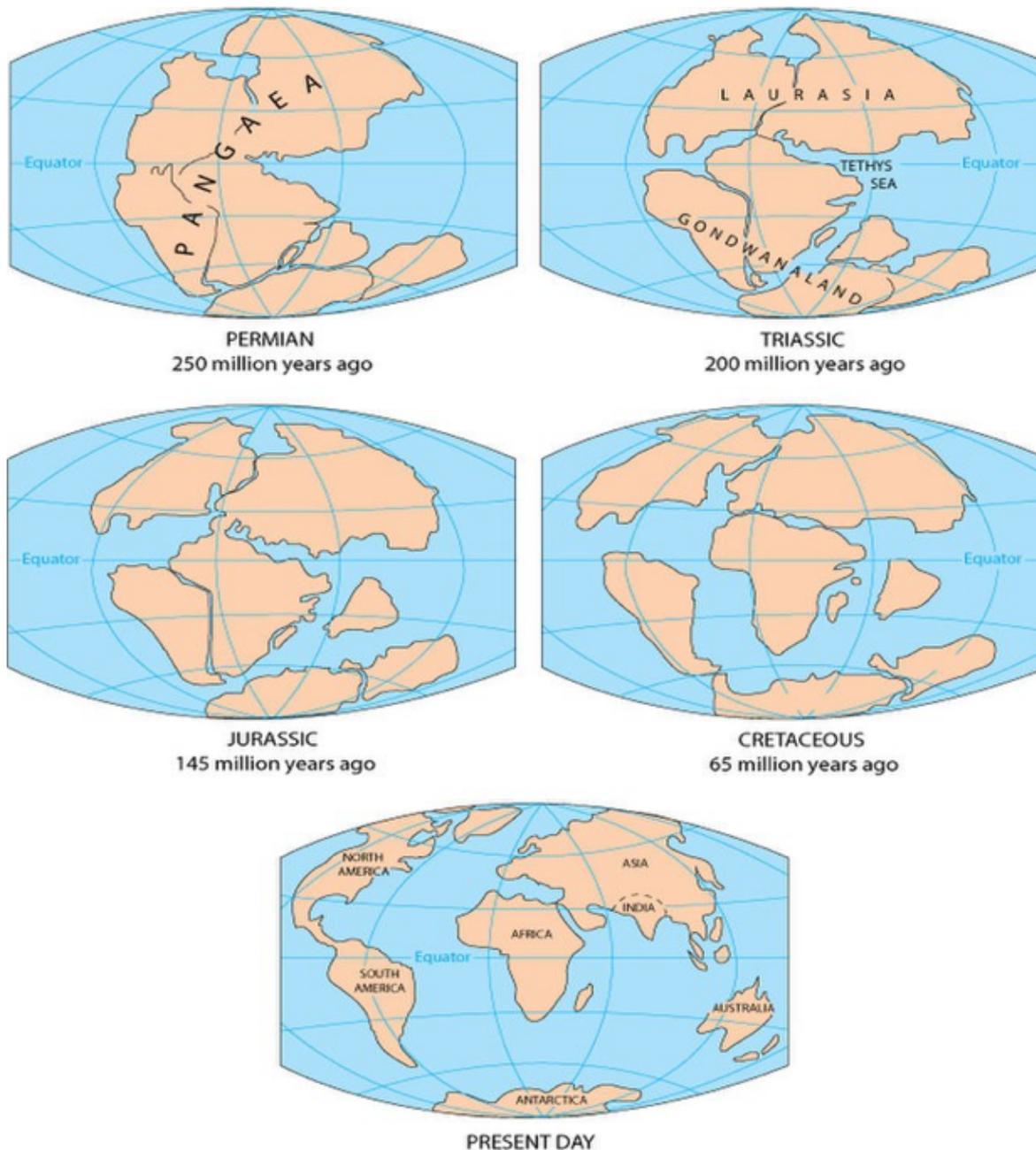


Figure 2: Maps showing continental drift since 250 million years ago (livescience.com)

A study done by Cubo and Wallace (2001) suggests that multiple occurrences of the loss of flight could happen relatively easily, and still result in the remarkable similar skeletal structure that all ratite have. Through analyzing bones of many different flightless birds, not only ratite, they discovered that they all have less developed chest muscles and more developed pelvic muscles and legs. These show that convergent evolution of flightless birds produces remarkably similar results in structural resemblance and functionality. This means it may be possible for multiple instances of the loss of flight to occur in ratite, and that the last common ancestor could have been able to fly. Flightlessness can occur in short time frames. Rails have lost the ability to fly after flying to small pacific islands in generations as oppose to the millions of years it is believed to only occur in (McNab, 1994 which shows that a bird like the ancestral kiwi, could have flown to New Zealand and then lost its ability to fly.

A study that analyzed the mitochondrial DNA of all ratite by Harshman et al. (2008) suggested three separate losses of flight. They found that the clade containing rheas, emus, and cassowaries had a common ancestor that lost the ability to fly, and that kiwis and elephant birds may be included in this group but also could have lost the ability to fly independently which concurs with Cubo and Wallace (2001). It is also suggested that ostriches lost flight independently and rheas did as well. They were unable to definitively place tinamou in any clade, because different methods and analyses put them in different places. However, they do state that there are no documented cases of a bird losing and regaining the ability to fly and so it is likely that it diverged before the common ancestor of a clade lost the ability to fly.

Conclusion

The Palaeognathae infraclass has long puzzled scientist because of its almost universal loss of flight across all of the continents in the southern hemisphere. With the exception of the tinamou, all other members, collectively known as ratite, are entirely flightless and lack the keel which anchors flight muscles to the chest, and have a number of other unique traits that are common among all families. It is thought that all of these families, including the tinamou, derived from one flightless common ancestor, however recent skeletal structure comparisons, DNA analysis, and geographic investigations, have suggested that multiple losses of flight occurred among the ratite. Although it seems unlikely that nearly all the families would independently lose the ability to fly, there may have been some aspect of the infraclass that enabled its members to more readily fill the niches left by the K-Pg extinction, and predispose them to a loss of flight. Perhaps their unique palate and nasal structure gave them an edge in finding food on the ground which enabled them to outcompete birds of the Neognathae infraclass for the ground dwelling, flightless niches. There is still abundant debate and further research and discovery is still needed to definitively map out the cladistics of the Palaeognathae infraclass, when their loss of flight occurred, and where it occurred.

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Department of Anthropology | Phone (603) 862-1864 | Fax (603) 862-1131
310 Huddleston Hall | 73 Main Street | Durham, NH 03824

College of Liberal Arts • 603-862-2062
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