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Review

The Evolution and Fossil Record of Palaeognathous Birds (Neornithes: Palaeognathae)

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Abstract: The extant diversity of the avian clade Palaeognathae is composed of the iconic flightless ratites (ostriches, rheas, kiwi, emus, and cassowaries), and the volant tinamous of Central and South America. Palaeognaths were once considered a classic illustration of diversification driven by Gondwanan vicariance, but this paradigm has been rejected in light of molecular phylogenetic and divergence time results from the last two decades that indicate that palaeognaths underwent multiple relatively recent transitions to flightlessness and large body size, reinvigorating research into their evolutionary origins and historical biogeography. This revised perspective on palaeognath macroevolution has highlighted lingering gaps in our understanding of how, when, and where extant palaeognath diversity arose. Towards resolving those questions, we aim to comprehensively review the known fossil record of palaeognath skeletal remains, and to summarize the current state of knowledge of their evolutionary history. Total clade palaeognaths appear to be one of a small handful of crown bird lineages that crossed the Cretaceous-Paleogene (K-Pg) boundary, but gaps in their Paleogene fossil record and a lack of Cretaceous fossils preclude a detailed understanding of their multiple transitions to flightlessness and large body size, and recognizable members of extant subclades generally do not appear until the Neogene. Despite these knowledge gaps, we combine what is known from the fossil record of palaeognaths with plausible divergence time estimates, suggesting a relatively rapid pace of diversification and phenotypic evolution in the early Cenozoic. In line with some recent authors, we surmise that the most recent common ancestor of palaeognaths was likely a relatively small-bodied, ground-feeding bird, features that may have facilitated total-clade palaeognath survivorship through the K-Pg mass extinction, and which may bear on the ecological habits of the ancestral crown bird.

Keywords: Palaeognathae; ostrich; tinamou; ratite; emu; kiwi; moa; elephant bird; rhea; Lithornithidae

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1. Introduction

Crown birds (Neornithes) comprise roughly 11,000 extant species [1]. They are divided into the reciprocally monophyletic Palaeognathae and Neognathae, with the latter including the hyperdiverse clade Neoaves [1]. At no point in time do total group palaeognaths appear to have been particularly diverse, especially in comparison with contemporaneous neognath diversity. Despite their relatively sparse taxonomic diversity, however, the position of palaeognaths as the sister group to all other neornithines makes them critical to efforts to understand the early evolutionary history of crown birds. Palaeognathae is diagnosed by several traits including a unique palatal structure characterized by enlarged basipterygoid processes and fused pterygoids and palatines (Figure 1), a grooved rhamphotheca, a single articular facet for the otic capitulum of the quadrate, and open ilioischiadic foramina (Figure 2) [2–6]. The palatal structure of palaeognaths was traditionally considered plesiomorphic for Neornithes [7], though recent evidence regarding the palatal structure of the near-crown Ichthyornithes may indicate that the palaeognathous palate is in fact a synapomorphy of Palaeognathae [8,9].

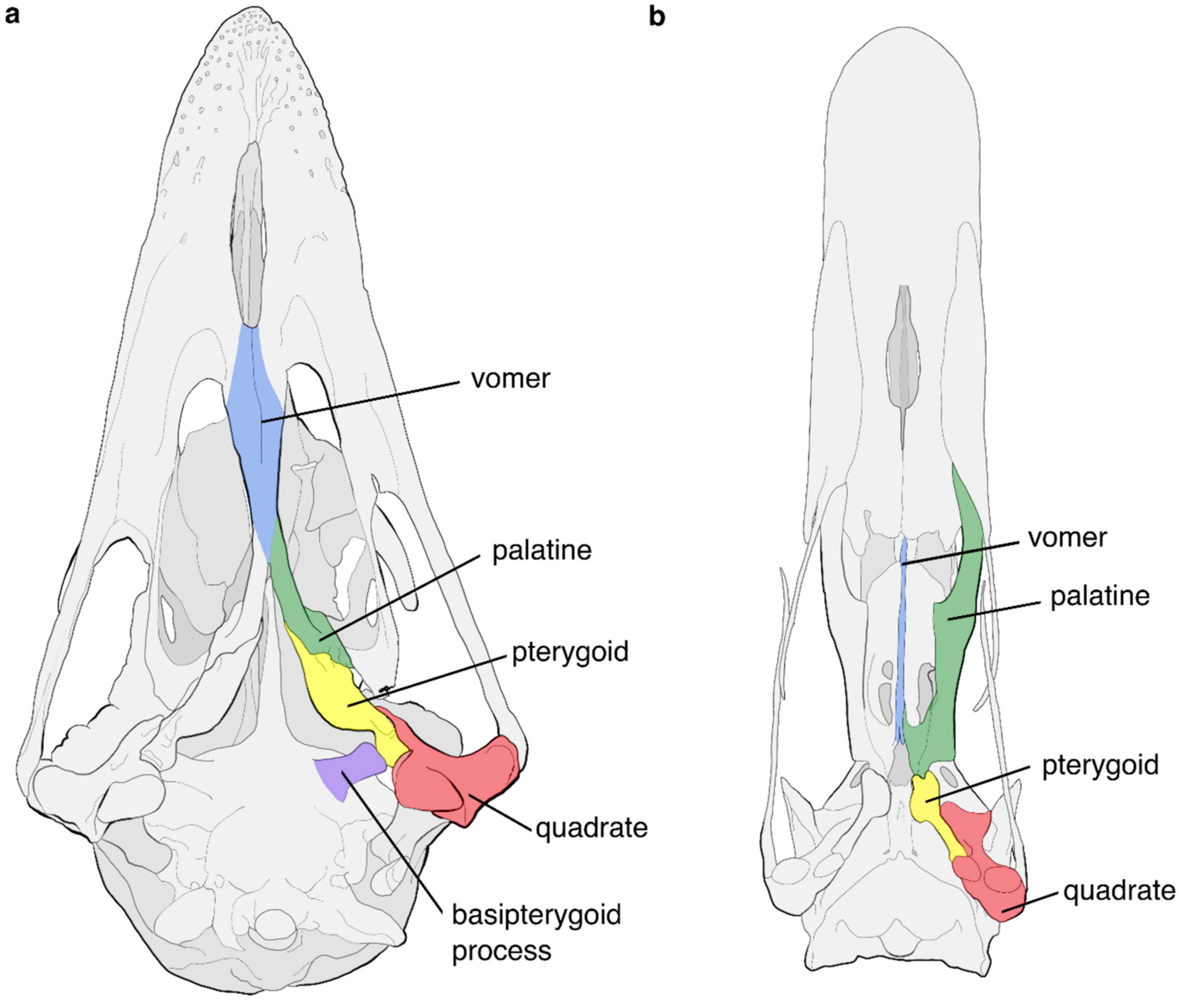

Figure 1. Comparison of the palate of a palaeognathous and a neognathous bird. (**a**) Palate of the palaeognathous Emu *Dromaius novaehollandiae*. The basipterygoid process is elongate, and the pterygoid and palatine are fused (demarcation between them is approximate). (**b**) Palate of the neognathous Mute Swan *Cygnus olor*. The pterygoid and palatine are connected by an intrapterygoid joint, and the short basipterygoid processes are mostly obscured by the pterygoids.

Extant palaeognaths are represented by 46 species of tinamou (Tinamidae) and two species of rhea (Rheidae) in Central and South America, two species of ostrich (Struthionidae) in Africa, the monotypic emu and three species of cassowaries (Casuariidae) in Australia and New Guinea, and approximately five species of kiwi in New Zealand (Apterygidae) [10]. Nine species of moa (Dinornithiformes) [11] and four species of elephant bird (Aepyornithidae) [12] survived into the Holocene in New Zealand and Madagascar respectively, before their extinction which may have been related to human activity that had a disproportionate impact on insular flightless birds [13].

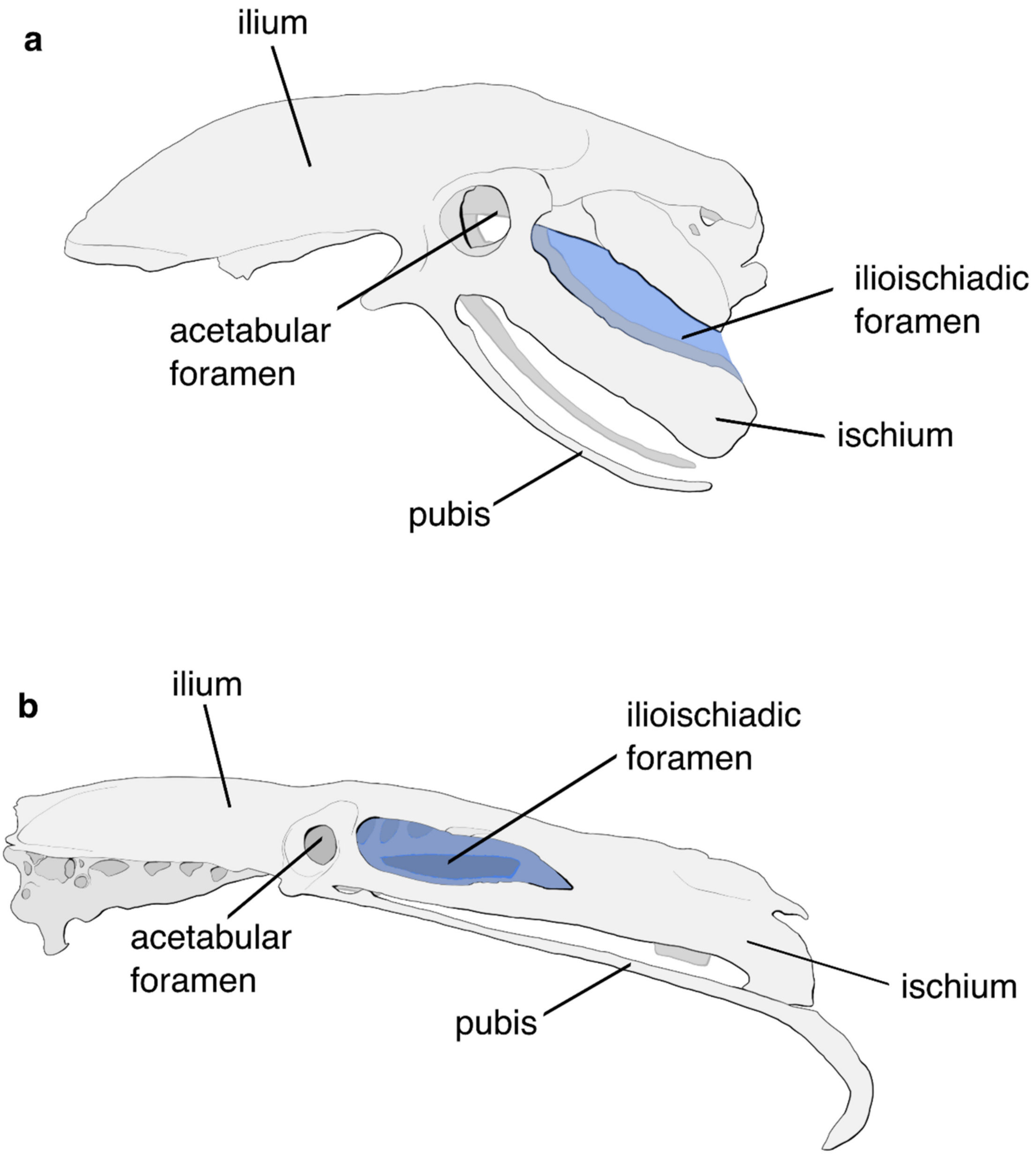

Figure 2. Comparison of the pelvis of a palaeognathous and a neognathous bird. The ilioischiadic foramen is highlighted in blue. (**a**) Pelvis of the Little Spotted Kiwi *Apteryx owenii*. The ilium and ischium are unfused throughout their lengths, leaving the ilioischiadic foramen open. (**b**) Pelvis of the Mute Swan *Cygnus olor*. The ilioischiadic foramen is closed due to the fusion of the posterior ilium and ischium.

Despite being relatively species-poor, extant and recently extinct palaeognaths encompass an impressive range of body sizes and ecologies. The group contains both cursorial open habitat specialists (e.g., emu) and graviportal forest dwellers (e.g., cassowaries), and feeding strategies ranging from cryptic nocturnal invertivores (e.g., kiwi) to megaherbivorous browsers (e.g., moa). Out of all extant palaeognaths, only tinamous (Tinamidae) are capable of flight [14]. This clade comprises small to medium-sized birds, ranging from 43 g in the smallest species (the Dwarf Tinamou *Taoniscus nanus*) [15], to 2080 g in the largest females of the Gray Tinamou (*Tinamus tao*) [16]. By contrast, flightless palaeognaths, from here on referred to collectively as “ratites” (acknowledging the paraphyletic nature of the group), are renowned for their gigantism. The Common Ostrich *Struthio camelus* is the world’s largest extant bird in both height and weight, with large males reaching sizes up to

2.8 m and 156 kg [17]. Recently extinct ratites were even larger: A body mass of 860 kg was estimated from femur measurements of an exceptionally large individual of the elephant bird *Vorombe titan*, making this species the heaviest-known bird ever discovered [12]. Females of the moa *Dinornis robustus* were less massive but appear to have constituted the tallest birds yet discovered, attaining heights of 3.6 m [18,19].

Several early authors argued that 'ratites' represented a non-monophyletic assemblage of large-bodied, flightless birds, and debate regarding the potential non-monophyly of ratites persisted through much of the 20th Century [4,20–24]. Opinion shifted with the widespread acceptance of continental drift theory in the latter half of the 20th century, as a monophyletic "Ratitae" became enshrined as a classic example of Gondwanan vicariance biogeography, a hypothesis stipulating that stem group ratites became flightless prior to the breakup of Gondwana, and that Gondwanan fragmentation drove the divergence of the extant ratite lineages as populations became geographically isolated from one-another [25–27]. This hypothesis of a monophyletic "Ratitae", sister to Tinamidae, was supported by a number of phenotypic features such as the absence of a triosseal canal and sternal keel, and the presence of a fused scapulocoracoid (Figure 3) [5]. Indeed, the term "ratite" refers to the flat, raft-like sterna of taxa lacking a sternal keel (Figure 4) [28]. This consensus opinion was upheld for several decades by most phylogenetic analyses of morphological characters [29–31], though analyses of cranial characters recovered alternative relationships [32–34]. However, over the past twenty years, molecular phylogenetic analyses have forced a wholescale revision of the Gondwanan vicariance paradigm of palaeognath evolution and historical biogeography. Evidence from analyses of both nuclear [35–43] and mitochondrial DNA [41,42,44–46], as well as large-scale phylogenomic analyses [47–50], demonstrate that tinamids are in fact phylogenetically nested within ratites, rendering "Ratitae" paraphyletic, once again reviving the early hypothesis of ratite non-monophyly [4,20–24] (Figure 5).

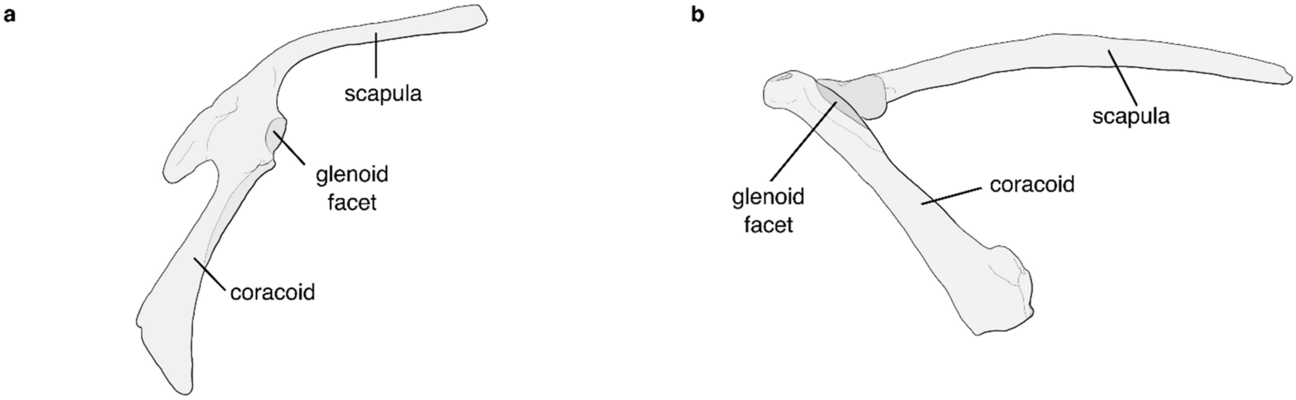

Figure 3. Comparison of the shoulder girdle of a flightless palaeognath displaying the fused 'ratite' condition, and that of a volant palaeognath in left lateral view. (**a**) Fused scapulocoracoid of the flightless Greater Rhea *Rhea americana*. (**b**) Unfused scapula and coracoid of the volant Andean Tinamou *Nothoprocta pentlandii*.

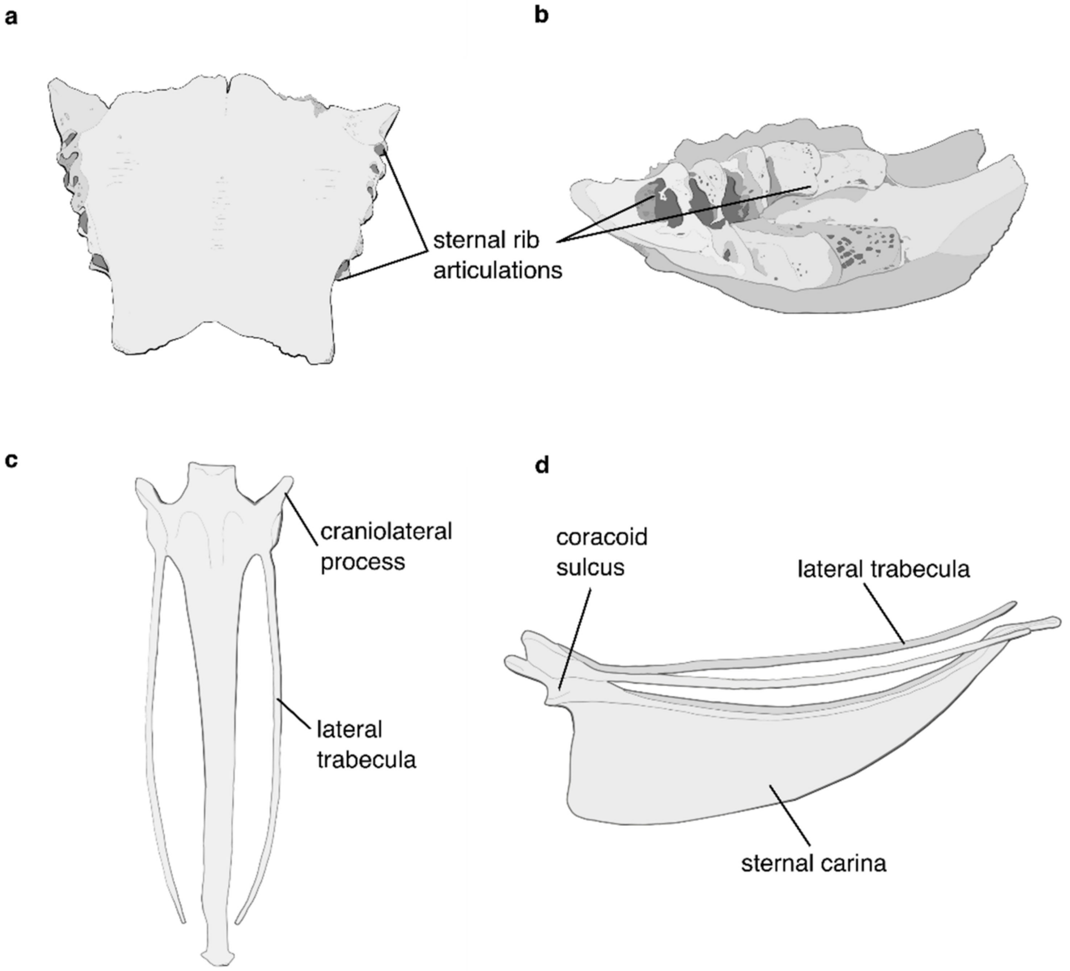

Figure 4. Comparison of the sterna of a flightless palaeognath, the Common Ostrich *Struthio camelus* and a volant palaeognath, the Andean Tinamou *Nothoprocta pentlandii*. (**a**) Sternum of *S. camelus* in dorsal view. (**b**) Sternum of *S. camelus* in left lateral view. A sternal keel is absent. (**c**) Sternum of *N. pentlandii* in dorsal view. (**d**) Sternum of *N. pentlandii* in left lateral view. A deep sternal keel provides an attachment area for the pectoralis and supracoracoideus muscles.

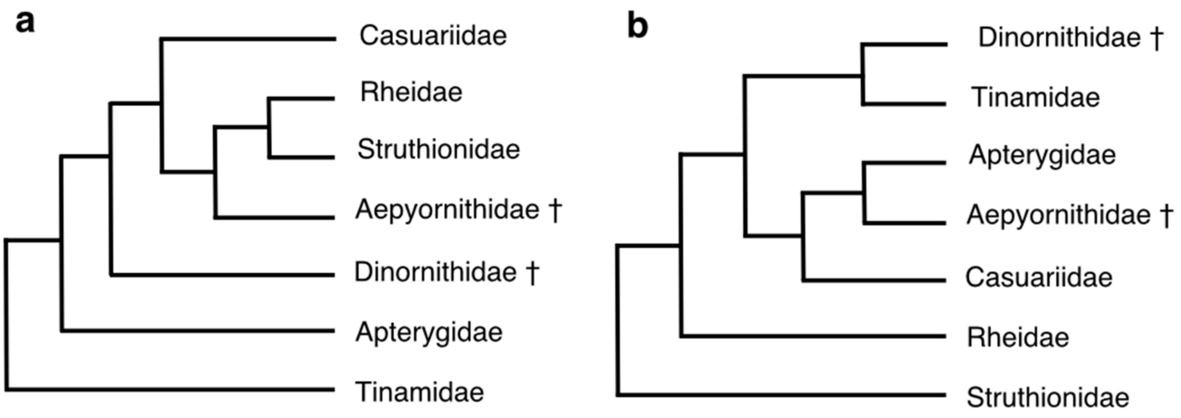

Figure 5. Old and new hypotheses of palaeognath interrelationships. Extinct clades are indicated by †. (**a**) Ratite monophyly based on the morphological study of Livezey and Zusi [30]. (**b**) Molecular phylogeny suggesting ratite paraphyly recovered by Mitchell, et al. [45], Grealy, et al. [41], Yonezawa, et al. [49], Urantówka, et al. [46], and Almeida, et al. [42].

The most parsimonious interpretation of this revised tree topology would be that the most recent common ancestor of crown Palaeognathae was flightless, with a reacquisition of flight arising along the tinamou stem lineage. This interpretation is indeed favoured by maximum likelihood analyses [44] and cannot be definitively rejected; however, this hypothesis would seem to be unlikely from first principles (after all, strong evidence exists for only four independent acquisitions of powered flight throughout the entire evolutionary history of animals [51]). By contrast, multiple independent transitions to flightlessness within the same crown bird subclade are not uncommon. For example, flightlessness has arisen dozens of times in Rallidae among island-dwelling taxa [52,53]. According to some recent molecular topologies, transitions to flightlessness arose a minimum of six times in palaeognaths, and transitions to gigantism a minimum of five [41,45].

The recent revival of a phylogenetic hypothesis stipulating that ratites repeatedly and independently lost the capacity to fly has largely been driven by molecular phylogenetic analyses [36–46,48–50,54–58], but has accrued supporting evidence from independent datasets. For instance, embryological studies have demonstrated important differences in patterns of wing growth among ostriches and emu, suggesting that alternative heterochronic mechanisms may underlie the acquisition of flightlessness in disparate ratite taxa and potentially supporting independent evolutionary transitions to flightlessness among ratites [59]. Furthermore, misexpression of the cardiac transcription factor *Nkx2.5* is associated with reduced wing growth in chicken embryos, and this transcription factor is expressed in the wings of emu embryos but not ostriches—again indicating the potential non-homology of flightlessness in emu and ostriches [60]. Sackton, et al. [50] found that many similarities in ratite forelimb morphology may be the result of convergence in gene regulatory networks, rather than the product of homologous changes to protein coding genes. Overall, the existing body of evidence is congruent with the hypothesis that ‘ratites’ are indeed paraphyletic, and have repeatedly converged on a suite of remarkably similar morphologies that were long interpreted as synapomorphies for the group. Much remains to be understood about the underlying drivers of these independent transitions to large size and flightlessness, as well as the developmental underpinnings of convergent ratite morphologies.

The recognition of ratite paraphyly, coupled with phylogenomic time trees that indicate an origin of crown palaeognaths long after the breakup of Gondwana commenced (e.g., [41,42,45,48,49,55]), makes the classic vicariance hypothesis untenable. Instead, present-day palaeognath biogeography must be the product of dispersal of volant ancestral palaeognaths to multiple landmasses preceding independent origins of flightlessness (Figure 6). However, this interpretation raises many questions regarding the nature of the volant last common ancestor of crown palaeognaths. Tinamous are the only extant volant palaeognaths available for reference, but they are primarily ground-dwelling and are only capable of flight over relatively short distances to flee predators or roost in trees [14,61]. It is difficult to imagine a burst-flying tinamou-like bird undertaking the transoceanic journeys needed to explain the distribution of extant palaeognaths (Figure 6), thus they would appear to be a poor analogue for hypothetical dispersive ancestral palaeognaths. Fossil evidence further suggests that the specialized burst flying of extant tinamous was not plesiomorphic for palaeognaths. The extinct lithornithids (Lithornithidae), known from the Paleocene and Eocene of Europe and North America, were apparently volant and appear to represent the oldest and most stemward known total-clade palaeognaths [49,62–65]. Importantly, they also appear to have been more capable long-distance fliers than extant tinamids are [62,65], and, as the earliest known palaeognaths in the fossil record, they may provide the best models for informing reconstructions of the dispersive ancestral palaeognaths that gave rise to extant palaeognath diversity.

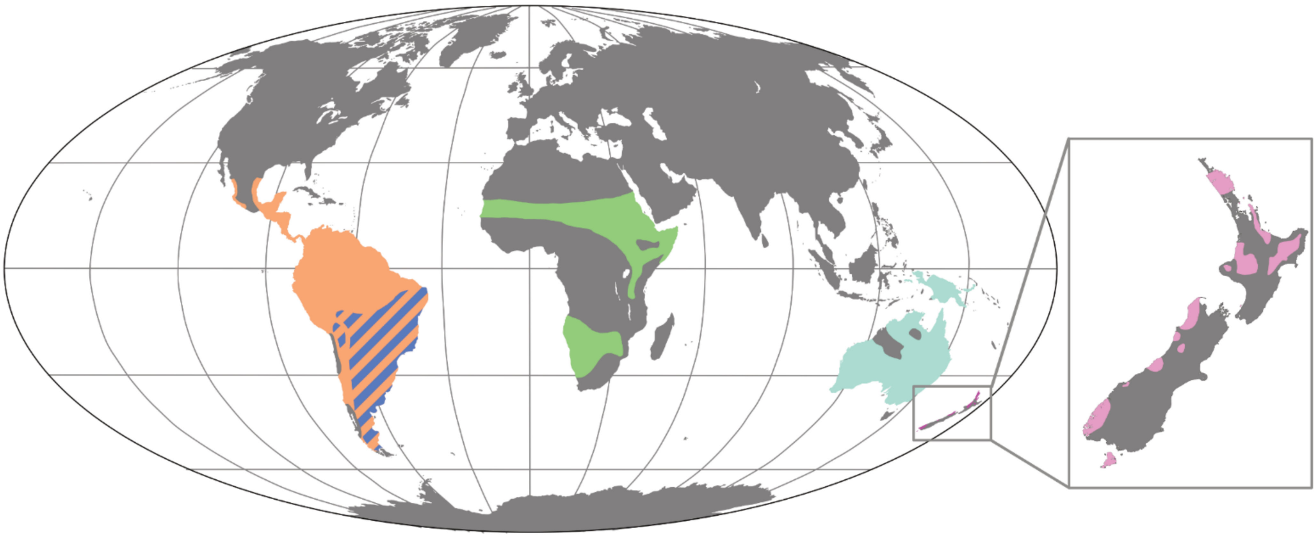

Figure 6. Present-day geographic ranges of extant palaeognath subclades. Range of Rheidae in dark blue, Tinamidae in orange, Struthionidae in green, Casuariidae in aqua, and Apterygidae in pink [10,14,66–68].

In order to probe deeper into the origin and early evolution of total group Palaeognathae, an in-depth understanding of the palaeognath fossil record is necessary. Early fossil palaeognaths are rare, and the phylogenetic interrelationships among them are poorly understood. For example, the monophyly and phylogenetic position of lithornithids are debated, and thus their relevance for clarifying the pattern and timing of the extant palaeognath radiation remains unclear. Due to the phylogenetic position of palaeognaths as the extant sister taxon of all other Neornithes, stem palaeognaths, which may include lithornithids, should provide key insight into the nature of the ancestral crown bird. Recent time-scaled phylogenies suggest that total-group palaeognaths were one of just a small number of extant neornithine lineages that passed through the Cretaceous-Paleogene (K-Pg) mass extinction event (e.g., [48,69–72]). A better understanding of the ecology and biology of early stem palaeognaths could therefore help clarify the biological attributes of avian survivors of the end-Cretaceous mass extinction, which appears to have eliminated all non-neornithine avialans [73]. Early palaeognath fossils from around the world will also be critical for illustrating how the remarkable convergent evolution of flightlessness and gigantism arose among crown palaeognaths, as well as providing insight into the biogeographic origins of extant palaeognath subclades and their responses to Cenozoic shifts in climate and environment [74,75].

Here, we summarize the current state of knowledge regarding the palaeognath fossil record. Useful reviews on palaeognath fossils and the evolutionary history of this group have previously been published, e.g., [76–78], and we refer interested readers to these excellent summaries, but the present review is the first attempt to systematically address the fossil record of palaeognaths in its entirety. We present the most specific locality data reported in the literature for each fossil occurrence, necessarily limited by the differential specificity available for certain records. We outline key lingering gaps in the known palaeognath fossil record, and suggest potential ways forward in hopes of narrowing those gaps. In addition, we provide an overview of strong inferences about palaeognath macroevolution that can be made on the basis of current molecular phylogenies and estimated divergence times, and summarise what can be reasonably inferred about the most recent common ancestor of crown group palaeognaths. We hope that this review provides both a solid base of information for those interested in the evolution and fossil record of palaeognaths, and helps inspire further work clarifying the evolutionary history of these remarkable birds.

Institutional abbreviations are as follows: AM—Australian Museum, Darlinghurst, Australia; AIM—Auckland Institute and Museum, Auckland, New Zealand; AMNH—American Museum of Natural History, New York, New York, USA; AU—Auckland University, Auckland, New Zealand; AUG—Aristotle University School of Geology, Thessaloniki, Greece; BGR—Bundesanstalt für Geowissenschaften Und Rohstoffe, Hanover, Germany; CICYTTP—Centro de Investigación Científica y de Transferencia Tecnológica a la Producción, Diamante, Argentina; CPC—Commonwealth Palaeontological Collections, Canberra, Australia; DK—Danekrae collections, Geological Museum, University of Copenhagen, Copenhagen, Denmark; FMNH—Field Museum of Natural History, Chicago, Illinois, USA; GHUNLP—Universidad Nacional de La Pampa, Santa Rosa, Argentina; GMB—Geological Museum of Budapest, Budapest, Hungary; GMH—Geiseltalmuseum, Martin Luther University, Halle, Germany; HLMD—Hessisches Landesmuseum, Darmstadt, Germany; IGM—Institute of Geology, Mongolian Academy of Sciences, Ulaan Baatar, Mongolia; IRSNB—Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; IVPP—Institute of Vertebrate Paleontology and Paleoanthropology, Beijing, People's Republic of China; KNM—Kenya National Museum, Nairobi, Kenya; MACN—Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina; MASP—Colección del Museo de Ciencias Naturales y Antropológicas, Paraná, Argentina; MFN—Museum für Naturkunde, Berlin, Germany; MGL—Geological Museum of Lausanne, Lausanne, Switzerland; MGUH—palaeontology type collection, Geological Museum, University of Copenhagen, Copenhagen, Denmark; MHNT—Muséum de Toulouse, Toulouse, France; MLP—Museo de La Plata, La Plata, Argentina; MNHN—Muséum National d'Histoire Naturelle, Paris, France; MPCN—Museo Patagónico de Ciencias Naturales, General Roca, Argentina; MPM—Museo Regional Provincal Padre Manuel Jesús Molina, Río Gallegos, Argentina; MUFYCA—Museo Florentino y Carlos Ameghino (Instituto de Fisiografía y Geología), Rosario, Argentina; MV—Musée Vivenel, Compiègne, France; NHMUK—Natural History Museum, London, UK; NJSM—New Jersey State Museum, Trenton, New Jersey, USA; NMNHS—National Museum of Natural History, Bulgarian Academy of Sciences, Sofia, Bulgaria; NMNZ—Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand; NNPM—National Museum of Natural History of the National Academy of Sciences, Kyiv, Ukraine; ONU—Odes'kiy Natsional'niy Universitet, Odessa, Ukraine; PIN—Palaeontological Institute, Russian Academy of Sciences, Moscow, Russian Federation; PU—Princeton University Collection (now at Yale Peabody Museum), Princeton, New Jersey, USA; QM—Queensland Museum, Brisbane, Australia; RAM—Raymond Alf Museum, Claremont, California, USA; ROM—Royal Ontario Museum, Toronto, Ontario, Canada; SAM—South Australian Museum, Adelaide, Australia; SGPIMH—Geologisch-Paläontologisches Institut und Museum der Universität Hamburg, Hamburg, Germany; UCMP—University of California Museum of Paleontology, Berkeley, California, USA; UCR—University of California Riverside, Riverside, California, USA; UM—Museum of Paleontology, University of Michigan, Ann Arbor, Michigan, USA; UNSW—University of New South Wales; Sydney, Australia; USNM—Smithsonian Museum of Natural History, Washington, DC, USA; WN—Michael C.S. Daniels collection, Essex, UK; YPM—Yale Peabody Museum, New Haven, Connecticut, USA; ZIUU—Zoologiska Museum, Uppsala Universitet, Sweden.

2. Overview of the Palaeognath Fossil Record

2.1. Lithornithidae

Lithornithids were small bodied, presumably volant birds that were first recognized as palaeognaths by Houde and Olson [79], and described in detail as a clade by Houde [62]. Thus far, they are only known from Europe and North America, contrasting with the Gondwanan distribution of extant palaeognaths. At first glance, they appear remarkably similar to tinamous, particularly in the shape of the skull. Fossil eggshells attributed to lithornithids are also very reminiscent of those of tinamous, and it has been hypothesized that lithornithids shared the same polygynandrous breeding behaviour of many extant palaeognaths [62]. However, numerous characters distinguish tinamous and lithornithids, which are detailed by Houde [62]. On the basis of a more distally positioned deltopectoral crest, longer and more curved humeral shaft, and a less distally elongated sternum in lithornithids compared with tinamous, Houde [62] also speculated that lithornithids were much more capable long-distance fliers than extant tinamous are. This idea received further support from a reconstruction of the wing of a specimen of the Eocene lithornithid *Calciavis grandei* with preserved carbonized feather traces, which indicated that this species may have been capable of long-distance flapping flight [65].

Since their fossils are most often recovered from nearshore lacustrine or marine environments, it was suggested that lithornithids may have exhibited a shorebird-like ecology [62], though this may be coincidental as these depositional settings are most likely to produce fossils in general. The lithornithid jaw apparatus appears well suited to distal rhynchokinesis, which allows a bird to capture food items in the ground without having to fully open the jaws [62]. This suggests they could have used their bills for probing the substrate for food items, in a manner more similar to kiwi than tinamous [62]. Additional evidence for this type of foraging behaviour comes from the recognition of mechanoreceptors known as Herbst corpuscles in the rostrum of lithornithids [80], which form a tactile bill-tip organ that picks up mechanical vibrations to detect buried prey.

A major unresolved question is whether Lithornithidae predate the K-Pg mass extinction. The cranial end of a right scapula with a distinctive pointed acromion was recovered from the latest Maastrichtian or earliest Danian Hornerstown Formation in New Jersey, USA [63]. If this material indeed belongs to a lithornithid, it would provide compelling evidence that the clade survived across the boundary. However, it should be noted that several Mesozoic stem ornithurines also have a hooked acromion that approaches the condition seen in Lithornithidae [64,81,82]. Thus, the identity of this fossil remains uncertain, and more material needs to be recovered from both this formation and other contemporaneous localities to clarify which groups of total-clade palaeognaths persisted across the K-Pg boundary.

2.1.1. North American Lithornithids

Definitive lithornithid fossils are known from North America from the middle Paleocene to the early Eocene (Figure 7, Table 1) [62,83–88]. The earliest uncontroversial record on this continent is *Lithornis celetius*, from the middle Paleocene (early to middle Selandian) Fort Union Formation of Montana and the Polecat Bench Formation of Wyoming [62]. The entire skeleton of this species is known from a composite series of individuals [62]. Slightly younger than *L. celetius* is a proximal end of a humerus from the middle Paleocene (Tiffanian) Goler Formation in southern California. Despite being fragmentary, its large, dorsally positioned humeral head and subcircular opening to the pneumotricipital fossa diagnose it as a probable lithornithid, and it was assigned to the genus *Lithornis* [88]. As nearly all North American lithornithids derive from the Rocky Mountain region, this fossil extends their known range significantly further west.

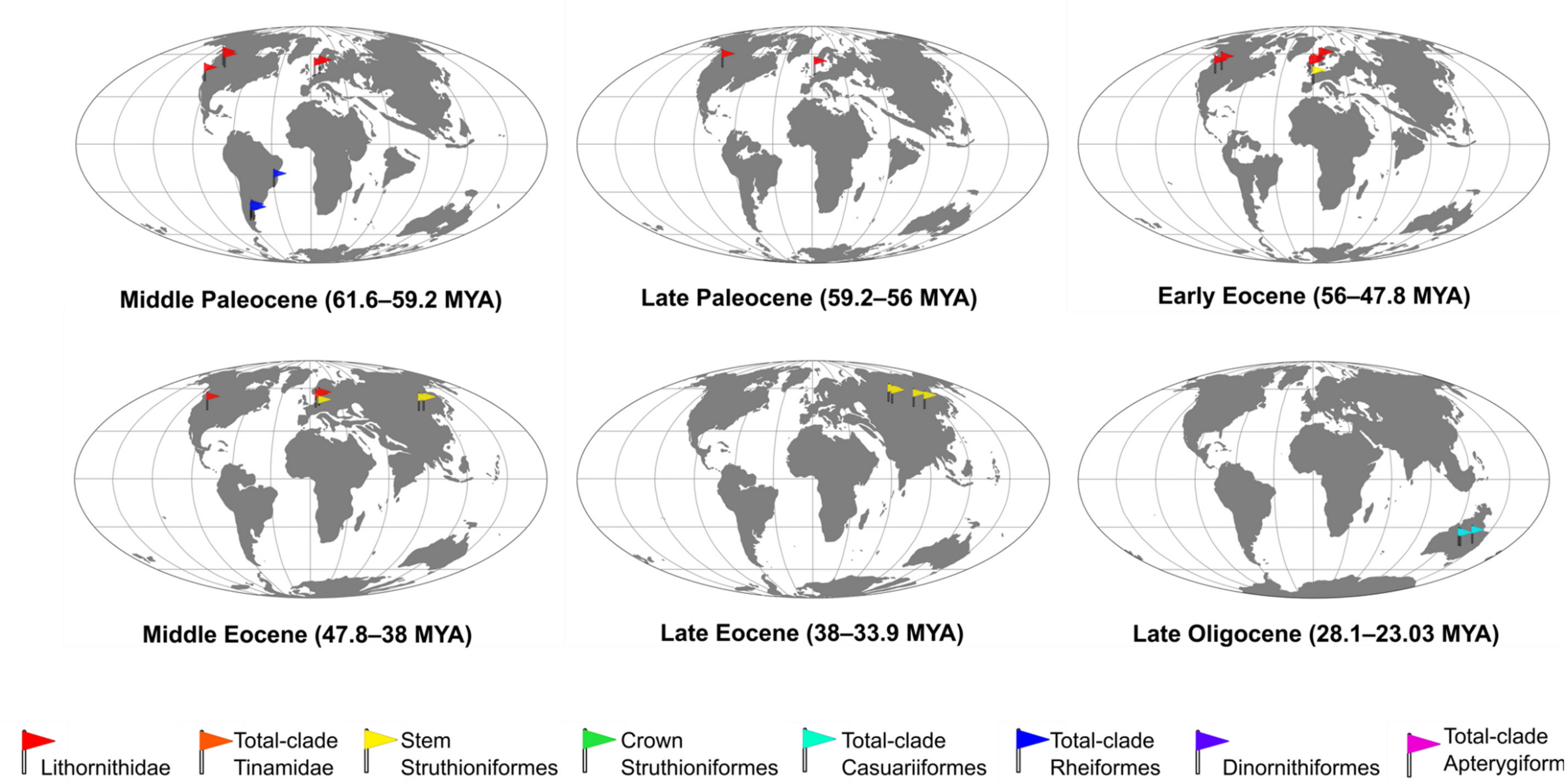

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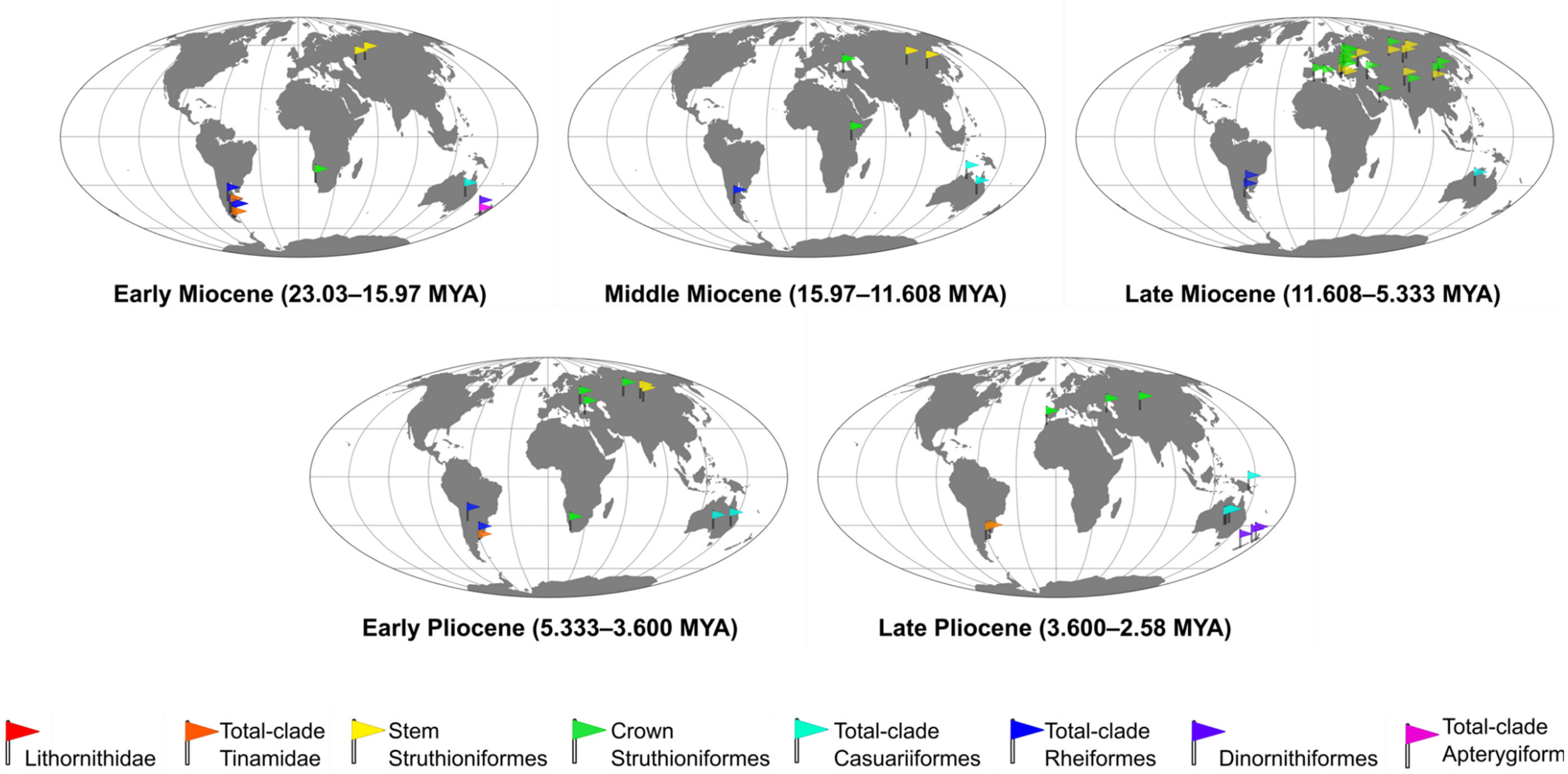
Figure 7. *Cont*.



(**b**)

Figure 7. Geographic distribution of palaeognath fossils illustrated on palaeogeographic globes. (**a**) Middle Paleocene, late Paleocene, early Eocene, middle Eocene, late Eocene, and late Oligocene. (**b**) Early Miocene, middle Miocene, late Miocene, early Pliocene, and late Pliocene. Palaeomaps modified from GPlates (www.gplates.org) [83,84].

Table 1. Lithornithid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
North America	Hornerstown Formation	New Jersey, USA	Late Cretaceous–early Paleocene	Maastrichtian-Danian	Olson and Parris [85]; Staron, et al. [86]	?Palaeognathae	NJSM	Parris and Hope [63]
	Fort Union Formation	Park County, Montana, USA	middle Paleocene	Selandian	Lofgren, et al. [87]; Stidham, et al. [88]	*Lithornis celetius*	USNM, PU	Houde [62]
	Polecat Bench Formation	Wyoming, USA	middle Paleocene	Selandian	Lofgren, et al. [87]; Stidham, et al. [88]	*Lithornis celetius*	PU, UM	Houde [62]
	Goler Formation	Kern County, California, USA	middle Paleocene	Selandian	Lofgren, et al. [89]; Albright, et al. [90]; Lofgren, et al. [91]	*Lithornis sp.*	RAM	Stidham, et al. [88]
	Willwood Formation, Sand Coulee beds	Park County, Wyoming, USA	late Paleocene	Thanetian	Lofgren, et al. [87]	*Lithornis promiscuus*, *Lithornis plebius*	USNM, UM, AMNH	Houde [62]
	Willwood Formation	Basin, Wyoming, USA	early Eocene	Ypresian	Lofgren, et al. [87]	*Lithornis nasi* (provisional), *Paracathartes howardae*	UM, ROM, USNM	Houde [62]
	Green River Formation, Fossil Butte member	Lincoln County, Wyoming, USA	early Eocene	Ypresian	Smith, et al. [92]	*Calciavis grandei*, *Pseudocrypturus cercanaxius*	AMNH, USNM	Houde [62]; Nesbitt and Clarke [64]
	Bridger Formation	Bridger Basin, Wyoming, USA	middle Eocene	Ypresian-Lutetian	Murphey and Evanoff [93]	*incertae sedis*	YPM	Houde [62]
Europe	Heers Formation, Orp Sand member	Maret, Belgium	middle Paleocene	Selandian	Smith and Smith [94], De Bast, et al. [95]	cf. Lithornithidae	IRSNB	Mayr and Smith [96]
	Fissure filling of Walbeck	Helmstedt, Germany	middle Paleocene	Selandian	Aguilar, et al. [97]	*Fissuravis weigelti*	GMH	Mayr [98]
	Tuffeau de Saint-Omer	Templeuve, France	late Paleocene	Thanetian	Steurbaut [99]; Moreau and Mathis [100]; Smith and Smith [94]	Lithornithidae gen. et sp. indet.	IRSNB	Mayr and Smith [96]

Table 1. *Cont.*

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
	Ølst Formation	Limfjord region, Denmark	early Eocene	Ypresian	Heilmann-Clausen and Schmitz [101]	*Lithornis nasi*, *Lithornis vulturinus*	MGUH	Bourdon and Lindow [102]
	Fur Formation	Denmark	early Eocene	Ypresian	Chambers, et al. [103]	*Lithornis vulturinus*	DK, MGUH	Leonard, et al. [104]; Bourdon and Lindow [102]
	London Clay Formation	Kent, Essex, Sussex, England	early Eocene	Ypresian	King [105]; Ellison, et al. [106]; Friedman, et al. [107]	*Lithornis vulturinus*, *Lithornis nasi*, ?*Lithornis hookeri*, *Pseudocrypturus cercanaxius* (provisional)	NHMUK, WN, PU	Houde [62]
	Messel Formation	Messel, Germany	middle Eocene	Ypresian-Lutetian	Franzen and Haubold [108]; Schaal and Ziegler [109]; Lenz, et al. [110]	*Lithornis sp.*	SGPIMH, IRSNB	Mayr [111]; Mayr [112]

Two sympatric species are known from the late Paleocene (late Thanetian) Sand Coulee Beds of the Willwood Formation in Wyoming. *Lithornis promiscuus* was the larger of the two, and is the largest species in its genus [62]. Like *L. celetius,* virtually all bones of the skeleton are known from a composite series [62]. The holotype, USNM 336535, preserves the entire forelimb skeleton. The smaller *Lithornis plebius* is known from all major appendicular elements [62]. Houde [62] acknowledged the possibility that *L. promiscuus* and *L. plebius* may belong to a single sexually dimorphic species, but erred on the side of a more conservative species diagnosis and retained them as separate taxa. Houde [62] tentatively referred specimen NHMUK A 5303 from the London Clay on the Isle of Sheppey, UK to the latter species. Owing to both the homogeneity of the global hothouse climate and the shorter distance across the North Atlantic at the time, North American and European avifaunas were remarkably similar during the late Paleocene and early Eocene (e.g., [76,113,114]). Finding the same species on both sides of the Atlantic should therefore not come as a surprise, and if NHMUK A 5303 is indeed an example of *L. plebius* it would hint towards the dispersal capabilities of these birds.

The remaining North American lithornithids are Eocene in age. *Paracathartes howardae* [115] was found in early Eocene strata of the Willwood Formation [62]. With the exception of the sternum and pelvis, all bones of this species are again known from a composite series [62]. The lacustrine Green River Formation deposited by the Gosiute, Uinta, and Fossil palaeolakes in what is now Utah, Wyoming, and Colorado has yielded an enormous wealth of fossils, most often preserved as slabs [116]. The Fossil Butte member of the formation, deposited by the short-lived early Eocene Fossil Lake [116], has produced the greatest number of lithornithid specimens thus far [64], as well as a great wealth of other bird fossils (e.g., [117–128]). A minimum of two lithornithid species have been found in this Lagerstätte [64]. The holotype of *Pseudocrypturus cercanaxius* [62] is a complete skull and mandible, with nine cervical vertebrae in articulation [62]. A spectacular crushed articulated specimen missing only the pelvis and caudal vertebrae is owned privately by Siber and Siber, and a cast of this specimen is in the collections of the USNM. Two skeletons collected from the London Clay in England were provisionally referred to this species [62], making it another lithornithid with a possible transatlantic distribution. The recently named *Calciavis grandei* [64] was described from a complete, mediolaterally compressed skeleton with preserved soft tissue including feathers, pedal scales, and claw sheaths. A referred specimen includes most of the postcranial skeleton minus the femora and pelvic region, and a disarticulated skull [64].

2.1.2. European Lithornithids

The fossil record of lithornithids in Europe also begins in the middle Paleocene, and stretches to the middle Eocene (Figure 7, Table 1) [96,111,112]. The Orp Sand member (early to middle Selandian) of the Heers Formation in Maret, Belgium yielded a distal humerus fragment and a partial carpometacarpus that were assigned to Lithornithidae, but the fossils are too incomplete to be assigned at a generic level [96]. The next oldest European lithornithid, *Fissuravis weigelti*, is also known from fragmentary remains, in this case the omal end of an isolated coracoid from the late middle Paleocene (Selandian) of the fissure filling of Walbeck, Germany [98]. A lack of clear diagnostic features has cast some level of doubt to this assignment. The coracoid lacks any lithornithid character other than similarity in size, and seems to be missing the small foramina on the posteroventral surface of the hooked acrocoracoid process that is an apomorphy of this clade [64]. Regardless of the true affinities of *Fissuravis weigelti*, the Maret fossils demonstrate that Lithornithidae stretch at least as far back in time in Europe as they do in North America.

As noted by Houde, one of the first fossil birds known to science was *Lithornis vulturinus* [62,129], the holotype specimen of which was purchased by the Royal College of Surgeons in 1798. The holotype was sadly destroyed in the Second World War, though detailed woodcut drawings of the holotype [130] allowed for the identification of a neotype by Houde [62]. The neotype, from the early Eocene (Ypresian) London Clay, was originally identified as an early relative of turacos and named *Promusophaga magnifica* by Harrison and Walker [131]. It consists of a right humerus, radius, ulna, and carpometacarpus, all missing the distal ends, a right scapula, partial sternum, distal left radius and ulna, proximal left femur, proximal right tibiotarsus, a vertebral series, and ribs within a clay nodule [62]. A large amount of fragmentary material from the London Clay, mainly hindlimb elements, has been referred to this species [102]. A slightly younger specimen from the early Eocene Fur Formation of Denmark preserves a three-dimensional skull in articulation with a nearly complete postcranial skeleton and has been described in great detail [102,104]. Another Danish fossil, a distal left humerus from the latest Paleocene-earliest Eocene Olst Formation, was also referred to this taxon [102].

Lithornis nasi [132], also from the early Eocene London Clay Formation, was considered a junior synonym of *L. vulturinus* by Bourdon and Lindow [102]. As the material comes from the type locality of *L. vulturinus*, these authors interpreted the differences between *L. nasi* and *L. vulturinus* as intraspecific variation. The holotype consists of proximal fragments of a left humerus and right ulna, distal fragments of a right femur and a right tibiotarsus, and two thoracic vertebrae [62]. Houde [62] tentatively assigned two specimens from Early Eocene Willwood Formation to *L. nasi*. Another bird from the London Clay, *?Lithornis hookeri* [132], was tentatively referred to the genus by Houde [62]. The holotype, a distal end of a tibiotarsus, suggests it was smaller than all currently known lithornithids [62]. The Messel lithornithid from the middle Eocene of Germany (47–48 MYA) is the youngest lithornithid material yet discovered [111,112]. Known from a partial postcranial skeleton and a skull that appear to represent the same species, it was assigned to the genus *Lithornis* but not to a species-level taxon [112].

2.1.3. Systematics of Lithornithidae

While it is generally accepted that lithornithids are indeed total-clade palaeognaths, important questions regarding their systematics remain: Do lithornithids represent a monophyletic radiation of volant stem or crown palaeognaths? Do they represent a paraphyletic grade of stem palaeognaths? Or, are they polyphyletic, with some taxa more closely related to certain extant palaeognath lineages than others (Figure 8)? All three scenarios would seem to be possible considering that the earliest members of several extant palaeognath subclades would most likely have been relatively small and volant. Houde [62] argued that lithornithids are not monophyletic and placed *Paracathartes* closer to other ratites on the basis of similar histological growth patterns, and the reduced, rounded postorbital process of its frontals. More recent authors have speculated that this histological similarity exists because *Paracathartes* is larger than other lithornithids, reaching approximately the size of a turkey [76].

The phylogenetic analyses of both Nesbitt and Clarke [64] and Yonezawa, et al. [49] recovered lithornithids as a monophyletic group. The character matrix used by Nesbitt and Clarke [64] contained 182 characters combined from the morphological datasets of Cracraft [5], Bledsoe [133], Lee, et al. [29], Mayr and Clarke [134], Clarke [81], Clarke, et al. [135], and new observations gathered by the authors for 38 terminal taxa. In their unconstrained analyses, Lithornithidae was recovered as the sister taxon to Tinamidae at the base of Palaeognathae, congruent with previous morphological phylogenetic hypotheses. This is unsurprising, given that lithornithids and tinamids share numerous skeletal similarities that often optimize as synapomorphies of a lithornithid + tinamou clade. When *Paracathartes* was constrained as sister to ratites, the resultant nonmonophyly of Lithornithidae added a significant number of steps to the analysis. The only character that supported this relationship was the reduction of the postorbital process of the frontal, which the authors considered to be convergent. When relationships of living palaeognaths were constrained to match those recovered by molecular phylogenies, lithornithids were recovered as a clade of stem group palaeognaths. Though Nesbitt and Clarke [64] were unable to achieve any resolution within Lithornithidae, lithornithid monophyly received relatively high support. However, the authors acknowledge the need for future analyses assimilating additional lithornithid character sets to further test the monophyly and phylogenetic position of lithornithids.

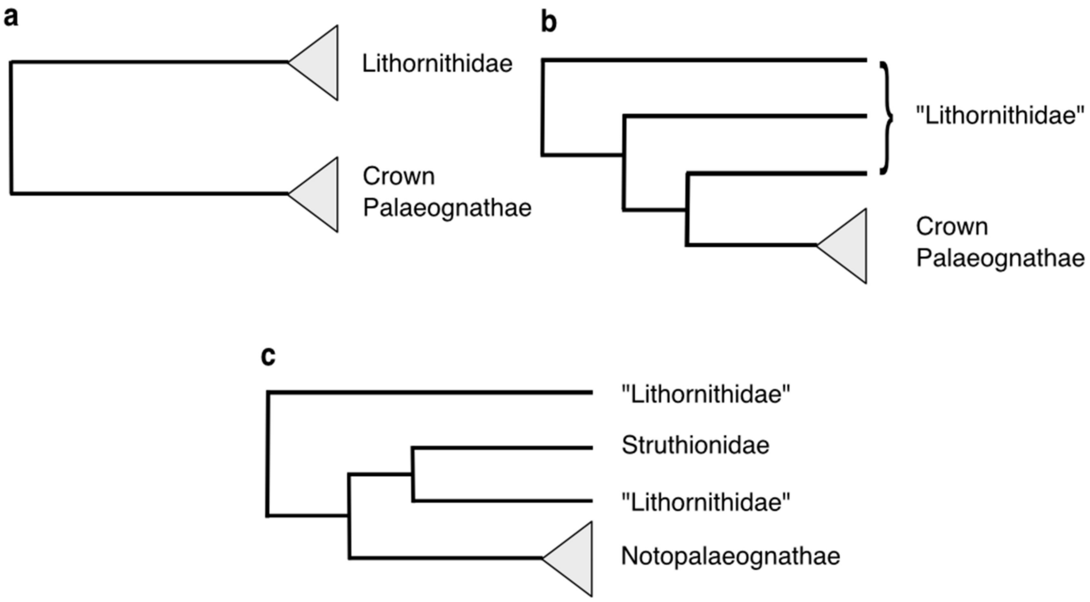


Figure 8. Possible relationships of Lithornithidae to the remainder of Palaeognathae. (**a**) Scenario A shows a monophyletic Lithornithidae, (**b**) Scenario B shows a paraphyletic Lithornithidae, and (**c**) Scenario C shows a polyphyletic Lithornithidae.

A strict consensus tree using parsimony constrained to match recent molecular phylogenetic topologies recovered a monophyletic Lithornithidae sister to Tinamidae, but when the molecular constraint was removed and replaced with constraints enforcing sister group relationships between Palaeognathae + Neognathae and Neoaves + Galloanserae, Lithornithidae instead resolved sister to a *Dinornis* + *Dromaius* + *Struthio* clade to the exclusion of tinamous [136]. In an analysis of this same dataset with new characters added and increased taxon sampling, Bayesian analysis placed lithornithids as stem palaeognaths, and a maximum parsimony analysis of this dataset with cranial characters weighted more strongly found strong support for a monophyletic Lithornithidae in this same position [137]. When characters were unweighted in the maximum parsimony analysis but constrained to a molecular backbone, a monophyletic Lithornithidae was once again sister to Tinamidae [137]. Almeida, et al. [42] also recovered lithornithids as sister to crown Palaeognathae in their Bayesian topology, but sister to tinamous in their maximum parsimony and maximum likelihood trees. Maximum likelihood trees inferred using characters exhibiting low homoplasy also supported a position on the palaeognath stem for Lithornithidae [49], though the monophyly of the clade was dependent on the matrix used. Ten non-homoplastic characters from Houde [62] yielded a paraphyletic Lithornithidae, while 92 non-homoplastic characters from Worthy, et al. [136] supported them as a monophyletic group. The authors considered their results as supportive of the hypothesis that all extant palaeognaths evolved independently from *Lithornis*-like birds [42]. Given lingering uncertainties regarding the monophyly and phylogenetic position of lithornithids, a careful revaluation of character states and species limits within the group would be timely, though this is beyond the scope of the present review.

2.2. *African and Eurasian Palaeognaths: Struthioniformes*

Two ostrich species are extant. The Common Ostrich *Struthio camelus* inhabits open areas across much of sub-Saharan Africa, and the Somali Ostrich *Struthio molybdophanes* of Eastern Africa was once considered conspecific with *S. camelus* but is now given species status [17,138]. While the two extant species of ostrich are now confined to Africa, their range extended into Asia during the Holocene. Ostriches may have persisted as far east as Mongolia until 7500 years ago based on Carbon-14 dating of eggshells [139] (though see Khatsenovich, et al. [140] regarding uncertainties surrounding the dating of ostrich eggs from Mongolia and Siberia), and ostriches of the subspecies *S. c. syriacus,* whose native range stretched from the Arabian Peninsula to Syria and Iraq, did not become extinct until 1966 [17]. Ostriches are arguably the most cursorial of all birds, able to run at speeds in excess of 70 km per hour [67]. Their extreme cursoriality is evinced by their unique foot morphology: ostriches are the only extant didactyl birds, an anatomical configuration that may be the result of similar selective pressures as those that drove digit reduction in horses [77]. The fossil record of ostrich eggshell is rich, and although the present review focuses only on skeletal remains, we note that the occurrence of palaeognath eggshells in the early Miocene of China 17 million years ago [77,141] supports the theory that struthionids either originated outside of Africa or else underwent rapid range expansion after their emergence. For a thorough review of the ostrich eggshell record, see Mikhailov and Zelenkov [78].

2.2.1. Eurasian Stem Struthionids

Our understanding of palaeognath evolution and particularly the transition to flightlessness in ratites has been hampered by a lack of recognizable stem group representatives of extant palaeognath lineages. Fortunately, recent research advances have provided a valuable window into the nature of early stem struthionids, which were previously unknown prior to the Miocene. The flightless palaeognaths *Palaeotis weigelti* and *Remiornis heberti* have long been known from the Paleogene of Europe [76,142–145], but their relation to the remainder of Palaeognathae was unclear [76,142]. *Palaeotis*, the better-known of the two taxa, has been variably recovered as the sister taxon to rheids [146], sister to a clade including Struthionidae, Rheidae, and Casuariidae [147], and sister to a clade comprised of lithornithids and tinamous [33]. The unconstrained analysis of Nesbitt and Clarke [64] recovered *Palaeotis* outside a *Struthio* + *Dromaius* + *Rhea* clade. When relationships of living palaeognaths were constrained to match those recovered by molecular phylogenies, the same authors recovered *Palaeotis* as the sister taxon of extant palaeognaths (to the exclusion of lithornithids). Mayr [142] noted the resemblance of the skull of *Palaeotis* to that of lithornithids, and that the scapulocoracoid differs from all extant ratites, but was unable to find a well-supported placement for *Palaeotis* and proposed that it may represent yet another independent acquisition of ratite features among palaeognaths. The phylogenetic position of *Remiornis heberti* was also challenging to estimate with confidence. Mayr [76] considered that it may belong with Palaeotididae before amending this hypothesis based upon the lack of a supratendinal bridge and extensor sulcus in *Remiornis*, both of which are present in *Palaeotis* [148].

Without information on its palatal anatomy, it would be extremely difficult to recognize *Palaeotis* as a palaeognath on the basis of its postcranial skeleton, as several aspects of its hindlimb morphology, such as a notch in the distal rim of the medial condyle of the tibiotarsus and intratendinous ossifications on the tarsometatarsus, are unusual for palaeognaths and are more reminiscent of Gruiformes [148]. Recently, Mayr [148] transferred *Galligeranoides boriensis* from the stem gruiform clade Geranoididae [149] to Palaeotididae. *G. boriensis* had been described on the basis of leg bones from the early Eocene of France [150]. Its initial assignment to Geranoididae was notable, as this clade was only known from the Eocene of North America [76,149,151]. The transfer of *G. boriensis* from Geranoididae to Palaeotididae raises the possibility that additional records of early palaeognaths could be hiding in plain sight in museum collections, misidentified due to their lack of obvious palaeognath synapomorphies.

This scenario was indeed the case with Eogruidae, a group of crane-sized birds known primarily from hindlimb elements from Central Asia. Since the remainder of the skeleton of eogruids was virtually unknown, these taxa were difficult to place phylogenetically. Eocene eogruids show a trend towards reduction in the size of the inner toe as a possible adaptation for cursoriality [152], and later eogruids of the subclade Ergilornithidae take this trend even further, to the point where the inner toe is vestigial or absent [148,152]. This feature led several earlier authors to hypothesize a placement for Eogruidae as stem struthionids [153–155]. However, this hypothesis was not widely accepted, and eogruids were generally viewed as representatives of Gruiformes (either as sister to a clade containing Aramidae and Gruidae [156] or sister to Gruidae [149]), implying that the didactyly of some eogruids was convergent with Struthionidae.

A previously undescribed partial skull PIN 3110–170 from the latest Eocene locality of Khoer Dzan, Mongolia has rendered the hypothesis of eogruids as gruiforms untenable [6]. Although the palate is missing, the skull preserves an articular surface for the otic capitulum of the quadrate, but apparently does not exhibit an articular surface for the squamosal capitulum of the quadrate. Both articular surfaces would be expected for a gruiform, and indeed for most neognaths, which have a bipartite otic process of the quadrate. Instead, the skull appears to genuinely exhibit only one articular facet for the quadrate, a condition seen only in palaeognaths [157]. This feature, in combination with the reduction and eventual loss of the inner toe, strongly indicate a stem struthioniform placement for Eogruidae. If taxa with greater toe reduction are more closely related to crown struthionids, eogruids would form a paraphyletic grade along the ostrich stem lineage [6] (Figure 9).

With the reassignment of Eogruidae, there is now a clear record of stem Struthionidae in Eurasia well before the first crown struthionids appear in the Miocene of Africa. It now appears likely that this iconic clade of extant African birds first arose outside the continent. In addition to recognizing eogruids as stem struthionids, Mayr and Zelenkov [6] also hypothesized that *Palaeotis* represents a total-clade struthionid based upon similarities in the shape of its skull with the newly described specimen. With palaeotidids interpreted as stem struthionids, the case for a Eurasian origin of Struthioniformes is strengthened even further (Figure 9).

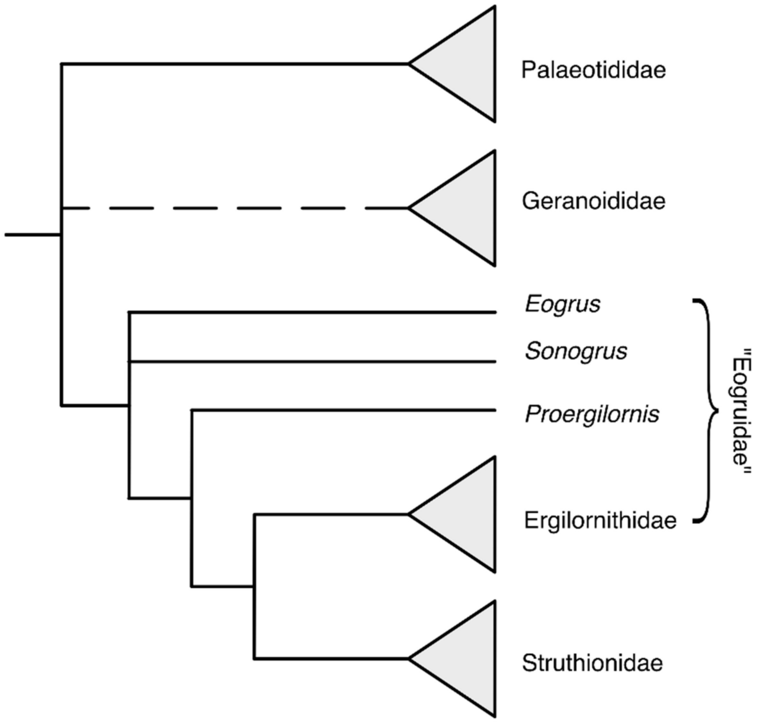


Figure 9. Relationships within Struthioniformes as hypothesized by Mayr and Zelenkov [6]. "Eogruidae" is here estimated to be a paraphyletic grade of crownward stem struthioniforms, and Geranoididae is tentatively inferred to be a clade of early stem struthioniforms.

The oldest flightless, non-lithornithid palaeognaths in Eurasia belong to Palaeotididae. *Galligeranoides boriensis* is now the oldest known probable palaeotidid, found in rocks ranging between the ages of 56 to 51 Ma [158]. It is known from a right tibiotarsus, a distal portion of a left tibiotarsus, and an incomplete right tarsometatarsus [150]. The nominate and best known palaeotidid, *Palaeotis weigelti*, was initially interpreted as a bustard [145] and subsequently as a crane [159] before it was finally recognized as a palaeognath by Houde and Haubold [143], who hypothesized that it was as a stem ostrich despite its lack of obvious cursorial adaptations, an assessment that, in light of the recent work discussed above, has gained robust support. *P. weigelti* is known from six specimens from the middle Eocene of the Messel and Geisel Valley sites of Germany (Table 2). One of these specimens is a complete two-dimensionally preserved skeleton. It stood slightly under 1 m tall, and was more gracile than the older *Remiornis* [76].

Table 2. Fossil record of stem struthioniforms.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
Europe	Châlons-sur-Vesles Formation	Cernay and Berru, Marne, France	late Paleocene	Thanetian	Buffetaut and Angst [160]	*Remiornis heberti*	MNHN	Lemoine [144]; Martin [161]; Mayr [76]
	Sables de Bracheux Formation	Rivecourt, France	late Paleocene	Thanetian	Smith, et al. [162]	*Remiornis heberti*	MV	Buffetaut and de Ploëg [163]
	Argiles rutilantes d'Issel et de Saint-Papoul	Saint-Papoul, France	early Eocene	Ypresian	Laurent, et al. [164]; Danilo, et al. [165]	*Galligeranoides boriensis*	MHNT	Bourdon, et al. [150]; Mayr [148]
	Messel Formation	Messel, Germany	middle Eocene	Ypresian-Lutetian	Franzen and Haubold [108]; Schaal and Ziegler [109]; Lenz, et al. [110]	*Palaeotis weigelti*	HLMD	Peters [146]; Houde and Haubold [143]; Mayr [142]
	Geiseltal brown coal	Geisel Valley lignite pits, Germany	middle Eocene	Lutetian	Franzen and Haubold [108]	*Palaeotis weigelti*	GMH	Lambrecht [145]; Houde and Haubold [143]; Mayr [142]; Mayr [148]
	unlisted	Kolkotova Balka, Tiraspol, Moldova	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis ukrainus*	PIN	Zelenkov and Kurochkin [166]
	unlisted	Hrebeniki, Odessa Oblast, Ukraine	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis ukrainus*	NNPM	Zelenkov and Kurochkin [166]
	unlisted	Morozovka, Odessa Oblast, Ukraine	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis ukrainus*	NNPM	Zelenkov and Kurochkin [166]
	unlisted	Armavir, Krasnodar Krai, Russia	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis ukrainus*	Armavir Regional Museum	Zelenkov and Kurochkin [166]
	unlisted	Samos, Greece	late Miocene	Tortonian	Zelenkov, et al. [167]	*Ampipelargus majori*	NHMUK	Lydekker [168]; Zelenkov, et al. [167]
	Triglia Formation	Kryopigi, Chalkidiki, Greece	late Miocene	Tortonian-Messinian	Tsoukala and Bartsiokas [169]; Lazaridis and Tsoukala [170]	?*Ampipelargus* sp.	AUG	Boev, et al. [171]; Zelenkov, et al. [167]
Asia	Irdin Manha Formation	Shara Murun region, Inner Mongolia, China	middle Eocene	Lutetian	Li [172]	*Eogrus aeola*	AMNH, PIN	Wetmore [173]; Kurochkin [152]; Zelenkov and Kurochkin [166]
	Khaichin Formation	Omnogvi Province, Mongolia	middle Eocene	Lutetian	Zelenkov and Kurochkin [166]	*Eogrus aeola*	PIN	Zelenkov and Kurochkin [166]

Table 2. *Cont.*

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
	Obayla Formation	Kalmakpai River, East Kazakstan	late Eocene	Priabonian	Clarke, et al. [156]	*Eogrus turanicus*	PIN	Bendukidze [174]; Zelenkov and Kurochkin [166]
	unlisted	Tsagan Khutel, Bayanhongor Province, Mongolia	late Eocene	Priabonian	Russell and Zhai [175]	*Eogrus crudus*	PIN	Kurochkin [176]; Zelenkov and Kurochkin [166]
	unlisted	Alag Tsav, Dornogovi Province, Mongolia	late Eocene	Priabonian	Dashzėvėg [177]; Clarke, et al. [156]	Eogruidae incertae sedis	IGM	Clarke, et al. [156]
	Kustovskaya Formation	East Kazakstan	late Eocene	Priabonian	Musser, et al. [178]	*Eogrus* sp.	PIN	Kozlova [179]; Kurochkin [176]; Musser, et al. [178]
	Ergilin Dzo Formation	Dornogovi Province, Mongolia	latest Eocene-earliest Oligocene	Priabonian-Rupelian	Dashzėvėg [177]	*Eogrus* sp., *Ergilornis rapidus*, *Ergilornis minor*, *Ergilornis* sp., Ergilornithidae incertae sedis, *Sonogrus gregalis*	PIN	Wetmore [173]; Kozlova [179]; Kurochkin [152]; Kurochkin [176]; Zelenkov and Kurochkin [166]; Mayr and Zelenkov [6]
	unlisted	Mynsualmas, Kazakstan	early Miocene	Aquitanian-Burdigalian	Karhu [180]; Zelenkov and Kurochkin [166]	*Urmiornis brodkorbi*	PIN	Karhu [180]; Zelenkov and Kurochkin [166]
	Upper Aral Formation	Altynshokysu, Kazakstan	early Miocene	Aquitanian-Burdigalian	Karhu [180]; Zelenkov and Kurochkin [166]	*Urmiornis brodkorbi*	PIN	Karhu [180]; Zelenkov and Kurochkin [166]
	Tunggur Formation	Shara Murun region, Inner Mongolia, China	middle Miocene	Serravallian	Wang, et al. [181]	*Eogrus wetmorei*	AMNH	[173]; Brodkorb [182]; Cracraft [183]
	unlisted	Sharga, Govi-Altai Province, Mongolia	middle Miocene	Serravallian	Musser, et al. [178]	*Ergilornis* sp.		Zelenkov, et al. [167]; Musser, et al. [178]
	Nagri and Chinji Formations	Gilgit-Baltistan, Pakistan	late middle- early late Miocene	Serravallian-Tortonian	Barry, et al. [184]	? *Urmiornis cracrafti*		Harrison and Walker [185]; Musser, et al. [178]
	unlisted	Maragheh, Iran	late Miocene	Tortonian-Messinian	Musser, et al. [178]	*Urmiornis maraghanus*	MNHN	Mecquenem [186]
	Lower Pavlodar Formation	Pavlodar, Kazakstan	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis* sp.	PIN	Kurochkin [176]; Zelenkov and Kurochkin [166]

Table 2. *Cont.*

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
	Karabulak Formation	Kalmakpai, Zaisan, East Kazakstan	late Miocene	Tortonian-Messinian	Zelenkov and Kurochkin [166]	*Urmiornis orientalis*	PIN	Kurochkin [176]; Zelenkov and Kurochkin [166]
	Liushu Formation	Zhuangeji town, Gansu, China	late Miocene	Messinian	Fang, et al. [187]	*Sinoergilornis guanheensis*	IVPP	Musser, et al. [178]
	Khirgis-Nur Formation	Khirgis-Nur, Sunur Province, Mongolia	late Miocene	Messinian	Zelenkov and Kurochkin [166]	*Urmiornis* sp.	PIN	Kurochkin [176]; Zelenkov and Kurochkin [166]
	Khirgis-Nur Formation	Chono-Khariakh, Kobdos Province, Mongolia	early Pliocene	Zanclean	Zelenkov and Kurochkin [166]	*Urmiornis dzabghanensis*	PIN	Kurochkin [188]; Zelenkov and Kurochkin [166]
	Khirgis-Nur Formation	Dzagso-Khairkhan-Obo, Ubsunur Province, Mongolia	early Pliocene	Zanclean	Zelenkov and Kurochkin [166]	*Urmiornis dzabghanensis*	PIN	Kurochkin [188]; Zelenkov and Kurochkin [166]

Eogruids are younger than Palaeotididae, occurring from the middle Eocene to the early Pliocene, and comprise fifteen named species in six genera (Table 2). The oldest species, *Eogrus aeola,* has been collected from the middle Eocene of Inner Mongolia and Mongolia's Omnogvi Province [152,166,173] (Table 2). Like nearly all eogruids, it is known only from hindlimb elements. Other members of this genus from the late Eocene include *Eogrus crudus* from central Mongolia [176], and *Eogrus turanicus* from Eastern Kazakhstan [174] (Table 2).

Outcrops of the latest Eocene-earliest Oligocene Ergilin Dzo Formation in Dorngovi Province, Mongolia have produced an enormous wealth of eogruid fossils. It is in this formation that Ergilornithidae first appear. Once recognized as a separate family [179], they are now considered a subclade of Eogruidae [156,167]. Ergilornithids recovered from this formation include *Ergilornis rapidus* [179], *Ergilornis minor* [176,179], and *Sonogrus gregalis* [176] (Table 2). The partial skull PIN 3110–170 was collected from the latest Eocene Sevkhul member of this formation [6,155]. As the Sevkhul member has produced huge quantities of hindlimb material belonging to *Sonogrus gregalis* and *Ergilornis minor* and no other large birds, the skull was presumed to belong to one of the two species [6].

We were unable to find any documented occurrences of this clade for the remainder of the Oligocene. The ergilornithid genus *Urmiornis* first appears in the early Miocene, with two occurrences of *Urmiornis brodkorbi* in western Kazakhstan [180]. The latest occurrence of the genus *Eogrus* is in the middle Miocene of Inner Mongolia with *Eogrus wetmorei* [173,182,183]. By the late Miocene, eogruids had expanded their range outside of Central Asia and reached their greatest generic diversity, with *Amphipelargus majori* occurring on Samos island [167,168] and another member of the same genus on the Greek mainland [167,171], *Urmiornis ukrainus* occurring in Ukraine, Moldova, and southwestern Russia [166,176], *Urmiornis maraghanus* in Iran [183,186,189], *?Urmiornis cracrafti* in the Siwaliks of northern Pakistan [185], and *Sinoergilornis guangheensis* in Gansu, China [178] (Table 2). Although Kurochkin [176] noted differences between *U. ukrainus* and *U. maraghanus*, the validity of *U. ukrainus* requires further conformation and *U. maraghanus* would take nomenclatural priority if they are shown to be the same species [166]. The group continued to thrive in their Central Asian stronghold, with *Urmiornis orientalis* found near Zaisan, Kazakhstan [166,176] and *Urmiornis* sp. in the Sunur province of Mongolia and Pavlodar, Kazakhstan [166,176]. The youngest species, *Urmiornis dzabghanensis*, was found in the early Pliocene Khirgis-Nur Formation of Mongolia [166,188] (Table 2).

The possibility that the eogruids were flightless has been proposed by several authors [152,173], though others contend that such a conclusion is premature based on existing evidence [156,178]. The trochlea for the second toe is vestigial or entirely absent in *Ergilornis*, *Sinoergilornis*, *Urmiornis*, and *Ampipelargus* [6,166,176,178], which is indicative of a highly cursorial lifestyle as seen in extant struthionids. In addition, a proximal humerus PIN 3110–60 from the Ergilin Dzo Formation attributed to *Ergilornis* has a greatly reduced deltopectoral crest (the portion of the humerus serving as the major insertion point for major flight muscles), and from this it was assumed that at least this taxon was flightless [152]. If some eogruids were volant, it could imply that multiple transitions to flightlessness occurred among stem struthionids, following the phylogeny of Mayr and Zelenkov (Figure 9) [6].

That the North American Geranoididae may also be struthioniforms has been suggested on several occasions, but unlike Eogruidae no strong evidence for such a placement has yet been found [6,148,155]. Geranoidids share several derived features with Palaeotididae, including an elongated tarsometatarsus, a pronounced extensor sulcus along the dorsal surface of the tarsometatarsus, a proximodistally elongated hypotarsus that forms a long medial crest, and a notched distal rim of the medial condyle of the tibiotarsus [148]. With the recent reassignment of *G. boriensis* (discussed above), an investigation into possible palaeognath affinities for fossils assigned to the remaining members of this clade is clearly merited. *Eogeranoides campivagus* from the Wilwood Formation of Wyoming has a deep extensor sulcus along the dorsal surface of the tarsometatarsus, a feature it shares with *Palaeotis* [142,148]. Considering that North American and European avifaunas were generally similar during the Eocene [114,148], and that certain flightless bird taxa such as Gastornithidae occurred on both sides of the Atlantic [76,77], the possibility that palaeotidids existed in North America is plausible. A clade uniting Palaeotididae, Geranoididae, Eogruidae, and Struthionidae is supported by the following characters highlighted by Mayr and Zelenkov [6]: a very long and narrow tarsometatarsus, a short trochlea for digits II and IV, a tubercle adjacent to the supratendinal bridge, and a shortening of all non-ungual phalanges on pedal digit IV.

Also uncertain is the placement of *Remiornis heberti* [144] from the late Paleocene of France [161] (Table 2). It is known from several isolated elements belonging to different individuals that include a tibiotarsus, tarsometatarsus, and fragmentary associated remains [76,161,163]. It appears to have been recognized as a palaeognath based on its overall resemblance to *Palaeotis*, as the two genera share a deep furrow on the dorsal surface of the tarsometatarsus and a similar configuration of the distal trochleae [76]. Mayr [148] excluded it from Palaeotididae based on its lack of an ossified supratendinal bridge and extensor sulcus, and Mayr and Zelenkov did not include *Remiornis* at all in their new hypothesis of struthioniform interrelationships [6]. However, in light of the variability exhibited by the supratendinal bridge, extensor sulcus, and hypotarsus among palaeognaths, rejecting a struthioniform affinity for *Remiornis* may be premature. An ossified supratendinal bridge of the tibiotarsus is present in Tinamidae and Dinornithidae and is variably present in Apterygidae, but is missing from all other crown palaeognaths [137,148]. Worthy et al. [137] note that given its variability in clades including crown Palaeognathae and Cariamiformes, the presence or absence of this feature should not be viewed to negate potential sister relationships. The extensor sulcus of the tibiotarsus is also variably present in palaeognaths. It is narrow in Lithornithidae, Apterygidae, Tinamidae, and Dinornithidae, and absent in Struthionidae, Casuariidae, Rheidae, and Aepyornithidae [148]. Eogruids have a hypotarsal canal, while all other palaeognaths lack this feature [148]. The putative gruid *Palaeogrus princeps* [190] from the middle Eocene of Italy also shares similarities in the distal tibiotarsus with *Palaeotis* and could represent yet another record of this clade [148].

Several other taxa that deserve further revision of their taxonomic placement are listed here, though it is far less likely that they belong within Palaeognathae. *Eleutherornis cotei* [191,192] from the middle Eocene of Switzerland and France is known from a partial pelvis and hindlimb elements and was originally assumed to be a ratite due to its large size, but was reinterpreted as a phorusrhacoid [193]. *Eremopezus eocaenus* [194] is known from hindlimb elements from the late Eocene Fayum Formation of Egypt [76,195]. Rasmussen, et al. [195] suggest that it could represent a non-palaeognathous endemic African group that independently became large and flightless. More material will be needed to firmly rule out palaeognathous affinities for this taxon [76]. Whether or not these species are indeed palaeognaths, we expect that further revaluation of Paleogene fossil collections is bound to reveal more palaeognaths from a critical time period that may capture their transitions to flightlessness.

2.2.2. African and Eurasian Crown Struthionids

As shown in Table 3.

Table 3. Crown struthionid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
Africa	Elisabethfeld silts	Northern Sperrgebiet, Namibia	early Miocene	Aquitanian	Pickford and Senut [196]	*Struthio coppensi*		Mourer-Chauviré, et al. [197]; Mourer-Chauviré [198]
	unlisted	Kadianga West, Kenya	middle Miocene	Langhian	Pickford [199]	*Struthio sp.*	KNM	Leonard, et al. [200]
	unlisted	Central Nyanza, Kenya	middle Miocene	Serravallian	Pickford [199]	*Struthio sp.*	KNM	Leonard, et al. [200]
	unlisted	Ngorora, Kenya	middle Miocene	Serravallian	Pickford [199]	*Struthio sp.*	KNM	Leonard, et al. [200]
	Beglia Formation	Bled el Douarah, Tunisia	late Miocene	Tortonian	Werdelin [201]	*Struthio sp.*		Rich [202]
	Varswater Formation	Langebaanweg, South Africa	early Pliocene	Zanclean	Roberts, et al. [203]	*Struthio cf. asiaticus*		Rich [204]; Manegold, et al. [205], but see Mikhailov and Zelenkov [78]
	unlisted	Ahl al Oughlam, Casablanca, Morocco	late Pliocene	Piacenzian	Geraads [206]	*Struthio asiaticus*		Mourer-Chauviré and Geraads [207], but see Mikhailov and Zelenkov [78]
	Olduvai series	Olduvai Gorge Bed I, Tanzania	early Pliestocene	Gelasian	Hay [208]	*Struthio oldawayi*		Lowe [209]; Leakey [210]
	unlisted	Aïn Boucherit, Algeria	early Pleistocene	Gelasian	Werdelin [201]	*Struthio barbarus*		Arambourg [211]; Mikhailov and Zelenkov [78]
Asia	Turgut strata	Çandir, Turkey	middle Miocene	Langhian	Becker-Platen, et al. [212]	*Struthio cf. brachydactylus*	BGR	Sauer [213]
	unlisted	Maragha, Iran	late Miocene	Tortonian		*Palaeostruthio karatheodoris*		Mecquenem [189]; Lambrecht [214]; Mikhailov and Zelenkov [78]
	Baynunah Formation	United Arab Emirates	late Miocene	Tortonian		*Palaeostruthio karatheodoris*		Louchart, et al. [215]
	unlisted	Pavlodar, Kazakhstan	late Miocene	Messinian (?)		*Palaeostruthio karatheodoris*		Tugarinov [216]; Kurochkin [188]; Mikhailov and Zelenkov [78]
	Liushu Formation	Gansu province, China	late Miocene	Tortonian-Messinian	Deng, et al. [217]	*Struthio (Orientornis) linxiaensis*		Hou, et al. [218]

Table 3. *Cont.*

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
	unlisted	Baode county, China	late Miocene	Messinian	Kaakinen, et al. [219]	*Struthio wimani*		Lowe [220]; Mikhailov and Zelenkov [78]
	Dhok Pathan Formation?, Siwalik series	Siwalik Hills, India	late Miocene-early Pliocene	Messinian-Zanclean	Sahni, et al. [221]; Sahni, et al. [222]; Stern, et al. [223]; Patnaik, et al. [224]	*Struthio asiaticus*		Davies [225]; Lydekker [226]; Mikhailov and Zelenkov [78]
	unlisted	Çalta, Ankara, Turkey	early Pliocene	Zanclean	Ginsburg, et al. [227]; Sen [228]; Janoo and Sen [229]	*Struthio sp.*		Janoo and Sen [229]
	unlisted	Pavlodar, Kazakhstan	early Pliocene	Zanclean		*Struthio chersonensis*		Beliaeva [230]
	upper Issykulian Formation	Akterek, Kyrgyzstan	late Pliocene	Piacenzian	Sotnikova, et al. [231]	*Pachystruthio transcaucasius*		Sotnikova, et al. [231]
	Nihewan Formation	Nihewan Basin, China	early Pleistocene	Gelasian	Cai, et al. [232]	*Pachystruthio indet.*	MNHN	Buffetaut and Angst [233]
	unlisted	Zhoukoudian, China	middle-late Pleistocene	Calabrian-Chibanian		*“Struthio anderssoni”*		Hou [234]
Europe	unlisted	Varnitsa, Moldova	late Miocene	Tortonian	Vangengeim and Tesakov [235]	*Struthio orlovi*		Kurochkin and Lungu [236]
	unlisted	Pikermi, Greece	late Miocene	Tortonian	Solounias, et al. [237]	*Palaeostruthio cf. karatheodoris*		Bachmayer and Zapfe [238]; Michailidis, et al. [239]
	Nikiti Formation	Nikiti, Greece	late Miocene	Tortonian		*Palaeostruthio cf. karatheodoris*		Koufos, et al. [240]
	unlisted	Hadzhidimovo, Bulgaria	late Miocene	Tortonian	Spassov [241]	*Palaeostruthio karatheodoris*	NMNHS	Boev and Spassov [242]
	unlisted	Novoelizavetovka, Ukraine	late Miocene	Tortonian- Messinian	Vangengeim and Tesakov [235]	*Struthio novorossicus*	ONU	Aleksejev [243]; Mikhailov and Zelenkov [78]
	unlisted	Kuyal’nik, Ukraine	late Miocene	Tortonian-Messinian		*Struthio sp.*		Burchak-Abramovich [244]; Mikhailov and Zelenkov [78]
	unlisted	Samos, Greece	late Miocene	Tortonian-Messinian		*Palaeostruthio karatheodoris*	MGL	Forsyth Major [245]; Mikhailov and Zelenkov [78]

Table 3. *Cont.*

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
	Strumyani Genetic Lithocomplex	Kamimantsi, Bulgaria	late Miocene	Tortonian- Messinian	Tzankov, et al. [246]; Spassov, et al. [247]	*Palaeostruthio cf. karatheodoris*	NMNHS	Boev and Spassov [242]
	unlisted	Kerassia, Greece	late Miocene	Tortonian-Messinian	Theodorou, et al. [248]	*Palaeostruthio karatheodoris*		Kampouridis, et al. [249]
	unlisted	Grebeniki, Ukraine	late Miocene	Tortonian	Vangengeim and Tesakov [235]	*Palaeostruthio karatheodoris, Struthio brachydactylus*		Burchak-Abramovich [250]; Mikhailov and Zelenkov [78]
	Odessa Catacombs	Odessa, Ukraine	early Pliocene	Zanclean		*Struthio sp.* "Odessa Ostrich"	ONU	Burchak-Abramovich [244]; Mikhailov and Zelenkov [78]
	unlisted	Kvabebi, Georgia	late Pliocene	Piacenzian		*Pachystruthio transcaucasius*		Burchak-Abramovich and Vekua [251]; Mikhailov and Zelenkov [78]
	Khapry Formation	Liventzovka, Rostovskaya Oblast, Russia	early Pleistocene	Gelasian	Tesakov [252]; Tesakov, et al. [253]	*Struthio sp.* "Odessa Ostrich"		Kurochkin and Lungu [236]
	Sésklo basin sedimentary fill	Sésklo, Thessaly, Greece	early Pleistocene	Gelasian		*Struthio cf. chersonensis*		Athanassiou [254]
	unlisted	Dmanisi, Georgia	early Pleistocene	Gelasian	Ferring, et al. [255]	*Pachystruthio dmanisensis*		Burchak-Abramovich and Vekua [256]; Mikhailov and Zelenkov [78]
	Taurida Cave	Taurida, Crimea	early Pleistocene	Gelasian	Lopatin, et al. [257]	*Pachystruthio dmanisensis*		Lopatin, et al. [257]; Zelenkov, et al. [258]
	unlisted	Kisláng, Hungary	early-middle Pleistocene	Gelasian-Calabrian	Mayhew [259]	*Pachystruthio pannonicus*	GMB	Kretzoi [260]; Mikhailov and Zelenkov [78]

The body fossil record of crown ostriches begins 21 million years ago in the early Miocene of Africa with *Struthio coppensi* (Figure 7, Table 3), named on the basis of the shaft and distal part of a left tibiotarsus, proximal left femur, distal left tarsometatarsus, right tarsometatarsus shaft, and a left fibula from the early Miocene of the Northern Sperrgebiet, Namibia [197]. As noted by Mourer-Chauviré [198], it was smaller and more gracile than *S. camelus*, and a vestigial trochlea metatarsi II shows this early ostrich was didactyl [197,198]. A late middle Miocene ostrich from western Kenya assigned to *Struthio* also had a didactyl foot and was smaller than extant ostriches, though still larger than *S. coppensi* [200]. Other Kenyan middle Miocene ostrich fossils have been discovered, but they remain undescribed [78,261]. A distal tarsometatarsus was found from the middle-late Miocene boundary in Tunisia [201,202], indicating their presence in North Africa. The size of this bone is roughly comparable with that of the extant *S. camelus* [78].

No late Miocene ostrich body fossils have yet been found from sub-Saharan Africa, but they are relatively common in Eurasia during this period (Figure 7, Table 3) [78]. A pedal phalanx from the middle Miocene of Turkey is the oldest body fossil of crown struthionids outside Africa [213]. From the late Miocene onwards, this clade occupied an enormous geographical range, from the Balkans to northeastern China and eastern Siberia, and south to India. The oldest ostrich from Eastern Europe, *Struthio orlovi*, was found in the early late Miocene of Moldova [236]. Late Miocene Southern and Eastern European ostrich species limits are somewhat contentious. *S. karatheodoris* [245] was larger than extant ostriches [78], and many specimens from the Balkans have been referred to this taxon [238–240,242,249]. A large pelvis from the late Miocene of the United Arab Emirates was assigned to this species based on its size [215], and sacral vertebrae of a very large ostrich found in the terminal Miocene of northern Kazakhstan [188,216] may also belong to *S. karatheodoris* [78]. *S. novorossicus* [243] is considered a *nomem dubium* by Mikhailov and Zelenkov [78], as it cannot be distinguished from *S. asiaticus.* Koufos, et al. [240] suggested that *S. brachydactylus* [250] may be a junior synonym of *S. karatheodoris*, but Mikhailov and Zelenkov [78] consider them separate taxa, as *S. brachydactylus* was roughly the size of *S. camelus* and therefore much smaller than *S. karatheodoris.* Mikhailov and Zelenkov [78] refer *Palaeostruthio sternatus* [244] to *S. karatheodoris*, creating the new combination *Palaeostruthio karatheodoris.*

Struthio (“*Orientornis*”) *linxiaensis* from the late Miocene of Gansu province, China is one of the oldest East Asian ostriches [77,218,262]. Slightly larger than *S. camelus*, Mikhailov and Zelenkov [78] argued that it likely belongs in its own genus, but tentatively treat it as *Struthio.* Other late Miocene Asian ostriches include *S. wimani,* known from a fragmentary pelvis from China [220], and *S. asiaticus* [263] from the Siwalik series in North India and Pakistan. The latter species has been treated as somewhat of a wastebasket taxon, with eggshell fragments attributed to it from sediments as young as the late Pleistocene of the Baikal region [264], and body fossils from as far away as South Africa [204,205] (Table 3). Ostrich eggshells ranging in age from 11 to 1.3 Ma are known from the Siwalik series [223]. However, the distribution, temporal range, and taxonomic identifications of these specimens are in need of revision.

Several large ostriches are known from the Pliocene. *S. transcaucasius* is known from a pelvis from the late Pliocene of Georgia [251] and was recently assigned to the genus *Pachystruthio* [258]. Many others have not been assigned to a species level taxon. It is evident from hindlimb fragments that a large ostrich existed in the lower Pliocene of South Africa, which was referred to *Struthio* cf. *asiaticus* [204,205]. Pliocene fossils from Ahl al Oughlam, Casablanca, Morocco, were also attributed to S. asiaticus [207]. Another large ostrich is known from the early Pliocene of Central Turkey [229]. An ostrich from Odessa, Ukraine, also from the early Pliocene, has only been assigned to *Struthio* [78,244].

Multiple species of large ostriches persisted through the Pleistocene. *Struthio oldawayi* of the early Pleistocene of Tanzania was similar to the extant *S. camelus*, though considerably larger [209,220]. Large Pleistocene ostrich bones from Kenya’s Olduvai Gorge site may also belong to this species [210]. A large ostrich from the early Pleistocene of

Algeria was assigned to *S. barbarus* [201,211], and a middle Pleistocene cervical vertebra from the Nefud desert in northeastern Saudi Arabia bears a close resemblance to the extant *S. molybdophanes* [265]. Two giant Eurasian ostriches of the early Pleistocene, *Pachystruthio pannonicus* and *Struthio dmanisensis,* may be one species [258]. These birds were truly massive; a femur from the lower Pleistocene Taurida Cave of Crimea yields a mass estimate of 450 kg [258] using the equation of Field, et al. [266]. A 1.8-million-year-old right femur from Nihewan, North China may also belong to *Pachystruthio.* Assigned to *Pachystruthio indet.*, its estimated mass is a smaller, though still enormous 300 kg [233]. *S. anderssoni* of the late Pleistocene of eastern China [234] was 1.5 times the size of *S. camelus*, at about 270 kg based on estimates from its minimum femur circumference [267]. Why ostriches disappeared across Eurasia remains a mystery. One hypothesis is that their decline was at least partially linked to climatic cooling throughout the Cenozoic [77]. However, fossil eggshells indicating the possible persistence of ostriches in Mongolia well into the Holocene [139] (though again, see Khatsenovich, et al. [140]) would seem to negate such an explanation, and a stronger explanation for their disappearance is needed.

2.3. South American Palaeognaths: Rheiformes and Tinamiformes

South America is notable for being the only continent to host two family-level palaeognath clades that have persisted to the present day. Two species belong to Rheidae, the Greater Rhea *Rhea americana* and the Lesser Rhea or Darwin's Rhea *Rhea pennata* (alternatively *Pterocnemia pennata* in certain taxonomies). Both species are cursorial and inhabit open areas, with the Greater Rhea's range covering much of eastern and southern South America while the Lesser Rhea is found in Patagonia and the Altiplano region [68,268,269]. The Lesser Rhea was formerly placed in its own genus, *Pterocnemia*, but genetic studies suggest it is closely related to the Greater Rhea, with which it can hybridize [268,270]. There is some debate surrounding species limits among Lesser Rheas populations, as some consider the Altiplano subspecies *R. p. garleppi* and *R. p. tarapacensis* to form a separate species from the nominate Patagonian subspecies, *R. p. pennata* [268].

Tinamous (Tinamidae) are by far the most speciose extant palaeognath clade, and occupy a wide range of habitats in Central and South America [14]. The clade is divided into two major subclades, the forest-adapted Tinaminae which contains 29 species in the genera *Tinamus, Crypturellus,* and *Nothocercus*, and the open and arid habitat-dwelling Nothurinae, with 17 species in the genera *Taoniscus, Nothura, Nothoprocta, Rhynchotus, Eudromia,* and *Tinamotis* [14,42,271,272]. Like many ground-dwelling birds, tinamous have short wings relative to their body size which results in high wing loading [273]. High wing loading is associated with rapid flight but makes flight energetically costly [273], therefore tinamous tend to escape from threats on foot unless flight is necessary [61]. The pectoral muscles in tinamids are enormous relative to their body size, and allow for rapid takeoff to escape potential predators [273,274].

2.3.1. Rheid Fossil Record

The oldest named ratite, *Diogenornis fragilis*, provides a key minimum-bound age estimate for the evolution of larger body size and flightlessness among palaeognaths. The type specimen was found in the middle-late Paleocene of Itaboraí, Brazil and consists of limb bones, vertebrae, and the tip of a premaxilla deriving from several individuals [76,275]. The precise age of the Itaboraí fauna has been subject to debate, and an early Eocene age has also been suggested [276]. However, the distal end of a right tibiotarsus missing most of its lateral condyle from the even older middle Paleocene Rio Chico Formation of Argentina was also referred to this genus [277]. It was about two-thirds the size of the Greater Rhea, and its wings were less reduced [77]. For biogeographical reasons, *Diogenornis* is often presumed to be a stem rheiform [77,275]. However, Alvarenga [278] reported casuariid affinities for *Diogenornis*, and [277] also noted dissimilarities between the referred tibiotarsus and those of rheids. The cranial end of the medial condyle in medial view is larger and projects further distally than the caudal portion, which optimizes as a synapomorphy of casuariids [5,29].

While we consider it unlikely that *Diogenornis* represents a casuariiform, the phylogenetic affinities of these fossils remain somewhat uncertain. We conservatively treat *D. fragilis* as a total-clade rheid (Figure 7, Table 4). Another possible Paleogene rheid is represented by pedal phalanges from the middle Paleocene of Patagonia [279].

Table 4. Rheid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
South America	Itaboraí Formation	São José, Brazil	late Paleocene	Selandian	Pascual and Ortiz-Jaureguizar [280]	*Diogenornis fragilis*		Alvarenga [275]
	Rio Chico Formation	Chubut province, Argentina	late Paleocene	Thanetian	Raigemborn, et al. [281]	*Diogenornis sp.*, Rheidae indet.	MACN	Tambussi [279]; Agnolín [277]
	Koluel Kaike Formation	El Gauchito, Chubut province, Argentina	late Paleocene	Thanetian	Krause and Bellosi [282]	gen. et sp. indet.	MLP	Agnolín [277]
	Sarmiento Formation	Chubut province, Argentina	middle Eocene to early Miocene	unknown	Paredes, et al. [283]	gen. et sp. Indet.	MACN	Agnolín [277]
	Chichinales Formation	Río Negro province, Argentina	early Miocene	Burdigalian	Kramarz, et al. [284]	*Opisthodactylus horacioperezi*	MPCN	Agnolín and Chafrat [285]
	Santa Cruz Formation	Santa Cruz province, Argentina	early Miocene	Burdigalian-Langhian	Marshall and Patterson [286]; Fleagle, et al. [287]; Blisniuk, et al. [288]; Perkins, et al. [289]; Cuitiño, et al. [290]	*Opisthodactylus patagonicus*	NHMUK, MPM, YPM, MNHN	Ameghino [291]; Buffetaut [292]; Diederle and Noriega [293]
	Aisol Formation	Mendoza province, Argentina	early Miocene	Burdigalian-Langhian	Forasiepi, et al. [294]	*Pterocnemia cf. mesopotamica*	FMNH	Agnolín and Noriega [295]
	Level 13 of Ganduglia (1977)	Río Negro province, Argentina	middle Miocene	Langhian	Ganduglia [296]	gen et sp. indet.	MLP	Agnolín [277]
	Ituzaingó Formation	Entre Ríos province, Argentina	late Miocene	Messinian	Cione, et al. [297]	*Pterocnemia mesopotamica*, *Pterocnemia* sp., Rheidae indet.	MACN, MASP, CICYTTP	Agnolín and Noriega [295]
	Cerro Azul Formation	La Pampa province, Argentina	late Miocene	Messinian	Cerdeño and Montalvo [298]; Verzi, et al. [299]	*Pterocnemia* sp.	GHUNLP	Cenizo, et al. [300]
	Andalhuala Formation	Tucumán province, Argentina	late Miocene-early Pliocene	Messinian-Zanclean	Marshall and Patterson [286]; Bossi and Muruaga [301]; Reguero and Candela [302]	*Opisthodactylus kirchneri*	MUFYCA	Noriega, et al. [303]
	Monte Hermoso Formation	Buenos Aires province, Argentina	early Pliocene	Zanclean	Deschamps, et al. [304]; Tomassini, et al. [305]	*Heterorhea dabbenei*, *Hinasuri nehuensis*	MLP	Rovereto [306]; Tambussi [279]

Other apparent ratite fossils from South America whose relations to modern palaeognaths are unclear are an incomplete right tibiotarsus from the middle Paleocene Koluel Kaike Formation of Argentina [277], a pedal phalanx from a poorly dated portion of the Sarmiento Formation that could be anywhere between middle Eocene and early Miocene in age [283], and a distal end of a tibiotarsus from the late Miocene of Patagonia [277]. By the late Miocene there was a marked increase in aridity across the continent, in contrast with the paratropical and warm temperate forests that stretched all the way south into Patagonia before this time [307]. Agnolín [277] puts forth the idea that this environmental change could have led to the extinction of hypothetical forest-adapted non-rheid ratites in South America, while favouring the open-habitat adapted rheids. Due to the high degree of anatomical homoplasy among the various ratite lineages, we may never know the true affinities of *Diogenornis* and these other unnamed ratite-like fossils with certainty, and can only hope that further fossil material will be found that can shed light on their proper phylogenetic placement and ecological habits.

Eocene bird records from South America are unfortunately rare in general [308]. The next oldest rheid fossils are significantly younger, dating from the Miocene (Figure 7, Table 4). *Pterocnemia mesopotamica* was found in the late Miocene of the Mesopotamia region of Argentina [295], and an isolated tarsometatarsus referred to *Pterocnemia cf. mesopotamica* could extend the temporal range of this species back to the middle Miocene [295]. *Opisthodactylus kirchneri*, another rheid from the late Miocene, was described on the basis of a right femur, a right and left tibiotarsus, left and right tarsometatarsi, and pedal phalanges [303]. The robust rheid *Hinasuri nehuensis* is known from a single left femur from the early Pliocene of Buenos Aires province, Argentina [309]. Extant rheid species appear in the Pleistocene, with *Rhea anchorenensis* [310] and *Rhea pampeana* [311] of the Pleistocene of Argentina reassigned to the extant Greater Rhea (*Rhea americana*) [312,313].

2.3.2. Tinamid Fossil Record

The oldest fossils belonging to crown group Tinamidae appear in the early Miocene Pinturas and Santa Cruz Formations of southern Patagonia (Figure 7, Table 5) [314–316]. This apparently abrupt appearance is most likely an artefact of the region's limited Eocene record. Molecular divergence time estimates suggest that the origin of crown Tinamidae occurred in the late Eocene or early Oligocene, concurrent with large-scale cooling and the emergence of open habitat in South America that led to turnover of the region's mammalian fauna [42,317]. Most of these early Miocene fossils are fragmentary and cannot be identified at a generic level, though phylogenetic analyses placed them within the open habitat-specialised tinamid subclade Nothurinae [42,315]. A left humerus from the Santa Cruz Formation was described as a new species, *Crypturellus reai* (*Crypturellus* is an extant genus within the tinamid subclade Tinaminae, which is sister to Nothurinae [316]). Fragmentary remains from the late Miocene were assigned to the extant genera *Eudromia* and *Nothoprocta* [300], both of which belong to Nothurinae. Only two species have been assigned to genera that are no longer extant: *Roveretornis intermedius* and *Tinamisornis parvulus*, both from the early Pliocene Monte Hermoso Formation [306,318], and *Tinamisornis* was later referred to the extant genus *Eudromia* [319]. The extinct *Eudromia olsoni* was also described from the same formation [320], and *Nothura parvula* was found alongside the extant *Nothura darwinii* and *Eudromia elegans* in the late Pliocene Chapadmalal Formation [308,321,322]. More recently, *Nothura parvula* was placed as sister to a *Nothura* + *Taoniscus* + *Rynchotus* + *Nothoprocta* clade [42]. As-yet undiscovered representatives of the Tinamidae stem group, which will likely be Eocene in age, are sorely needed to better understand the evolutionary history of this group, and whether the ancestors of crown tinamids were adapted for flight styles other than the highly specialized burst flight seen in tinamous today.

Table 5. Tinamid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
South America	Pinturas Formation	Santa Cruz province, Argentina	early Miocene	Burdigalian	Fleagle, et al. [287]	Tinamidae gen. et sp. indet	MACN	Bertelli and Chiappe [315]
	Santa Cruz Formation	Santa Cruz province, Argentina	early Miocene	Burdigalian	Marshall and Patterson [286]; Fleagle, et al. [287]; Blisniuk, et al. [288]; Perkins, et al. [289]; Cuitiño, et al. [290]	*Crypturellus reai*, Tinamidae gen. et sp. indet	MPM, MACN, AMNH	Bertelli and Chiappe [315]; Chandler [316]
	Cerro Azul Formation	La Pampa province, Argentina	late Miocene	Messinian	Cerdeño and Montalvo [298]; Verzi, et al. [299]	*Eudromia* sp., *Nothura* sp.	MLP, GHUNLP	Cenizo, et al. [300]
	Monte Hermoso Formation	Buenos Aires province, Argentina	early Pliocene	Zanclean	Deschamps, et al. [304]; Tomassini, et al. [305]	*Eudromia olsoni*, *Eudromia cf. elegans*, *Roveretornis intermedius*, *Tinamisornis parvulus*	MACN	Brodkorb [318]; Tambussi and Tonni [320]; Tomassini, et al. [305]
	Chapadmalal Formation	Buenos Aires province, Argentina	late Pliocene	Zanclean-Piacenzian	Marshall, et al. [323]; Deschamps, et al. [304]	*Eudromia elegans*, *Eudromia* sp., *Nothura parvula*, *Nothura darwinii*	MLP	Tambussi and Noriega [324]; Tambussi and Degrange [308]

2.4. Australian Ratites: Casuariiformes

Both the cursorial emu and the graviportal cassowary belong to the family-level clade Casuariidae [325]. The Emu *Dromaius novaehollandiae* is the only member of its genus, with the recently extinct dwarf Kangaroo Island Emu *D. baudinianus* [326], King Island Emu *D. minor* [327], and Tasmanian Emu *D. diemenensis* [328] now considered to be subspecies of *D. novaehollandiae* [329–331]. Emu are found across most of continental Australia, with the exception of areas of sandy desert and dense forest [332]. Cassowaries have an extremely distinctive appearance, with a casque on the head and wattles on the neck. Unlike Emu, cassowaries typically inhabit dense rainforest habitats. Three cassowary species are currently accepted: the Southern Cassowary *Casuarius casuarius*, the Dwarf Cassowary *Casuarius bennetti*, and the Northern Cassowary *Casuarius unappendiculatus* [66]. All three species inhabit the island of New Guinea, and the Southern Cassowary's range extends into northeastern Queensland, Australia, and some adjacent islands. No casuariiform fossils are known before the Late Oligocene [333], and thus far there is no indication that any other palaeognath lineage has ever been present in Australia (Figure 7, Table 6).

Table 6. Casuarid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
Australia	Etadunna Formation	Lake Palankarinna, South Australia, Australia	late Oligocene	Chattian	Woodburne, et al. [334]; Megirian, et al. [335]	*Emuarius guljaruba*	SAM	Boles [333]
	Wipajiri Formation	Etadunna Station, South Australia, Australia	latest Oligocene-early Miocene	Chattian-Aquitanian	Woodburne, et al. [334]; Megirian, et al. [335]	*Emuarius gidju*	SAM, AM	Patterson and Rich [336]; Boles [337]
	Riversleigh faunal zones A-C	Riversleigh, Queensland, Australia	latest Oligocene-middle Miocene	Chattian-Langhian	Archer, et al. [338]; Travouillon, et al. [339]; Megirian, et al. [335]	*Emuarius gidju*	AM, QM	Boles [337]; Boles [340]; Worthy, et al. [341]
	Camfield beds	Bullock Creek, Northern Territory, Australia	middle Miocene	unknown	Woodburne, et al. [342]	*Dromaius* sp.		Rich [343]; Rich and Van Tets [344]
	Waite Formation	Alcoota, Northern Territory, Australia	late Miocene	unknown	Rich [343]	*Dromaius* sp.	QM, UCMP	Woodburne [345]; Stirton, et al. [346]; Rich [343]; Rich and Van Tets [344]
	Chinchilla Sands	Chinchilla, Queensland, Australia	early Pliocene	Zanclean	Rich and Van Tets [344]	*Dromaius novaehollandiae*	QM	Woods [347]; Stirton, et al. [346]; Rich and Van Tets [344]
	Tirari Formation	Lake Palankarinna, South Australia, Australia	late Pliocene-early Pleistocene	Piacenzian-Gelasian	Stirton, et al. [348]; Rich and Van Tets [344]	*Dromaius ocypus*	UCMP	Miller [349]; Rich [343]; Rich and Van Tets [344]
New Guinea	Otibanda Formation	Morobe, Papua New Guinea	late Pliocene	Piacenzian	Hoch and Holm [350]	*Casuarius* sp.	UCMP	Plane [351]; Rich and Van Tets [344]
	Cave deposits	unknown	Pleistocene?	Unknown	Lydekker [168]; Miller [352]	*Casuarius lydekkeri*	AM	Lydekker [168]; Rothschild [353]; Miller [352]; Worthy, et al. [341]
	Pleistocene swamp deposits	Pureni, Papua New Guinea	late Pleistocene	Chibanian	Williams, et al. [354]	*Casuarius lydekkeri*	CPC	Rich, et al. [355]

One of these earlyfossil Casuariiformes, *Emuarius gidju* [337], had a temporal range spanning from approximately 24 Ma to 15 Ma and is known from a large number of specimens [341]. *E. gidju* was first described on the basis of a distal tibiotarsus, proximal tarsometatarsus and shaft, and a complete pes from the Lake Ngapakaldi Leaf Locality of the Wipajiri Formation in South Australia [336]. Two more specimens were found in late Miocene deposits in Alcoota, Northern Territory [336,356], and even more from formations spanning the late Oligocene to early late Miocene of Riversleigh, Queensland [337,340]. The genus *Emuarius* differs from *Dromaius* in its retention of a cassowary like-femur, while the tibiotarsus and tarsometatarsus have cursorial modifications and are emu-like [337,340]. The pedal phalanges are of an intermediate morphology between the extant emu and cassowary, being more dorsoventrally compressed than those of cassowaries but less than those of emu [337,341]. This taxon is frequently used to calibrate molecular divergence dates between *Casuarius* and *Dromaius*, and a phylogenetic analysis of morphological characters provided robust confirmation for *E. gidju* and *Dromaius* being sister taxa [341]. The derived tibiotarsus and tarsometatarsus of *Emuarius* and *Dromaius* likely evolved after the emu-cassowary split as the emu lineage began to evolve towards a more cursorial mode of life [337,341]. The humerus is less reduced than in *Dromaius,* which may represent the plesiomorphic state of a bird less removed in time from its volant ancestors than extant Emu and cassowaries are [341]. *E. gidju* was smaller than the extant *D. novaehollandiae*, with an estimated weight of 19–21 kg [340] compared with 30–55 kg in emus [332]. Smaller orbits than *Dromaius* indicates *Emuarius* had smaller eyes relative to its skull, and this feature combined with the limited extent of its cursorial specialisations have been interpreted as being representative of the less open habitats present in Australia before the continent underwent extensive aridification beginning in the latter half of the Miocene [341,357].

Emuarius guljaruba, from the 24.1 Ma late Oligocene Etadunna Formation [333–336], is known from a single complete left tarsometatarsus [333]. It is larger than *E. gidju* and most likely a separate species, but its allocation to *Emuarius* remains provisional because no femur has yet been discovered. The extant genus *Dromaius* first appears in the middle Miocene Camfield beds of the Northern Territory [336,343]. *Dromaius arleyekweke* from the late Miocene Waite Formation in the Alcoota scientific reserve, Northern Territory [358] is the oldest named species in this genus. Small and gracile, it is notable in that it exhibits extreme cursorial adaptation, with the tarsometatarsus even more elongated than in *D. novaehollandiae* [358]. It was a small emu, with an estimated body mass based on tibiotarsus least shaft circumference using the algorithm of Campbell and Marcus [359] between 16 and 17.2 kg [358]. Derived features including a distally flattened external condyle of the distal tibiotarsus, the elongated tarsometatarsus, a reduced trochlea metatarsi II as compared with trochlea metatarsi IV, and a shallow median sulcus of the distal trochlea metatarsi II indicate a close affinity with *Dromaius* rather than *Emuarius* [358]. The oldest occurrence of the extant *Dromaius novaehollandiae* is in the early to middle Pliocene-aged Chinchilla Sands of Queensland [336,346,347]. Another species, *Dromaius ocypus*, is known from a tarsometatarsus from the Pliocene Tirari Formation of Lake Palankarinna, South Australia [349]. *D. arleyekweke* was found as the sister taxon of *D. ocypus* and *D. novaehollandiae* [358]. With *D. ocypus* interpreted as less cursorial than either *D. arleyekweke* or *D. novaehollandiae*, this relationship implies an independent acquisition of cursoriality in *D. arleyekweke* or a loss in *D. ocypus*, which may complicate the traditional view of emu evolutionary history as having involved a trend towards increasing cursorial specialisation [358].

The cassowary fossil record is very poor, likely owing to the clade’s preference for tropical forest habitats in which fossils are unlikely to form or be found. Phalanges found from the late Pliocene-aged Otibanda Formation of Papua New Guinea most closely match the extant *C. bennetti* in size but do not appear similar enough to justify being considered conspecific [351]. *Casuarius lydekkeri* [353] is known from a distal right tibiotarsus that is likely Pleistocene in age. The provenance of this fossil is debated [355], and may be from Darling Downs, Queensland based on its preservation [331,341]. Worthy, et al. [341]

assessed the *C. lydekkeri* type material and concluded that its placement within *Casuarius* is likely correct, but there are significant differences between it and the extant *C. bennetti* and *C. casuarius*. A partial skeleton from swamp deposits dating to the late Pleistocene of Pureni, Papua New Guinea was assigned to *C. lydekkeri*, and it was noted to be smaller than any extant cassowary, with a more gracile femur [355]. Unfortunately, no elements from this specimen overlap with those from the Otibanda Formation specimen [355], so the relationship between the only known fossil cassowaries remains a mystery. Naish and Perron [360] speculated that crown cassowaries may be a relatively young clade that evolved in post-Pliocene Australia, with movement into New Guinea occurring during the Pleistocene with the appearance of land bridges between the two landmasses. Of course, this scenario will remain purely speculative until more of these elusive fossils come to light.

2.5. New Zealand Ratites: Apterygiformes and Dinornithiformes

Until just a few centuries ago, New Zealand hosted two ratite lineages: Apterygiformes (kiwi) and Dinornithiformes (moa). Without mammalian competition, kiwi and moa filled the niches of small terrestrial insectivorous and large browsing mammals respectively. Five extant species of kiwi (Apterygidae) are currently recognized, all in the same genus: the Southern Brown Kiwi *Apteryx australis*, the North Island Brown Kiwi *Apteryx mantelli*, the Great Spotted Kiwi *Apteryx haastii*, the Little Spotted Kiwi *Apteryx owenii*, and the Okarito Brown Kiwi *Apteryx rowi* [10]. Convergence between kiwi and small ground mammals is often noted, and is indeed remarkable [361]: kiwi are relatively small-bodied and nocturnal, with hair-like plumage and a superb sense of smell that compensates for their poor vision. Their long bills are used to probe the soil and leaf litter for invertebrates. Their eggs, which are the largest relative to body size of any bird, are laid in burrows [10]. Additionally, they are unique in that they are the only known crown birds with two functioning ovaries [362]. All five species face serious threats from introduced mammalian predators, and introduction of kiwi to predator-free offshore islands has been key to their continued survival [363]. Because of their sedentary nature, substantial local diversity exists, and a study examining thousands of mtDNA loci found 16 to 17 genetically distinct lineages within the five extant kiwi species [364].

Moa took the trend of forelimb reduction in flightless birds to the furthest possible extreme by losing the forelimbs entirely. There is no indication of a humeral articular facet on the scapulocoracoid, which itself is highly reduced and, along with the sternum, is the only vestige of the pectoral girdle [77]. A vestigial furcula is present in the genus *Dinornis* but is absent in all other moa [77]. Curiously, the forelimb-specific gene *tbx5* that is essential for the induction of forelimb development appears to have been fully functional in moa, suggesting that other developmental pathways were responsible for the loss of their wings [365]. The moa clade exhibited an extreme degree of reverse sexual dimorphism that for some time led to confusion regarding the number of known species-level taxa. The accepted number of recent taxa based on ancient DNA is nine species in three families: Dinornithidae, containing *Dinornis robustus* and *Dinornis novaezealandiae,* Megalapterygidae containing the monotypic *Megalapteryx didinus*, and Emeidae, containing *Anomalopteryx didiformis*, *Emeus crassus*, *Euryapteryx curtus*, *Pachyornis geranoides*, *Pachyornis elephantopus*, and *Pachyornis australis* [11]. In the largest-bodied genus, *Dinornis*, females could be up to three times larger than males, and it required a study of ancient sex-linked DNA sequences to reveal that individuals of the previously recognized *D. struthoides* actually represented the much smaller males of *D. giganteus* and *D. novaezealandiae* [366]. The extinction of moa is believed to have occurred extremely rapidly, within 200 years of human settlement approximately 600 years BP [367]. Evidence of their existence remains in New Zealand's flora, some of which retains anachronistic defenses against browsing by moa [368,369]. Moa coprolites and preserved gizzard contents indicate that they were generalist herbivores, though some degree of species-specific dietary niche partitioning existed [370].

How and when moa and kiwi arrived in New Zealand is still unknown [371], as unfortunately neither group has a clear fossil record from before the Pliocene [372]. Molecular phylogenetic evidence generally supports the hypothesis that moa and tinamous are sister taxa [371], suggesting that moa and kiwi colonised New Zealand and became flightless independently. Depending on the timing of their arrival, both clades may have been greatly affected by the Oligocene drowning of New Zealand, which culminated 25 Mya [373,374]. Coincidentally, this time frame appears to have been a key interval for the emergence of recognizable crown group representatives of other palaeognath clades on different landmasses (Tables 3–6).

Debates regarding how much of Zealandia was above water during the Oligocene drowning episode, and how this event impacted the origins of New Zealand's endemic flora and fauna continue [375,376]. Cooper and Cooper [377] postulate that only 18% of the present land area was above sea level during peak inundation as a low-lying archipelago. Trewick, et al. [376] and Landis, et al. [374] proposed that the islands were inundated completely, meaning that the entirety of New Zealand's terrestrial flora and fauna must have arrived in the past 22 million years. An increasing amount of biological evidence suggests at least some land must have remained above sea level during this period and has shifted the consensus against a total inundation [372]. Divergence dating of taxa with poor dispersal ability including frogs of the genus *Leiopelma* [378], *Craterostigmus* centipedes [379], mite harvestmen [380], and zopherid beetles [381] indicates that taxa within these groups diverged well before the drowning event, suggesting that all of them would have needed to independently disperse to New Zealand post-flooding had it been fully submerged. Wallis and Jorge [382] reviewed 248 published divergence dates between New Zealand lineages and their closest relatives elsewhere and found evidence for 74 lineages that diverged before 23 Mya, and of those, 25 lineages dated back before Zealandia split from Australia, making them of true Gondwanan vicariant origin. Interestingly, they found no evidence for a spike in extinctions or new arrivals around the time of the transgression. No study has yet presented unequivocal geological evidence for complete submergence [376,383], and clastic sediments deposited during the Waitakian stage in the southern Taranaki Basin suggests a nearby terrestrial sediment source [384].

Cooper and Cooper [377] examined mitochondrial genetic diversity in kiwi, moa, and acanthisitid wrens and found it to be unusually low compared to other ratites and other avian taxa, and interpreted this as evidence for a bottleneck effect due to the Oligocene drowning. They estimated that re-radiation of these endemic New Zealand lineages began 19–24 Mya. Could this be evidence that moa and kiwi survived the drowning in situ on small islands, or that small volant founding populations arrived afterwards? The apparent survival through the drowning event by other New Zealand taxa means the first scenario is certainly possible. If absence of volant non-tinamid palaeognaths after the middle Eocene is not an artifact of the fossil record, then the ancestral founding populations that ultimately gave rise to kiwi and moa must have arrived before the drowning of New Zealand. Ultimately, only new fossil discoveries from before the drowning event are likely to be able to resolve this question completely.

2.5.1. Apterygid Fossil Record

The oldest kiwi and moa fossils are from the St. Bathans terrestrial vertebrate faunal assemblage from the early Miocene of St. Bathans, in the central Otago region of the South Island (Figure 7, Table 7). The site is dated to 19–16 Ma [385,386], and has provided a rare glimpse at New Zealand's Neogene fauna just after the drowning of New Zealand. The earliest known kiwi, *Proapteryx micromeros*, was described on the basis of a right femur missing its distal condyles [387]. The only referred specimen is also fragmentary, consisting of a left quadrate missing the orbital process anterior to the pterygoid condyle and much of the lateral mandibular condyle [387]. Based on the femur circumference, the estimated body mass of *P. micromeros* was between 234.1 and 377 g, making it only slightly larger than the smallest extant kiwi, *A. owenii* [387]. If this species is representative of size of the earliest total-clade apterygids, its size would seem to refute the hypothesis that kiwi are phyletic dwarfs. The classic explanation for the extremely large eggs of kiwi was that kiwi evolved from a large-bodied ancestor, and body size decreased over time while egg size remained the same [361,388,389]. Instead, it may be more likely to have arisen as a novel feature related to producing highly precocial young [387,390]. Based on the gracile shape of the femur, the authors went as far as to propose that *P. micromeros* may have been volant, though that hypothesis is impossible to assess on the basis of presently known fossil material. If *P. micromeros* was volant, it would represent the only known example of a volant stem member of an extant ratite lineage, and would indicate that kiwi may have arrived in New Zealand after the drowning event. Recently, a 1-million-year-old kiwi fossil from the North Island [391] was identified as a new species *Apteryx littoralis* [392]. No other fossils of intermediate age are yet known between the St. Bathans fauna and the Holocene, making it difficult to trace the origins of crown kiwi.

Table 7. Apterygid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
New Zealand	Bannockburn Formation	Otago, South Island, New Zealand	late early Miocene	Burdigalian	Mildenhall and Pocknall [385]; Pole and Douglas [386]	*Proapteryx micromeros*	NMNZ	Worthy, et al. [387]
	Kaimatira Pumice	Marton, North Island, New Zealand	middle Pleistocene	Calabrian	Worthy [393]	*Apteryx littoralis*	NMNZ	Tennyson and Tomotani [392]

Thus far, the only molecular studies that sample multiple *Apteryx* species yield alternative estimates of the timescale over which species-level diversification within *Apteryx* took place. Using concatenated sequences of nuclear and mitochondrial DNA, Grealy, et al. [41] estimated that *Apteryx mantelli* diverged from other kiwi approximately 13 MYA, whereas *A. haastii* and *A. owenii* diverged at about 4 MYA. The phylogenomic time tree produced by Yonezawa, et al. [49] included nuclear and mitochondrial sequences from all five extant kiwi species, and is in agreement with those divergence time estimates, inferring an origin of crown group kiwi at approximately 12 MYA. By contrast, Weir, et al. [364] inferred a much younger origin of the kiwi crown group at 3.85 MYA using mitochondrial DNA from a large sample of individuals. This was interpreted as evidence that the kiwi radiation coincided with the last glacial period when populations were isolated in glacial refugia, particularly those on the South Island [364].

2.5.2. Dinornithid Fossil Record

The St. Bathans fauna also provides a window into moa evolution (Figure 7, Table 8), though the moa fossils known from this locality are even more fragmentary than those of kiwi. Eggshell fragments found at the site suggest at least two species of moa were present [372,394,395]. Several large avian bone fragments have been found, including one that was identified as a portion of the proximal shaft of a right tibiotarsus [395]. Other large New Zealand landbirds such as flightless adzebills and giant geese existed at the time, but the fibular and outer cnemial crests are separated further on this tibiotarsus fragment than they would be in those groups, and instead resemble those of palaeognaths most closely [395]. One can only hope that the St. Bathans site yields bones that can be more conclusively identified as belonging to early representatives of the moa lineage. Many late Pleistocene-Holocene moa fossils are known [391,396], but Pliocene-Pleistocene moa fossils are much scarcer, and very few are known from before the Otira glaciation event which began ~75,000 years ago [397]. A tibiotarsus assigned to *Euryapteryx* was found in marine mudstone reported to be Pliocene in age [397], and *Dinornis* was present on the North Island at least two million years ago [397]. A tibiotarsus and tarsometatarsus fragments belonging to *Anomalopteryx didiformis* were found in a clay bed below a basalt [398], and if they are indeed older than the basalt and not fissure-fill, they would be about 2.5 million years old [397].

Table 8. Dinornithid fossil record.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
New Zealand	Bannockburn Formation	Otago, South Island, New Zealand	late early Miocene	Burdigalian	Mildenhall and Pocknall [385]; Pole and Douglas [386]	Dinornithidae indet.	NMNZ	Tennyson, et al. [395]
	unlisted	Timaru, South Island, New Zealand	early Pleistocene	Gelasian	Mathews and Curtis [399]	*Anomalopteryx didiformis*		Forbes [398]; Worthy, et al. [397]
	unlisted	Hawke's Bay, North Island, New Zealand	early Pleistocene?	Gelasian?	Beu and Edwards [400]	*Eurapteryx curtus*	AIM	Worthy, et al. [397]
	unlisted	Wairapa, North Island, New Zealand	early Pleistocene?	Gelasian?	Oliver [401]; Beu and Edwards [400]	*"Eurapteryx geranoides"*	NMNZ	Worthy, et al. [397]
	Tewkesbury Formation	Wanganui, North Island, New Zealand	early Pleistocene	Calabrian	Beu and Edwards [400]	*Dinornis novaezealanidae*, *Emeidae* indet.	NMNZ	Marshall [402]; Worthy, et al. [397]

As with kiwi, molecular time trees have yielded divergent hypotheses regarding the timing of the moa radiation. Bunce, et al. [11] found evidence for the radiation being relatively recent. The deepest divergence (between Megalapterygidae and the remaining family-level moa taxa) was estimated at 5.8 MYA, within the same time frame as rapid mountain formation on the South Island during the Miocene-Pliocene [11]. Indeed, the uplift of the Southern Alps would have led to greater habitat diversity [403], and may have spurred the diversification of moa. Interestingly, Haddrath and Baker [38] placed this earliest moa divergence much earlier, at 19 MYA, which roughly coincides with the end of the Oligocene drowning event. Regardless of when the earliest phylogenetic divergence within the moa clade occurred, the fossil record suggests moa crossed onto the North Island via a land bridge 1.5–2 million years ago, which may have led to even greater species diversity as the land bridge reappeared and disappeared during Pleistocene glacial cycles [11]. Whether kiwi were similarly restricted to the South Island before the Pleistocene is unknown, and more fossils from sediments of intermediate age between the Miocene and Pleistocene are needed to make any further advances.

2.6. Malagasy Ratites: Aepyornithiformes

Extremely little is known of the evolutionary history of Madagascar's giant elephant birds. The island's Cenozoic terrestrial vertebrate record is notoriously poor, and thus far all fossil finds are restricted to the last 80,000 years [404–406]. What little we do know comes from subfossil bones and eggshells, the latter of which are extremely abundant in some areas. Detailed records of late Pleistocene and Holocene aepyornithid subfossils are beyond the scope of this paper, but can be found in Angst and Buffetaut [407]. Isotopic analysis of eggshells from southern Madagascar reveals that the birds that laid them mainly browsed on non-succulent trees and shrubs [408], some of which retain anachronistic defenses against ratite browsing similar to plants in New Zealand [369]. Palaeoneurological evidence shows that elephant birds had extremely reduced optic lobes, presumably associated with a predominantly nocturnal or crepuscular lifestyle [409].

Even the number of elephant bird species that existed into the Holocene is not known with certainty. Morphometric analysis of subfossil limb bones by Hansford and Turvey [12] recovered evidence for four species-level taxa: *Mullerornis modestus, Aepyornis hildebrandti, Aepyornis maximus,* and the heaviest bird ever discovered, *Vorombe titan. M. modestus, A. maximus,* and *V. titan* were found to be sympatrically distributed across much of Madagascar, while *A. hildebrandti* was restricted to the central highlands [12]. Molecular studies are needed to evaluate this morphology-based taxonomic scheme, as well as additional fossil collecting in other regions of Madagascar, as most known specimens come from the south of the island and the central highlands [12]. Nuclear and mitochondrial DNA recovered from eggshells suggested that *Aepyornis* and *Mullerornis* diverged approximately 27.6 MYA [41]. A divergence at 3.3 MYA between *A. hildebrandti* and *A. maximus* had previously been estimated [45]. The third genus found by Hansford and Turvey [12] appears not to have been sampled, highlighting the need to extract aDNA from additional eggshells and subfossil specimens.

Unraveling the decline and eventual demise of elephant birds in Madagascar is less straightforward than for moa, which went extinct within a brief window of time following human arrival in New Zealand [367]. Debate as to how long humans have been present on Madagascar, and thus for how long they coexisted with the island's endemic megafauna, is ongoing. Based on rare findings of stone tools and butcher marks on elephant bird bones, humans may have arrived early, between 10,000 and 4000 years BP [410,411]. Some anthropologists advocate a more recent arrival, between 1600 and 1000 BP [412], while an intermediate arrival time between 2000 and 1600 BP is supported by ^{14}C data associated with human activity [413]. If humans and elephant birds indeed coexisted for a long period of time, their extinction cannot be easily attributed to the rapid overkill of a naïve population as with moa [411,414]. Instead, a more complex scenario for the extinction of the Malagasy megaherbivores, which also included giant lemurs and tortoises, as well as dwarf hippopotami, has been proposed. Instead of overhunting, the key factor in their decline may have been the introduction of livestock such as Zebu cattle and a shift towards pastoralism. The introduction of large herbivores by humans coincides with the time frame of Malagasy megafaunal extinction, and under this scenario a combination of resource competition with introduced herbivores, alteration of the landscape by humans to suit the needs of livestock, and increased bushmeat hunting due to the expanding human population could have led to the demise of the Malagasy megafauna [414]. Whatever the direct cause or causes, the extinction of Aepyornithidae occurred roughly 1000 years BP according to radiometric data [415], concurrent with the drastic decline and extinction of the remainder of the endemic megafauna of the island [416], though some colonial records suggest they may have survived in isolated areas into the 17th century [407,417].

2.7. Antarctic Ratites

Antarctica was once a very different place from the frozen continent we recognize today. The formation of a continental ice sheet did not occur until the Eocene—Oligocene boundary [418]. Up until this time, the continent boasted thriving flora and fauna that were isolated from large mammalian predators—an ideal environment for flightless birds to evolve. Palynological records from sediment cores dated to 53.6–51.9 MYA from the eastern Antarctic Wilkes Land coast reveal that a diverse paratropical rainforest with frost-free winters existed during the early Eocene climatic optimum [419,420]. Sparse pollen from more cold-tolerant trees such as *Nothofagus* (southern beech) and *Araucaria* ("monkey puzzle") trees suggest temperate rainforests further inland [419,420]. By the middle Eocene, cores from 49.3–46 MYA indicate species diversity had decreased [420] and that cool temperate *Nothofagus*-dominated forests had taken over [419,420]. As a point of comparison, petrified wood samples from King George island in the South Shetland Islands aged 49–43 MYA (Middle Eocene) indicate a forest similar in composition to the cold temperate Valdivian rainforest of Chile [421], which is not dissimilar to the temperate rain forests of New Zealand that moa once inhabited.

There is fossil evidence of large terrestrial birds in Antarctica during this time, but they are too fragmentary to allow firm diagnoses (Table 9). A distal fragment of a right tarsometatarsus purported to be a ratite was found in the middle Eocene of the La Meseta Formation of Seymour Island, just off the Antarctic peninsula [422]. Unfortunately, there is no evidence for its ratite affinities other than its large size. Its unusually large trochlea for the second toe is different from that of all other known ratites [76], and it bears consideration that misattribution of large bones to ratites is not uncommon [423]. An anterior part of a premaxilla originally attributed to a phorusrhacid, also from the La Meseta Formation [424–428], was recently suggested to belong to a palaeognath [429,430]. The presence of ratites on Seymour Island would not be surprising given the environmental conditions at the time, as evidenced by abundant petrified conifer wood from the La Meseta Formation [431]. Confirmation of their existence will have to await more complete specimens, but remains a tantalizing possibility.

Table 9. Putative Antarctic ratites.

Continent	Geological Unit	Location	Epoch	Stage	Age Reference	Taxa	Institutions	Reference
Antarctica	La Meseta Formation	Seymour Island	late Eocene	Lutetian-Priabonian	Amenábar, et al. [432]	"ratititae"	MLP, UCR	Tambussi, et al. [422]; Cenizo [429]; Acosta Hospitaleche, et al. [430]

The majority of Cenozoic Antarctic bird fossils belong to penguins and other marine birds, but Seymour Island was also host to a thriving terrestrial fauna during the Eocene. The stem falconid *Antarctoboenus carlinii* [433,434] was named from a distal end of tarsometatarsus from the early Eocene portion of the La Meseta Formation [430]. Small mammals were abundant, and included the extinct and highly enigmatic sudamericid gondwanatheres [435,436] as well as didelphimorphid, polydolopimorphid, and microbiotheriid marsupials [436–440]. Seymour Island also hosted South American meridiungulates [436,441–445], and a large sparnotheriodont with an estimated body mass of 395–440 kg [446] indicates the ecosystem was fully capable of sustaining large herbivores. The presence of meridiungulates also indicates that overland dispersal from South America was possible, and there is no reason why South American ratites could not have made the journey as well. The Drake passage between South America and the Antarctic Peninsula did not begin to open until approximately 41 Ma [447], meaning these faunas lived during an era where biotic interchange was possible. Such interchange with Australia was also hypothetically possible for a brief window during the Paleocene and early Eocene, as dinocyst assemblages indicate the flow of ocean water across the Tasman gateway by 50–49 Ma [448]. It is also possible for a unique ratite lineage to have arisen on Antarctica, though—as with all other ideas regarding Antarctic palaeognaths—this will remain highly speculative until more fossils are recovered. Regardless of whether the Antarctic terrestrial fauna included ratites, the complete glaciation of the continent in the Oligocene would have doomed them to extinction.

3. Molecular Phylogenetic Hypotheses of Palaeognath Interrelationships

Interpreting phylogenetic relationships among extant and fossil palaeognaths was historically challenging due to morphological homoplasy, and although molecular phylogenetic approaches have yielded some consensus on palaeognath interrelationships, areas of disagreement remain. Thus far, all recent molecular phylogenetic studies of palaeognaths have recovered ostriches as the sister taxon to the rest of the clade, yielding congruent support for a reciprocally monophyletic clade called Notopalaeognathae comprising rheas, tinamous, kiwi, moa, and elephant birds [36–41,44–46,48–50,54–58,449,450]. Limited morphological evidence has also been found in support of a monophyletic Notopalaeognathae [33,77]. In addition, all molecular phylogenetic studies investigating ancient DNA from palaeognath subfossils have strongly supported elephant birds as sister to kiwi [41,45,46,49,57], and tinamous as sister to moa [38,40,41,44–46,49,50,57].

The internal relationships of Notopalaeognathae remain controversial, particularly in regard to the position of rheids. The internal branches at the base of Notopalaeognathae appear to be very short, indicating that the clade may have undergone relatively rapid diversification early in its history, which may have led to incomplete lineage sorting and limited phylogenetically informative character acquisition along deep internodes [38,39,56]. This may have pushed Notopalaeognathae into an empirical anomaly zone in which the most common gene trees from molecular phylogenetic analyses do not match the species tree [56]. Rheids are most often recovered in one of two phylogenetic positions:

1. As the sister taxon of the remaining notopalaeognaths [36,37,39,41,42,44–46,48,49,54–56], though this position is generally weakly supported (Figure 10) [41,44,49].

2. As sister to a casuariid + apterygid + aepyornithid clade ("Novaeratitae") [38,43,48,50,56–58,450] (Figure 11). Several alternative topologies in addition to these have been recovered that place rheas sister to the tinamid-dinornithid clade [37,39,449] or sister to casuariids [38].

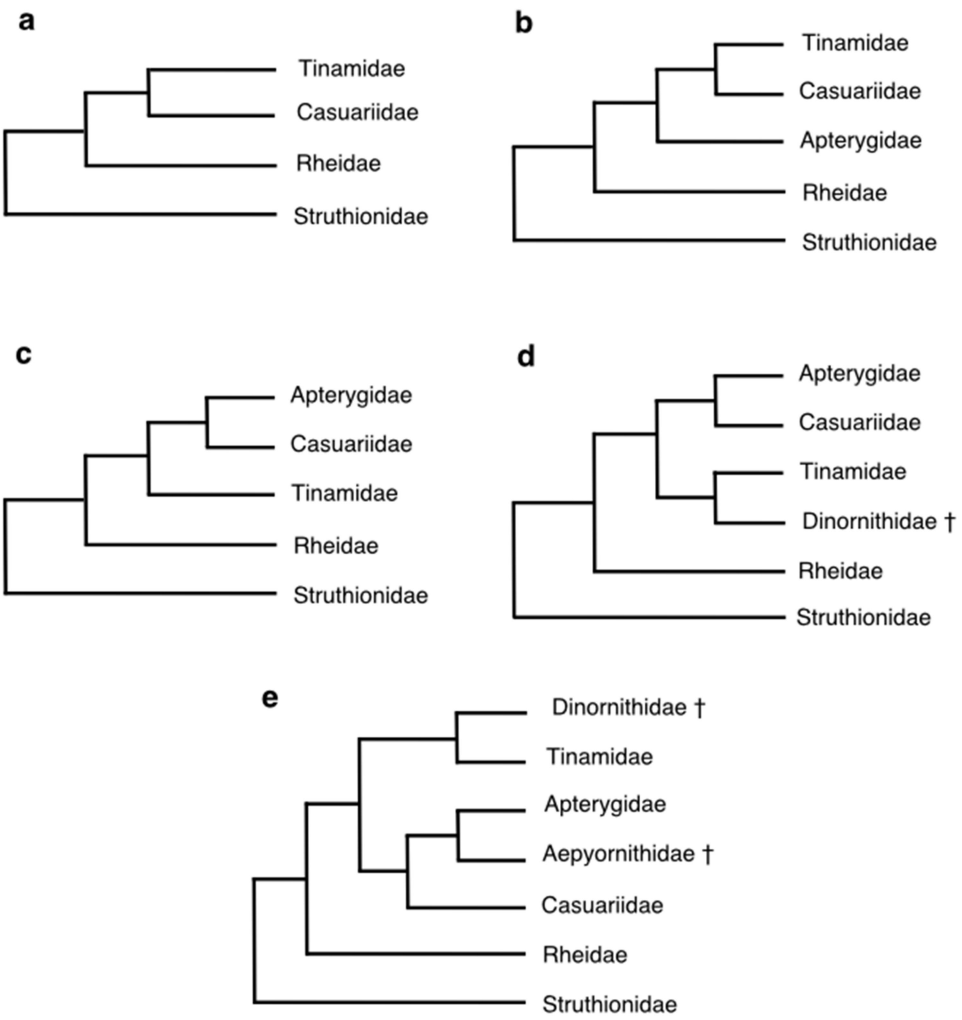


Figure 10. A summary of recent molecular phylogenetic studies that recover Rheidae as sister to the remaining notopalaeognaths. Extinct clades are indicated by †. (**a**) Smith, et al. [39] primary concordance and total evidence tree. (**b**) Prum, et al. [48] concatenated dataset; Kuhl, et al. [54]. (**c**) Hackett, et al. [36]; Harshman, et al. [37] maximum likelihood and Bayesian tree; Claramunt and Cracraft [55]. (**d**) Phillips, et al. [44]; Cloutier, et al. [56] concatenated dataset. (**e**) Mitchell, et al. [45]; Grealy, et al. [41]; Yonezawa, et al. [49], Urantówka, et al. [46], Almeida, et al. [42].

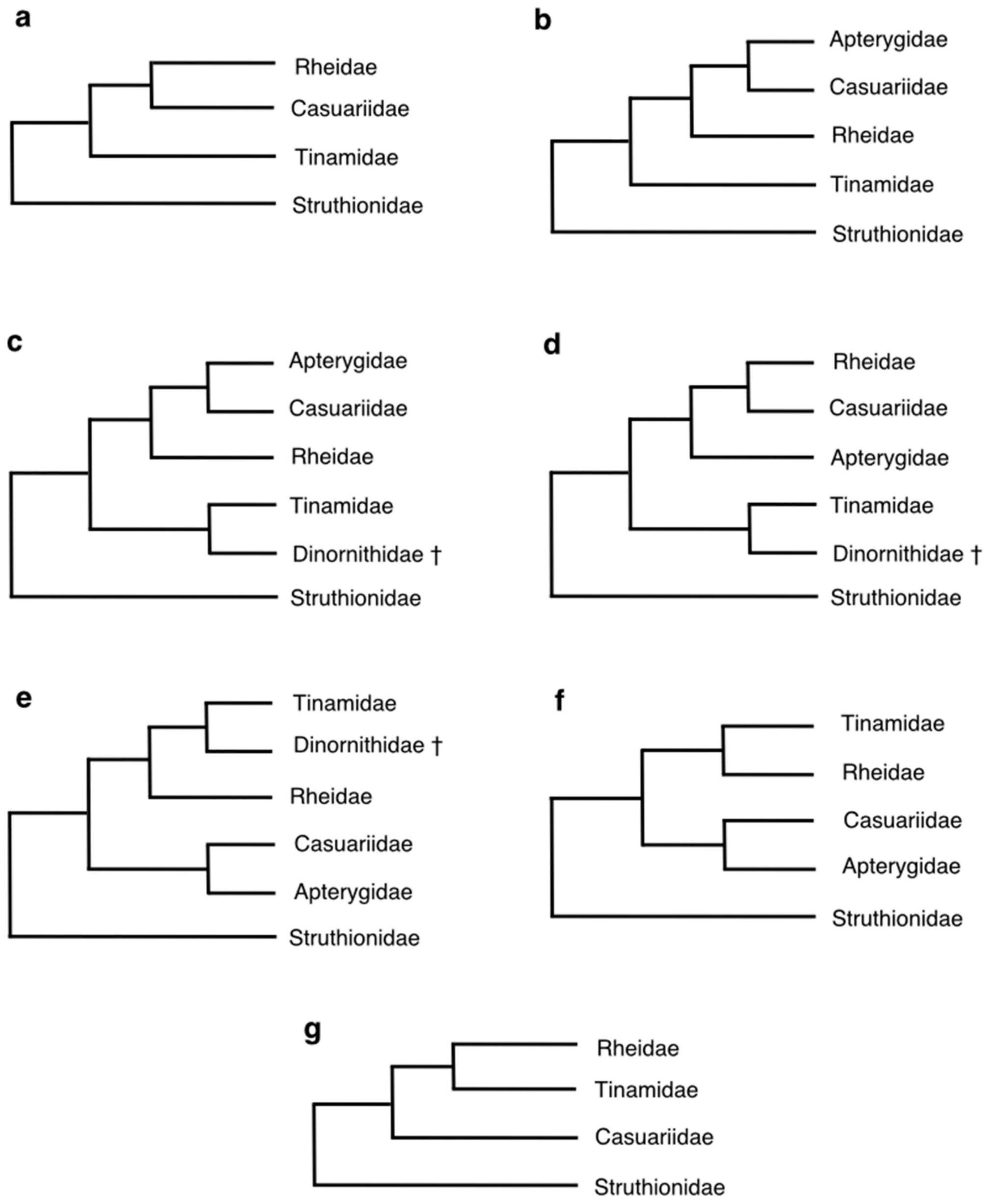


Figure 11. A summary of recent molecular phylogenetic studies that do not recover Rheidae as sister to the remaining notopalaeognaths. Extinct clades are indicated by †. (**a**) Kimball, et al. [450]. (**b**) Prum, et al. [48] binned ASTRAL analysis; Reddy, et al. [58]; Sackton, et al. [50]; Feng, et al. [43] maximum likelihood analysis of avian growth hormone gene copies. (**c**) Haddrath and Baker [38] 10 and 27 gene concatenated dataset, 27 gene consensus tree; Baker, et al. [40]; Cloutier, et al. [56] total evidence consensus tree. (**d**) Haddrath and Baker [38] 10 gene consensus tree. (**e**) Smith, et al. [39] maximum likelihood reanalysis of Phillips, et al. [44]; (**f**) Harshman, et al. [37] maximum parsimony and RY coded maximum likelihood analysis; Wang, et al. [449]; (**g**) Smith, et al. [39] using 40 loci.

Determining why these discrepancies exist could be key to finally resolving the internal branching order of Notopalaeognathae. In their attempt to address this question using genome-wide datasets of conserved nonexonic elements, introns, and ultraconserved elements, Cloutier, et al. [56] found that the consensus species tree building methods MP-EST and ASTRAL-II placed rheids sister to the casuariid-apterygid-aepyornithid clade with maximal bootstrap support from MP-EST for all three datasets. Their concatenated supermatrix dataset recovered rheids as sister to all other notopalaeognaths, but with weaker statistical support. In general, concatenated analyses have often yielded different results to consensus tree building methods regarding the interrelationships of Notopalaeognathae, with concatenated data more frequently recovering rheids as sister to all other notopalaeognaths [56]. Sackton, et al. [50] found similar results and claim that their genome-wide approach is more robust to incomplete lineage sorting than concatenation, which is what leads to discrepancies between studies. "Novaeratitae", a proposed clade that places casuariids sister to an elephant bird + kiwi clade, received high bootstrap support when mitochondrial and genomic data were combined but not when each were analysed individually [41]. In order to finally resolve the messy internal relationships of notopalaeognaths, a greater number of faster-evolving retrotransposons and introns may need to be analysed [41], and the models of sequence evolution employed must fit the type of genomic data being investigated [58].

Molecular Divergence Time Estimates

The vast majority of molecular divergence time analyses have recovered an estimate for the palaeognath-neognath divergence in the Cretaceous Period, preceding the K-Pg extinction event (e.g., [38,41,42,44,45,47–49,54,55,449]), an estimate that is consistent with the known (yet sparse) fossil record of Mesozoic neornithines [72]. However, estimates of the age of the neornithine root vary enormously, ranging from 131 Ma [38] to 63.2 Ma [42]. Importantly, the oldest published divergence time estimates do not invalidate Gondwanan vicariance as a potential driver of crown palaeognath divergences [38]. The enormous temporal breadth of deep neornithine divergence time estimates have stimulated discussion about the role of model misspecification in driving erroneously ancient divergence time estimates [451]. Hypothesized selection for reduced body size across the end-Cretaceous mass extinction event could have transiently increased molecular substitution rates along the deepest branches within neornithine phylogeny, which would be expected to drive overestimates of node ages around the neornithine root [452]. Indeed, simulations suggest that 40 million years' worth of age disparity for the neornithine root node can plausibly be explained by the effect of body size on nucleotide substitution rates [452]. Importantly, the palaeognath stem lineage is inferred to have exhibited high nucleotide substitution rates, consistent with ancestral palaeognaths having been small-bodied (the last common ancestor of crown palaeognaths was estimated to have weighed approximately 2.9 kg) [452]. With smaller body sizes and shorter generation times than other extant palaeognaths, tinamous exhibit anomalously high nucleotide substitution rates compared with other palaeognaths [37,449], which may additionally drive erroneously ancient divergence time estimates near the neornithine root [45,453].

Lingering uncertainty regarding the phylogenetic divergence times of crown palaeognaths complicates attempts to place lithornithids within the broader context of palaeognath evolution. Since most palaeognath divergence time estimates pre-date the earliest well corroborated lithornithid fossils [41,45,49,449] (with the possible exception of the ~66 million year old isolated scapula from the Hornerstown Formation [63]), the hypothesis that at least some lithornithids represent early stem group representatives of major palaeognath subclades is temporally viable. However, Prum, et al. [48] estimated the origin of the palaeognath crown group at 51 Ma, during the Ypresian stage of the early Eocene. In this temporal scenario, most lithornithid fossils predate the crown palaeognath radiation, in which case nearly all lithornithids with the exception of those found in the younger Messel Formation could only represent stem palaeognaths. This relatively young age for the palaeognath crown group would also imply that early Paleogene remains such as *Diogenornis*, Palaeotididae, and the Middle Paleocene fossils identified as belonging to a stem rheid fall outside the palaeognath crown group.

4. Key Gaps in the Palaeognath Fossil Record

4.1. Cretaceous Stem Palaeognaths

Virtually no examples of Cretaceous stem palaeognaths have yet been identified, despite consensus—on the basis of divergence time estimates as well as the presence of fossil total-clade neognaths—that they must have existed at this time. This is perhaps the most glaring gap in the known palaeognath fossil record, but is perhaps an unsurprising one given the general scarcity of well-supported Cretaceous neornithines at present. A probable example of a Cretaceous total-clade neognath is *Vegavis iaai*, recovered from the late Maastrictian of Vega Island, Antarctica [69]. This fossil taxon shows apparent specialisations for foot-propelled diving, and has been variably placed within Anatoidea [69], as a stem neognath, or even outside of Neornithes altogether [72,454]. *Asteriornis maastrichtensis*, from the Maastrichtian of Belgium, is another probable Cretaceous total-clade neognath. At 66.7–66.8 million years old, *Asteriornis* is slightly older than *Vegavis*, and therefore the oldest well-corroborated neornithine yet discovered [72]. A relatively small bird (estimated to have weighed roughly 490 grams), *Asteriornis* was identified as a total-clade galloanseran [72], although a recent study raised the (weakly supported) hypothesis that it instead represents a total-clade palaeognath [8]. The presence of probable total-clade neognaths from before the K-Pg mass extinction, such as *Vegavis* and *Asteriornis*, implies that the palaeognath-neognath split must have occurred even earlier in the Cretaceous (though, as described above, molecular divergence dates do not agree on the true antiquity of the basal neornithine phylogenetic divergence).

Longstanding biogeographic hypotheses held that Neornithes originated in Gondwana [26,55], partly on the basis that there are far more extant endemic bird clades on the southern continents of South America, Africa, and Australia than there are on the northern continents of North America and Eurasia [455]. However, the discovery of *Asteriornis* in Europe indicates that deeply diverging crown bird lineages have a long evolutionary history in the Northern Hemisphere [72]. More broadly, many clades that are currently restricted to tropical latitudes have fossil stem group representatives in the Paleocene and Eocene of the Northern Hemisphere (e.g., [70,74,120,124,455–457]), implying far more widespread geographic distributions early in these clades' evolutionary histories. Given the generally dispersive capacity of birds, as well as the fact that hothouse climatic conditions predominated throughout the early Paleogene and led to the expansion of paratropical forests into high latitudes, the present-day geographic distributions of many extant tropical clades may not reliably indicate their ancestral areas of origin [74]. In light of these considerations, determining the most likely fossil localities for revealing the first evidence of a Cretaceous stem palaeognath is challenging, and it would seem equally probable that an early palaeognath could derive from Late Cretaceous deposits of either the northern or the southern hemisphere.

4.2. Stem Group Representatives of Extant Palaeognath Subclades

If contemporary hypotheses of ratite paraphyly and dispersal are accurate, small volant palaeognaths should have been present on landmasses where extant palaeognaths are found during the Paleocene or Eocene [45]. However, the timing of each independent palaeognath transition to large body size and flightlessness is uncertain. Transitions to complete flightlessness among island-dwelling birds typically necessitate few terrestrial predators and a food source that does not require flight [458,459]. If these conditions are met, flightlessness may be advantageous because it allows for energy conservation through reduction in the size of the pectoral musculature [460]. Indeed, the basal metabolic rates of flightless rails are lower than those of closely related flighted rails [460]. Given the right circumstances, transitions to flightlessness and large body size can apparently arise quite rapidly. The extinct giant flightless Hawaiian goose *Branta rhuax* is nested within the Canada Goose *Branta canadensis* species complex, and its presence on the main island of Hawai'i means it must have become large and flightless in less than 500,000 years [461].

Most geologically recent transitions to avian flightlessness occurred on oceanic islands in the absence of predation and competition from terrestrial mammals [458,459]. Were these conditions met on continents in the wake of the K-Pg mass extinction event, allowing multiple lineages of ratites to evolve flightlessness and large body sizes before mammalian predators and competitors could evolve? These conditions appear to have been met on at least some landmasses, as even 10 million years after the extinction event most mammals remained relatively small and unspecialized [462]. The Corral Bluffs site in Colorado suggests that the mammalian fauna in the immediate aftermath of the K-Pg was dominated by small omnivores and insectivores [463], and generally there was a dearth of specialized mammalian carnivores in the early Paleocene [76,464,465]. The makeup of terrestrial mammalian faunas at the time could well have favoured the evolution of flightlessness in birds that could obtain food on the ground, and other large flightless Paleogene bird clades such as Gastornithidae, Phorusrhacidae, and Dromornithidae may have followed a similar pattern along with ratites [76]. In particular, the lack of placental carnivores in South America through most of the Cenozoic may have contributed to the diversity of flightless birds on that continent, which also included Phorusrhacoidea and the giant anseriform *Brontornis* [76].

If volant stem group representatives of various palaeognath subclades evolved into large-bodied, flightless forms during a relatively narrow temporal window in the early Paleogene, the chances of finding direct fossil evidence of these small-bodied ancestral forms might be relatively low. Indeed, short internodes near the root of Notopalaeognathae indicate a rapid diversification of palaeognath lineages during the Paleogene [41,56]. However, if some transitions to flightlessness were protracted, the chances of identifying informative fossils documenting such transitions would be more likely. With their recent reassignment to total clade Struthionidae, eogruids are a superb example of previous unrecognised stem group representatives of an extant ratite lineage, though better data on their wing apparatus are needed in order to assess whether all known taxa were flightless. If some taxa were volant, Eogruidae could provide an illuminating window into the relative timing of transitions to cursoriality, large body size, and loss of flight in a ratite lineage.

A further challenging aspect of reconstructing the early evolutionary history of the various ratite lineages is that, if flightlessness and large body size arose numerous independent times, confidently assigning a given volant palaeognath fossil from the Paleogene to the correct palaeognath subclade may prove difficult due to convergence. However, the ongoing exploration of certain localities may yield further insight into transitions to flightlessness among certain ratite lineages—for example, additional finds from the St. Bathans fauna could shed more light on the origins of moa and kiwi, and help elucidate whether the stem kiwi *Proapteryx* was indeed small and volant as initially hypothesized [387].

5. Reconstructing the Most Recent Common Ancestor of Palaeognaths

Understanding the nature of the most recent common ancestor (MRCA) of extant palaeognaths will reveal much about palaeognath macroevolution, and neornithine macroevolution more broadly. For instance, insight into the flight apparatus of the crown palaeognath MRCA will help explain how the geographic distributions of extant palaeognaths arose. Moreover, stem palaeognaths (along with stem galloanserans and stem neoavians) are inferred to have survived the end-Cretaceous mass extinction event [41,48,71,72], while all non-neornithine birds appear to have perished [73]. Strong evidence regarding the morphology and ecology of early palaeognaths may also help clarify ecological factors that may have favoured the survivorship of crown birds with respect to non-neornithine avialans—one of the more contentious questions in contemporary palaeornithology [71,77]. Inevitably, given that the palaeognath-neognath split is the deepest divergence within crown birds, a better understanding of the nature of the palaeognath MRCA will in turn shed light on the common ancestral condition of all extant birds. Although much remains to be learned, there are several inferences that can be made regarding the nature of the most recent common ancestor (MRCA) of palaeognaths based upon the information currently available.

5.1. The Flight Apparatus of the Crown Palaeognath MRCA

Due to the relaxation of stabilizing selection, significant polymorphism exists in the wing musculature of ratites [466], complicating attempts to infer features of the ancestral crown palaeognath wing. As the only extant flighted palaeognaths, tinamids presumably provide the best source of data on the muscular anatomy of the wings of early flighted palaeognaths. Nearly all flight muscles present in neognaths are found in tinamids, with the exception of the biceps slip [274,467,468]. Extant phylogenetic bracketing [469] therefore indicates that the same suite of muscles would be expected to be present in both the crown palaeognath and crown neornithine MRCAs. Of course, tinamids are specialized for burst flight over relatively short distances, and as such are probably imperfect analogues of the ancestral crown palaeognaths that must have colonized distant landmasses in the early Cenozoic [470]. Subsequent losses of dispersal capacity, and the extinction of dispersive ancestral lineages, can leave the inaccurate impression that poorly dispersive taxa underwent oceanic dispersal via stochastic events. For example, the phasianid galliforms *Margaroperdix* (Madagascar) and *Anurophasis* (New Guinea) are poor dispersers, yet are found on isolated islands [470]. Phylogenomic analyses revealed that these taxa are nested within *Coturnix* quails and likely evolved from a dispersive *Coturnix*-like ancestor. Both taxa apparently independently evolved towards a non-dispersive partridge-like morphotype, reminiscent of how the ratite condition appears to have repeatedly evolved in palaeognaths [470]. As discussed in this review, some lithornithids appear to have been reasonably capable fliers and could provide more accurate insight into the nature of dispersive ancestral crown palaeognaths.

5.2. Inferred Ecology of the Palaeognath MRCA and K-Pg Survivorship

Non-neornithine avialans thrived throughout the Cretaceous and remained diverse through the Maastrichtian, before suddenly disappearing at the K-Pg boundary [73]. Until this point, Enantiornithes were the dominant Mesozoic avialan clade with more than 60 known species and a worldwide distribution [471–473]. Why did they become extinct, while neornithines survived? The answer may be associated with their ecology and habitat preferences. The K-Pg impact was devastating to the world’s forests and resulted in significant species turnover [71,77,474–478]. Palynology of K-Pg boundary sections across the globe indicates that ground cover following the impact consisted primarily of ferns. This “fern spike” is interpreted as evidence of a disaster flora following the destruction of forests worldwide [71,464,474–476] by widespread fires ignited by the impact and subsequent cold and darkness [479,480]. This fern spike persisted for approximately 1000 years, and closed-canopy forests appear to have remained generally rare during this interval [481]. Indeed, it may have taken as long as 1.4 Ma for floral diversity hotspots to reappear [482]. This widespread habitat destruction would have been a powerful agent of selection against the mostly arboreal Enantiornithes, though this hypothesis does not explain the extinction of contemporaneous marine avialans such as Ichthyornithes and Hesperornithes. Instead, the demise of these marine piscivorous taxa may have been part of a broader collapse of marine food chains in the aftermath of the Chicxulub impact [77,81,483–486]. Importantly, ancestral state reconstructions of crown birds predict that the MRCAs of crown birds and the deepest crown bird subclades (Neornithes, Palaeognathae, Neognathae, and Neoaves) were all non-arboreal [71]. As such, the ancestors of palaeognaths may have made it through this mass extinction event partly by virtue of having exhibited terrestrial non-arboreal lifestyles.

As the most stemward palaeognaths known [49,64], lithornithids provide the best opportunity to draw fossil-informed inferences about the nature of the crown paleognath MRCA. Vibrotactile bill tips in *Lithornis promiscuus* and *Paracathartes howardae* may have been associated with probe-feeding in the ground, an interpretation congruent with the hypothesis of predominant K-Pg survivorship among non-arboreal taxa. A vibrotactile bill tip organ composed of mechanoreceptors known as Herbst corpuscles embedded within the bone was hypothesized to be a plesiomorphy of Neornithes by du Toit, et al. [80], which would support the neornithine MRCA and its immediate descendants as having been ground-foraging birds. Such organs are found in palaeognathous and neognathous probe-foragers, enabling them to locate prey buried in substrate through vibration detection [487,488]. In non-probe-foraging palaeognaths, the vibrotactile bill tip organ is vestigial [80,489]. The hypothesis that lithornithids and the palaeognath MRCA were probe-feeders agrees with ideas put forth by Houde [62], who suggested that lithornithids may have preferred to live near water and probed for food using their long beaks, noting the similarity of their jaw apparatus to those of kiwi. Additionally, the genus *Lithornis* appears to have had relatively large olfactory lobes, similar to olfactory foraging taxa including Procellariiformes and kiwi [490]. Since ground feeding birds are more likely to become flightless than arboreal taxa, a volant, non-arboreal, probe-feeding taxon would seem to be a provide a reasonable expectation for the ecology of the MRCA of crown palaeognaths.

6. Conclusions

Our understanding of palaeognath evolution has progressed markedly over the past two decades thanks to the development and application of sophisticated molecular phylogenetic approaches and the continued interrogation of the fossil record; however, many fundamental questions about the origins of extant palaeognath diversity remain unanswered. The present review affirms that the palaeognath crown group has a reasonably thorough fossil record from the late Oligocene-early Miocene onwards, with the exception of early elephant birds and early representatives of the New Zealand ratites, whose fossil record remains sparse until the Pleistocene [392,397,409]. However, the fossil record still fails to clearly illuminate how and when independent transitions to large body size and flightlessness arose among the multiple lineages of "ratites". As yet, volant stem members of these extant flightless clades remain unknown (besides the possible exception of Proapteryx [387]), leaving the early evolutionary history of crown group palaeognaths shrouded in mystery. Lithornithids currently provide the best insight into the nature of the earliest total-clade palaeognaths, and their relatively small size, probable non-arboreal ecology, and apparent capacity for sustained flight may make them useful models for understanding the nature of avian survivors of the end-Cretaceous mass extinction event. In the coming years, we anticipate increased consensus on both the evolutionary relationships and age of Palaeognathae and its major subclades, and hope that such advances are accompanied by the recognition of new fossil total-group palaeognaths from the Mesozoic and early Cenozoic. Such advances will be necessary to fill the many gaps in the palaeognath fossil record identified in this review, and to shed light on the repeated independent origins of "ratites"—one of the most striking examples of convergent evolution in birds, or indeed any other vertebrate clade.

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