A review of the Cenozoic fossil record of avian eggs, eggshells, and nests

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Keywords: avian reproduction; Cenozoic; fossil eggs; eggshell microstructure; oology; palaeobiogeography; palaeoecology; nesting behaviour; isotopes; palaeogenetics

Abstract

Modern avian lineages evolved and radiated during the Cenozoic Era (66 Ma–present) following the end-Cretaceous extinction. Despite a wealth of isolated eggshells and nest structures, the global oological record remains unevenly studied. This review integrates the scattered literature on Cenozoic oological remains to produce the first comprehensive synthesis of their distribution, structure, palaeobiogeography, and palaeobiological significance. This record reconstructs temporal patterns in eggshell microstructure, nesting ecology, and biogeography. Methodological advances in microscopy, electron backscatter diffraction, isotopic geochemistry, and biomolecular preservation have permitted transformed refined taxonomic attributions and ecological inferences of oological material. This synthesis highlights key gaps—particularly in Africa, Antarctica, and Oceania—and outlines research priorities aimed at linking palaeontology, molecular biology, conservation, de-extinction, and Earth-system science to better understand the evolutionary trajectory of avian reproduction. Furthermore, this dynamic avian fossil record provides a foundation for understanding past ecosystems and conserving biodiversity for the future.

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Introduction

Birds are the most diverse group of non-marine tetrapods, with estimates ranging from 10,906[1] to over 18,000[2] species of extant taxa. The ancestry of modern birds can be traced back to the Late Jurassic, with *Archaeopteryx* from the Tithonian

representing a pivotal early bird species[3,4]. Having survived the mass extinction at the end of the Cretaceous, birds underwent a rapid adaptive radiation, filling ecological niches left vacant by non-avian dinosaurs, pterosaurs, and terrestrial reptiles. They subsequently colonised all continents, adapting to an extraordinary range of environments and developing a remarkable diversity of ecological and behavioural strategies[5–7].

Bird reproduction, more than that of any other vertebrate group, reflects the interplay between physiological constraint, ecological opportunity, and environmental context[8–12]. The avian reproductive record offers a rare and durable archive of behaviour through geological time, owing to the production of calcareous eggs and the construction of nests leave abundant physical traces[8–16]. The morphology and microstructure of eggshells encapsulate critical information on gas exchange, nesting environment, incubation strategy, and phylogenetic affinity. When examined alongside body and trace fossils, sedimentological context, and isotopic data, eggs and eggshells reveal the complex evolutionary history of avian adaptation following the end-Cretaceous mass extinction[5–7].

The Cenozoic Era witnessed the complete restructuring of global ecosystems and the rapid diversification of crown-group birds. From the large, flightless taxa of the early Palaeocene to the extensive radiation of Neognaths and Palaeognaths, fossil evidence of eggs, eggshells, and nests provides a complementary dimension to skeletal data. Despite over a century of discoveries, the avian oological record remains geographically and stratigraphically patchy. Fossil eggshells are often recovered in isolation and described under parataxonomic systems, sometimes with limited phylogenetic resolution. Regional and temporal biases—driven by

depositional environments, taphonomic processes, and uneven research intensity—have hindered a holistic understanding of avian reproductive evolution[5,6] (5, 6). Recent methodological advances have reinvigorated the study of fossil avian reproduction. Techniques such as scanning electron microscopy (SEM), cathodoluminescence imaging, and electron backscatter diffraction (EBSD) characterise eggshell ultra and microstructures in high-resolutions[17,18]; while stable-isotope and trace-element analyses yield insights into palaeoclimate and avian physiology[19–21]. In rare but remarkable cases, preserved biomolecules and fragments of ancient DNA provide molecular constraints that complement morphological interpretations[9–13]. Collectively, these approaches allow reconstructions of nesting strategies, incubation behaviours, and environmental adaptations at unprecedented resolution.

Nevertheless, profound gaps persist in the avian reproductive record, particularly across the Cenozoic. Although Mesozoic enantiornithine and early ornithuromorph eggshells have illuminated primitive reproductive stages[7], the transition from these ancestral conditions to the derived strategies of modern birds remains only partly understood[5,6]. The rarity and fragmentary preservation of Palaeogene and Neogene nests and eggshells, together with the scarcity of integrative analyses, limit our ability to trace continuous evolutionary trends. Earlier studies have enriched specific aspects of Cenozoic palaeoology but are often restricted to narrow regional or taxonomic scopes[8–15]. For instance, Mikhailov and Zelenkov[15] combined eggshell and skeletal evidence to reconstruct ostrich evolution through climatic fluctuations, while Vieco-Gálvez et al.[14] established modern analogues using *Apteryx* eggshells to infer palaeoenvironmental adaptations. Such research underscores the value of

integrating extant and extinct data but also highlights the need for a global, synthetic framework.

Understanding how birds adapted their reproductive systems to changing Cenozoic climates is essential to interpreting the evolutionary success of modern lineages. Climatic transitions—from the greenhouse conditions of the early Palaeogene to the icehouse regimes of the Neogene and Quaternary—transformed habitats, selective pressures, and reproductive strategies. Variations in eggshell thickness, porosity, and nesting architecture reflect physiological and behavioural responses to shifts in temperature, humidity, and predation risk. Simultaneously, continental drift and the emergence of novel biomes shaped avian biogeography and reproductive evolution. This review provides the first comprehensive synthesis of Cenozoic avian eggs, eggshells, and nests, drawing together disparate regional studies to construct a coherent evolutionary and palaeobiogeographical framework. It evaluates fossil evidence across all epochs of the Cenozoic, identifies large-scale patterns in eggshell structure and nest ecology, and interprets them within the broader context of climatic and tectonic change. By integrating methodological, biogeographical, and palaeobiological perspectives, the review aims to advance understanding of avian reproductive evolution and establish priorities for future research[17,19].

Methodological and Conceptual Framework

Approaches to the Study of Fossil Eggs and Eggshells

Current parataxonomic analysis uses destructive methods (e.g., fracturing, thin-sectioning, polishing, etching and powdering) (Table 1)[22]. No available, genuinely non-destructive scanner or workflow can yet recover the requisite macro-, micro-, and ultrastructures of eggs. This constrains access to materials, limits sample sizes, hampers replication, and discourages investigation of rare or type material[17,23]. Even

techniques often regarded as low-damage at the point of analysis—most notably electron backscatter diffraction (EBSD)—remain intrinsically consumptive because they generally require embedding and ultra-polishing. Although modern EBSD detectors have become substantially faster, more sensitive, and less costly than earlier systems, sample preparation continues to be the primary bottleneck for the technique, and large-area mapping still entails significant time, effort, and expense (Table 1)[24–28]. Interpretation of fossil avian eggs therefore draws on an integrated toolkit that combines classical description with modern analytical approaches. While macroscopic and microscopic attributes—eggshell thickness, layer architecture, pore geometry and surface ornament—continue to provide the foundation for comparative diagnosis[22,29]; scanning electron microscopy (SEM) provides high-resolution imaging of calcite fabrics and layering and analytical capabilities such as qualitative to semi-quantitative elemental characterisation, mineralogical assessment, and texture analysis[22,30,31]. Stable-isotope measurements of eggshell carbonate ($\delta^{18}O$, $\delta^{13}C$) provide complementary environmental and physiological proxies—such as palaeotemperature, humidity and vegetation signals—with further constraints obtainable from clumped-isotope thermometry and trace-elements analyses[32–34]. However, they require the physical removal of material by powdering or micro-drilling, which may modify carbonate record by diagenetic alteration after burial. Consequently, samples must be screened for preservation prior to isotopic analysis[22,30,31]. Elemental mapping using Electron Probe Microanalysis (Electron Probe Micro-Analyzer or synchrotron-based X-ray fluorescence can resolve mineralogical heterogeneity and diagenetic pathways but typically demands destructive preparation and access to specialist facilities. In rare instances, preserved organic residues (proteins, lipids, even ancient DNA) provide molecular

143 evidence of affinity and function, although rigorous authentication is mandatory given
144 the risks of contamination and recrystallisation artefacts[7,32,34–36].
145 Among recent advances, EBSD has substantially expanded what can be inferred
146 about eggshell growth, crystallography and homology by quantifying lattice
147 orientation, misorientation, grain size/shape and boundary character at micrometre
148 scales[32–34].These data have clarified the organisation of the mammillary, squamatic
149 and external zones across living and fossil taxa and have informed revised
150 interpretations of eggshell evolution. Yet EBSD's strengths are offset by practical
151 limitations: meticulous preparation, sensitivity to polish quality and charging, long
152 mapping times for large areas, and the need for specialist expertise—all of which
153 elevate per-sample costs and slow throughput[32–34].
154 In summary, current best practice remains intrinsically sample-consumptive, and a
155 truly non-destructive modality capable of resolving crystallography and ultrastructure
156 at the necessary spatial scales is not yet available. EBSD epitomises the trade-off:
157 uniquely powerful for microstructural and evolutionary inference, yet comparatively
158 expensive, slow, and dependent on destructive preparation[32–34].

159 **Taxonomic and Parataxonomic Systems**

160 Assigning fossil eggs to specific avian taxa remains challenging because eggshells
161 are seldom preserved in unambiguous association with skeletal material such as *in*
162 *ovo* embryos, brooding postures, gravid individuals with oviductal eggs,
163 perinatal/neonate remains in nest structures with trace association, stratigraphic co-
164 occurrence in restricted facies, and in coprolites and gut residues[33,37–44]. Oologists
165 address this uncertainty by applying parataxonomy. Based on microstructural
166 attributes and comparisons with modern avian eggshells—layering, crystalline
167 organisation and pore geometry—rather than on assumed biological lineage,

oologists group material into oofamilies such as *Ornitholithidae*, *Ratitiolithidae* and *Struthiolithidae*[22,45]. This framework enables reproducible comparison across sites but risks over-splitting or conflating convergent morphologies; robust attribution therefore requires integration with body fossils, sedimentological context and geochemical screening[17,46–48]. However, A recurring weakness in parts of the oological literature is the reliance on macromorphology—overall egg size and outline, pigmentation, and low-magnification surface features—in lieu of a microstructurally grounded parataxonomy. Harrison[49] and Harrison and Msuya[50]'s Laetoli studies exemplify this emphasis: eggshell thickness, pore-pit form and simple counts assessed with a hand lens underpin their taxonomic and biochronological inferences, with little or no deployment of thin-section petrography, SEM/EBSD fabrics or formal oofamilial assignments. The result is serviceable description and coarse taxonomic placement, but limited comparability beyond the local record and reduced value for broader questions in palaeobiogeography, palaeoecology and correlation.

Taphonomy and Preservation of Oological Material

The preservation potential of calcareous eggshells is strongly governed by depositional environment, geochemical conditions, and post-burial diagenetic history[51–53]. Although composed primarily of stable calcite or aragonite in standard conditions, eggshells are susceptible to degradation of finer morphological features, such as pores and surface ornamentation, which are extremely sensitive to physicochemical alteration[51–53]. Arid and lacustrine depositional settings, where rapid burial and carbonate-saturated pore waters are common, generally enhance preservation[52]. In contrast, acidic soils or environments characterised by high groundwater percolation typically promote dissolution or recrystallisation of the

193 calcareous matrix, resulting in partial or total loss of microstructural fidelity[7,36].
194 Mechanical deformation during compaction, transport abrasion, and microbial
195 alteration can further distort or obscure diagnostic features[52].These taphonomic
196 variables collectively influence the fidelity of the oological record, determining
197 whether observed morphological variation reflects biological evolution or post-
198 depositional modification. Consequently, the accurate interpretation of eggshell
199 remains requires explicit assessment of taphonomic alteration at both macroscopic
200 and microscopic scales. Recognition of diagenetic pathways—such as
201 recrystallisation fronts, dissolution textures, or cement overgrowths—is vital for
202 distinguishing original eggshell fabric from secondary mineral phases[7,36,51–53]. For
203 example, caution is warranted when recovering material associated to nests. A study
204 of the modern debris from an arboreal great blue heron (*Ardea herodias*) colony
205 shines on avian nesting taphonomy[54]. Surface and subsurface sampling near the
206 Missouri River (2012–2013) recorded accumulations dominated by disarticulated
207 juvenile heron bones, with lesser fish, small mammals, and invertebrates. Eggshell
208 was scarce and variably oriented with size and tree proximity; subsurfaces lacked
209 eggshell and fragile invertebrates. These filters bias preservation towards robust
210 elements. Limited spatial–temporal scope cautions against generalisation as fossil
211 inferences require taphonomic evaluation[54].

212 **Analytical Integration and Limitations**

213 Robust interpretation of fossil eggshells demands an integrative analytical approach
214 combining microstructural, geochemical and contextual data. Quantitative techniques
215 such as pore-density analysis and gas-conductance modelling can provide valuable
216 insight into nesting depth, incubation strategy, and palaeoenvironmental
217 conditions[17,48,55]. Stable-isotope analyses of eggshell carbonate can further elucidate

palaeotemperature and hydrological regimes[7,36]. However, the fragmentary and often diagenetically altered nature of eggshell specimens imposes significant analytical constraints, reducing statistical robustness and complicating functional inference. Synthesis across multiple stratigraphic units and geographic regions therefore provides the most reliable framework for identifying large-scale evolutionary and ecological patterns. Such meta-analytical approaches mitigate the limitations of individual localities, allowing assessment of both genuine evolutionary trends and preservation-driven biases[52]. Nevertheless, caution is warranted when extrapolating behavioural or physiological interpretations from modern analogues, given the potential for taxon-specific variation and environmental contingency[56–58].

Overall, eggshell preservation reflects a dynamic interplay between biological composition, environmental context and diagenetic processes. Arid and carbonate-rich systems generally promote eggshell integrity, while acidic and hydrologically active settings accelerate degradation. Integrating taphonomic evaluation with quantitative and geochemical analysis remains essential for distinguishing true evolutionary change from preservational artefact.

Chronological Review of the Cenozoic Record

The Cenozoic Era marks the establishment and diversification of modern avifaunas following the terminal Cretaceous extinction. Across this interval, fossil eggs, eggshells and nests provide crucial evidence for the adaptive radiation of birds into a wide range of ecological niches. Although the record is uneven, each epoch reveals distinctive trends in reproductive morphology and ecology.

Palaeocene (66–56 Ma)

The earliest Cenozoic record is scarce (Figure 1), but it captures ecosystems recovering from the Cretaceous–Palaeogene (K–Pg) mass extinction, during which

avian lineages diversified to occupy newly vacant ecological niches[12,29,59–61]. In the absence of non-avian dinosaurs, large flightless birds became dominant terrestrial vertebrates across several continents. Among these, the Gastornithidae of Europe and North America and the Lithornithidae of the Northern Hemisphere represent key early lineages (Table2; Figures 2C, 3). Their eggshells are relatively thick, with coarse mammillary layers and simple pore systems, indicating ground-nesting behaviour and low gas conductance compatible with open or semi-open nest environments (Figure 2C)[12,61].

Gastornithids, typified by *Gastornis*, occur from the Selandian to the Lutetian, spanning at least 15 million years (Figure 3)[12,61]. Fossil eggshells from southern France and Iberia potentially assigned to Gastornithids, are referred to the oogenus *Ornitholithus*, with thin-shelled *Ornitholithus biroi* and thick-shelled *Ornitholithus arcuatus* representing ecological adaptations to humid and arid settings respectively[12,61,62]. Thick-shelled specimens from the Iberian Tremp Formation predate those in Provence, implying regional succession during the Palaeocene–Eocene transition, when gastornithids intermittently coexisted with ratites and phorusrhacids[12,29,59,63].

In North America, Mikhailov[22] described altered prismatic eggshells attributed to Presbyornithidae from Wyoming, while Houde[64] reported abundant *Lithornis* eggs and associated bones from the Clark Quadrangle (Table 2). The glossy, thick eggshells with conspicuous pores resemble tinamou eggs[65] and suggest complex reproductive strategies, including potential polyandry and polygyny. However, the conclusions are conjectural. Houde[64] only analysed a few specimens among thousands of eggshells in the accumulations. Besides, the absence of immature

bones could be due to either low mortality or some peculiar seasonal condition represented in the accumulations. Houde[64] also ascribed *Lithornis celetius* to *Rhynchotus rufescens*.from the Bangtail Quarry, Fort Union Formation (Gallatin National Forest, Montana). He noted that the eggshells of *L. celetius* (PU 16961) are glossy with large, widely spaced pores that are clearly visible to the naked eye, closely resemble those of Rhynchotus rufescens, albeit *L. celetius* eggshells are significantly thicker (Houde, 1988, p. 25, fig. 31). This was based on a sections of an outer layer resembling the cuticular layer of true eggshell as described in *Rhea* by Tyler and Simkiss[65]. However, Grellet-Tinner et al.[66] reinterpreted the layer as an aprismatic and composed of calcium carbonate, a character of all palaeognath eggshells.

Overall, the Palaeocene oological record indicates early experimentation in nesting ecology and continuity in eggshell microstructure across the K–Pg boundary, marking the foundation of modern avian reproductive diversity[12,22,29,60–63,63–65,67].

Eocene (56–34 Ma)

The Eocene represents a pivotal interval in the evolutionary history of birds characterised by a marked diversification and global dispersal of avian lineages. This epoch provides a far more substantial oological record than the preceding Palaeocene, offering direct evidence of reproductive strategies and nesting behaviours among early avian families [65,67]. Numerous well-preserved eggs and eggshell fragments have been recovered from lacustrine and fluvial deposits across Europe, North America, and Asia, notably from the Paris Basin, the Green River Formation, and the Messel oil shales (Table 3 and Figure 2C). These assemblages document a wide spectrum of ecological adaptations among waterfowl, shorebirds,

and early terrestrial birds, reflecting the diversification of both neognathous and palaeognathous groups within a variety of Eocene habitats (Figures 2A,B, C).

Presbyornithidae and the Expansion of Early Waterfowl

Among the best represented taxa are the Presbyornithidae, a family of duck- and goose-like anseriforms combining morphological traits of ducks and flamingos (Table 3)[67]. The family was considerably more widespread during the Eocene than in the Palaeocene, extending across North America, Asia, and Afro-Arabia[67]. In North America, four fossil colonies within Wyoming's Green River Formation—particularly at Fossil Basin and Lake Gosiute—record early to early middle Eocene lacustrine environments (Figure 2C)[68–70]. At these sites, prismatic eggshells attributed to *Presbyornis* sp. were found in association with monospecific bone beds, providing compelling evidence of autochthonous nesting. Such assemblages indicate gregarious or colonial breeding similar to that of modern anseriforms in saline-lake systems, for instance Kenya's Lake Nakuru[68–70].

Comparable material has been described from the late to early middle Eocene Glib Zegdou Formation (~49–46 Ma) in the Gour Lazib area of Algeria, where García et al.[71] documented the first African Presbyornithidae eggs and eggshells (Table 3). The thin eggshells closely resemble those of *Presbyornis* from Wyoming, while their association with a presbyornithid carpometacarpus supports taxonomic attribution. These finds extend the family's known range into Afro-Arabia, reinforcing hypotheses of a cosmopolitan Palaeogene distribution. Further evidence from Asia[72–74], as well as skeletal remains from Australia and South America[75], suggests Gondwanan origins and early dispersal routes facilitated by intercontinental wetland systems.

Cohabitation of Presbyornithidae with other basal anseriforms strengthens the notion of a Gondwanan radiation of early waterfowl during the early Eocene.

Palaeognath Eggs and Ratite-like Taxa

Contemporaneous with these neognath lineages, the Eocene also preserves important evidence for early palaeognaths (Table 3). Scanning electron microscopy (SEM) analyses of *Lithornis* eggshells from the London Clay Formation (~54 Ma) revealed a tri-layered, aprismatic microstructure akin to that of extant tinamous, confirming Palaeognath affinities[66]. These eggshell characteristics are consistent with the interpretation that Lithornis combined features associated with volant palaeognaths with reproductive traits reminiscent of ratites [66], implying that early palaeognaths may have occupied an intermediate position between fully flighted and flightless strategies. In this context, they may have nested on the ground—consistent with the widespread ground-nesting habit inferred for non-avian dinosaurs and many early birds[57,58,76,77]—while retaining greater dispersal potential than modern flightless forms."

Kohring and Hirsch[78] identified a palaeognathous morphotype egg, *Medioolithus geiselensis*, from the Lutetian Geiseltal quarry in Germany (Middle Eocene), representing one of the earliest records of large, cursorial palaeognaths in Europe (Table 3). Its compact crystalline organisation, reduced pore density, and small size imply ground-nesting behaviour akin to modern ostriches, with adaptations to thermally variable environments. The bifurcating pore canals, rather than increasing gas conductance, may instead have functioned to maintain effective diffusion pathways by reducing the impact of localised pore blockage or sediment infilling (Figure 2C). Mayr[79] later attributed *M. geiselensis* to the struthioniform *Palaeotis*

weigelti, but provided no justification. He also questioned the association between eggshells and disarticulated avian remains found on a fossil slab, which he proposed was a dissociated snake pellet (Table 3). Notwithstanding, it seems improbable that a snake, in a single ingestion event, consumed two adult birds (potentially females) and the eggs from potentially one or two nests, given the size constraints and typical dietary behaviour of most Eocene snakes[80]. Alternatively, the slab may be representing two separate ingestion events and therefore evidence of multiple predation or scavenging occurrences within the same depositional context. Regardless, it provides valuable insight into Eocene ecological interactions, where bone fragmentation and mixed faunal content suggest repeated predation or scavenging events by snakes[80], underscoring the ecological role of egg and nest predation as a selective pressure in Eocene avifaunas. Further research, including microscopic analyses of the eggshells and comparative analysis of fossilised snake pellets and modern analogues, could establish what depicts the slab.

Novel Ootaxa and Microstructural Diversity

Further Eocene material from other continents adds to the growing recognition of morphological diversity in avian eggs (Table 3). Hirsch et al.[81] described *Incognitoolithus ramotubulus* from the lower Eocene DeBeque Formation (Colorado), a novel ratite oospecies exhibiting a smooth external surface with branching and non-branching pore canals clustered in grooves and pits, recalling “aepyornithid” patterns. Such structural complexity suggests physiological control over gas exchange, possibly linked to incubation in partially buried nests.

In addition, Jackson et al.[82] reported two partial eggs from the lower Eocene Willwood Formation (Wyoming) containing indeterminate embryonic remains. Their

two layered smooth eggshells indicate neognath affinity. These were assigned to *Microolithus wilsoni*, whose microstructure closely resembles that of extant neognaths, supporting an avian–theropod continuum in eggshell evolution. Conversely, the egg *Metoolithus nebraskensis* from the Chadron Formation displays features more akin to non-avian theropods, highlighting mosaic retention of ancestral characters within Eocene taxa[82]. This variability demonstrates that the prismatic structure often associated with neognath eggs is not an apomorphy exclusive to crown birds, but rather a feature with deeper evolutionary roots in the Cretaceous–Palaeogene transition. Hirsch and Bowles[83] further reported crane-like eggs from Wyoming, including one with an embryo (Table 3). Although the mammillary layer closely resembles that of the sandhill crane (*Grus canadensis*), differences in radial structure suggest microstructural variation within early gruiforms. Such diversity aligns with Hirsch's unpublished data and Miller's comparative studies across seven extant crane species, revealing early experimentation in reproductive morphology among large wading birds[83]. Panadès i Blas et al.[84,85], reported that avian eggshells were unearthed in the early Eocene of Australia in lacustrine sediments along with crocodylian eggshells. The avian eggshells are being analysed and could provide palaeobiogeographic insights of ratites and/or early branching galloanseres.

The Eocene oological record, though geographically fragmented, reveals remarkable morphological and ecological diversity among early avian taxa. From the colonial *Presbyornis* of saline lakes to the ground-nesting palaeognaths of Geiseltal, early birds exhibited a spectrum of reproductive strategies reflecting both phylogenetic inheritance and environmental constraint. These eggs, through their microstructural complexity and taphonomic associations, provide direct insight into the interplay of physiology, behaviour, and environment at a formative stage of avian evolution. The

period thus stands as a cornerstone for understanding the adaptive radiation and reproductive innovation that underpin modern avian diversity.

Oligocene (34–23 Ma)

The Oligocene fossil record is comparatively sparse and has often been described as a “dark age” of the Cenozoic due to limited continuity between Eocene and Miocene avifaunas[79,86] (Table 4). Global cooling and the onset of Antarctic glaciation induced major ecological reorganisation, leading to habitat contraction and taphonomic discontinuities[87,88]. Nevertheless, a series of exceptional deposits—particularly in North America and Eurasia—preserve key insights into avian reproductive evolution during this transitional epoch. In the North American Oligocene Badlands (South Dakota, Nebraska, and Wyoming), rare avian eggs and eggshell fragments illustrate morphological diversification among neognaths (Table 4)[29,89–91]. Hirsch and Packard[29] examined over 100 eggs Oligocene Badlands in South Dakota and Nebraska, including eggs described previously by Farrington[89], Troxell[90] and Sinclair[92] (Table 4). The eggs that were not fully recrystallised were associated with owls[29]. Chandler and Wall[91] described the earliest Oligocene bird eggs (~32.5 Ma) from the Scenic Member of the Brule Formation (South Dakota), attributing them to gruiform birds (Table 4). Lawver and Boyd[93] later established *Metoolithus jacksonae* from the Brule Formation of North Dakota (~33.7–30 Ma), characterised by high gas conductance and microstructural adaptations for ground or vegetative nesting. Collectively, these assemblages demonstrate that, despite limited diversity, Oligocene birds maintained reproductive specialisations inherited from Eocene ancestors. A unique fossilised nesting chamber from Egypt, featuring a chiselled entrance, short corridor, and internal cavity, provides rare evidence of early

avian behavioural innovation[94]. The morphology suggests excavation in woody substrate, consistent with the nesting behaviour of modern piciform or passeriform birds. Though undated precisely, the specimen underscores the emergence of specialised nesting behaviours by the Oligocene.

The Oligocene illustrates persistence and environmental adaptation amid climatic deterioration. The widespread occurrence of prismatic eggshell structure and a distinct external zone across taxa is consistent with their early establishment within modern avian lineages, in line with Mikhailov's model of eggshell biomineralisation[22]. These patterns indicate a combination of phylogenetic continuity and ecological plasticity, from the saline lake colonies of *Presbyornis* to the steppe-adapted ratite forms of the Oligocene.

Miocene (23–5.3 Ma)

The Miocene epoch represents one of the most oologically diverse and palaeobiologically informative intervals of the Cenozoic (Table 5; Figure 1; Figure 2A, B, and C; Figure 3). Following the climatic instability of the Oligocene, global temperatures stabilised, facilitating the expansion of open grasslands, savannahs, and semi-arid environments across Africa, Eurasia, and Australasia[95–97]. These ecological transformations were accompanied by major faunal radiations, including the diversification of large flightless ratites and the proliferation of neognathous lineages, resulting in an extensive fossil record of avian eggs, eggshells, and nests that provides insight into evolutionary adaptation, palaeoecology, and reproductive strategy .

Ratite Evolution and the Emergence of Ostriches

The earliest unambiguous ostrich eggs (*Struthio*) occur in early Miocene deposits of Africa and Eurasia, marking the beginning of a lineage that persists into the Holocene (Tables 5-8)[15,98,99]. The Miocene record reveals remarkable variation in ostrich eggshell microstructure, pore morphology, and eggshell thickness, reflecting adaptation to the increasingly arid continental interiors. The eggs are large, thick-shelled, and characterised by well-developed external layers with complex pore systems[15,48,100,101]; these features are consistent with open-ground incubation in hot, desiccating conditions[18,102–104].

Mikhailov and Zelenkov[15] correlated ostrich eggshell microstructures with palaeoenvironmental gradients, identifying two principal pore morphologies (Table 5). The aepyornithoid pattern, comprising long, slit-like pores parallel to the egg's long axis, occurs in thicker eggshells associated with large-bodied ostriches inhabiting stable semi-arid savannahs, where consistent gas exchange was vital for embryonic survival. In contrast, the struthioid type, consisting of smaller, round pores arranged in clusters or pits, corresponds to species adapted to more variable steppe or shrubland climates, requiring greater moisture retention and diffusion control[15].

Regional fossil evidence substantiates this evolutionary trend. *Diamantornis* eggs from the early Miocene of Namibia[105–107] exhibit the aepyornithoid pore system and represent transitional forms bridging Palaeogene ratites and modern ostriches. Conversely, Smith[108] described in Egypt (North Africa) aepyornithoid eggshell fragments from the Moghra Formation (≈17–18 Ma), associated with deltaic and estuarine deposits. Their 2.1 mm thickness and linear pores indicate nesting near deposition sites and suggest adaptation to fluvio-marine plains with fluctuating water levels and moderate humidity[108].

From the middle Miocene onwards, particularly during the early Serravallian (14.5–13.5 Ma), ostrich populations underwent rapid diversification and dispersal from Africa and Arabia into southern Europe, central Asia, and beyond[15,50,59]. Medium-sized ostriches with thinner aepyornithoid eggshells adapted to semi-arid savannahs spread across Anatolia, Kazakhstan, and Mongolia, forming early populations of *Struthio oshinensis*. These eggs display moderate wall thickness and pores suited to open steppe environments. In the late Miocene, *Struthiolithus chersonensis* from Central Asia shows more rounded, clustered pores and thicker eggshells, indicative of adaptation to cooler, fluctuating climates where moisture retention and protection from thermal stress were increasingly critical[15].

The North African record of *Psammornis rothschildi*[15,109] from the late Miocene Segui Formation in Tunisia exemplifies this trend (Table 5). Its eggs exceed 3 mm in thickness and exhibit large, funnel-like pores and a thickened mammillary layer, consistent with nesting in arid, open habitats. Buffetaut[109] confirmed the taxonomic distinctiveness of *Psammornis* based on its robust morphology, distinguishing it from both *Struthio camelus* and other ratites. The highly reinforced eggshell structure suggests selection for enhanced mechanical resistance to temperature extremes and predation. Together, these records highlight the Miocene as the key period for ostrich evolution and the emergence of modern reproductive strategies among ratites.

Bravo et al.[110] documented fragments of aepyornithoid eggshells from the late Miocene of Torrellano locality near Alicante, on the Iberian Peninsula. These eroded eggshells were recovered from Messinian-aged deposits associated with shallow lagoonal and palustrine environments. The eggshells are thick (2.13–3.05 mm) and

display unique pore structures within elongated grooves, indicating adaptations to specific nesting environments near freshwater or brackish lagoons, potentially shielded by oolitic coastal barriers[110]. Microstructural analysis revealed three layers: a thick mammillary layer, a continuous layer with a squamatic texture, and a thin external layer, consistent with those of giant ratites like *Aepyornis maximus*. Phylogenetic analysis placed the eggshells within the crown group of ratites, closely related to *Struthio* and *Diamantornis*. The work emphasises the utility of eggshell microstructure in resolving evolutionary relationships and provides valuable insights into the evolutionary history and biogeography of Miocene European ratites[110].

Ratites Beyond Africa and Eurasia

Comparable ratite oological records occur globally (Table 5). In New Zealand, early-to-middle Miocene deposits of the Bannockburn Formation (16–19 Ma) preserve thick-shelled eggs attributed to *Dinornithiformes* (moas)[111–113]. The eggshells exhibit tightly packed crystalline layers and a well-defined pore system optimised for embryonic gas exchange in humid lacustrine environments. These features indicate adaptation to the dynamic wetland landscapes of Lake Manuherikia, where fluctuating water levels and seasonal variability governed nesting behaviour[111–113]. The moa eggs' resilience suggests synchronised breeding cycles and demonstrates Zealandia's significance as a Miocene biodiversity hotspot for Gondwanan avifauna.

In Australia, giant eggshells from the Etadunna Formation in Queensland[114,115] represent the Dromornithidae—giant flightless birds phylogenetically allied to *Anseriformes* (Table 5). Their eggshell measure approximately 4 mm in eggshell thickness and is estimated to have formed eggs 30–43 cm long, weighing up to 14 kg. Their microstructure, consisting of dense calcitic layers with a complex pore

network, is consistent with incubation in open, semi-arid habitats. The combination of extreme size and robust shell construction suggests a reproductive strategy that balanced embryonic protection with adequate gas exchange." Together with aepyornithids and other flightless taxa, dromornithids illustrate that extreme egg size evolved convergently in multiple lineages rather than being restricted to ratites.

Neognaths: Diversification and Ecological Breadth

Sellés et al.[116] reported a rare direct evidence of avian nest-site fidelity from the Middle–Late Miocene (Aragonian) deposits of the Vallès-Penedès Basin (northeastern Iberian Peninsula). The exceptionally preserved concentration of dozens of eggs and hundreds of eggshell fragments of phasianids suggests philopatric behaviour despite the increasing environmental fragmentation that characterised the Middle–Late Miocene transition[117–119]. It indicates a notable degree of ecological resilience of phasianids from maintain breeding-site fidelity and potentially behavioural stability under changing landscape and habitat conditions.

Neognathous bird eggs from Miocene lacustrine and fluvial deposits demonstrate wide ecological and behavioural diversity (Table 5) [59,120–122]. Eggshells attributed to *Neognathoolithus* oosp. and *Aves indet.* from Slovenia and central Europe show the characteristic tripartite structure—mammillary, palisade, and external zones—typical of modern birds[120]. These specimens have been linked to Galloanserae, Palaelodidae, and Gruiformes, indicating varied nesting strategies ranging from open ground to aquatic environments.

In the Barstow Formation of California, ornithoid eggshells[68] preserve prismatic layers consistent with galloanserine morphology, suggesting shoreline nesting near saline-alkaline lakes. The Fuentes de Ebro locality in Iberia yielded thin (0.13–0.14

mm) prismatic eggshells attributed to nightjar-like birds (*Caprimulgiformes*)[121], indicative of nesting in lacustrine settings. Eggshells with similar microstructures from Dolnice (Czech Republic) and Heiligenstadt (Austria) show thicker eggshells, perhaps reflecting species-specific or climatic differences[120]. These finds confirm the potential of Miocene lacustrine and fluvio-lacustrine sediments to preserve delicate avian reproductive materials (Table 5).

At the Mataschen clay pit in Styria (Austria), a late Miocene (≈11 Ma) songbird egg constitutes the earliest known passeriform oological record (Table 5)[123]. Measuring 16 mm, the egg displays a basal mammillary zone and an outer layer with brown speckled pigmentation, interpreted as an original biological feature rather than diagenetic alteration. It attests to the early establishment of arboreal nesting and rapid incubation cycles in passerines, consistent with their ecological diversification during the Miocene[124–126].

A remarkable mid-Miocene nesting chamber from northern Bohemia[127,128] carved into fossilised *Castanoxylon*, exhibits an oval entrance and funnel-shaped cavity surrounded by peck marks, strongly suggesting piciform (woodpecker) activity.The presence of heavy bill markings around the entrance indicates deliberate chiselling, showcasing intricate avian interactions with forested ecosystems of the mid-Miocene[127,128]. This indicates that cavity nesting was established by the mid-Miocene.

Tropical and Island Records

Amber inclusions from the Dominican Republic preserve minute eggs and eggshell fragments representing the oldest hummingbird (*Trochilidae*) reproductive record in the Americas (Table 5)[129–132]. The smooth, white egg (9 × 6.2 mm) lacks predation

554 marks, indicating successful hatching before entrapment. Microscopic analysis
555 reveals mammillary and prismatic layers characteristic of modern avian eggshells,
556 underscoring the continuity of reproductive structures across tens of millions of
557 years.

558 In the Iberian Peninsula, the first twig-built nest referred to *Phoenicopteriformes*
559 (flamingos) was unearthed at the Tudela Formation (Table 5)[133]. The five, thin,
560 porous eggs indicate adaptation to oligohaline lacustrine settings under semi-arid
561 conditions. Microstructural transitions between grebes and modern flamingos reflect
562 evolutionary experimentation within aquatic taxa[133]. The upper Miocene deposits
563 from Bardenas Reales and Lardero (Iberia) and middle Miocene strata in the
564 Calatayud–Daroca Basin[121,134–136] yielded ornithoid-prismatic eggshells from aquatic
565 birds, highlighting wetlands as key reproductive habitats (Table 5). In the Ebro Basin,
566 Anatidae eggshells display fine lamination and distinct pore systems, optimised for
567 moisture retention and embryonic respiration under variable climatic regimes[9,137,138].
568 In the North Atlantic, Seabird fossils from the Miocene deposits of the Selvagens
569 Islands[139–141] document nesting within volcanic coastal sediments (Table 5). Eggs
570 attributed to *Puffinus* (shearwaters) and *Calonectris* (cagarros) exhibit neognath
571 microstructure and variable eggshell thickness, corresponding to species size. Their
572 preservation beneath basaltic layers indicates resilience to volcanic activity and
573 reveals the ecological role of seabirds in early Atlantic Island ecosystems.

574 **Pliocene (5.3–2.6 Ma)**

575 The Pliocene epoch was characterised by significant climatic transitions and faunal
576 turnovers that profoundly influenced avian evolution[142,143] (Table 6; Figure 2A-C;
577 Table 3). In ratites, ostriches underwent final consolidation of xeric-adapted

strategies: thick eggshells with characteristic struthioid pore systems—rounded, often branched clusters—optimised moisture retention while maintaining adequate gas conductance during incubation on exposed substrates[15,50,144]. Skeletal trends toward larger body size and cursoriality paralleled these oological changes, reflecting selection for efficient high-speed locomotion across open savannah–steppe mosaics[105]. Regionally, advanced *Struthio* lineages (e.g., *S. coppensi* in eastern Africa; *S. chersonensis* in Central Asia) attest to diversification in seasonally variable grassland–woodland ecotones; while associated eggshells (*S. chersonensis*) preserve the diagnostic struthioid pores and locally thicker walls, consistent with heightened predation pressure and climatic unpredictability[15].

At Laetoli (Tanzania), *Struthio* eggshells—attributed to ancestors of *S. camelus*—occur in both lower (4.3–3.8 Ma) and upper (3.8–3.6 Ma) Beds, with broader Late Pleistocene–Holocene abundance across African archaeological contexts (Table 6)[15,50]. Historical distributions of *S. camelus* encompassed Africa north and south of the Sahara and parts of Asia Minor; genetic and fossil data further imply late Quaternary presence on the Indian subcontinent[22,145]. Mid-20th-century extinction of the Arabian ostrich (*S. camelus syriacus*) exemplifies recent anthropogenic loss, whereas living populations persist in savannah to true desert, including the Sahel and southwestern Africa[15,50]. Dispersal histories remain debated: some evidence favours an African origin with subsequent Eurasian incursions, whereas others infer bidirectional movements during the Mio-Pliocene, supported by Eurasian eggshells and bones[15,59,144].

Laetoli also yielded diverse galliform and numidin eggs (e.g., *Francolinus* spp., *Numida meleagris*) preserved within rapidly emplaced carbonatite tuffs, implying subaerial nesting on open ground within a mosaic of bushland–savannah habitats

(Table 6; Figure 2C)[49,50]. Beyond Africa, Pliocene oology records stable neognath strategies: anseriform, ciconiiform and charadriiform eggshells in lacustrine–alluvial settings (Figure 2C)[9,146,147]; a woodpecker-type nesting chamber from Arizona gravels reinterpreted as Pliocene (*Eocavum picifactum*) evidences cavity-nesting behaviour(Figure 2C)[148,149]; and unusually thick, terrestrial eggs from Lanzarote (2.1–2.9 mm) indicate large insular birds unrelated to odontopterygiform seabirds (Table 6; Figure 2C)[19,150,151]. Collectively, Pliocene eggs and nests highlight conservative yet ecologically tuned reproductive architectures across lineages occupying wetlands, woodlands and expanding xeric biomes.

Pleistocene and Holocene (Quaternary) (2.6 Ma–present)

The Quaternary preserves one of the richest palaeontological archives of avian reproductive evolution (Tables 7 and 8; Figure 1; Figure 3). Fossilised eggs, eggshells, and nesting structures from this interval document the culmination of adaptive trends established during the Neogene and the increasing influence of humans and climate change on avian ecology. The record spans continental, lacustrine, coastal, and insular deposits across Africa, Eurasia, Australasia, the Americas, and Antarctica. Eggshell microstructure, isotopic signatures, and nesting traces illuminate evolutionary strategies among both extinct and extant taxa, revealing the interplay between morphology, environment, and behaviour. The persistence of ratites such as *Struthio* and the extinction of giants like *Genyornis* and *Aepyornis* demonstrate the dual forces of climatic oscillation and anthropogenic pressure shaping avian biogeography and reproductive biology.

Ostrich Evolution and Adaptation during the Pleistocene

627 The Pleistocene represents the zenith of ostrich diversification and adaptation (Table
628 7)[15]. Global cooling and glacial–interglacial cycles transformed much of Africa and
629 Eurasia into expansive grasslands and steppe habitats, promoting the evolution of
630 *Struthio* as a highly specialised cursorial bird[15,152,153].
631 Early Pleistocene fossils of *S. asiaticus* from India, Mongolia, and southern Siberia
632 illustrate the genus's broad ecological tolerance[15]. This large-bodied species
633 exhibited elongate limbs and a robust pelvic girdle, enabling high-speed locomotion
634 across open terrains[105]. Eggshell fragments associated with these fossils exhibit
635 struthioid microstructures comparable to modern *S. camelus* but slightly thicker,
636 implying adaptation to drier, colder continental climates[15,105]. Accelerator Mass
637 Spectrometry dating of Siberian eggshells places their persistence between 41,700–
638 10,000 years BP, spanning the Last Glacial Maximum[154].
639 In Africa, *S. camelus* emerged as the dominant lineage by the middle Pleistocene,
640 expanding from eastern to southern Africa[15,155]. The species' eggshells display
641 increased density of pores and uniform eggshell thickness, reflecting fine-tuned
642 adaptation to seasonal aridity. By the late Pleistocene, *S. camelus* had replaced
643 earlier Eurasian and African congeners, including *S. chersonensis* and *S. asiaticus*[15].
644 The skeletal morphology of *S. camelus*—light but robust bones, elongated
645 tarsometatarsi, and reduced wings—underscored an evolutionary commitment to
646 terrestrial locomotion.

647 Mikhailov and Zelenkov[15] emphasised that the Pleistocene marks the final
648 consolidation of ostrich evolutionary traits: efficient respiration through eggshell
649 design, large clutch sizes, and exceptional running capacity. These traits refined
650 over successive glacial–interglacial cycles, facilitated *Struthio*'s persistence into the
651 Holocene as the only surviving giant ratite outside Australasia.

Extinction and Ecological Replacement in Australasia

In contrast to *Struthio*'s success, Australasia witnessed the extinction of its giant avifauna at or near the Pleistocene–Holocene boundary (Tables 7 and 8; Figure 3)[156–158]. The most significant was *Genyornis newtoni*, a massive, flightless bird within the Dromornithidae[159]. Fossilised eggshell fragments recovered from aeolian and lacustrine sediments across South Australia, dated to 37,000–50,000 years BP, indicates that *G. newtoni* co-existed with Emus in savannah-grasslands and both species laid eggs in sand dunes [159,160].

Early interpretations attributed the thick-shelled eggs (2.2–2.7 mm) to *Genyornis*, associating their widespread occurrence with human exploitation, as evidenced by charring and fragmentation near hearths[156–158]. However, subsequent re-evaluations challenged this view. Grellet-Tinner et al.[161] demonstrated that the "Spooner Egg" from South Australia, long attributed to *Genyornis*, exhibited microstructural features more consistent with extinct megapodes (*Progura* spp.), including Y-shaped pores and a thin accessory phosphate layer. However, Chan[162] highlighted that the eggs were surprisingly small for a bird of *G. newtoni*'s size and prompted a revision of the eggshells. Morphometric comparisons suggested the egg was too small for *Genyornis*, whose body mass exceeded 250 kg. However, Miller et al. [163]countered that hundreds of fragments across inland dunes were consistent with *Genyornis* in size and distribution, whereas *Progura*—a small, mound-nesting megapode—was limited to eastern forests unsuited to arid dune incubation. Subsequent proteomic analysis by Demarchi et al.[164] reaffirmed the eggshell's affiliation with Galloanseres but aligned it more closely with *Genyornis* than with megapodes. The consensus now favours *Genyornis* as the parent species, with human exploitation contributing to

its extinction through egg predation and habitat modification[156–158,163]. However, the Demarchi et al.[164] study raises significant concerns. Firstly, it appears designed to confirm a predetermined conclusion rather than to evaluate competing hypotheses objectively. The taxa chosen for comparison were largely irrelevant, including ratites, anatids, and phasianids, while using the megapode *Alectura lathami*, a mound-building species, rather than a non-mound-building species (such as *Eulipoa* or *Macrocephalon*) to address the hypothesis that the eggs may have been laid by a basal, non-mound-nesting species. Furthermore, the phylogenetic tree constructed in their analysis shows significant discrepancies with well-established Galloanseran relationships. Notably, methodological oversights undermine confidence in the study's conclusion. The researchers did not apply the standard practice of constraining the fossil protein taxon within a tree reflecting known phylogenetic relationships. As the tree failed to accurately to reconstruct the familiar relationships among extant taxa with high-quality protein sequences, the placement of the *Genyornis* sample close to anseriforms is doubtful. In contrast, the megapode hypothesis may predict a position of the eggshells closer to galliforms. Nonetheless, Demarchi et al.[164] (personal communication) have clarified that their analysis was constrained by the access to avian genomes of extant and extinct bird lineages available at that point. Their objective was not to reconstruct a comprehensive avian phylogeny, but rather to test a focused hypothesis: whether the *Genyornis* eggshell proteins showed closer affinity to megapodes or not. Within these constraints, they argue that the clustering recovered was sufficient to evaluate that specific question, with further methodological detail provided in their original study.

Elephant Birds of Madagascar

Madagascar's Quaternary record reveals an equally striking case of giant avian extinction. Eggshells of *Aepyornis* and *Mullerornis* (Aepyornithidae) occur widely in late Pleistocene–Holocene sediments, offering insights into ecological differentiation and environmental change (Table 8; Figure 2C; Figure 3)[34,165,166]. Morphometric analyses classify three eggshell thickness morphotypes—thin (1.1 mm), intermediate (1.9 mm), and thick (3.3 mm)—corresponding to distinct taxa within the family[166]. Stable isotope studies indicate that *Aepyornis* species inhabited wetter regions, feeding on groundwater-dependent vegetation, whereas *Mullerornis* occupied drier, open habitat[34,166]. Genetic analyses of subfossil eggshells confirm deep lineage divergence, suggesting regional endemism and adaptation to local aridity gradients. The survival of elephant birds into the late Holocene coincides with increasing human activity, including hunting and habitat clearance, leading to extinction by ~1 ka BP[34,166,167].

Aepyornithid eggs, the largest known in the avian fossil record (up to 34 cm long, 10 kg in weight), exhibit remarkable mechanical strength and resistance to diagenesis. Their survival across diverse depositional contexts has made them invaluable for isotopic, palaeogenomic, and ecological studies[34]. Grealy et al.[34] extracted complete mitochondrial genomes from 1,100-year-old eggshells, demonstrating a sister relationship between elephant birds and kiwis. This finding refutes earlier vicariance models of ratite evolution and supports dispersal by volant ancestors followed by independent evolution of flightlessness[34,35]. Notably, the exceptional size of aepyornithid eggs should be regarded as part of a broader pattern of convergent gigantism among flightless birds rather than a trait unique to ratites.

Pleistocene Avifaunae and Wetland Ecosystems

Beyond ratites, Pleistocene avifaunas from Europe reveal rich assemblages of waterbirds, raptors, and passerines preserved in travertine and lacustrine deposits[168] (Table 7). In Germany, Burkhard[169] described eggshells from the Weimar–Ehringsdorf travertines (~100 ka BP) representing *Anser*, *Anas*, and *Aythya* species, along with smaller passeriform and caprimulgiform forms. The calcareous spring environment facilitated exceptional preservation, including embryonic remains, allowing reconstruction of breeding activity in temperate interglacial wetlands. Similarly, Kahlke[170] documented Taubach travertine assemblages containing eggshells of swans, geese, ducks, and waders, indicating a rich riparian ecosystem during the last interglacial (Table 7). In the Iberian Peninsula, avian eggshells from Atapuerca's Sima del Elefante and Gran Dolina sites represent taxa such as *Perdix paleoperdix*, *Corvus corax*, and *Anas sp.* (Table 7)[171–174]. These deposits reflect open woodland and wetland settings that supported mixed avifaunas. The absence of cut marks or burning suggests natural nesting accumulations rather than human collection.

Polar and Insular Records

Pleistocene eggshells from oceanic islands and polar regions add further dimensions to avian reproductive history (Tables 7 and 8). In Bermuda, eolianite deposits preserve interglacial eggs of seabirds including *Pterodroma cahow* and *Pelecanus occidentalis*[175–179]. These records document alternations between marine and terrestrial nesting faunas corresponding to glacio-eustatic sea-level fluctuations. In Antarctica, the fossil record of Adélie penguins (*Pygoscelis adeliae*) from the Ross Sea region provides a near-continuous archive of reproductive activity spanning 7,000 years (Tables 7 and 8)[180–183]. Eggshell fragments from ornithogenic soils on

748 Inexpressible Island and Cape Irizar indicate long-term occupation of refugia
749 maintained by open-water polynyas (Tables 7 and 8). Radiocarbon data and isotopic
750 analyses reveal cycles of colony expansion and abandonment driven by Holocene
751 climate variability. The penguin “optimum” (~4–2 ka BP) corresponds with reduced
752 sea-ice cover and increased marine productivity, while subsequent Neoglacial
753 cooling caused contraction of nesting ranges[180–183]. On the Channel Islands
754 (California), Guthrie et al.[184] described *Fratercula dowi*, an extinct puffin species with
755 preserved eggs and burrow nests dated 38–12 ka BP. The findings illustrate the
756 vulnerability of island seabird populations to sea-level rise and climatic change.

757 **Human–Avian Interactions and Extinction Dynamics**

758 The late Pleistocene–Holocene transition marks intensified human impacts on avian
759 populations. Burnt eggshells and butchery marks attest to consumption of both
760 adults and eggs[167]. In Africa and the Middle East, *S. camelus* persisted but suffered
761 range contraction due to hunting and habitat fragmentation[15]. By contrast, in
762 Madagascar and Australia, human exploitation directly contributed to the extinction
763 of *Aepyornis* and *Genyornis*[156–158].

764 The first record of Flamingo eggs from the late Pleistocene of the Santa Lucía site
765 (Mexico) represent a remarkable addition to an exceptionally sparse record of fossil
766 bird eggs in the Americas[185]. The authors also reassigned eggs unearthed in
767 Texcoco Lake in the Mexican Basin in the 1940s to flamingos[185,186], and established
768 shallow, saline palaeolakes systems and warmer and wetter climate in Mexico during
769 the Late Pleistocene[185,186].
770 Scott et al[187] demonstrated through analyses of breeding activity of Holocene and
771 Pleistocene sediments around the saline to hypersaline Lake Bogoria and Lake

772 Magadi, that their compacted mounds nests can stabilise shoreline and delta
773 sediments, resist erosion, and even influence minor channel patterns[187].
774 Ksepka[188,189] integrated bones and eggshells from key sites in Antarctica, New
775 Zealand, and South America to understand the evolutionary and ecological history of
776 Sphenisciformes (penguins). Eggshells offer information on reproductive biology,
777 such as egg size and structure, which correspond to body size and nesting
778 behaviour. Comparisons with extant penguins suggest that fossilised eggshells were
779 exapted to nesting environments ranging from coastal rocky areas to sandy or
780 forested habitats. The in-situ preservation indicates favourable conditions for
781 fossilisation, such as rapid burial and mineralisation in calcareous environments.
782 Eggshell and bone evidence from sites such as the La Meseta Formation in
783 Antarctica and the Pisco Basin in Peru established a timeline for penguin
784 diversification, linking body size and morphological traits to ecological niches and
785 environmental conditions. This suggests that penguins rapidly diversified following
786 the Cretaceous-Cenozoic extinction event, exploiting marine niches in the Southern
787 Hemisphere. Eggshell and bone evidence collectively underscore the importance of
788 tectonic shifts, ocean currents, and climatic changes in shaping penguin evolution
789 and dispersal patterns. The biogeographical distribution inferred from these fossils
790 aligns with key dispersal and vicariance events, illustrating the influence of
791 environmental and geological factors on penguin history[188,189].

792 Kuhn et al.[190] analysed avian eggshell fragments recovered from the Pleistocene
793 (~2.8 Ma) Dart Deposits at Taung (South Africa), where the skull of a child with
794 predation marks was discovered. Encased within breccia, the eggshells were
795 attributed to the helmeted guinea fowl (*N. meleagris*), eagle owl (*Bubo* sp.), and
796 black eagle (*Aquila* sp.)[190]. The isotope analyses agree with the hypotheses by

797 Berger and Clarke[191] that eagles and raptors rather than leopards were the
798 significant contributors of mammal faunal remains[20,192,193]. However, the isotopes
799 pointed at the black eagle as the potential predator of the Taung Child[190].

800 **Holocene Transitions and Ratite Persistence**

801 During the Holocene, post-glacial climatic stabilisation favoured open savannahs and
802 deserts, facilitating the persistence of *S. camelus* as the sole surviving ratite in Afro-
803 Eurasia[15,155] (Table 8;Figure 3). Radiocarbon data indicate ostriches survived in
804 Central Asia until ~7.5 ka BP[151,184,194]. Morphological continuity in eggshells—
805 maintaining rounded, clustered struthioid pores—demonstrates conservative
806 reproductive adaptations over millennia. Archaeological assemblages across Africa
807 and the Arabian Peninsula reveal extensive human utilisation of ostrich eggs for food
808 and material culture such as ornaments and water containers occur (Table 8) [15].
809 Despite exploitation, *S. camelus* endured due to reproductive resilience, broad
810 dietary flexibility, and ability to inhabit extreme environments. In South America, rhea
811 eggs from Holocene deposits in Argentina reveal parallel patterns of adaptation and
812 human interaction[195,195–198] (Table 8). Variations in pore density between *Rhea*
813 *americana* and *R. pennata* reflect microhabitat preferences and local environmental
814 gradients. Stable isotope and taphonomic analyses show their importance as human
815 dietary resources and indicators of semi-arid climatic conditions.

816 **Avian Diversity in Holocene Australasia and the Pacific**

817 Abundant eggshell remains of extinct flightless birds, illustrating rapid ecological
818 turnover following human arrival, were preserved during the Holocene of New
819 Zealand and Australia (Table 8). Moa (*Dinornithiformes*) eggs, varying from 120–240
820 mm in length, display species-specific thickness patterns (0.54–1.74 mm)

corresponding to ecological niche differentiation[199–202]. Radiocarbon dating of eggshells from rock shelters and archaeological sites demonstrates that moas were extirpated within centuries of Polynesian settlement through overhunting and habitat destruction[199–202]. Wood[203] described nesting materials from Holocene moa sites in New Zealand, including twigs and bark suggesting deliberate nest construction (Table 8). The presence of eggs of *Megalapteryx didinus* and *Pachyornis elephantopus* in upland contexts indicates adaptation to alpine and subalpine habitats. Gill[199] showed that eggshell thickness can serve as a proxy for species identification and relative abundance, complementing genetic and osteological data. Associated avifaunas, including Anatidae species such as *Tadorna variegata* and *Anas chlorotis*, demonstrate persistence of wetland ecosystems in late Holocene Canterbury despite climatic fluctuations[202].

Insular and Temperate Avifaunas

The Holocene record from the Canary Islands and other Atlantic archipelagos highlights insular avian adaptation (Table 8). A complete Procellariiform egg from Fuerteventura's Lobos 3 site (27 BCE–37 CE) was assigned to *Puffinus*. The bigger egg was tentatively assigned to *Calonectris* or *Puffinus*. Both eggs preserved mammillary reabsorption patterns indicative of embryonic development[173]. The specimens, associated with Roman coastal activity, exemplify the co-occurrence of natural nesting and anthropogenic influence. In New Zealand's Gibraltar Rock deposit, subfossil moa and kākāpō (*Strigops habroptilus*) eggshells occur together, providing rare insights into coexistence of species within late Holocene woodlands (Table 8)[204–207]. The kākāpō's thin-shelled eggs and nesting debris reveal ground-nesting in secluded forest habitats, correlating with its present-day reproductive

ecology. Building on the previous research, Boast[207] revised the fossil and subfossil records of the kākāpō (*Strigops habroptilus*), focusing on late Holocene deposits dating from approximately 2,500 to 124 years BP. Eggshell fragments and nesting materials were predominantly recovered from caves and rock shelters in regions such as Fiordland and northwest Nelson. The nesting sites, typically located in secluded, forested environments, were closely associated with abundant food sources, as evidenced by plant remains and faecal deposits. The eggshells were characterised by a thin calcareous structure, reflective of the kākāpō's unique reproductive biology[207]. The presence of eggshell remains of kākāpō in diverse fossil deposits suggests that kākāpō historically occupied a much wider area.

Polar Faunas and Climate Adaptation

Holocene Antarctic records of Adélie penguins provide some of the most continuous avian palaeoecological datasets (Table 8)[181–183,208]. Sites along the Ross Sea coast, including Cape Irizar and Inexpressible Island, preserve eggshells, bones, and guano spanning over 7,000 years. Stratigraphic analyses reveal alternating phases of colony expansion and retreat aligned with sea-ice dynamics. Periods of reduced sea ice during the mid-Holocene “penguin optimum” allowed range expansion inland, while Neoglacial cooling led to site abandonment. The eggshells’ calcitic composition and excellent preservation enable isotopic reconstruction of dietary and climatic conditions. Millar et al.[183] demonstrated correlations between isotopic variation and marine productivity, linking breeding intensity with nutrient availability. Millar et al.[183] built a model for understanding penguin resilience and vulnerability under contemporary warming scenarios.

Late Quaternary Wetland and Crane Records

Fossilised eggs and nests of *Grus canadensis* (Sandhill Crane) from Lago de Texcoco, Mexico, dated to the early Holocene, represent rare examples of crane reproductive remains (Table 8). The eggs' morphology parallels modern specimens, confirming ecological continuity in wetland habitats despite Holocene climatic oscillations. These finds demonstrate the utility of eggshells as bioindicators of ecosystem stability and migratory behaviour.

Avian Biomolecules and Evolutionary Insights

The Quaternary record has also transformed understanding of molecular preservation in calcitic substrates (Table 8). Oskam et al.[209] demonstrated that eggshells from moa, emu, and elephant birds preserve ancient DNA and proteins distributed around mammillary cones. Such biomolecules allow reconstruction of phylogenetic relationships where skeletal remains are absent. Subsequent studies have recovered near-complete mitochondrial genomes from *A. maximus* eggshells[34,35] and genetic data from ostrich and moa specimens, elucidating evolutionary relationships among ratites. Proteomic and isotopic analyses complement these data, revealing diet, habitat, and even microbial resistance mechanisms encoded in eggshell microstructure[35,164]. References to seminal works, such as those of Rowley[210], Grandidier[211], and Monnier[212], as well as later studies using advanced High-Resolution Computed Tomography (HRCT) techniques, including Rowe et al.[213] and Ketcham and Carlson[214] have emphasised the role of eggshells in elucidating the palaeobiology of this extinct giant. Similarly, moa eggshells from New Zealand exhibit regional morphological diversity, reflecting adaptive radiation into varied ecological niches, including both forested and open landscapes, during the Holocene[215].

Synthesis and Implications

Across the Pleistocene and Holocene, avian reproductive evolution reflects the complex interplay of climatic, ecological, and anthropogenic factors. Ratites such as *Struthio*, *Genyornis*, and *Aepyornis* demonstrate divergent fates: persistence through adaptability versus extinction through overspecialisation and human impact. Smaller taxa—flamingos, cranes, penguins, seabirds, and passerines—illustrate corresponding adjustments in eggshell structure and nesting behaviour to shifting habitats. Eggshell microstructure offers a direct window into these evolutionary processes. The persistence of struthioid and aepyornithoid pore systems into the Holocene underscores functional optimisation, while variation in eggshell thickness and crystallography records responses to humidity, temperature, and nesting substrate. Integrating isotopic, molecular, and sedimentological data has transformed eggshells from simple taphonomic curiosities into quantitative proxies for palaeoecology and climate. By the close of the Holocene, human activity had become the dominant selective force shaping avian distribution and reproductive success. Yet the survival of *S. camelus* and numerous modern bird lineages demonstrates remarkable resilience. The Quaternary record—spanning climatic upheavals, continental shifts, and cultural revolutions—thus encapsulates both the fragility and the endurance of avian life.

Palaeobiogeographical Synthesis

Global Overview

The distribution of Cenozoic avian eggs, eggshells and nests reveals complex palaeobiogeographical patterns shaped by continental drift, climate oscillations and ecological specialisation. Although preservation is patchy, the cumulative record

demonstrates that the broad outlines of modern avian biogeography were already established by the Miocene. Oological assemblages track not only the phylogenetic diversification of birds but also the expansion of habitats—from Eocene wetlands to Neogene savannas and Quaternary deserts.

Africa

Africa has the most continuous record of avian eggshells from the Miocene to the Holocene, dominated by ostrich and related ratite forms. Early Miocene occurrences in the Rift Valley document the emergence of *Struthio* contemporaneous with the development of open grasslands. Subsequent dispersal across northern Africa corresponds with the establishment of arid zones following the retreat of the Tethys Sea. The density of Pleistocene ostrich eggshell assemblages in North Africa and the Levant attests to both ecological abundance and extensive human utilisation. Isotopic analyses from isolated eggshells fragments of waterbirds and raptors from southern African caves indicate cyclical shifts between humid and arid conditions that influenced breeding distributions of birds.

Eurasia

Eurasia preserves an exceptionally diverse oological record that spans the entire Cenozoic. In the early Palaeogene, European localities such as the Paris Basin and Messel yielded eggs of aquatic and ground-nesting birds associated with subtropical wetlands. By the Miocene, extensive steppe habitats in central Eurasia supported a proliferation of large ratites, including *Struthiolithus*, *Pachystruthio* and early *Struthio*. Eggshell fragments from the Caucasus and Transcaspian regions document successive dispersal events of large ratites between Africa and Eurasia, probably facilitated by intermittent land bridges and corridor habitats.

The Asian record extends eastward to China and Mongolia, where Miocene–Pliocene sequences preserve abundant eggshells of waterbirds and terrestrial species. The presence of *Struthio* eggs in northern China and Mongolia during the Late Miocene demonstrates the eastward expansion of ostriches into temperate latitudes, likely tracking the spread of arid grasslands. In contrast, southern Asia retained more humid conditions supporting anseriform and charadriiform breeders in lacustrine settings.

Australia

The Australian Cenozoic oological record depicts an of avian reproductive evolution under long-term isolation. The record is dominated by the Dromornithidae, giant flightless birds that occupied ecological roles analogous to ratites elsewhere. Their eggshells, characterised by thick palisade layers and dense crystalline textures, are well represented in Miocene and Pliocene deposits of the Lake Eyre Basin and northern territories. These forms demonstrate convergent adaptation to arid climates, with reduced pore density minimising evaporative water loss.

Late Pleistocene and Holocene eggshells of *G. newtoni* extend this lineage into the human era. Stable-isotope data from burnt fragments provide the earliest direct evidence of anthropogenic exploitation of eggs in Australia and their eventual demise. Alongside these megafaunal records, fragmentary eggshells of waterbirds and parrots indicate continued diversity within volant lineages despite increasing aridity through the Neogene.

South America

The South American record is less abundant but provides key insights into palaeobiogeographical isolation. Variations in pore density between *R. americana*

and *R. pennata* reflect microhabitat preferences and environmental gradients. Stable isotope and taphonomic analyses of *Rhea* sps. indicate adaptation to semi-arid climates and their role as human dietary resource. Together, these findings show how humans exploited rhea eggs while adapting to ecological variability across the Holocene.

Antarctica

In Antarctica, eggshell microstructure resembling that of modern penguins indicates colonial breeding was established before major glaciation, after which expanding ice curtailed terrestrial nesting archives. A Holocene Adélie penguin record from the Ross Sea spans around 7,000 years, with eggshells from ornithogenic soils on Inexpressible Island and Cape Irizar marking refugia sustained by open-water polynyas. Radiocarbon and isotopic data show repeated cycles of colony expansion and abandonment, a mid-Holocene “penguin optimum” with reduced sea-ice and higher productivity, and subsequent Neoglacial contraction. Analysis of bones and eggshells from Antarctica, New Zealand and South America link eggshell traits to body size and nesting behaviour, with in-situ preservation implying rapid burial and calcareous mineralisation. Together, these lines of evidence support the rapid post-Cretaceous–Palaeogene diversification shaped by tectonics, ocean currents and climate outlined by genetic studies[216–219].

North America

North American Cenozoic sequences yield a varied but discontinuous record. Eocene lacustrine deposits of the Green River Formation contain waterbird eggshells akin to presbyornithids, while Miocene assemblages from the Great Plains and western basins show increasing representation of ground-nesting forms adapted to

989 expanding grasslands. Late Pleistocene and Holocene caves preserve subfossil
990 eggshells of raptors, owls and passerines.

991 **Dispersal and Vicariance**

992 The distributional history of avian eggs and eggshells mirrors the complex interplay
993 of dispersal and vicariance that structured avian evolution. During the early
994 Cenozoic, dispersal between Laurasian continents was facilitated by continuous
995 northern land connections. Subsequent fragmentation and climatic differentiation
996 promoted regional endemism, most clearly expressed in the independent evolution
997 of ratites on Gondwanan fragments—Africa, South America, Australia, Madagascar
998 and New Zealand.

999 The spread of *Struthio* from Africa into Eurasia during the Miocene exemplifies
1000 successful intercontinental dispersal following climatic corridor formation.
1001 Conversely, the persistence of unique lineages such as the Dromornithidae and
1002 Aepyornithidae reflects long-term isolation. Eggshell evidence thus corroborates
1003 molecular phylogenies that infer multiple independent losses of flight and convergent
1004 adaptation to open habitats[220–222].

1005 **Latitudinal and Environmental Gradients**

1006 Analyses of eggshell microstructure across latitudes reveal consistent environmental
1007 signatures. Equatorial and subtropical regions tend to yield thin, highly porous
1008 eggshells corresponding to humid conditions and open or shallow nesting sites,
1009 whereas temperate and arid regions produce thick-shelled forms with reduced pore
1010 density. These gradients suggest strong selective pressure on gas conductance and
1011 water-vapour exchange, tightly linked to climatic parameters such as temperature

and humidity. This data provides a geographically coherent picture of how avian reproduction responded to Cenozoic climatic reorganisation.

Temporal Integration

The progressive shift from equable early Cenozoic climates to the cooler, more variable regimes of the Neogene and Quaternary reshaped global avian distributions. Early Palaeogene records cluster around mid-latitudes, corresponding to widespread forested environments. By the Miocene, eggshell evidence indicates a poleward expansion of birds following the emergence of open biomes. Quaternary glacial cycles imposed repeated range contractions and expansions, generating secondary contact zones and hybridisation events reflected in genetic data from modern taxa.

Palaeobiological and Evolutionary Trends

Eggshell Structure and Function

The Cenozoic fossil record documents a broad spectrum of avian eggshell morphologies that reflect both phylogenetic constraint and ecological adaptation. Eggshell architecture—comprising the mammillary, palisade and external layers—varied primarily in thickness, pore geometry and degree of crystallite organisation. Comparative analyses reveal two major evolutionary trajectories: (1) progressive refinement of thin, high-porosity eggshells among volant waterbirds and passerines, and (2) stabilisation of thick, low-porosity eggshells among flightless terrestrial taxa such as ratites and dromornithids.

In general, eggshell thickness correlates positively with egg mass and incubation environment. Ground-nesting birds in exposed habitats developed robust eggshells

capable of withstanding mechanical stress, while arboreal or burrow-nesting species maintained thinner, more porous structures promoting efficient gas exchange in humid conditions. The transition from the Eocene's warm, equable climates to the variable regimes of the Miocene and Pliocene coincided with increased heterogeneity in eggshell traits, reflecting expansion into a wider array of habitats. Miocene oological evidence indicates the epoch was pivotal in moulding modern bird diversity. Ratites diversified along latitudinal climate gradients, evolving eggshell structures that mitigated aridity and thermal stress. Neognaths expanded into emerging habitats—from deserts to wetlands and tropical forests—producing a spectrum of eggshell forms ranging from thick, multi-layered ratite shells to the fine prismatic shells of passerines and nightjars. Differences in pore geometry, microstructure, and shell thickness reveal adaptations to nesting substrates, ambient humidity, and incubation behaviour, including evidence for philopatric behaviour and on the ecological resilience shown by some taxa in maintaining breeding-site fidelity under changing environmental conditions. These reproductive shifts parallel contemporary plant and animal turnovers, reinforcing interpretations of the Miocene as a time of global ecological experimentation and specialisation.

Microstructural conservatism within major clades suggests strong functional optimisation early in avian evolution. Ratite-type eggshells, for example, display minimal architectural change from the early Miocene to the present, indicating a design finely tuned to ground incubation in arid environments. Conversely, neognath groups exhibit greater plasticity: the diversification of pore arrangements and eggshell textures in anseriforms and charadriiforms tracks the shift from forested wetlands to open lacustrine and coastal systems.

Nesting Behaviour and Ecology

Nesting traces, though rare, provide a behavioural dimension to the fossil record of avian reproduction. From the simple ground scrapes inferred for early Palaeogene taxa to the complex cup and mound nests of the Neogene, nesting strategies evolved in tandem with ecological opportunity and climatic constraint (Figure 3).

The fossil record indicates that ground nesting was probably predominant throughout much of the Cenozoic, particularly among large-bodied and aquatic species, albeit this pattern is undoubtedly shaped by fossilisation bias that favours the preservation of terrestrial nests. As importantly, there is a strong preservation and sampling bias towards thicker eggshells: thin-shelled eggs, such as those of passerines and many small waterbirds, are highly fragile and preserve poorly even over archaeological timescales[18,51,223,224], let alone in deeper-time contexts. This differential preservation likely skews the apparent taxonomic distribution of nesting strategies in the fossil record and must be considered when interpreting broad evolutionary patterns. Buried nests constructed from vegetation or sediment are well documented among palaeognaths and early anseriforms and would have supported thermoregulation in environments where parental attendance was limited. By contrast, aerial and arboreal nesting—suggested by the delicate, thin-shelled eggs of passerines and swifts—appears to have become more widespread alongside the expansion of trees and shrubs during the Miocene, potentially providing protection from ground-dwelling predators (Figure 2C).

The Miocene radiation of passerines coincided with the evolution of diverse nest architectures, including domed, pendant and cup-shaped structures. These innovations enabled exploitation of microhabitats and facilitated expansion into both temperate and tropical ecosystems. The fossilised remains of nest impressions and

adhered sediment layers in Miocene and Pliocene strata of Europe and North America attest to this behavioural diversification.

Fossilised nesting structures and eggs from the Oligocene to Pliocene reveal early avian behavioural innovation and ecological diversification. A carved nesting chamber from Egypt and wood-bored cavities from Europe and the USA suggest early excavation behaviour akin to woodpeckers and passerines. Miocene and Pliocene eggs, including the earliest passeriform specimen from Austria, demonstrate established arboreal nesting, rapid incubation, and lineage-specific reproductive adaptations across forested, lacustrine, and arid environments.

In island and continental interior settings, reproductive adaptations often mirrored isolation and resource limitation. The giant eggs of the Aepyornithidae in Madagascar and the Dromornithidae in Australia represent extreme cases of K-selected strategies, where large egg size and prolonged incubation compensated for low clutch numbers and reduced predation. Conversely, small-bodied birds in variable environments likely adopted r-selected strategies with rapid reproduction and minimal parental investment. Although direct evidence is rare, comparative morphology and isotopic proxies permit these inferences.

Reproductive Physiology and Environmental Correlates

The Cenozoic record reveals consistent physiological trends linking eggshell properties to environmental parameters. One of the most conspicuous patterns is the inverse correlation between eggshell porosity and aridity. As global climates shifted towards increasing dryness during the Neogene, many avian lineages developed thicker eggshells with restricted pore openings, effectively reducing water-vapour

conductance. Such modifications mirror adaptations observed in extant desert-nesting species, including ostriches and sandgrouse.

Although egg shape has been linked to flight adaptations[225], we found that egg size and shape may also reflect climatic and ecological factors as previously outline by Duursma et al.[226]. Elliptical or elongated eggs are more common in cavity or cliff nesters, enhancing packing efficiency and preventing rolling on inclined surfaces. Spherical eggs dominate among ground nesters, providing structural strength and even heat distribution. These morphological variations are readily observable in fossil assemblages and align closely with inferred nesting .

Reproductive periodicity appears to have evolved in response to the onset of pronounced seasonality during the Miocene–Pliocene transition. Stable-isotope analyses suggest that breeding in many taxa became synchronised with rainfall cycles and resource availability. Such plasticity may have contributed to the resilience of avian populations through climatic perturbations, while the inability of large, slow-breeding species to adjust may explain their vulnerability to late-Quaternary extinction.

Convergent and Divergent Evolution

A recurring theme in avian oology is the balance between convergent adaptation and phylogenetic divergence. Similar environmental pressures repeatedly produced comparable eggshell architectures across unrelated lineages. The independent emergence of thick, compact eggshells among the Dromornithidae and African ratites exemplifies functional convergence, whereas fine-scale microstructural differences preserve phylogenetic identity. Conversely, closely related groups

occupying distinct habitats exhibit divergent oological traits, demonstrating rapid evolutionary response to ecological differentiation.

The fossil record also captures transitional morphotypes that blur conventional boundaries between palaeognaths and neognaths. For instance, certain Eocene and Oligocene eggshells combine ratite-like mammillary bases with neognath-style external zones, suggesting either ancestral retention or parallel modification. Such forms underscore the mosaic nature of avian reproductive evolution, in which structural innovation and constraint interacted over tens of millions of years.

Evolutionary Stability and Innovation

Despite substantial climatic and ecological upheavals, avian reproductive systems display remarkable evolutionary stability. The fundamental architecture of the eggshell and the behavioural repertoire of nesting have remained consistent since the early Cenozoic. Innovations occurred primarily in materials and microstructural refinement rather than in overall design. This conservatism reflects the success of the basic avian reproductive strategy: external calcareous eggs coupled with parental incubation.

Nevertheless, the record reveals episodic bursts of innovation linked to major environmental transitions (Figure 2C and 3). The Miocene expansion of grasslands and the concomitant diversification of open-country birds triggered adaptive modification of eggshell texture and pigmentation for camouflage and thermoregulation. The colonisation of new habitats, including alpine and desert zones, necessitated physiological adjustments in eggshell gas conductance and embryonic tolerance to temperature extremes. Such episodes of innovation punctuate an otherwise stable evolutionary trajectory.

Integration with Molecular and Developmental Data

Comparisons between fossil oological evidence and molecular phylogenies reinforce the interpretation that key reproductive traits were established early and maintained through deep time. Genomic data indicate that genes controlling eggshell mineralisation, pigmentation and pore formation are highly conserved across avian orders. The fossil record thus provides the temporal framework for these molecular observations, demonstrating when and under what environmental conditions particular traits emerged.

Emerging studies integrating developmental biology with palaeontology—through experimental modelling of crystallisation and gas diffusion—are beginning to illuminate the functional basis of fossil eggshell variation. Such cross-disciplinary approaches hold promise for linking macroscopic patterns in the geological record to underlying biological mechanisms.

Human interactions, extinction dynamics and conservation implications

Human Exploitation of Avian Eggs

The late Quaternary and Holocene mark a pivotal stage in avian history, when the cumulative effects of human exploitation and environmental modification began to override natural selective processes. Archaeological and palaeontological records document widespread harvesting of bird eggs for nutrition[145,227], ornamentation and ritual use. Ostrich eggshell fragments from African and Eurasian caves exhibit burning, incision and deliberate perforation, demonstrating both dietary and symbolic utilisation extending back more than 60,000 years.

Extinction of Megafaunal Birds

Large flightless birds were especially susceptible to overexploitation and environmental stress. The Aepyornithidae of Madagascar, the Dromornithidae of Australia and extinct Eurasian ostrich lineages such as *Pachystruthio* and *Struthio syriacus* all vanished within a few millennia of human arrival. Burnt and fragmented eggshells provide unequivocal evidence of human predation. Although climatic oscillations contributed to ecological stress, human activity accelerated decline through habitat burning and direct egg collection.

Anthropogenic Modification of Reproductive Environments

Beyond direct exploitation, humans have reshaped nesting habitats on a global scale. Agricultural expansion, urbanisation and the drainage of wetlands reduced the availability of breeding sites for numerous species, while others exploited novel niches created by human structures[228–230]. Eggshell geochemistry provides an independent record of these transformations, preserving signatures of industrial pollution, fertilisers and altered food webs[231–233].

Conservation and the Legacy of the Oological Record

The oological record offers unique insights for modern conservation. Understanding how birds historically adjusted reproductive traits to environmental fluctuation can inform management of contemporary species threatened by climate change. By reconstructing the limits of past adaptation, palaeobiologists can help predict species' resilience or vulnerability under future scenarios. Long-term datasets derived from fossil and subfossil eggshell isotopes can calibrate models of breeding phenology and migration, assisting conservationists in defining critical habitat windows.

De-extinction and Genetic Reconstruction

Advances in ancient DNA and proteomic recovery from eggshell fragments have added an important new dimension to avian research, including discussion of de-extinction and genetic rescue[34,234,235]. However, such possibilities remain highly constrained: to date, only short fragments of proteins or DNA have been recovered from deep-time eggshells, and mitochondrial DNA has been retrieved only from comparatively recent subfossil contexts. Although complete genome reconstruction is therefore not currently feasible, partial sequences from subfossil ostrich, moa and elephant-bird eggshells have nonetheless provided valuable insights into evolutionary relationships and patterns of gene persistence. While full resurrection of extinct birds remains speculative, biomolecular data from fossil eggshell contribute to more robust phylogenetic placement, inform the design of conservation breeding programmes, and enhance understanding of developmental pathways involved in eggshell formation.

Ethical Dimensions

The intersection of de-extinction and conservation raises ethical and ecological questions. Restoring a lost species without restoring its original environment risks superficial success and ecological imbalance[236–238]. The fossil record serves as a cautionary narrative: extinction is often the product of complex ecosystem disruption rather than the loss of a single lineage. Conservation strategies should prioritise habitat restoration, genetic diversity and the maintenance of functional ecological networks.

Conclusions and Future Directions

The Cenozoic fossil record of avian eggs, eggshells, and nests is a continuous chronicle of reproductive evolution, environmental adaptation, and, in the most

recent millennia, human influence. Over the past 66 million years, birds have repeatedly adjusted their reproductive strategies in response to shifting climates, habitats, and ecological pressures. The palaeoological record reveals both resilience and vulnerability: evolutionary continuity expressed through conserved structural motifs, and local innovation driven by environmental and behavioural change.

The main conclusions of this synthesis are as follows:

1. **Parataxonomic standardisation — widely adopted and essential —**We advocate the routine, comprehensive use of parataxonomy—now standard across oological and palaeontological studies—as the primary framework for classifying eggshells. This will deliver robust cross-basin correlation, support large-scale meta-analyses, and integrate seamlessly with biological and environmental datasets.

2. **Evolutionary continuity and innovation** — Fundamental features of avian reproduction were established early in the Cenozoic and have been preserved through successive radiations, while morphological and physiological refinements track adaptive diversification.

3. **Environmental sensitivity** — Egg morphology, microstructure, and geochemistry provide robust proxies for palaeoclimate and habitat reconstruction, capturing both regional and global environmental trends.

4. **Biogeographical structure** — Continental drift, climatic corridors, and habitat fragmentation dictated the spatial and temporal distribution of reproductive forms, generating distinct regional and evolutionary trajectories.

5. **Human impact and conservation relevance** — The late Quaternary introduced direct anthropogenic control over avian reproduction through exploitation, habitat modification, extinction, and modern conservation interventions.

6. **Prospects for de-extinction and restoration** — Genetic and proteomic information preserved in fossil eggs contributes to the ethical and scientific frameworks underpinning assisted evolution, functional restoration, and rewilding.

Future Research Priorities

Future work should prioritise:

- **Expansion and refinement of parataxonomic frameworks** — Broaden and standardise the application of parataxonomy in oological research to establish a coherent global classification system.
- **Expanded geographic coverage**, targeting under-represented regions and depositional settings to refine global biogeographical models.
- **Integration of multi-proxy analyses**, combining microstructural, isotopic, and biomolecular data with ecological and climatic modelling.
- **Developmental and genomic synthesis**, linking fossil and modern eggshell traits to underlying genetic and biochemical mechanisms of biomineralisation.
- **Conservation palaeobiology**, employing fossil baselines to predict reproductive and ecological responses to ongoing climate change.

- **Ethical evaluation of de-extinction initiatives**, ensuring that restoration efforts complement rather than compromise the preservation of existing biodiversity.

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Table 1. Summary of analytical methods used in the study of fossil and modern eggshell micro- and ultrastructure. The table outlines each method's main advantages ("plus"), limitations ("minus"), sample preparation requirements and degree of destructiveness, cost and throughput, and typical analytical outputs[17,22,32,37,45,48].

Method	Plus (advantages)	Minus (limitations)	Sample prep / Destructiveness	Cost / Throughput	Typical outputs
Hand specimen description & stereomicroscopy[19]	Rapid triage; minimal damage; documents surface ornament and pore openings.	Limited resolution; no crystallographic information; easily confounded by diagenesis.	None to very low (non-destructive).	Low cost; high throughput.	Qualitative notes, macro/micro photographs.
Cross-polarised light microscopy (thin sections)[19]	Low cost; reveals optical textures, first-order layering and alteration.	Requires thin-sectioning (destructive); largely qualitative for crystallography.	Thin-sectioning, polishing (destructive).	Low–moderate cost; moderate throughput.	Photomicrographs; layer thickness; optical fabrics.
Cathodoluminescence (CL) imaging[19]	Sensitive to recrystallisation and trace-element zoning; useful for diagenetic screening.	Destructive prep; interpretative ambiguities; instrument access required.	Polished section; usually coated (destructive).	Moderate cost; moderate throughput.	CL mosaics highlighting alteration domains.

SEM (SE/BSE imaging) [19]	High-resolution fabrics; pore geometry; microfractures; widely available.	Often requires coating/sectioning; no direct orientation (crystallography).	Fracture or polished section; conductive coating (destructive).	Moderate cost; moderate throughput.	SE/BSE micrographs; layer architecture; pore morphometry.
EBSD (SEM-based crystallography) [20, 38]	Quantitative orientation/misorientation; grain size/shape; growth directions; decisive for homology tests.	Embedding and ultra-polishing (destructive); slow for large maps; higher per-sample cost; sensitive to polishing and charging.	Embedded, sectioned, colloidal-silica polished; usually coated (destructive).	High cost; slow throughput.	Orientation maps (IPF, pole figures), grain-boundary statistics.
Elemental mapping (EPMA; synchrotron XRF) [20, 38]	Resolves elemental/mineral distributions; tracks diagenetic pathways; complements textures.	Destructive mounting; facility access; calibration/matrix effects.	Polished mounts/sections; coating common (destructive).	Moderate–high cost; variable throughput (beamtime).	Element maps; profiles; phase/oxide totals.
Stable-/clumped-isotope & trace-element geochemistry[22]	Environmental and physiological proxies (temperature, humidity, vegetation; incubation context).	Requires powdering/micro-drilling (destructive); potential diagenetic overprint; needs rigorous screening.	Powder drilling; micro-milling (destructive).	Moderate–high cost; moderate throughput.	δ18O, δ13C, Δ47 (clumped), trace-element ratios.
Biomolecular assays[145] (proteins, lipids, aDNA)	Potentially direct evidence of phylogenetic affinity and	Very rare preservation; destructive; high	Powdering/extraction (destructive).	High cost; low	Peptide/protein fragments, lipids, sequence

physiological function.	contamination risk; stringent authentication required.		through put.	data (when authentic).	

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1855 Table 2. Palaeocene avian record of eggs, eggshells, and nests.

Families	Species	Oospecies	Material	Epoch	Location	References
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: La Mourotte	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: Les Bardouine	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: St-Maurin	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002);

						Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Catalonian coastal range	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Claret and Tendruy	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Llimiana	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: La Mourotte	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: Les Bardouine	Hirsch and Packard (1987); Mourer-Chauviré (1996a);

						Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: St-Maurin	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Catalonian coastal range	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Claret and Tendruy	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Llimiana	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: La Mourotte	Hirsch and Packard (1987); Mourer-

						Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: Les Bardouine	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus biroi*	eggshells	Palaeocene	France: St-Maurin	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Catalonian coastal range	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Claret and Tendruy	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)

Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Palaeocene	Iberia: Llimiana	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Lithornithidae	*Lithornis indeter.*		eggshells	Palaeocene	USA: Clark Quagrangle Park County (Wyoming)	Houde (1988); Mikhailov (1997); Grellet-Tiner and Dyke (2005)
Lithornithidae	*Lithornis celetius*		eggshells	Palaeocene	USA: Fort Union Formation (Gallatin National Forest, Montana)	Grellet-Tinner and Dyke (2005)
Lithornithidae	*Lithornis indeter.*		eggshells	Palaeocene	USA: Clark Quagrangle Park County (Wyoming)	Houde (1988); Mikhailov (1997); Grellet-Tiner and Dyke (2005)
Lithornithidae	*Lithornis celetius*		eggshells	Palaeocene	USA: Fort Union Formation (Gallatin National Forest, Montana)	Houde (1988); Mikhailov (1997); Grellet-Tiner and Dyke (2005)
Lithornithidae	*Lithornis indeter.*		eggshells	Palaeocene	USA: Clark Quagrangle Park County	Houde (1988); Mikhailov (1997); Grellet-

				(Wyoming)	Tiner and Dyke (2005)
Lithornithidae	*Lithornis celetius*	eggshells	Palaeocene	USA: Fort Union Formation (Gallatin National Forest, Montana)	Grellet-Tinner and Dyke (2005)
Presbyornithidae	*Aves indeter.*	eggshells	Palaeocene	USA: Western Interior of the USA	Mikhailov (1997b)
Presbyornithidae	*Aves indeter.*	eggshells	Palaeocene	USA: Western Interior of the USA	Mikhailov (1997b)
Presbyornithidae	*Aves indeter.*	eggshells	Palaeocene	USA: Western Interior of the USA	Mikhailov (1997b)

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1867 Table 3. Eocene avian record of eggs, eggshells, and nests.

Families	Species	Oospecies	Material	Epoch	Location	References
Aves	*Aves indeter.*		eggs	Eocene	Dominican Republic: La Bucara mine	Kosmowska-Ceranowicz et al. (2013)
Aves	Ornithoid		eggshells	Eocene	Germany: Geisetal quarry Munchen-Sudfeld near Halle/Salle	Kohring and Hirsch (1996); Mlíkovský (2002)
Aves	*Aves indeter.*	*Incognitoolithus ramotubulus*	eggshells	Eocene	USA: DeBeque Formation North Western Colorado	Hirsch et al. (1997)
Aves	*Aves indeter.*	*Metoolithus nebraskensis*	eggs	Eocene	USA: Willwood Formation of Wyoming	Jackson et al. (2013)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Aude (Rivel and Fa)	Villatte (1966); Dughi et al. (1966); Buffetaut and Angst (2014); Angst et al. (2014)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Bouxviller	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002);

						Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Fontcouverte	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Lagrasse	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Les Bardouines	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Les Bardouines	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002);

						Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Les Mauquiers	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Ponteves	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Sillans	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: St-Antonin	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002);

						Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	France: Suberoque;	Hirsch and Packard (1987); Mourer-Chauviré (1996a); Mlíkovský (2002); Angst et al. (2015)
Gastornithidae	*Gastornis indeter.*	*Ornitholithus arcuatus*	eggshells	Eocene	Iberia:Tremp Formation	Donaire and López-Martínez (2009); Buffetaut and Angst (2014)
Gruiformes	Gruiformes		eggs	Eocene	USA: Big Horn basin and Piceance Creek (Wyoming)	Hirsch and Bowles (1978)
Lithornithidae	*Lithornis vulturinus*		eggshells	Eocene	United Kingdom: Walton−on−the−Naze (London Clay Formation)	Grellet-Tinner and Dyke (2005)
Palaeotididae	*Palaeotis weigelti*	*Medioolithus geiseltalensis*	eggshells	Eocene	Germany: Geisetal quarry Munchen-Sudfeld near Halle/Salle	Kohring and Hirsch (1996); Mlíkovský (2002)
Passeriformes	Neognathous		eggshells	Oligocene	Germany: Kärlich (Rheinland-Pfalz W)	Gross et al. (2008): Mörs (2010)
Presbyornithidae	*Aves indeter.*		eggshells	Eocene	Algeria :Glib Zegdou Formation	Garcia et al. (2020)

Presbyornithidae	*Aves indeter.*	eggs	Eocene	Algeria: Glib Zegdou Formation	Garcia et al. (2020)
Presbyornithidae	*Aves indeter.*	eggshells	Eocene	Algeria: Gour Lazib	Garcia et al. (2020)
Presbyornithidae	*Presbyornis indeter.*	colony	Eocene	USA: Bear Divide and Warfield Creek (Southern Western Wyoming)	McGrew (1980); Leggitt et al. (1998a and b); Naish (2013)
Presbyornithidae	*Presbyornis indeter.*	colony	Eocene	USA: Green River Formation of Lake Gosiute	McGrew (1980); Leggitt et al. (1998a and b); Naish (2013)
Presbyornithidae	*Presbyornis indeter.*	colony	Eocene	USA: Powerline	McGrew (1980); Leggitt et al. (1998a and b)
Presbyornithidae	*Presbyornis indeter.*	colony	Eocene	USA: Wilkins Peak, Southern Western Wyoming	McGrew (1980); Leggitt et al. (1998a and b)
Sandcoleidae	?*Eoglaucidium pallas*	eggshells	Eocene	Germany: Geisetal quarry Munchen-Sudfeld near Halle/Salle	Mayr (2020)
Trochilidae	*Aves indeter.*	eggs	Eocene	Dominican Republic: La Toca mine	Poinar et al. (2007)

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1875 Table 4. Oligocene avian record of eggs, eggshells, and nests.

Families	Species	Oospecies	Material	Epoch	Location	References
Aves	*Aves indeter.*	*Metoolithus jacksonae*	eggs	Oligocene	USA: Fitterer Ranch locality in Stark County, North Dakota (The Brule Formation)	Lawver and Boyd (2018)
Galloanseraе	Galloanserae		eggs	Oligocene	USA: Badlands near Harrison, Nebraska	Troxell (1916);Hirsch and Packard (1987); Hirsch and Bray (1988)
Gruiformes	*Badistornis aramus*		eggs	Oligocene	USA: Badlands National Park Shannon County (South Dakota)	Chandler and Wall (1999)
Piciformes	*Aves indeter.*		nests	Oligocene	Egypt	Hasiotis et al. (1993)
Strigidae	Strigiformes		eggs	Oligocene	USA: White River	Troxell (1916); Hirsch and Bray (1988); Hirsch

					Badlands of South Dakota	and Packard (1987); Lawver and Boyd (2018)
Strigiformes	owl eggs		eggs	Oligocene	USA: Badlands, near Dakota City, South Dakota	Farrington (1899); Hirsch and Packard (1987)
Strigiformes	owl eggshells		eggshells	Oligocene	USA: Badlands, near Dakota City, South Dakota	Farrington (1899); Hirsch and Packard (1987)
Ratite	owl eggshells		eggshells	Oligocene	Khatorin-Dondzhi (Mongolia)	Mikhailov and Zelenkov (2020)

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1883 Table 5. Miocene avian record of eggs, eggshells, and nests.

Families	Species	Oospecies	Material	Epoch	Location	References

Aepyornithidae	Aepyornithoid	eggshells	Miocene	Egypt: Moghra Formation	Smith (2013)
Aepyornithidae	*Aepyornis indeter.*	eggshells	Miocene	Iberia: Torrellano site (Alacant)	Bravo et al. (2009)
Aepyornithidae	Aepyornithidae?	eggshells	Miocene	Kenya: Apak Nawata	Mourer-Chauviré et al. (1996a, 1996b); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Aepyornithidae	Aepyornithidae?	eggshells	Miocene	Kenya: Fort Ternan	Mourer-Chauviré et al. (1996a, 1996b); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Aepyornithidae	Aepyornithidae?	eggshells	Miocene	Kenya: Lothagam	Mourer-Chauviré et al. (1996a, 1996b); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Aepyornithidae	Aepyornithoide	eggs	Miocene	Namibia: Elisabethfeld	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide	eggshells	Miocene	Namibia: Elisabethfeld	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide	eggs	Miocene	Namibia: Fiskus	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide	eggshells	Miocene	Namibia: Fiskus	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide	eggs	Miocene	Namibia: Grillental	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)

Aepyornithidae	Aepyornithoide		eggshells	Miocene	Namibia: Grillental	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide		eggs	Miocene	Namibia: Kamberg	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoide		eggshells	Miocene	Namibia: Kamberg	Senut and Pickford (1995); Senut (2000);Mikhailov and Zelenkov (2020)
Aepyornithidae	*Struthiobrachydactylus*	*Struthiolithus brachydactylus*	eggshells	Miocene	Romania: Fălciu at Prut River valley (North Black See area)	Mikhailov and Zelenkov (2020)
Aepyornithidae	*Aepyornis indeter.*		eggshells	Miocene	India: Hasnot	Sauer (1972); Sahni et al., 1990; Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid		eggshells	Miocene	Turkey: Çankiri-Delibayir Surti; Gölbaşi-Zivra	Sauer (1976);Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid		eggshells	Miocene	Turkey: Gölbaşi-Zivra; Süleymanli	Sauer (1976);Mikhailov and Zelenkov (2020)
Aepyornithidae	*Aepyornis maximus*		eggshells	Miocene	Iberia: Elx (Catalonian Countries)	Mein and Dauphin (1995); Bravo et al. (2009); Mikhailov and Zelenkov (2020)
Anatidae	?anatid		eggshells	Miocene	New Zealand: Otago	Worthy et al. (2007)
Anatidae	*Anser indeter.*		eggs	Miocene	Iberia: Cevico de	Sánchez Marco (1996); Mlíkovský (2002)

					la Torre (Palencia)	
Anatidae	*Aves indeter.*		eggs	Miocene	USA: Bad Lands near Dakota City,	Farrington (1899)
Aves	*Aves indeter.*	*Neognathoolithus sps.*	eggshells	Miocene	Czech Republic: Dolnice (NW Bohemia)	Kohring (1998 , 1999); Mlíkovský (2002)
Aves	*Aves indeter.*		eggshells	Miocene	Czech Republic: Heiligenstadt; Schönweg	Mlíkovský (1996a and 2002)
Aves	*Aves indeter.*		eggshells	Miocene	Germany: Hahnenberg	Mlíkovský and Hesse (1996); Mlíkovský (2002)
Aves	*Aves indeter.*		eggshells	Miocene	Germany: Lierheim	Mlíkovský and Hesse (1996); Mlíkovský (2002)
Aves	*Aves indeter.*		eggs	Miocene	Savage Islands	Meijer (2009)
Aves	*Aves indeter.*		eggs	Miocene	USA: Western interior of the USA Sheep Creek Formation	Hirsch and Bray (1988)
Aves	neognathous		eggshells	Miocene	USA: Mountains in California	Leggittt (2002)
Caprimulgidae			eggs	Miocene	Iberia: Fuentes de Ebro	Amo-Sanjuán and Laplana (2001).
Dinornithidae	*Dinornis indeter.*		eggshells	Miocene	New Zealand: Otago	Worthy et al. (2007); Tennyson et al.(2010); Cole and Wood (2018)

Dinornithiformes	Dinornithiformes		eggshells	Miocene	New Zealand: Otago	Worthy et al. (2007); Tennyson et al.(2010); Cole and Wood (2018)
Dromornithidae	*Dromornis indeter.*		eggshells	Miocene	Australia: Snake Dam (Clayton River Australia)	Williams and Rich-Vickers (1992); Grellet-Tinner (2001)
Passeriformes	Passeriformes		eggs	Miocene	Austria: Mataschen (Styria, Austria)	Gross et al. (2008)
Phoenicopteridae	Phoenicopteridae		eggshells	Miocene	Iberia: Bargota	Murelaga et al. (2006)
Phoenicopteridae	Phoenicopteridae		eggshells	Miocene	Iberia: Jumilla (Murcia)	Sánchez Marco (1999)
Phoenicopteridae	Phoenicopteridae		eggshells	Miocene	Iberia: Monte de la Pila Lardero (La Rioja)	Hernández et al. (2003); Gamonal González (2015)
Phoenicopteridae	Phoenicopteridae		eggshells	Miocene	Iberia: Toril 3A (Daroca)	Hernández et al. (2003); Gamonal González (2015)
PhoenicopteridaeAY48:BE54	Phoenicopteridae		nests	Miocene	Iberia: Bardenas	Murelaga (2000); Grellet-Tinner et al. (2012);
Piciformes	Piciformes		nests	Miocene	Czech, Republic: Velká Černoc (Northern Bohemia)	Mikuláš and Zasadil (2002, 2004)
Procellariidae	*Aves indeter.*		eggshells	Miocene	Savage Islands	Hutterer et al. (2001)
Procellariidae	*Aves indeter.*		eggs	Miocene	Savage Islands	Hutterer et al. (2001)

Struthionidae	*PachyStruthio indeter.*	eggshells	Miocene	Azerbaijan: Eldari	Mikhailov and Kurochkin (1988); Bukhsianidze and Koiava (2018); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio cf. karatheodoris*	eggshells	Miocene	United Arab Emirates: Baynunah Municipality Site Abu Dhabi Emirate	Bibi et al. (2006); (Stewart and Beech 2006); Louchart et al. (2022)
Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: Awasib	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggshells	Miocene	Namibia: Awasib	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: Cairn 2	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggshells	Miocene	Namibia: Cairn 2	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: Karingarab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggshells	Miocene	Namibia: Karingarab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: Rooilepel Depression	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: Vreemdelingspoort	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggshells	Miocene	Namibia: Vreemdelingspoort	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Diamantornis corbetti*	eggs	Miocene	Namibia: West Pan (Namibia)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs hells	Miocene	Namibia: West Pan (Namibia)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis corbetti*	eggs hells	Miocene	Namibia:Rooilepel Depression	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Awasib Cairn 1	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs hells	Miocene	Namibia: Awasib Cairn 1	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Diep Rivier	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs hells	Miocene	Namibia: Diep Rivier	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Elim Gullies (Tsondab sandstone)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs hells	Miocene	Namibia: Elim Gullies (Tsondab sandstone)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Middle Haiber Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs hells	Miocene	Namibia: Middle Haiber Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Rooilepel Depression	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Diamantornis iaini*	eggshells	Miocene	Namibia: Rooilepel Depression	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Schmidtfeld	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggshells	Miocene	Namibia: Schmidtfeld	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Tjirundo	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggshells	Miocene	Namibia: Tjirundo	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Tree Pan	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggs	Miocene	Namibia: Tsauchab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggshells	Miocene	Namibia: Tsauchab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Diamantornis iaini*	eggshells	Miocene	Namibia:Tree Pan	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Awasib	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Awasib	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Awasib (NNE of water hole)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Awasib (NNE of water hole)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Awasib (West of	Senut and Pickford (1995); Senut (2000)

				waterhole inselberg)	
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: Awasib (West of waterhole inselberg)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Elbow Dune	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: Elbow Dune	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Etosha Subcrop Beisebvlakte	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: Etosha Subcrop Beisebvlakte	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: GP Pan East	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: GP Pan East	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: GP Pan North	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: GP Pan North	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Haiber Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs hells	Miocene	Namibia: Haiber Hill	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Karingarab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Karingarab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Narabeb	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Narabeb	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Rooilepel Depression	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Rooilepel Depression	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Rooilepel West	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Rooilepel West	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Sesriem North of Airstrip	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Sesriem North of Airstrip	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Tsauchab Valley	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggshells	Miocene	Namibia: Tsauchab Valley	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*	eggs	Miocene	Namibia: Vreemdelingspoort (aeolianite cliffs)	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Namornis oshanai*		eggs hells	Miocene	Namibia: Vreemdelingspoort (aeolianite cliffs)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*		eggs	Miocene	Namibia: Vreemdelingspoort (fossil dune upper)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Namornis oshanai*		eggs hells	Miocene	Namibia: Vreemdelingspoort (fossil dune upper)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*PachyStruthio indeter.*		eggs hells	Miocene	Kazakhstan	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio daberasensis*	*Struthiolithus oosps.*	eggs hells	Miocene	South Africa: Prospect Hill Formation	Stidham (2004); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggs hells	Miocene	Turkmenistan: Badkhyz Desert Region	Burchak-Abramovich, and Konkova (1967); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggs hells	Miocene	Ukraine: Apostolovo	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio indeter.*		eggs hells	Miocene	Ukraine: Čebotarevkac	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio indeter.*		eggs hells	Miocene	Ukraine: Il'inka	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio indeter.*		eggs hells	Miocene	Ukraine: Malynivcy	Mlíkovský (1996d and 2002)

Struthionidae	*Struthio indeter.*	eggshells	Miocene	Ukraine: Snigirevka	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio indeter.*	eggshells	Miocene	Ukraine: Vojničevo	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio indeter.*	eggshells	Miocene	Ukraine:Jur'yvka	Mlíkovský (1996d and 2002)
Struthionidae	*Struthio asiaticus*	eggshells	Miocene	Transbaikalia (Russian Federation)	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio brachydactylus*	eggshells	Miocene	Ukraine: Cherevichnoe	Burchak-Abramovich (1953); Mikhailov (1988); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio brachydactylus*	eggshells	Miocene	Unkraine: Novaya Emetovka	Burchak-Abramovich (1953); Mikhailov (1988); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio cf Kakesiensis*	eggshells	Miocene	Kenya: Kaiyumung Member	Harris and Leakey (2003); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio cf Kakesiensis*	eggshells	Miocene	Kenya: Lothagam	Harris and Leakey (2003); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio cf. brachydactylus*	eggshells	Miocene	Turkey: Çandir	Sauer (1976); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio cf. brachydactylus*	eggshells	Miocene	Turkey: Eskişchir-Akçayir	Sauer (1976); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Awasib (NNE of water hole)	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Awasib (NNE of water hole)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Awasib (West of waterhole inselberg)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Awasib (West of waterhole inselberg)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Daberas (main aeolianite)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Daberas (main aeolianite)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Daberas (near inselberg)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Daberas (near inselberg)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Diep Rivier (Namibia)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Diep Rivier (Namibia)	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Elim	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Elim	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Fiskus	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Fiskus	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Haiber Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Haiber Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Kamber cliff	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Kamber cliff	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Kolmanskop	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Kolmanskop	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Obib Gorge	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggshells	Miocene	Namibia: Obib Gorge	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Tsauchab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*	eggs	Miocene	Namibia: Tsauchab 3	Senut and Pickford (1995); Senut (2000)

Struthionidae	*Struthio daberasensis*		eggshells	Miocene	Namibia: Tsauchab 3	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*		eggs	Miocene	Namibia: West Pan	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*		eggshells	Miocene	Namibia: West Pan	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*		eggs	Miocene	Namibia: Zebra Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*		eggshells	Miocene	Namibia: Zebra Hill	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio daberasensis*		eggshells	Miocene	Namibia:Tsauchab	Senut and Pickford (1995); Senut (2000)
Struthionidae	*Struthio indeter.*	*Struthiolithus oshinensis*	eggshells	Miocene	India: India Hasnot (Siwalik)	Sahni et al. (1990); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Mongolia: Buk-A	Bibi et al. (2006); Zelenkov (2011)
Struthionidae	*Struthio indeter.*	*Struthiolithus oshinensis*	eggshells	Miocene	Mongolia: Oshin-Boro-Udzur-Ula (Oshin Formation)	Sauer (1976); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Mongolia: Shargan	Bibi et al. (2006); Zelenkov (2011)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Oman: Marsawdad Formation	Pickford et al. (2023)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Oman: Rub' Al-Khali	Pickford et al. (2023)
Struthionidae	*Struthio indeter.*	*Struthiolithus*	eggs	Miocene	Republic of Moldovia:	Mikhailov (1988); Mlíkovský (1996a and

		sarmaticus			Cherevichnoe	2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	*Struthiolithus sarmaticus*	eggs	Miocene	Republic of Moldovia: Çimislia	Mikhailov (1988); Mlíkovský (1996a and 2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Republic of Moldovia: Çimişlia	Mikhailov and Kurochkin (1988); Mlíkovský (2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	*Struthiolithus sarmaticus*	eggs	Miocene	Republic of Moldovia: Pocşeşti	Mikhailov (1988); Mlíkovský (1996a and 2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Republic of Moldovia: Varniţa	Mikhailov and Kurochkin (1988); Mlíkovský (2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	*Psammornis rothschildi*	eggshells	Miocene	Tunisia: Segui Formation (Chebket Safra)	Robinson and Wiman (1976); Buffetaut (2020)
Struthionidae	*Struthio orlovi*		eggs	Miocene	Republic of Moldovia: Cherevichnoe	Mikhailov (1988); Mlíkovský (1996a and 2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio orlovi*		eggs	Miocene	Republic of Moldovia: Çimislia	Mikhailov (1988); Mlíkovský (1996a and 2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio orlovi*		eggs	Miocene	Republic of Moldovia: Pocşeşti	Mikhailov (1988); Mlíkovský (1996a and 2002); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio sp. cf. Struthiolithus*		eggshells	Miocene	India: Dharamsala (Dhok Pathan,	Patnaik et al. (2009)

					Middle Siwaliks)	
Struthionidae	*Struthio wimani*		eggshells	Miocene	China: Shanxi and Gansu	Andersson (1923); Lowe (1931); Wang et al. (2011)
Struthionidae	*Struthio indeter.*	*Struthiolithus caucasicus*	eggshells	Miocene	Georgia: Eldar	Kurochkin and Lungu (1970); Burchak-Abramovich and Vekua (1971); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Miocene	Mongolia: Camp Margetts Iren Dabasu	Sauer (1972); Bibi et al. (2006);Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio orlovi*	*Struthiolithus oshinensis*	eggshells	Miocene	Kyrgyz Republic: lower Dzhunarakskaya Svita	Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)
Struthionidae	*Str. Dzabkhanensis*		eggshells	Miocene	Turkmenistan	Mikhailov (1988 and 1997); Mikhailov and Kurochkin (1988)

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1887 Table 6. Pliocene avian record of eggs, eggshells, and nests.

Families	**Species**	**Oospecies**	**Material**	**Epoch**	**Location**	**References**
Aepyornithidae	*Aepyornis maximus*		eggshells	Pliocene	Iberia: Gloria 4 (Teruel)	Mein and Dauphin (1995); Bravo et al. (2009); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid		eggs	Pliocene	Namibia: Gamsberg	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)

Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Gamsberg	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Gobabeb	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Gobabeb	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Nutab	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Nutab	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Pass	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aepyornithidae	Aepyornithoid	eggs	Pliocene	Namibia: Pass	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aves	*Aves indeter.*	eggshells	Pliocene	Iberia: La Puebla de Almuradiel (Toledo)	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Aves	*Aves indeter.*	eggs	Pliocene	Canary Archipelago: Valle Chico Órzolarzola Lanzarote	Sauer and Rothe (1972); García-Talavera (1990); Sánchez Marco (2010); Lazzerini et al. (2016); Mikhailov and Zelenkov (2020)
Numididae	*Numida indeter.*	eggs	Pliocene	United Republic of Tanzania: Laetoli	Harris and Leakey (2003); Harrison and Msuya (2005)

Phasianidae	*Francolinus indeter.*		eggs	Pliocene	United Republic of Tanzania: Emboremony	Harris and Leakey (2003); Harrison and Msuya (2005)
Phasianidae	*Francolinus indeter.*		eggshells	Pliocene	United Republic of Tanzania: Laetoli	Harrison (2005); Harrison and Msuya (2005)
Picidae	Picidae	*Eocavum picifactum*	nests	Pliocene	USA: Yuma, Arizona	Buchholz (1986); Benson (2000)
Struthionidae	*Struthio cf Kakesiensis*		eggshells	Pliocene	Kenya: Kanapoi	Harris and Leakey (2003); Harrison and Msuya (2005); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio oshanai*		eggshells	Pliocene	Namibia: Elim Gullies	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio oshanai*		eggshells	Pliocene	Namibia: Elim Gullies	Senut and Pickford (1995); Senut (2000); Mikhailov and Zelenkov (2020)
Struthionidae	*Str. Dzabkhanensis*		eggshells	Pliocene	Turkmenistan	Mikhailov (1988 and 1997); Mikhailov and Kurochkin (1988)
Struthionidae	*Struthioanderssoni*		eggshells	Pliocene	Ukraine: Odesa Catacombs	Mlíkovský (1996d and 2002); Mikhailov and Zelenov (2020)
Struthionidae	*Str. Kakesiensis*		eggshells	Pliocene	United Republic of Tanzania: Kakesio	Harrison, 2005; Harrison and Msuya 2005); Mikhailov and Zelenov (2020)
Struthionidae	*Str. Kakesiensis*		eggshells	Pliocene	United Republic of Tanzania: Laetoli	Harrison, 2005; Harrison and Msuya 2005); Mikhailov and Zelenov (2020)

Struthionidae	*Str. chersonensis)*	eggshells	Pliocene	Russian Federation: (Kabakova Balka locality near Krymskin Stavropol	Mikhailov (1997 and 1988); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	eggshells	Pliocene	Canary Archipelago: Fuente de Gusa (Lanzarote)	Sauer and Rothe (1972); García-Talavera (1990); (Casañas 1990)
Struthionidae	*Struthio indeter.*	eggshells	Pliocene	Canary Archipelago: Valle Chico Órzola Lanzarote	Sauer and Rothe (1972); García-Talavera (1990);Sánchez Marco (2010); Lazzerini et al. (2016); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	eggs	Pliocene	Canary Archipelago: Valle Grande Lanzarote	Sauer and Rothe (1972); García-Talavera (1990); Sánchez Marco (2010); Lazzerini et al. (2016); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	eggshells	Pliocene	Canary Archipelago: Valle Grande Lanzarote	Sauer and Rothe (1972); García-Talavera (1990);Sánchez Marco (2010); Lazzerini et al. (2016); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*	eggshells	Pliocene	Morocco: Ouarzazate	Sauer and Sauer (1978); Mikhailov and Zelenkov (2020)

Struthionidae	*Struthio linxiaensis and/or Struthio asiaticus*	*Struthioli thus dzabkhan ensis*	eggshells	Pliocene	Mongolia: Altan-Teli Formation	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio linxiaensis and/or Struthio asiaticus*	*Struthioli thus dzabkhan ensis*	eggshells	Pliocene	Mongolia: Hyargas-Nuur Formation	Mikhailov (1997); Mikhailov and Zelenkov (2020)

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1889 Table 7. Pleistocene avian record of eggs, eggshells, and nests.

Families	**Species**	**Oospecies**	**Material**	**Epoch**	**Location**	**References**
Accipitridae	Aquilinae		eggshells	Pleistocene	South Africa: Taung	Kuhn et al. (2015)
Aepyornithidae	*Aepyornis indeter.*		eggs	Pleistocene	Madagascar: Cave	Samonds et al. (2019)
Aepyornithidae	*Aepyornis indeter.*		eggshells	Pleistocene	Madagascar: Ankilitelo Cave	Samonds et al. (2019)
Aepyornithidae	*Aepyornis indeter.*		eggs	Pleistocene	Madagascar: FauxCap	Samonds et al. (2019)
Aepyornithidae	*Aepyornis indeter.*		eggshells	Pleistocene	Madagascar: FauxCap	Samonds et al. (2019)
Alcidae	Alcidae		eggs	Pleistocene	USA: Channel Islands of California of San Miguel	Guthrie et al (2000)
Alcidae	Alcidae		eggs	Pleistocene	USA: San Nicolas islands	Guthrie et al (2000)

Alcidae	*Fratercula dow*		eggs	Pleistocene	USA: The west end of San Nicolas Island (California)	Guthrie et al (2000)
Anatidae	*Cygnus sp.*		eggs	Pleistocene	Germany: Tabuch	Kahlke (1977)
Anatidae	*Anser sp.*		eggs	Pleistocene	Germany: Tabuch	Kahlke (1977)
Anatidae	*Anas sp.*		eggs	Pleistocene	Germany: Tabuch	Kahlke (1977)
Anseriformes	Anseriformes		eggshells	Pleistocene	Iberia: Atapuerca (Burgos)	Núñez-Lahuerta et al. (2021 and 2022)
Aves	*Aves indeter.*	*Incognitoolithus ramotubulus*	eggshells	Pleistocene	Germany: Weimar-Ehringsdorf	Burkhard (1968)
Aves	*Aves indeter.*		eggs	Pleistocene	USA: Lovelock (Nevada, USA)	Wetmore (1939)
Aves	*Aves indeter.*		eggshells	Pleistocene	India: Kilar Lower Karewas	Mikhailov (1988 and 1997); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)
Aves	*Aves indeter.*		eggshells	Pleistocene	India: Sombur Upper Karewas	Mikhailov (1988 and 1997); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)
Aves	*Aves indeter.*		eggshells	Pleistocene	Iberia: Atapuerca (Burgos)	Rosas et al. (2006); Marqueta et al. (2022)
Aves	*Aves indeter.*		eggs	Pleistocene	Iberia: Atapuerca (Burgos)	Rosas et al. (2006); Marqueta et al. (2022)

Casuariidae	*Dromaius indeter.*	eggshells	Pleistocene	Australia: Tunnel Cave	Oskam et al. (2010)
Charadriiformes		eggshells	Pleistocene	Iberia: Gran Dolina de Atapuerca (Burgos)	Núñez-Lahuerta et al. (2021 and 2022)
Diomedeidae	*Phoebastria albatrus*	eggs	Pleistocene	Bermuda: Cooper's Island; Yucker's Bay	Olson and Hearty (2003 and 2013); Olson et al. (2005)
Dromornithidae	*Genyornis indeter.*	eggshells	Pleistocene	Australia: Eurobilli	Oskam et al. (2010)
Dromornithidae	*Genyornis indeter.*	eggshells	Pleistocene	Australia: Popiltah	Oskam et al. (2010)
Dromornithidae	*Genyornis indeter.*	eggshells	Pleistocene	Australia	Williams (1981); Grellet-Tinner et al. (2016); Miller at al. (2017)
Dromornithidae	*Genyornis indeter.*	nests	Pleistocene	Australia: Wallaroo	Demarchi et al. (2022)
Dromornithidae	*Genyornis indeter.*	nests	Pleistocene	Australia: Wood point	Demarchi et al. (2022)
Gruidae		eggshells	Pleistocene	Iberia: Gran Dolina de Atapuerca (Burgos)	Núñez-Lahuerta et al. (2021 and 2022)
Gruidae	Gruidae	eggshells	Pleistocene	Iberia: Atapuerca (Burgos)	Núñez-Lahuerta et al. (2021 and 2022)
Megapodiidae	*Progura indeter.*	egg	Pleistocene	Australia: Dunes in Lake Menindee and Lake Mungo Western New	Williams and Rich-Vickers (1991); Williams and Rich-Vickers (1992); Grellet-Tinner (2001); Tinner et al. (2016)

				South Wales	
Megapodiidae	*Progura indeter.*	egggshells	Pleistocene	Australia: Dunes in Lake Menindee and Lake Mungo Western New South Wales	Williams and Rich-Vickers (1991); Williams and Rich-Vickers (1992); Grellet-Tinner (2001); Tinner et al. (2016)
Megapodiidae	*Progura indeter.*	egg	Pleistocene	Australia: Scott River south-eastern Western Australia;	Williams and Rich-Vickers (1991); Williams and Rich-Vickers (1992); Grellet-Tinner (2001); Tinner et al. (2016)
Megapodiidae	*Progura indeter.*	egggshells	Pleistocene	Australia: Scott River south-eastern Western Australia;	Williams and Rich-Vickers (1991); Williams and Rich-Vickers (1992); Grellet-Tinner (2001); Tinner et al. (2016)
Numididae	Numidinae	eggshells	Pleistocene	South Africa: Taung	Kuhn et al. (2015)
Pelecanidae	*Pelecanus occidentalis*	eggs	Pleistocene	Bermuda: Cooper's Island; Yucker's Bay	Olson and Hearty (2003 and 2013); Olson et al. (2005)
Phoenicopteridae	*Phoenicon ais minor*	eggs	Pleistocene	Kenya: Bogoria and Magadi basins	Scott et al. (2012)
Phoenicopteridae	*Phoenicon ais minor*	eggshells	Pleistocene	Kenya: Bogoria and	Scott et al. (2012)

				Magadi basins	
Phoenicopteridae	Phoenicopteridae	eggs	Pleistocene	Mexico: International Airport 'Felipe Angeles', Santa Lucía	Cruz et al. (2023)
Procellariidae	*Pterodroma cahow*	eggshells	Pleistocene	Bermuda: Bermuda eolianite deposits	Lewis (1928); Olson et al. (2005)
Procellariidae	*Pterodroma cahow*	eggshells	Pleistocene	Bermuda: Cooper's Island; Yucker's Bay	Olson and Hearty (2003 and 2013); Olson et al. (2005)
Procellariidae	*Puffinus indeter.*	eggs	Pleistocene	Canary Archipelago: La Graciosa	Lazzerini et al. (2016)
Procellariidae	*Puffinus indeter.*	eggshells	Pleistocene	Canary Archipelago: La Graciosa	Lazzerini et al. (2016)
Rheidae	*Rhea americana*	eggshells	Pleistocene	Argentina	Giardina et al. (2015)
Rheidae	*Rhea americana*	eggshells	Pleistocene	Argentina	Giardina et al. (2015)
Spheniscidae	*Eudyptula minor*	eggs	Pleistocene	New Zealand: Wanbrow	Worthy et al. (2003); Ksepka (2011)
Strigidae	*Bubo indeter.*	eggshells	Pleistocene	South Africa: Taung	Kuhn et al. (2015)
Strigopidae	*Strigops Habroptilus*	eggs	Pleistocene	New Zealand: Gibraltar Rock; Sawer's	Boast (2020)

					Rockshelter	
Strigopidae	*Strigops Habroptilus*		eggshells	Pleistocene	New Zealand: Gibraltar Rock; Sawer's Rockshelter	Boast (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia:Tuwairifa Umm al Qurun (II)	Lowe (1933); Buffetaut (2020);Mikhailov and Zelenov (2020)
Struthionidae	*Struthio anderssoni*	*Struthiolithus anderssoni*	eggs	Pleistocene	China	Lowe and Bate (1931); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio anderssoni*	*Struthiolithus anderssoni*	eggshells	Pleistocene	China	Lowe and Bate (1931); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*	*Struthiolithus anderssoni*	eggs	Pleistocene	China: loess of northern China	Andersson (1923); Lowe (1931); Young (1933 and 1960); Wang et al. (2011); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*	*Struthiolithus anderssoni*	eggshells	Pleistocene	China: loess of northern China	Andersson (1923); Lowe (1931); Young (1933 and 1960); Wang et al. (2011);Mikhailov and Zelenov (2020)
Struthionidae	*Struthio camelus*		eggshells	Pleistocene	India: Gujarat	Sanhi et al. (1989;Mikhailov and Zelenov (2020))
Struthionidae	*Struthio molybdophanes*	*Struthiolithus indicus*	eggshells	Pleistocene	India: ChandresalKota (Rajasthan)	Mikhailov (1997); Mikhailov and Zelenov (2020);Mikhailov and Zelenov (2020)

Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	India: Katoati, Rajasthan	Blinkhorn et al. (2015);(Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	India: Naliya Kachchh	Mohabey (1989); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio molybdophanes*	*Struthiolithus indicus*	eggshells	Pleistocene	India: Viri village (Anjar Kachchh)	Mikhailov (1997); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio transcaucasicus*		eggshells	Pleistocene	Kazakhstan	Mikhailov (1997); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Libya: El Greifa Complex Wadi el Adjal (near Ubari)	Mikhailov and Zelenov (2020)
Struthionidae	*Struthio daberasensis*	*Struthiolithus oosps.*	eggshells	Pleistocene	Malawi: Lake Malawi	Stidham (2004); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio daberasensis*	*Struthiolithus oosps.*	eggshells	Pleistocene	Malawi: Mwimbi	Stidham (2004); Mikhailov and Zelenkov (2020)
Struthionidae	*Psammornis rothschildi*		eggshells	Pleistocene	Mauritania: Aguerguerian	Tessier et al. (1971); Buffetaut (2020)
Struthionidae	*Struthio camelus molybdophanes*		eggshells	Pleistocene	United Republic of Tanzania: Lake Manyara	Harris and Leakey (2003); Harrison and Msuya (2005); Mikhailov and Zelenov (2020)
Struthionidae	*Psammornis rothschildi indeter.*		eggshells	Pleistocene	United Republic of Tanzania: Oldaway (Tanganyi	Lowe (1933); Tyrberg (2008); Mikhailov and Zelenov (2020)

					ca Territory)	
Struthionidae	*Struthio oldawayi*		eggshells	Pleistocene	United Republic of Tanzania: Oldaway (Tanganyica Territory)	Lowe (1933); Tyrberg (2008); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*	*Struthiolithus chersonensis*	eggshells	Pleistocene	Russian Federation: Transbaikalia	Mikhailov (1997); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: ‘Ain Sala	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Abu Sabbau	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Bani Ma’ridth	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Bani Ma’ridth	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Edge of Qua’amiyat	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio indeter.*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Shuqqat al Khalfat	Lowe (1933); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia:	Lowe (1933); Buffetaut (2020)

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Struthionidae	*Struthio camelus syriacus*	*Psanormis* oosps.	eggshells	Pleistocene	Saudi Arabia: Umm Tina	Lowe (1933); Buffetaut (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Baian-Dzak (Omnogov)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Naran-Bulak (Omnogov),	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Ongon (Sukhebator)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Tsagaan Aguii Cave (Gobian Altai)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Tugrikijn-Us (Omnogov)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio transcaucasicus*		eggshells	Pleistocene	Kazakhstan	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio asiaticus*		eggshells	Pleistocene	Transbaikalia	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio asiaticus*		eggshells	Pleistocene	Transbaikalia	Mikhailov (1997); Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Baian-Dzak	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)

					(Omnogov)	
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Naran-Bulak (Omnogov),	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Ongon (Sukhebator)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Tsagaan Aguii Cave (Gobian Altai)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struthio indeter.*		eggshells	Pleistocene	Mongolia: Tugrikijn-Us (Omnogov)	Mikhailov and Kurochkin (1988); (Mikhailov and Zelenkov (2020)
Struthionidae	*Struhio indeter.*	*Psammornis rothschildi rothschildi*	eggshells	Pleistocene	Algeria: Kachba	Mikhailov and Kurochkin (1988); Mlíkovský (2003); Buffetaut (2022)
Struthionidae	*Struhio indeter.*	*Psammornis rothschildi rothschildi*	eggshells	Pleistocene	Algeria: Mokrani	Mikhailov and Kurochkin (1988); Mlíkovský (2003); Buffetaut (2022)
Struthionidae	*Struhio indeter.*		eggshells	Pleistocene	Libya: Libyan Cyrenaica	Mikhailov and Kurochkin (1988); Mlíkovský (2003); Mikhailov and Zelenkov (2020)
Struthionidae	*PachyStruthio pannonicus*		eggshells	Pleistocene	Hungary: Kisláng	Mikhailov (1988 and 1997); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)

Struthionidae	*Struthio chersonensis*		eggshells	Pleistocene	Ukraine: Snigirevka	Mlíkovský (1996d and 2002); Mikhailov and Zelenov (2020)
Struthionidae	*Str. Chersonensis*		eggshells	Pleistocene	Russian Federation: Malinowka (Kherson region)	Mikhailov (1997 and 1988); Mikhailov and Kurochkin (1988); Mikhailov and Zelenkov (2020)

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1899 Table 8. Holocene avian record of eggs, eggshells, and nests.

Families	**Species**	**Oospecies**	**Material**	**Epoch**	**Location**	**References**
Aepyornithidae	*Aepyornis indeter.*		Egg/skeleton	Holocene	Madagascar	Balanoff and Rowe (2007)
Aepyornithidae	*Aepyornis indeter.*		eggshells	Holocene	Madagascar: Meandrare Estuary	Oskam et al. (2010)
Aepyornithidae	*Aepyornis indeter.*		eggs	Holocene	Madagascar: Ankilitelo Cave	Goodman et al. (2013)

Aepyornithidae	*Aepyornis indeter.*	eggshells	Holocene	Madagascar: Ankilitelo Cave	Goodman et al. (2013);
Aepyornithidae	*Aepyornis indeter.*	eggs	Holocene	Madagascar: Meandrare Estuary	Oskam et al. (2010)
Aepyornithidae	*Mullerornis indeter.*	eggs	Holocene	Madagascar: North and South	Grealy et al. (2023)
Aepyornithidae	*Aepyornis indeter.*	eggshells	Holocene	Madagascar: North and South	Grealy et al. (2023)
Aepyornithidae	*Mullerornis indeter.*	eggs	Holocene	Madagascar: Talaky	Grealy et al. (2023)
Aepyornithidae	*Aepyornis indeter.*	eggshells	Holocene	Madagascar: Talaky	Grealy et al. (2023)
Aepyornithidae	*Aepyornis indeter.*	eggshells	Holocene	Madagascar	Grealy et al. (2017)
Anatidae	*Tadorna variegata*	eggs	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Anatidae	*Tadorna variegata*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Aves	*Aves indeter.*	eggshells	Holocene	New Zealand: Hukanui (South Island)	Oskam et al. (2010)
Aves	*Aves indeter.*	eggshells	Holocene	New Zealand: Hukanui Pool (South Island)	Oskam et al. (2010)
Aves	*Aves indeter.*	eggshells	Holocene	New Zealand: Rosslea	Oskam et al. (2010)

				(South Island)	
Aves	*Aves indeter.*	eggshells	Holocene	Australia: Tallering Hill	Oskam et al. (2010)
Casuariidae	*Dromaius indeter.*	eggshells	Holocene	Australia: Witchcliffe Rock Shelter	Oskam et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: Castlepoint	Huynen et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: Gisborne	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Glendhu Bay	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Glenmark	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Hamiltons	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Kapua Swamp	Oskam et al. (2010); Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Karamea	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Mt Cookson	Huynen et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: North Cape	Huynen et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: Ocean Beach	Huynen et al. (2010)

Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Pleasant River	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Pyramid Valley (South Island)	Oskam et al. (2010); Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Takata	Huynen et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: Tokerau Beach	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: West Coast	Huynen et al. (2010)
Dinornithidae	*Dinornis novaezealandiae*	eggshells	Holocene	New Zealand: Whananaki	Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand: Whanganui inlet	Oskam et al. (2010); Huynen et al. (2010)
Dinornithidae	*Dinornis robustus*	eggshells	Holocene	New Zealand:Roxburgh Gorge	Huynen et al. (2010)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Alexandra South Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Awamoa, Otago	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Chatto	Gill (2000 and 2022)

				Greek, Otago	
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Clutha river, Otago	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Ettrick, Otago	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Kaiiwi Wanganui, North Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis maximus*	eggs	Holocene	New Zealand: Kaikoura Marlborough South Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Omakau, Otago	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Otago Central	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Otago North	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Poolburn, South Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis robustus*	eggs	Holocene	New Zealand: Pyramid Valley, Cantebury, South Island	Gill (2000 and 2022)

Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Shag River, Otago	Gill (2000 and 2022)
Dinornithidae	*Dinornis maximus*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Tokerau Beach, North Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Tokerau Beach, North Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Tukituki River in Hawkes Bay, North Island	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Pounawea (South Island)	Oskam et al. (2010)
Dinornithidae	Dinornithiformes	eggshells	Holocene	New Zealand: Karikari Peninsula	Gill (2000 and 2022)
Dinornithidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Wairau River in Marlborough South Island	Gill (2000 and 2022)

Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Blackhead	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Castle Point	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggs	Holocene	New Zealand: Central Otago	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Dannevirke	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggshells	Holocene	New Zealand: Geraldine	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Gisborne	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Haurangi	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Havelock North	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Hebertville	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Hukanui	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Matai Bay	Huynen et al. (2010)
Emeidae	*Pachyornis geranoides*	eggshells	Holocene	New Zealand: North Cape	Huynen et al. (2010)

Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: North Cape	Huynen et al. (2010)
Emeidae	*Emeus crassus*	eggshells	Holocene	New Zealand: Oamaru	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Oamaru	Huynen et al. (2010)
Emeidae	*Pachyornis geranoides*	eggshells	Holocene	New Zealand: Ocean Beach	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Ocean Beach	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Otago	Huynen et al. (2010)
Emeidae	*Pachyornis geranoides*	eggshells	Holocene	New Zealand: Tokerau Beach	Huynen et al. (2010)
Emeidae	*Euryapteryx indeter.*	eggshells	Holocene	New Zealand: Tokerau Beach	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Unknown	Huynen et al. (2010)
Emeidae	*Anomalopteryx didiformis*	eggs	Holocene	New Zealand: Waitomo	Huynen et al. (2010)
Emeidae	*Pachyornis indeter.*	eggs	Holocene	New Zealand: Cromwell Otago South Island	Gill (2000 and 2022)

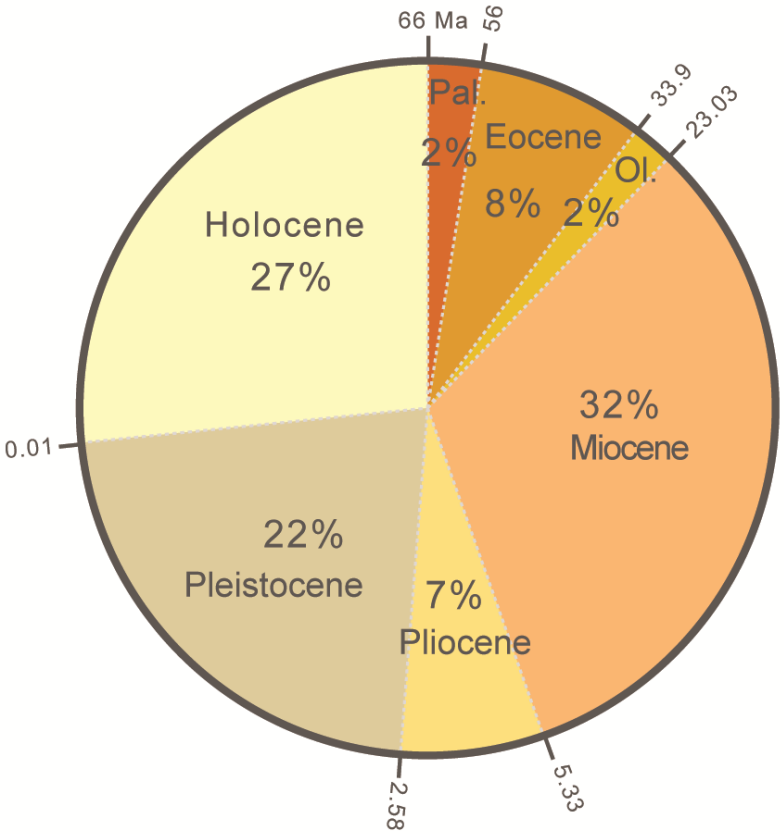
Emeidae	*Emeus crassus*	eggs	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Emeidae	*Pachyornis indeter.*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Emeidae	*Emeus indeter.*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Emeidae	*Emeus crassus;*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Emeidae	*Dinornis indeter.*	eggshells	Holocene	New Zealand: Redcliffs (South Island)	Oskam et al. (2010)
Gruidae	*Grus canadensis*	eggs	Holocene	Mexico: Lago de Texcoco	Martin del Campo (1944); Corona (2002 and 2009)
Megalapterygidae	*Megalapteryx didinus*	eggs	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Megalapterygidae	*Megalapteryx didinus*	eggs	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Megalapterygidae	*Megalapteryx didinus*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)
Megalapterygidae	*Megalapteryx indeter.*	eggshells	Holocene	New Zealand: Southwest of Timaru	Worthy (1997)

Phoenicopteridae	*Phoenicona is minor*	eggs	Holocene	Kenya: Bogoria and Magadi basins	Scott et al. (2012)
Phoenicopteridae	*Phoenicona is minor*	eggshells	Holocene	Kenya: Bogoria and Magadi basins	Scott et al. (2012)
Phoenicopteridae	*Phoenicona is minor*	nests	Holocene	Kenya: Lake Bogoria at Sandai delta	Scott et al. (2012)
Phoenicopteridae	*Phoenicona is minor*	nests	Holocene	Kenya: Lake Bogoria at Sandai delta	Scott et al. (2012)
Rheidae	*Pterocnemia pennata*	eggshells	Holocene	Argentina: Arroyo Talainín 2 (Provincia de Córdoba)	Apolinaire et al. (2010); medina et al. (2011); Medina et al. (2018)
Rheidae	*Rhea americana*	eggshells	Holocene	Argentina: Arroyo Talainín 2 (Provincia de Córdoba)	Apolinaire et al. (2010); medina et al. (2011); Medina et al. (2018)
Rheidae	*Rhea americana*	eggshells	Holocene	Argentina: Boyo Paso 2 (Sierras of Córdoba, Argentina)	Medina et al. (2011)
Spheniscidae	*Pygoscelis adeliae*	eggshells	Holocene	Antarctica: Dunlop Island	Miller et al. (2012); Yang et al. (2021); Gao et al. (2022); Emslie and Patterson (2007)
Spheniscidae	*Pygoscelis adeliae*	eggshells	Holocene	Antarctica: Scott Coast	Miller et al. (2012); Yang et al. (2021); Gao et al. (2022); Emslie and Patterson (2007)
Struthionidae	*Struthio indeter.?*	eggshells	Holocene	Argentina: Cañada Rocha y Arroyo Corro	Ameghino and Torcelli (1915)

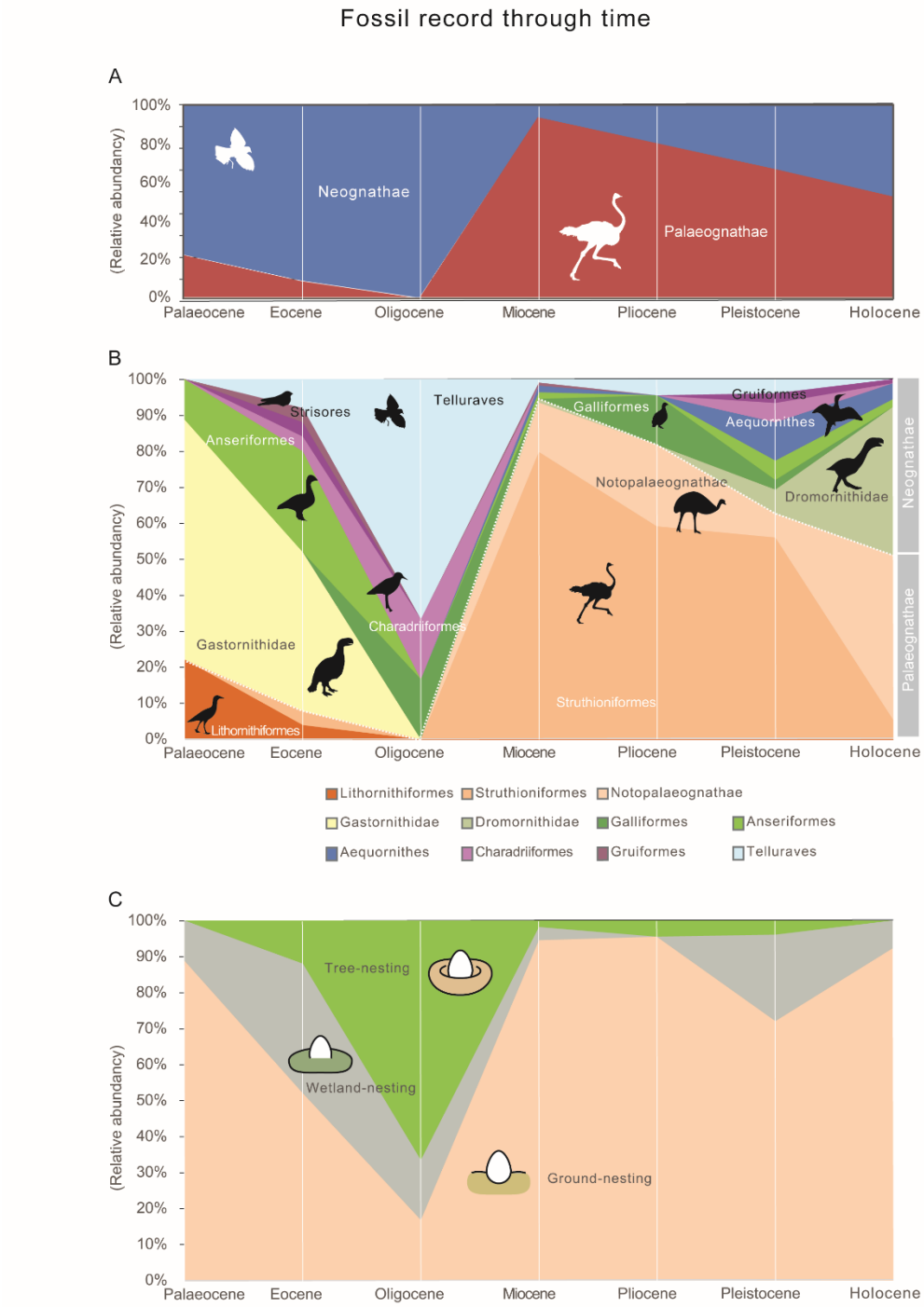
Struthionidae	*Struthio transcaucasicus*	eggshells	Holocene	Kazakhstan	Mikhailov (1997); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio asiaticus*	eggshells	Holocene	Russian Federation: Transbaikalia	Mikhailov (1997); Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*	eggs	Holocene	China	Janz et al. (2015);Mikhailov and Zelenov (2020)
Struthionidae	*Struthio indeter.*	eggs	Holocene	Mongolia	Janz et al. (2015);Mikhailov and Zelenov (2020)

1900

Figure 1. Percentage contribution to the whole record; Pl.=Pliocene; Ol=Oligocene; Ma=million years ago.

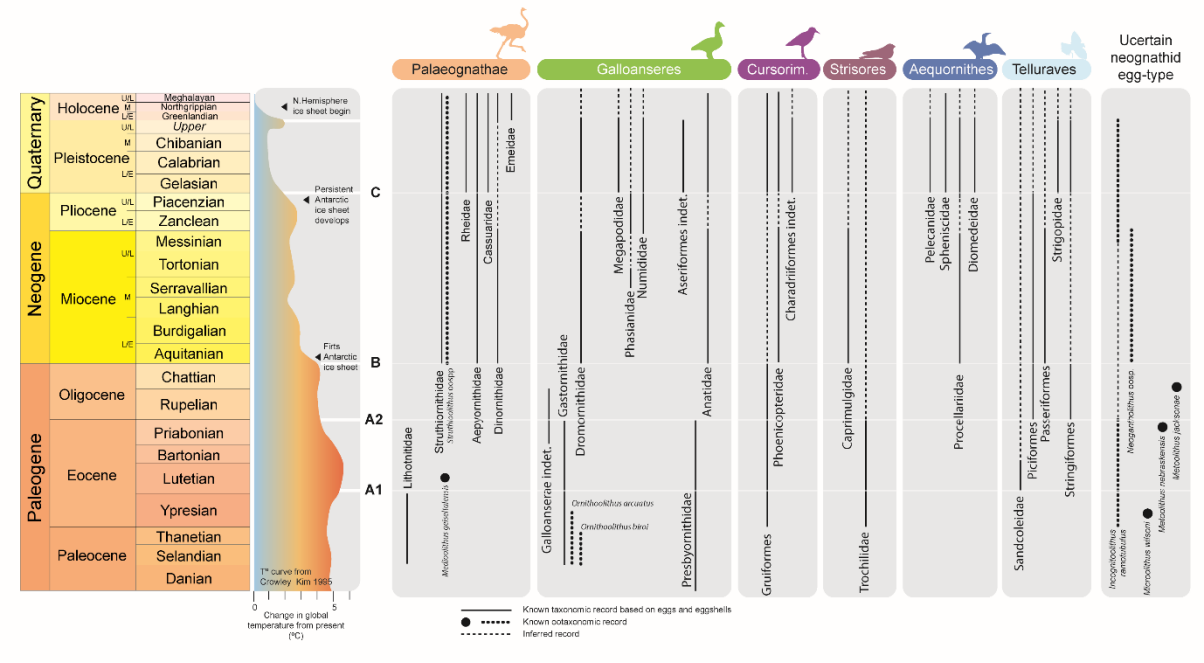


1909 Figure 2. The Cenozoic fossil record of avian eggs, eggshells, and nests through
1910 time. A. Relative abundance of Infraclasses. B. Relative abundance of clades. C.
1911 Relative abundance of nest types.



1912

Figure 3. Chronostratigraphic record of main avian groups based on the oological record and the major events involving change on faunal assemblage and their correlation with global climatic trends



Events:

A1 & A2: Demise of basal groups – lithornithid palaeognathids, and gastornithid and presbyornithid galloanserans / Appearance (A1) and diversification (A2) of early Telluravaves.

B: Appearance of new groups – several lineages of palaeognathids and galloanserans, first Aequornithes and Caprimulgidae (Strisores).

C: Diversification of previous groups – mainly notopalaeognathids, Galliformes, and Aequornithes / Appearance of Charadriiformes.