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The enigmatic fossil bird eggs of Lanzarote (Canary Islands): review and perspectives

Running title fossil bird eggs of Lanzarote

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Abstract Large ostrich-like eggs of about 16 cm length were found at three places in a fossil, four Mio. years old Pliocene sand layer in the north of Lanzarote (Canary Islands). Taxonomic identification is still under debate. Derivation from an ostrich-like palaeognath is questionable, because no land bridge between Africa and Lanzarote ever existed. An alternative hypothesis declaring an extinct large odontopterygian seabird having used the fossil habitat as its breeding site was not substantiated by isotope analysis. It revealed that the egg laying bird was a terrestrial-feeding one. Alternatively, as in other isolated oceanic islands gigantism and flightlessness could have evolved in a yet unknown neognath flighted ancestor belonging to a completely different taxonomic group, taking profit out of the herbivory niche open due to the absence of mammal competition.

Resumen Se encontraron huevos grandes similares a los de avestruz, de unos 16 cm de longitud, en tres lugares de una capa de arena del Plioceno, con una antigüedad de cuatro millones de años, en el norte de Lanzarote (Islas Canarias). La clasificación taxonómica sigue siendo objeto de debate. La derivación de un paleognato similar al avestruz es cuestionable, ya que nunca existió un puente terrestre entre África y Lanzarote. Una hipótesis alternativa que afirmaba que una gran ave marina odontopterigia extinta había utilizado el hábitat fósil como lugar de reproducción no fue corroborada por el análisis

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isotópico. Este reveló que el ave que ponía los huevos era una ave terrestre. Alternativamente, al igual que en otras islas oceánicas aisladas, el gigantismo y la incapacidad de volar podrían haber evolucionado en un antepasado neognato volador aún desconocido perteneciente a un grupo taxonómico completamente diferente, aprovechando el nicho herbívoro abierto debido a la ausencia de competencia de los mamíferos.

Introduction

Large fossil eggs with a longitudinal diameter of about 16 cm have been discovered in Lanzarote (García-Talavera 1990). This discovery initially led to two conclusions (Fig. 1): Firstly, based on the shell structure, the eggs were attributed to a flightless ostrich-like bird and secondly this record seemed to substantiate the geological hypothesis that between Africa and Lanzarote a land bridge had previously existed (Rothe 1964, Sauer & Rothe 1972). However, recent geological studies show that such a connection never existed (Zaczek et al. 2015). Thus, the origin and interpretation of the eggs is still under debate. The theories range from a questionable arrival of ostriches in Lanzarote on rafts consisting of plant and tree material washed into the sea from African rivers, as is well known from lizards, snakes, and tortoises, but questionable in the case of such a large bird, to being the eggs of a fossil large seabird breeding on the island (Sánchez-Marco et al. 2025, García-Talavera 1990). In this article, the current state of knowledge is reviewed and a third alternative is proposed.

Fig. 1 The enigmatic bird egg from Lanzarote in comparison to that of a chicken (Photo: Ulrike Strecker).

Location of the eggs in Lanzarote

The eggs were discovered at three sites, two on the north-eastern and the third on the north-western edge of the Famara massif in the north of Lanzarote, near the village of Órzola (Fig. 2). In one place, they were found lying very close together, indicating their position within a nest (García Talavera 1990). The fossils are enclosed by a layer of bioclastic calcarenite up to 6 m thick. The location is about 20 to 50 metres above present-day

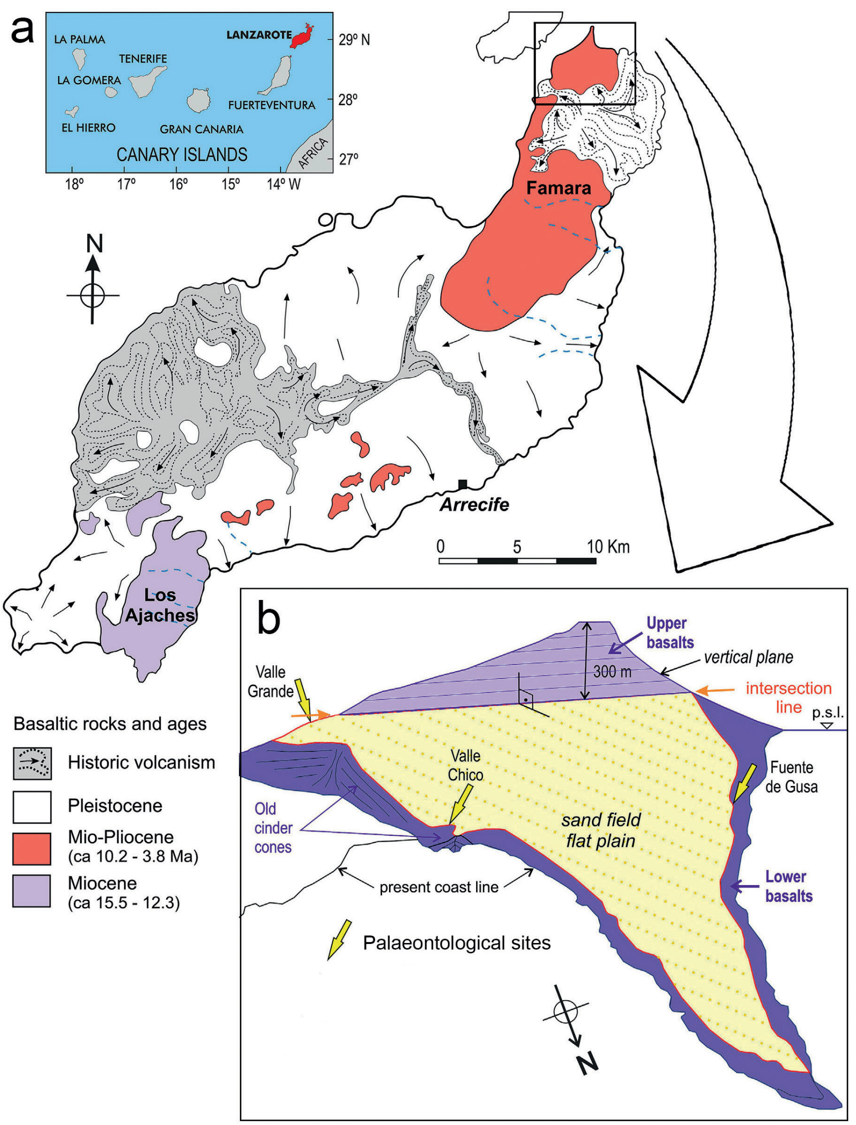

Fig. 2 a) Geology of Lanzarote and position of the fossil sand plain in the North of the island; b) Reconstruction of the fossil sand plain; overlying basalts shown in schematic vertical section at top of drawing (p. s. l. = present sea level; adapted from Lomoschitz et al. 2016; ages from Coello et al. 1992). Please spun b) around to have the same orientation.

sea level (Lomoschitz et al. 2016). Potassium-argon dating (K/Ar ages) of the fossiliferous deposits range between ca. 4.3 and 3.6 million years (Lomoschitz et al. 2016). They consist of carbonate sands that had emerged from shells, skeletons and cuttle bones of marine animal species that had been broken up by the surf. It was driven inland from the former beach by the northeast trade winds and accumulated here on the volcanic underground. Later volcanism covered the fossiliferous layer with lava flows up to 300 metres thickness.

The current extent of the fossiliferous layer, on the eroded edge of which the Valle Grande, Valle Chico and Fuente de Gusa sites are located, is at least 16 km². It probably originally extended between 25 and 100 km² further northward, but was eroded and reduced in size over time by the surf (Lomoschitz et al. 2016). The fossilised beach, as the place of origin of the sand building this habitat therefore no longer exists. In addition to the eggs, the shells of four extinct land snail species *(Leptaxis orzolae, Canariella orzolae, Pupoides orzolae, Theba orzolae)*, eggshells of a large turtle, a back vertebra of a snake from the boa family (Boidae), a large undetermined bone fragment, and great numbers of breeding chambers of solitary bees were also found (Gittenberger & Ripken 1985, García-Talavera 1990, Barahona et al. 1998, Lomoschitz et al. 2016). The ancient landscape probably had a semi-open character. It may have been very similar to the recent El Jable semi-desert in the north of Lanzarote, which also consists of marine carbonate sand blown in from the beach by the trade winds. Even the snail genus *Theba* and countless fossilised breeding chambers of extinct solitary bees are present (Fig. 3). As concerns the bird species today inhabiting El Jable, they are steppe birds, the up to 0.75 m tall hubara bustard *(Chlamydotis undulata fuertaventurae)* being the largest in size (Wilkens et al. 2025).

Discussion of current hypotheses

As mentioned before the large eggs in Lanzarote were attributed, based on the shell structure, to flat-breasted birds, the ratites. These are palaeognathous birds, which include the ostriches (*Struthio spp.*, Africa), the extinct moas (e. g. *Dinornis* spp.) and the kiwis (*Apteryx* spp., New Zealand), the nandu (*Rhea americana,* South America), the emu (*Dromaius novahollandiae,* Australia), the cassowaries (*Casuarius* spp., Australia and New Guinea), the extinct elephant birds (*Aepyornis* spp., *Mullerornis* spp., Madagascar), and the volant tinamous birds from South America.

Molecular genetic studies have revealed that the flightless palaeognathous ratite birds are paraphyletic rather than monophyletic and that the flying tinamous birds from South America are deeply nested within paleognaths and appear as the sister taxon of moas (Phillips et al. 2010, Mitchell et al. 2014). The recognition of ratite paraphyly, coupled with phylogenomic time trees indicating an origin of palaeognaths long after the Gondwanian breakup makes the vicariance hypothesis explaining their recent distribution untenable. Instead, present-day palaeognath biogeography must be the product of dispersal of able-to-fly ancestors preceding independent origins of flightlessness and gigantism (Mitchell et al. 2014, Widrig & Field 2022).

The eggshells were primarily recognized as remains of Miocene to Pliocene ostriches because of their structure (Rothe 1964, Sauer 1972, Sauer & Rothe 1972). Their thickness ranges between 2 and 3 mm. The shape of the pore openings of the eggshells was described as circular struthioid (similar to the African ostrich, *Struthio c. camelus*) and slit-like aepyornithoid (similar to an extinct elephant bird *Aepyornis* sp.). It was left open, whether the eggs were assumed to belong to two species, possibly from different geological periods. The assumption of the co-existence of two large bird species on Lanzarote was rejected because the island possibly was too small in area (García-Talavera 1990).

However, differences based on pore structure have become questionable as a means of species determination. The struthionid and aepyornithid pore patterns, established by Sauer (1972) for the pore system in ratite eggshells, are suggested to be an adaptive response to environmental factors like climate or aridity and thus are not diagnostic for the identification (Mikhailov 1992). In some ratite species, the two different pore types represent just different parts of the egg (Bibi et al. 2006, Choi et al. 2023).

The struthioform birds evolved into the modern, two-toed ostriches in the steppes of Central Asia and first occurred in Africa about 20 million years ago (Mikhailov & Zelenkov

Fig. 3 Breeding chambers of extinct solitary bees in the recently existing semidesert El Jable in Lanzarote (Photo: Ulrike Strecker).

2020, Mayr & Zelenkov 2021). This time range matches with the possibility of an ostrich like bird living on the island. However, as mentioned before, the assumption that the fossilised eggs would belong to a flightless ratite having reached Lanzarote by using a permanent land connection or a chain of volcanoes existing at that time between Lanzarote and Africa is no longer valid. It is geologically certain that there was never such a land connection between Africa and Lanzarote (Zaczek et al. 2015, Schmincke & Sumita 2010, Tomasi et al. 2023).

Thus, the question remains, to which bird species the fossil eggs belong. The volant palaeognath tinamous from South America, which are possible candidates, are considered out of question, because they are no long distance flyers (Widrig & Field 2022). Apart from tinamous, the only other palaeognathous birds that are known to have been volant are the extinct palaeognath Lithorniformes known from the Palaeocene (66 – 56 Mio. years) and Eocene (56 – 34 Mio years) of Europe and North America (Mayr 2009, 2017, Torres et al. 2020, Widrig & Field 2022). They appear to represent the oldest and most stemward known total-clade palaeognaths. They may provide the best candidates of the dispersive ancestral palaeognaths that gave rise to extant palaeognath diversity (Widrig & Field 2022. However, Lanzarote is a geologically young island, having risen out of the sea some 15 Mio. years ago, too late for a lithorniforme species to be the ancestor.

Alternatively, García-Talavera (1990) discussed the possibility that the eggs might belong to an extinct pseudotooth or bony-toothed bird (Pelagornithidae, Odontopterygiformes), the largest seabirds that ever existed with a wingspan of up to 6 m (Mayr & Rubilar-Rogers 2010). Like albatrosses, they might permanently have flown over the oceans – enabled by dynamic sailing – and only landed on islands to lay eggs and breed. The localisation of the fossil eggs and thus the probable breeding ground and nests on fossil dunes in the extreme north of Lanzarote could suggest that this place was particularly suitable for these birds to breed. Here the strong northeast trade wind, blowing almost constantly from the open ocean, might have provided the necessary updraft for these giant birds to take off again. Still today, a large number of seabird species seek out the Canary Islands to breed on every year.

This hypothesis, though, is not supported by the ratite structure of the eggshell (Sauer & Rothe 1972). However, although in principle the eggshell of flightless ratite palaeognaths in its basic biocrystalline structure and external morphology was characterised as well distinguishable from that of any family of large neognathous birds (Mikhailov 1997, Kohring 1999, Mikhailov & Zelenkov 2020), the identification of fossil eggshell types is not always straightforward, because a ratite-like eggshell morphotype is also found in some neognathous bird taxa, such as Cuculiformes and Piciformes (Hirsch et al. 1997). Furthermore, in thick eggshells of some neognathous birds like the genera *Anser, Cygnus* and *Aptenodytes,* the ratite like features can be seen (Mikhailov 1992). A ratite-like eggshell microstructure also occurred in the Eocene *Ornitholithus*-type eggshell, which is considered to stem from the neognathous anseriform Gastornithidae (Mikhailov 1991). Thus, more detailed microstructural and crystallographic approaches, which seem to provide a better basis for identifying palaeognath eggshells (Choi et al. 2023), are needed for the enigmatic eggs found in Lanzarote.

The hypothesis of a large seabird laying the eggs is also questionable by another observation. A comparative study of the composition of oxygen and carbon isotopes of the eggshells of two extinct fossil shearwater species *(Puffinus holeae, P. olsoni)* from Lanzarote and the extant Atlantic shearwater *(P. puffinus)* with those of the enigmatic large bird from Lanzarote does not support the assumption of García-Talavera (1990). Both $\delta^{13}C_{calc}$ and $\delta^{18}O_{calc}$ values of *Puffinus* eggshells point to a semi-aquatic marine bird ingesting mostly seawater, whereas low $\delta^{13}C_{calc}$ and high $\delta^{18}O_{calc}$ values of eggshells from the Pliocene giant bird suggest a terrestrial lifestyle (Lazzerini et al. 2016, Schaffner & Swart 1991).

Under the current state of knowledge, another alternative solution should not be disregarded: Here I propose that a completely different neognath able to fly bird species might have reached Lanzarote and that gigantism and flightlessness have only evolved after arriving on the island. Many examples for this exist on other isolated oceanic islands (Maderspacher 2022, Wright et al. 2016).

The Canary Islands provide several examples of gigantism. Among the reptiles, giant tortoises *(Centrochelys burchardi)* up to 1 metre in size once existed on Tenerife from the Middle Pleistocene, ca. 670,000 to 200,000 years before present (ybp), as well as in Gran Canaria *(C. vulcanica)* in the late Pliocene ca. 4 million ybp (Hutterer et al. 1997, Rhodin et al. 2015). The discovery of fossil eggshells from the Pliocene indicates the presence of other, undescribed large tortoises on Lanzarote and Fuerteventura (García-Talavera 1990, Hutterer et al. 1997, Lomoschitz et al. 2016). A giant, more than 1.5 metres long lizard *(Gallotia goliath)* only became extinct in Tenerife in the 15th century (Castillo et al. 1994).

The development of gigantism relies on several factors: An important one is that not all species of the adjoining continental ecosystems are able to reach isolated islands. Due to this, “ecological vacua” exist here and various niches remain open. Such an interpretation was in principle also applied for the initial evolution of flightless ratites beginning in the ecological vacuum after the Cretaceous-Paleogene (K-Pg) mass extinction event and the extinction of the dinosaurs (Mitchell et al. 2014). At that time, most mammals appear to have remained relatively small, potentially providing a window of opportunity for the evolution of large flightless herbivores.

This scenario also applies to the occurrence of mammals in the Canary Islands. Except for the ancestral forms of an extinct small rodent *(Malpaisomys insularis)* and an extant little shrew *(Crocidura canariensis),* no other mammal species reached Lanzarote and its neighbouring island Fuerteventura (Hutterer et al. 1987, 1988). Thus, there were open niches, because large herbivores usually are mammals. The ancestral bird could potentially profit from this missing competition for food and evolve to large size.

Another important factor is that the number of mammalian predators is lower. In general, on smaller islands with fewer predators, birds exhibit shifts in investment from forelimbs to hind limbs and tend to evolve on a trajectory toward flightlessness, even if most remain volant (Wright et al. 2016). Such species are preadapted to reduce their wings entirely in the case where mammalian predators are missing completely, because rapid escape is no longer necessary. The wings including the ordinary feather structure become entirely functionless – comparable to eyes and dark pigmentation in cave animals living in constant darkness (Wilkens & Strecker 2017). Under such conditions, the wings are submitted to regressive evolution. This process is driven by mutation pressure because under relaxed selection negative mutations may accumulate as proven by the variability of vestigial structures (Wilkens 2021, 2023, Wilkens & Strecker 2017). For example, studies of the flightless Emu *(Dromaius novaehollandiae)* revealed variability of the number, size, and structure of wing muscles, of origin and insertion sites, number of heads, as well as presence-absence variation, dramatically exceeding that found in flying birds (Maxwell & Larsson 2007). Also in most individuals of the Brown Kiwi *(Apteryx mantelli),* in which the wings consist of a single functional digit, the degree of intraspecific variability, both in the overlying musculature as well as in the skeleton itself, is immense (McGowan 1982).

It has been argued that Lanzarote might have been too small in area for the evolution of a large ground dwelling bird. However, on the one hand at least the sandy plain, in which the eggs were found, was originally much larger and extended between 25 and 100 km^2 further northward, but was eroded and reduced in size over time by the surf (Lomoschitz et al. 2016). On the other hand, during geological history the extent of the whole island sometimes became larger, when the sea level was lower, and the coastal shelves turned into firm land and even a terrestrial connection to Fuerteventura arose (Perez-Torrado et al. 2022, Rijsdijk et al. 2014).

In summary, it is proposed that the ancestral species of the large bird of Lanzarote might have been a flying neognath bird, which became large and flightless once being on the island.

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