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Fossil avian eggs from the Palaeogene of southern France: new size estimates and a possible taxonomic identification of the egg-layer

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Abstract – Eggshell fragments attributed to large birds have been known from the Palaeogene of southern France for half a century, but reconstructing their original dimensions and identifying the birds that laid the eggs has been fraught with difficulties. On the basis of numerous newly collected specimens and using geometrical calculations, the original size of the thick-shelled eggs is reconstructed, showing that they were slightly larger than ostrich eggs, with a greatest length of 17.8 cm and a mean diameter of 12.0 cm in transversal section. The estimated volume is 1330.4 cm^3. The fossil eggs from southern France are thus among the largest known avian eggs, being only surpassed by *Aepyornis* and some moas. Estimated egg mass is about 1.4 kg. On the basis of egg mass, the body mass of the parent bird is estimated at between 135.4 kg and 156.4 kg, assuming that the hatchlings were precocial. These calculations are in good agreement with the dimensions and mass estimates for the Palaeogene giant bird *Gastornis*, a probable anseriform, which lived in Europe at the time the eggs were laid. Other large Early Tertiary birds from Europe (*Remiornis*, *Palaeotis*) are too small to have laid these eggs. In all likelihood, the large eggs from the Palaeogene of southern France were laid by gastornithid birds.

Keywords: eggs, Aves, Palaeogene, France, size estimates, *Gastornis*.

1. Introduction

The bird eggshells from the Tertiary of southern France have been known since the 1950s, with the first discovery in 1957 by Philippe Biro, and the first published study in 1959 by Dughi & Sirugue (1959). During the 1960s–1970s, several studies on the stratigraphic distribution of eggshells, their ornamentation and their microstructure were conducted (Dughi & Sirugue, 1959, 1962, 1968; Fabre-Taxy & Touraine, 1960; Touraine, 1960, 1961, 1962, 1963, 1967, 1978; Martini, 1961; Dughi, Plaziat & Sirugue, 1969). Since the 1970s, interest in these avian eggs has waned, with only a few contributions to the topic, including remarks on the microstructure (Penner, 1983) and a semi-popular review paper (Kerourio & Aujard, 1987).

The estimation of the egg size is a significant point of interest because it may have some important consequences for the attribution of these eggshells to a specific group of Palaeogene birds. Since these eggshells have never been found in association with skeletal remains, there is still considerable uncertainty as to the type of bird that may have laid them. The first estimation of the egg size was provided by Dughi & Sirugue (1959) in the first published study of eggshells from southern France (Table 1). These authors, however, only compared the fossil eggshell curvature with that of ostrich eggs, and concluded that the fossil eggshells are more curved than the ostrich eggshells, without applying any quantitative method. They proposed an egg size of about 24.0 cm by 10.0 cm based on an observation of an egg section with a thick eggshell. One year later, Touraine (1960; Table 1) mentioned some sub-complete eggs that had been observed, and used them to estimate the size of the egg. An egg with a thick eggshell was sectioned along the major diameter, allowing an estimation of the maximal length of 24.0 cm. A second egg sectioned along the minor axis presented a circular diameter of 15.0 cm. On the other hand, the eggs of the thin-shelled type measured 15.0 cm in length and 10.0 cm in diameter. All the following authors used these estimates without further

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Table 1. Summary of the different estimates of egg size based on the fossil eggshells from southern France, proposed in previous publications

Method to estimate the egg size	Estimated egg size	Reference
Estimation with the naked eye, based on the observation of sub-complete eggs	Fossil egg more cambered than the ostrich egg Egg with a thick eggshell: ~ 10 cm × ~ 24 cm	(Dughi & Sirugue, 1959)
Based on the observation of sub-complete eggs	Egg with a thick eggshell: ~ 24 cm × ~ 15 cm Egg with a thin eggshell: ~ 10 cm × ~ 15 cm	(Touraine, 1960)
Unspecified	Two types of eggs: • Large: 14 cm × 24 cm • Small: 10 cm × 15 cm	(Fabre-Taxy & Touraine, 1960)
Unspecified	Two types of eggs: • Large: 14 cm × 20 cm And later in the text: 20 cm × 40 cm. • Small: < 20 cm for the greatest axis	(Dughi & Sirugue, 1962)
Based on Touraine (1960) and Dughi & Sirugue (1962), and on a 'reconstructed' egg	• 15 cm × 24 cm • 15 cm × 25 cm • 20 cm × 40 cm	(Donaire & Lopez-Martinez, 2009)
Egg size calculated for the eggs from southern France	Egg with a thick eggshell: 12 cm (11–13) × 17.8 cm (16.3–19.2)	This study

measurements or calculations (Fabre-Taxy & Touraine, 1960; Dughi & Sirugue, 1962; Kerourio & Aujard, 1987; Donaire & Lopez-Martinez, 2009; Table 1). Several problems arose, however, the first major one being a direct outcome of the publications of Dughi & Sirugue (1959) and Touraine (1960). They did not indicate the localities where they found the sub-complete eggs, and following these two succinct descriptions, no one has ever found other sub-complete eggs, but only isolated eggshell fragments. No photograph or drawing was made available to document these sub-complete eggs, and none of them has been deposited in a museum because they could not be extracted. Secondly, Dughi & Sirugue (1962) gave some measurements of these eggs, in which they somewhat modified their original data (Dughi & Sirugue, 1959), proposing a maximal length of 20.0 cm for the large eggs, instead of 24.0 cm as proposed originally, without any explanation for the discrepancy. Furthermore, in the same paper, a length of 40.0 cm was also mentioned, which we think was probably a misprint, and therefore erroneous. The latest publication (Donaire & Lopez-Martinez, 2009) (Table 1) used all the previous measurements to estimate the mass of these eggs, and added new measurements coming from a purported sub-complete egg exhibited at a fossil show. However, the more or less 'complete' eggs exhibited at such shows are artificial reconstructions made by gluing isolated eggshell fragments onto a plastic form (N. Houles, pers. comm.) and should by no means be used to estimate the size of real eggs. Based on these previous studies, the fossil eggs from the Palaeogene of southern France were certainly large, but no real consensus was reached about their real size. Therefore, we propose a new quantitative estimate of the size of these eggs, which provides evidence about the identification of the bird that may have laid these eggs.

Institutional abbreviations: MNHN – Muséum National d'Histoire Naturelle, Paris; MC – Musée des Confluences, Lyon; APSO – Association Paléontologique du Sud-Ouest; MDE – Musée des Dinosaures d'Espéraza.

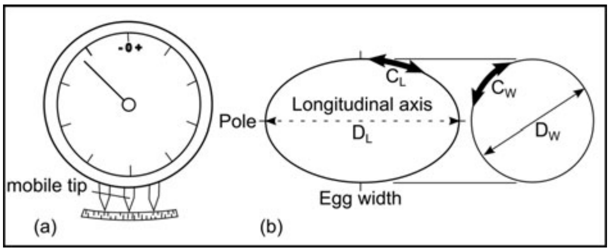

Figure 1. Explanations of the egg measurements from Williams (1981). (a) Measurement of the curvature of the eggshells with a spherometer; (b) egg geometry: C_W is the transversal curvature, C_L is the longitudinal curvature.

2. Material and methods

2.a. Methods

The method proposed by Williams (1981) was used to estimate the average egg size. This author measured the shell curvature, with a spherometer (Fig. 1a), in all spatial directions. This method allowed the acquisition of the maximal curvature (C_W) and the minimal curvature (C_L), corresponding, respectively, to the transversal curvature and the longitudinal curvature (Fig. 1b). The curvature measurements were obtained in diopters and converted into diameter (D) in millimetres by using Eq. (1) (Table 2):

$$D = ((1.523 - 1)/\text{curvature} \times 1000) \times 2 \qquad (1)$$

The greatest curvature (C_W) gives the smallest diameter (D_W) (Fig. 1b), which corresponds to the transversal diameter and to the egg width, if we postulate that the transversal section of the egg is circular. The smallest curvature (C_L) permits the obtention of the greatest diameter (D_L), which, however, does not correspond to the egg length because the egg is probably

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Table 2. Equations used in this work

(1)	$D = ((1.523 - 1)/\text{curvature} \times 1000) \times 2$	
(2)	$V_{egg} = K_v{}^*L^*B^2$	Hoyt, 1979
(3)	$M_{egg} = K_w{}^*L^*B^2$	Hoyt, 1979
(4)	$\log(\text{fem length}) = 0.4503 \log(M_{egg}) + 1.0336$	Dyke & Kaiser, 2010
(5)	$M_{egg} = -0.659394 + 0.7889097\, M_{body}$	Dyke & Kaiser, 2010
(6)	$M_{egg} = -0.164615 + 0.6451872\, M_{body}$	Dyke & Kaiser, 2010
(7)	$\log_{10} M_{body} = 2.424 \log_{10} LC_t - 0.076$	Campbell & Marcus, 1992
(8)	$\log_{10} M_{body} = 2.411 \log_{10} LC_f - 0.065$	Campbell & Marcus, 1992

not spherical. The egg width is the point that corresponds to the highest D_W and D_L values. This value represents the flattest part of the eggshell in all spatial directions, which must be at the middle of the egg. Considering that the egg was circular in section, the obtained D_W value corresponds to the egg width. To estimate the egg length we cannot use the same method because it is only applicable for a circular section: as the eggs were in all likelihood not spherical, we cannot consider that the longitudinal section was circular. We used the ratio 1.48 proposed by Williams (1981) to calculate the length (L) based on the mean width value, itself obtained on the basis of numerous egg ratios.

Using these values with Eq. (2) (Table 2), the volume of a bird egg (V_{egg}) can be obtained according to the work of Hoyt (1979), where K_v is a factor defined by Hoyt and equal to 0.51, L is the length and B the width, both measured in centimetres.

$$V_{egg} = K_v{}^*L^*B^2 \quad (2)$$

The egg mass (M_{egg}) can be obtained using Eq. (3) (Table 2; Hoyt, 1979), with K_w a factor defined by Hoyt and equal to 0.55, and L the length and B the width, both in centimetres.

$$M_{egg} = K_w{}^*L^*B^2 \quad (3)$$

2.b. Material

The material consists of fossil avian eggshell fragments from southern France collected during two field trips in 2011 and 2012, during which 1343 eggshell fragments were unearthed from 13 localities of late Paleocene and early Eocene age. Eggshells of two distinct average thicknesses have been observed, most of them (95 %) being thick (around 2 mm in thickness), while the thin ones (around 1 mm in thickness) are very rare (5 %). Only the first group (thick eggshells), named *Ornitholithus arcuatus* by Dughi & Sirugue (1962), has been used in this study, because the fragments belonging to the thin group are too small to be measured with the spherometer. Among the 1343 fragments collected, only 106 are large enough in all the spatial directions to apply Williams's method. These 106 eggshell fragments come from eight different sites in southern France: Saint Antonin-sur-Bayon, Sillans-la-Cascade, Cengle indet., Suberoque, Pontevès, Rians-Les Bardouines, Vinon-sur-Verdon and Lagrasse (online Supplementary Material Table S1 available at http://journals.cambridge.org/geo). The *Ornitholithus arcuatus* eggshells are always stratigraphically younger than the thin eggshells (*Ornitholithus biroi*) and occur in the upper part of the Calcaire de Saint-Marc Formation and in overlying red marls, which are Sparnacian in age (Cojan, Moreau & Stott, 2000), whereas the thin eggshells come from underlying Paleocene deposits. Dughi & Sirugue (1962) distinguished several oospecies among the thick eggshells, on the basis of small differences in thickness, ornamentation and microstructure, but our observations are in agreement with Penner's (1983) and Mikhailov's (1997) conclusions, viz. that the subdivision into several oospecies is questionable. We therefore recognize a single thick-shelled oospecies, namely *Ornitholithus arcuatus*.

Size and mass estimates obtained for the fossil eggshells have been compared with some values for large living ground birds, such as the Ostrich (*Struthio camelus*), the Greater Rhea (*Rhea americana*), the Emu (*Dromaius novaehollandiae*) and the Cassowary (*Casuarius casuarius*). For each group the length and the diameter have been measured for several eggs using a caliper (online Supplementary Material Table S2 at http://journals.cambridge.org/geo). These estimates have also been compared to large fossil birds for which complete eggs are known, such as the Dromornithidae (Williams, 1981), the Aepyornithidae (Mlikovsky, 2003) and the Dinornithiformes (Gill, 2000, 2006, 2007).

3. Results: discussion

Based on these 106 eggshell fragments, we selected for size and mass calculations the two fragments (eg124 and eg515) that had the highest D_W value and the highest D_L value, and estimated an egg width of between 11.0 cm and 13.0 cm (Fig. 2). Using the ratio of 1.48 proposed by Williams (1981), the calculated egg length ranged between 16.3 cm and 19.2 cm (Table 1). These values correspond to a very large egg, which is in agreement with the thickness of the eggshells, around 2 mm.

3.a. Comparisons with the previous estimates for these eggs

The egg size we estimated is smaller than the sizes previously proposed with a mean width around 12.0 cm versus 14.0 cm (Fabre-Taxy & Touraine, 1960; Dughi & Sirugue, 1962) to 15.0 cm (Touraine, 1960; Donaire & Lopez-Martinez, 2009), and a mean length of around 17.8 cm versus 20.0 cm (Dughi & Sirugue, 1962; Donaire & Lopez-Martinez, 2009) to 25.0 cm (Dughi &

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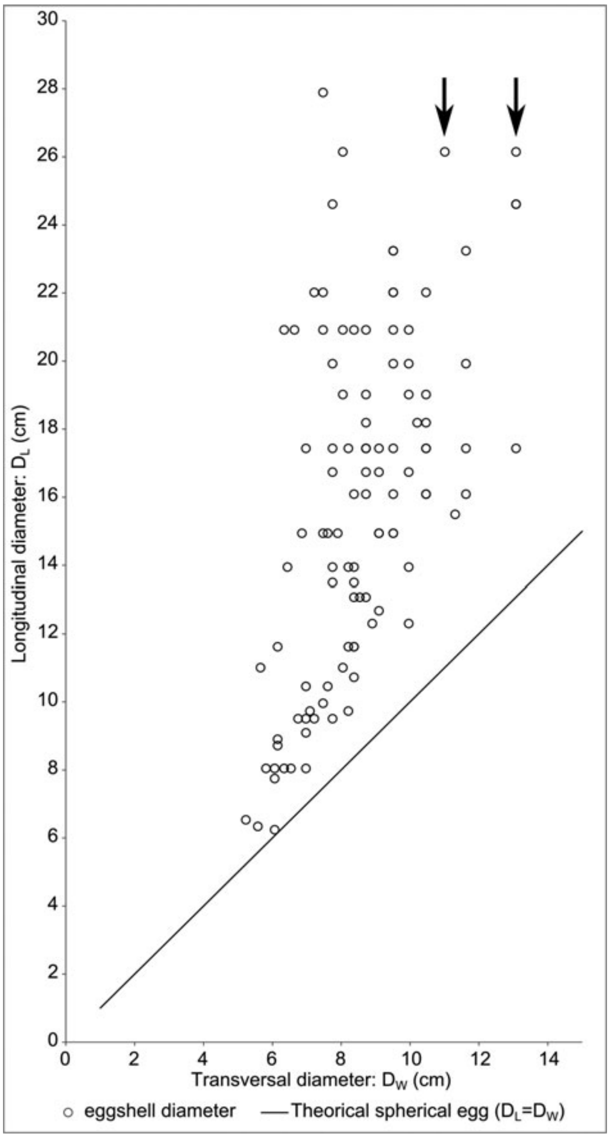

Figure 2. Estimation of the egg width using Williams's graph (1981) representing the transversal diameter (D_W) as a function of the longitudinal diameter (D_L) in centimetres. The two upper-right-most values used for the estimation of the width are indicated by arrows.

Sirugue, 1959; Touraine, 1960; Fabre-Taxy & Touraine, 1960; Donaire & Lopez-Martinez, 2009). The new estimate of 12.0 cm for the diameter is, however, relatively close to the first value proposed by Dughi & Sirugue (1959), which was close to 10.0 cm (Table 1). This new estimate poses the question of the validity or the repeatability of the field observations made by Touraine (1960) and Dughi & Sirugue (1959), even more so that during our two field trips, we never found any sub-complete eggs. Even finding two associated fragments is exceptional, and never permitted the direct estimation of the size of the complete egg.

3.b. Comparisons with modern and fossil large bird eggs

The comparison between these estimates and the eggs of living large birds shows that these fossil eggs were larger than those of the Emu, Cassowary and Greater Rhea, which are about 11.1 cm to 15.1 cm in length by 7.6 to 12.6 cm in diameter (Table 3; Fig. 3). The fossil eggs correspond to the highest part of the ostrich egg range of dimensions (maximum about 15.0 cm by 17.0 cm) or are even larger. The comparison with large fossil bird eggs, including mainly the Aepyornithidae (*Aepyornis maximus*), the Dromornithidae (*Genyornis* sp.) and the Dinornithiformes, shows that the fossil eggs studied here are larger than the *Genyornis* eggs, measuring 12.5 cm by 15.5 cm, and than the eggs of the smallest Dinornithiformes (*Euryapteryx curtus, Megalapteryx didinus* and *Anomalopteryx didiformis*), measuring 12.0 cm by 9.4 cm, 16.2 cm by 11.1 cm and 16.5 cm by 11.8 cm, respectively. They are, however, much smaller than the *Aepyornis* eggs, which measure on average 30.4 cm by 22.4 cm and than the eggs of the largest Dinornithiformes (Table 3; Fig. 3; online Supplementary Material S2 available at http://journals.cambridge.org/geo). Therefore, these fossil eggs are among the largest known fossil ones, with only the *Aepyornis* eggs and some of the largest dinornithiform ones being larger.

The use of Eq. (2) (Table 2) leads to a calculated egg volume of 1330.4 cm^3 for *Ornitholithus arcuatus*. It is close to the ostrich egg mean volume (1284.1 ± 235.1 cm^3) and significantly larger than the volume of the eggs of the other living and fossil large ground birds (Table 3), except for the largest Dinornithiformes and *Aepyornis* eggs with mean values of 1721.6 ± 778.5 cm^3 and 7751.5 ± 1323.4 cm^3, respectively, which are the largest known bird eggs.

3.c. Estimated mass of the egg

On the basis of both length and diameter values, we obtained a mean mass of around 1.4 kg (Table 3) for the *Ornitholithus arcuatus* egg according to Eq. (3) (Table 2). This value is much lower than that proposed by Donaire & Lopez-Martinez (2009), with a weight between 2.9 kg and 8.7 kg. These differences, however, can be explained by the values for length and width used by these authors, which are largely overestimated or false.

Hoyt's method was applied to some modern birds (*Struthio, Rhea, Dromaius, Casuarius*), and well-studied fossil birds (Aepyornithidae, Dromornithidae, Dinornithiformes) in order to test its validity when applied to fossil eggs studied here. The comparison with these other large birds shows that the values obtained using Hoyt's equation are totally in accordance with the measured and published values, which demonstrates the robustness of this method (Table 3). The egg mass estimated for the *Ornitholithus arcuatus* eggshells matches the egg weight of the ostrich in the range of uncertainties (1.4 ± 0.3 kg) (Amadon, 1947; Ar *et al.* 1974) and is larger than that of all the other large bird eggs studied here, except Aepyornithidae (Amadon, 1947; Rahn & Ar, 1974), as well as the larger Dinornithiformes (Gill, 2007). The egg corresponding to the

Table 3. Values estimated using the different equations presented in Table 2, for living and fossil birds, and for the eggshell *Ornitholithus arcuatus*

Group		Measurements mean L (length) B (width) (cm)		Egg volume (cm³) (3)	Egg mass (kg) (4)	Egg mass expected (kg)
Fossil egg *(Ornitholithus arcuatus)*						
	L	17.8 (16.3–19.2)	n = 2	1330.4 (1005.9–1654.8)	1.4 (1.1–1.8)	2.9–8.7 (Donaire & Lopez-Martinez, 2009)
	B	12.0 (11.0–13.0)	n = 2			
Ostrich *(Struthio camelus)*						
	L	15.1 (13.1–16.6)	n = 45	1284.1 (793.8–1804.6)	1.4 (0.9–1.9)	1.7 (Hoyt, 1979) 1.3 (Amadon, 1947)
	B	12.9 (10.9–14.6)	n = 45			
Greater Rhea *(Rhea americana)*						
	L	13.1 (11.1–14.8)	n = 50	529.2 (327.0–1198.3)	0.6 (0.4–1.3)	0.6 (Rahn & Ar, 1974; Ar *et al*. 1974)
	B	8.9 (7.6–12.6)	n = 50			
Emu *(Dromaius novaehollandiae)*						
	L	13.3 (12.6–13.8)	n = 11	525.3 (416.4–621.9)	0.6 (0.4–0.7)	0.6 (Hoyt, 1979) 0.5 (Amadon, 1947)
	B	8.8 (8.1–9.4)	n = 11			
Cassowary *(Casuarius casuarius)*						
	L	13.3 (12.5–15.1)	n = 19	513.0 (428.7–651.8)	0.6 (0.5–0.7)	0.6 (Amadon, 1947)
	B	8.6 (8.2–9.2)	n = 19			
Aepyornithidae *(Aepyornis maximus)*						
	L	30.4 (28.0–40)	n = 43	7751.5 (5655.0–13161.3)	8.3 (6.1–14.2)	7.8 (Amadon, 1947) 0.9–1.3 (Rahn & Ar, 1974)
	B	22.4 (19.9–25.4)	n = 43			
Dromornithidae *(Genyornis)*						
	L	15.5	n = 1	1235.2	1.3	1.3 (Williams, 1981)
	B	12.5	n = 1			
Dinornithiformes						
Euryapteryx curtus						
	L	12.0 (12.0–12.1)	n = 2	543.0 (506.8–580.6)	0.6 (0.5–0.6)	
	B	9.4 (9.1–9.7)	n = 2			
Megalapteryx didinus						
	L	16.2 (15.5–17.0)	n = 3	1015.9 (871.5–1248.5)	1.1 (0.9–1.3)	
	B	11.1 (10.5–12.0)	n = 3			
Anomalopteryx didiformis						
	L	16.5 (15.2–18.0)	n = 7	1182.3 (1025.2–1321.9)	1.3 (1.1–1.4)	
	B	11.8 (11.8–12.0)	n = 7			
Eurapteryx gravis						
	L	20.4 (19.4–21.6)	n = 13	2128.4 (1750.1–2750.0)	2.3 (1.9–3.0)	
	B	14.3 (13.3–15.8)	n = 13			

Table 3. Continued.

Group		Measurements mean L (length) B (width) (cm)		Egg volume (cm^3) (3)	Egg mass (kg) (4)	Egg mass expected (kg)
Emeus crassus	L	17.9 (17.9–18.0)	n = 2	1583.0 (1519.2–1648.4)	1.7 (1.6–1.8)	
	B	13.1 (12.9–13.4)	n = 2			
Pachyornis elephantopus	L	22.3 (22.1–23.0)	n = 3	2885.2 (2536.0–3390.0)	3.1 (2.7–3.7)	
	B	15.8 (15.0–17.0)	n = 3			
Dinornis novaezealandiae	L	19.0	n = 1	2180.3	2.4	
	B	15.0	n = 1			
Dinornis robustus	L	24.0	n = 1	3878.1	4.2	4.0 (Amadon, 1947)
	B	17.8	n = 1			

Numbers in brackets are min.–max.; n – number of measurements.

eggshell named *Ornitholithus arcuatus* was therefore a large egg close to the ostrich egg in terms of size and mass.

Calculations based on geometrical properties of eggs show that the oospecies *Ornitholithus arcuatus* of Dughi & Sirugue (1962) was a very large egg, measuring on average 12.0 cm in diameter and 17.8 cm in length. An egg with such proportions must have been laid by a very large bird. In Europe, only a few large birds are known from the Palaeogene. The ratite *Remiornis* had a size similar to that of a Greater Rhea and is known from two late Paleocene localities in France, Mont-de-Berru and Cernay (Martin, 1992). *Palaeotis*, also a ratite, is another relatively large bird, but smaller than *Remiornis*, with a size close to that of a Bustard (a little less than 1 m in height), known from the Middle Eocene of the Geiseltal and Messel in Germany (Lambrecht, 1928; Houde & Haubold, 1987). The only very large bird known from the Palaeogene of France is *Gastornis*, a probable anseriform, described from several French localities such as Meudon (Hébert, 1855*a*,*b*), Cernay-les-Reims (Lemoine, 1878, 1881, 1884) and Mont-de-Berru (Andors, 1992; Martin, 1992; Buffetaut, 1997; Angst & Buffetaut, 2013). In southern France, *Gastornis* is known from the Early Eocene of Saint-Papoul (Buffetaut, 2008; Laurent *et al.* 2010). The eggshells found in the Early Tertiary basins of southern France may therefore be referred to *Gastornis* on the basis of the very large size of the reconstructed egg and of the considerable mass of the birds which laid these eggs.

Results from Dyke & Kaiser's (2010) study were used to test this association between these two separate kinds of fossils, the avian eggshells and the bones of *Gastornis*. These authors proposed a relationship between the egg mass and the femur length (as a proxy of mass) of the birds having laid the eggs, based on various modern birds. On the basis of our study the mass of our fossil eggs is estimated at 1.4 kg on average. Using the regression equation (Eq. (4); Table 2) proposed by Dyke & Kaiser (2010), the relationship between the femur length and the mass of the egg is expressed as follows:

$$\log(\text{fem length}) = 0.4503 \log(M_{egg}) + 1.0336 \quad (4)$$

Thus we obtain a log of the femur length of 2.45 (Table 4), which is comparable to that obtained for European *Gastornis* specimens, the femora of which have a mean length of 28.2 cm, which corresponds to a log of the egg mass of 3.15 (Fig. 4). If we use the same method with the femora of *Palaeotis* we obtain an estimated point clearly distinct from the two former ones. Using this method, we can strongly support the association of the eggshells from southern France with *Gastornis*. This association between the two different kinds of fossils had already been suggested by Dughi & Sirugue (1959, 1962, 1968) and by Touraine (1960), who tentatively referred the fossil eggs to gastornithids on the basis of contemporaneity of both fossil

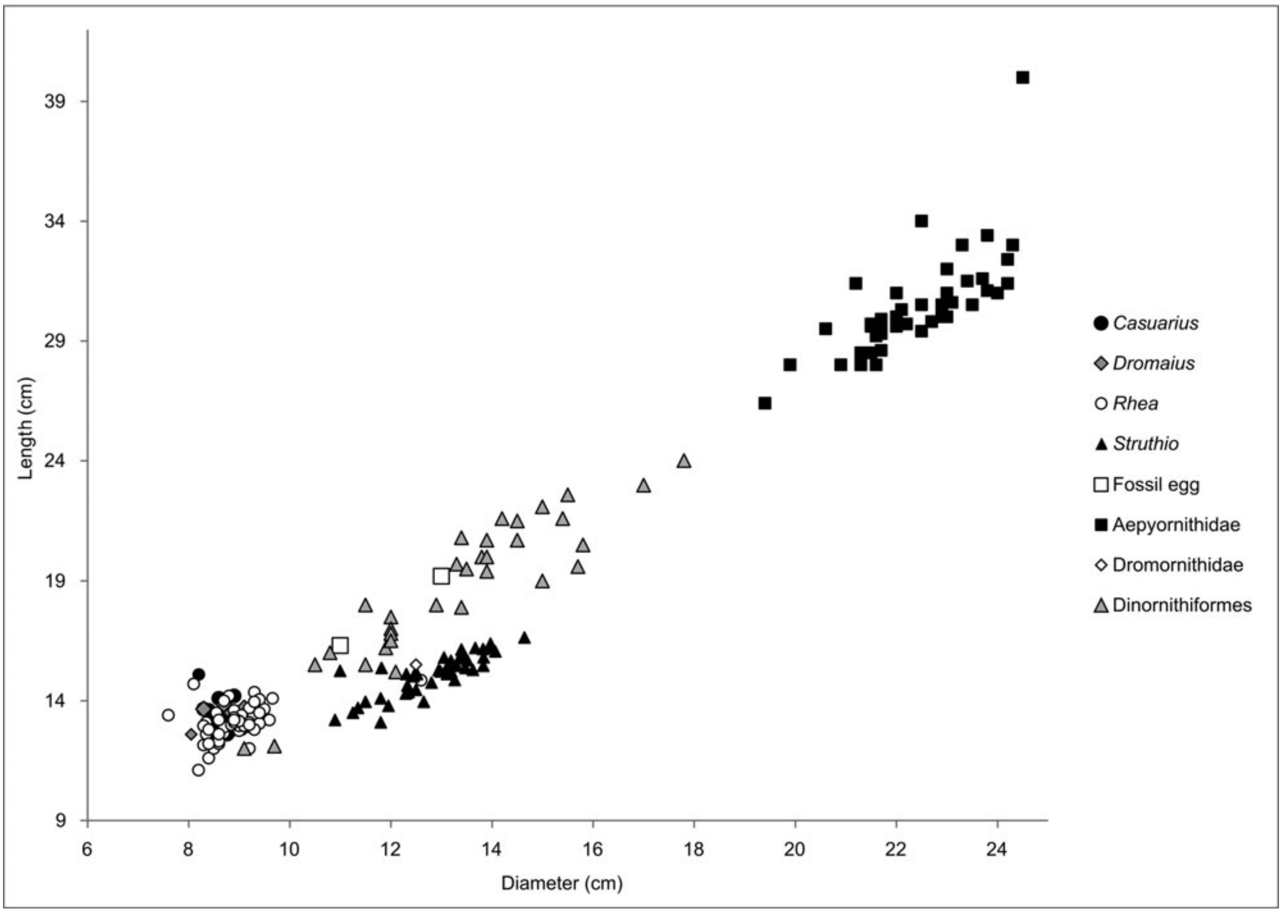

Figure 3. Egg size comparison between the studied fossil eggs (white square), and modern and fossil known bird eggs, using the diameter (in centimetres) as a function of the length (in centimetres).

occurrences, a suggestion supported by Mayr (2009). The quantitative study of the eggshell size and mass proposed in this study provides more solid evidence to support this hypothesis.

3.d. Estimated body mass of the bird that laid these eggs

Assuming that these eggs have been laid by *Gastornis*, the body mass of the female bird which laid these eggs can be estimated using two other equations (Eqs (5) and (6); Table 2) determined by Dyke & Kaiser (2010). These two equations correlate the log of the egg mass to the log of the body mass, depending on the developmental mode of the young: 'altricial' (helpless, Eq. (5)) or 'precocial' (independent, Eq. (6)).

$$M_{egg} = -0.659394 + 0.7889097\ M_{body} \quad (5)$$

$$M_{egg} = -0.164615 + 0.6451872\ M_{body} \quad (6)$$

As we do not know what type of development the *Gastornis* hatchlings had, we tested both equations using the egg mass calculated before. Therefore, in the case of an altricial bird, we obtain a female body mass of between 66.6 kg and 79.3 kg. For a precocial bird, the estimated body mass is between 135.4 kg and 156.4 kg. These values are smaller than the previous body mass estimates for *Gastornis* proposed by Andors (1992) and Murray & Vickers-Rich (2004), which were around 175.0 kg and 199.0 kg, respectively. But both estimates were based on measurements of *Gastornis* specimens from North America, which were larger than the European form. This size difference can easily explain the differences in estimated body mass, because our study is based on European specimens. Body mass estimates for European *Gastornis* using Campbell & Marcus's method (1992) based on minimal circumference (LC) of the tibiotarsus (Eq. (7)) and femur (Eq. (8)) (Tables 2, 5), are between 133.4 kg and 156.4 kg, respectively, a result which is in good agreement with our estimates based on egg mass.

$$\log_{10} M_{body} = 2.424\ \log_{10} LC_t - 0.076 \quad (7)$$

$$\log_{10} M_{body} = 2.411\ \log_{10} LC_f - 0.065 \quad (8)$$

The values obtained using the altricial equation appear rather small for *Gastornis*, but could be explained if this bird presented a large sexual dimorphism. The precocial estimates of between 135.4 kg and 156.4 kg are more in agreement with the estimated weight of *Gastornis*, which is not unexpected since all the large

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Table 4. Calculations to estimate the log egg mass from the femur length, and the log femur length from the egg mass, based on the equation proposed by Dyke & Kaiser (2010)

Group	Site	Sample n°	Femur length (cm)	Log femur length	Log egg mass	Egg mass (g)	References
Ornitholithus arcuatus							
	Southern France		28.20 (25.30–31.58)	2.45 (2.40–2.50)	3.15 (3.04–3.26)	1400 (1100–1800)	this study
Gastornis sp.							
	Geiseltal	Dia.6	30.00	2.48	3.21	1606	Fischer, 1978
	Messel	Me 6116	30.00	2.48	3.21	1606	Berg, 1965
	Geiseltal	Dia.18	31.2	2.49	3.24	1752	Fischer, 1978
	Geiseltal	Dia.19	34.00	2.53	3.33	2120	Fischer, 1978
			31.30 (30.00–34.00)	2.49 (2.48–2.53)	3.25 (3.21–3.33)	1759 (1606–2120)	

Table 5. Estimation of the body mass of *Gastornis* based on the method of Campbell & Marcus (1992)

Bone	Sample n°	Locality	Sources	LC (mm)	Body mass (kg)
Tibiotarsus	/	Meudon (France)	This study	131.4	162.8
	MDE	St-Papoul (France)	This study	119.5	129.3
	APSO2008 SP5–12	St-Papoul (France)	This study	111.0	108.1
			Mean:	120.6	133.4
			Range:	111–131.4	108.1–162.8
Femur	Me 6116	Messel (Germany)	This study	161.0	180.2
	/	Meudon (France)	This study	156.0	167.0
	APSO 2007 SP2–145	St-Papoul (France)	This study	137.0	122.1
			Mean:	151.3	156.4
			Range:	137.0–161.0	122.1–180.2

LC – minimal circumference

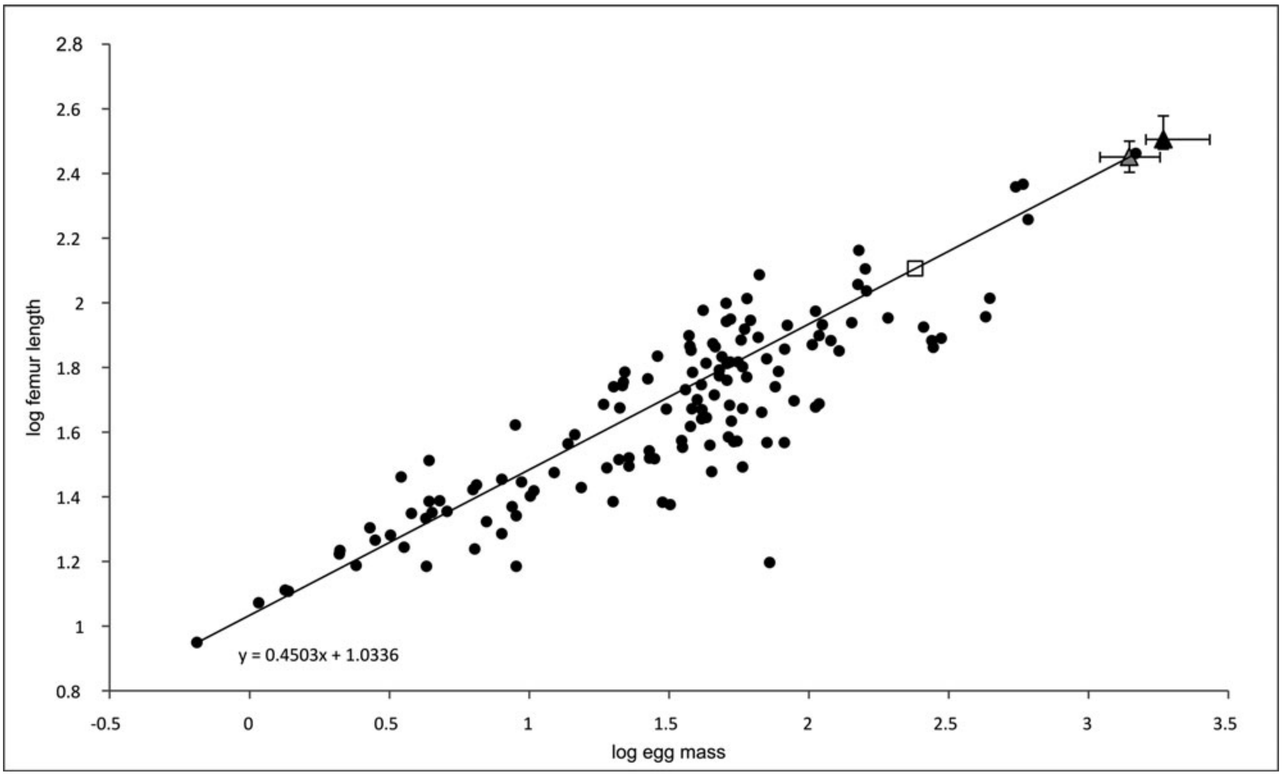

Figure 4. Estimation of the log(femur length) from the log(egg mass), using the measurements and the regression equation proposed by Dyke & Kaiser (2010) (log femur length = 0.4503 log egg mass + 1.0336) (grey triangle); compared with the log(egg mass) estimated from the log(femur length) measured for the European *Gastornis* (black triangle). Both values are very close, showing that the fossil eggshells studied here can be referred to *Gastornis*. For comparison, the white square corresponds to *Palaeotis*, based on the measurements of the femur.

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living ground birds, including the present-day ostrich, are precocial (Dyke & Kaiser, 2010).

4. Conclusion

This new study of the bird eggshells from the Early Tertiary of southern France permits us to associate the fossils eggs with *Gastornis*, as well as to propose a body mass estimate for the female of *Gastornis*, which is totally in accordance with the estimates independently obtained for this Early Tertiary giant ground bird. This association raises some questions about the ecology of *Gastornis*: are the very large quantities of eggshell fragments found at some sites only due to a specific taphonomic environment or do they reflect nesting sites? If the eggshell localities correspond to nesting sites, the fact that only fragments are found (unlike the situation of dinosaur nesting sites in the Cretaceous of the same areas of southern France, where complete eggs and clutches are common) probably reflects the fact that the eggs were laid unprotected on the ground and not buried. Because the eggs are broken, it is difficult to assess how many there were in a clutch and how many eggs were laid each year by a single bird. Similarly, it is difficult to evaluate how many laying periods are represented at each site, or how many birds used the nesting sites. The large accumulations of eggshell fragments found at some sites may suggest gregarious nesting of *Gastornis* flocks. Another fact worth noting is that these eggshell sites only occur in southern France and northern Spain while *Gastornis* skeletal remains are mainly known (with the exception of the Saint-Papoul locality) from localities further north, in northeastern France, Belgium, England and Germany. This fact was already commented on by Touraine (1960), who noted that no bones had been found in association with the eggshell fragments (this also applies to Cretaceous dinosaur nesting sites in southern France, where skeletal remains do not occur). Conversely, in their review of fossil eggs from the Geiseltal, where *Gastornis* bones are known, Kohring & Hirsch (1996) did not describe any eggshell type that could be referred to gastornithids. However, it seems difficult to envision migrations of the flightless *Gastornis* to distant regions for egg-laying to explain this geographical pattern. What the reasons were why some specific locations were chosen by gastornithids to lay their eggs is an additional question. Further studies on the numerous and productive Early Tertiary eggshell localities of southern France, using approaches such as sedimentology and geochemical analysis, may provide answers to at least some of these questions.

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Declaration of Interest

None

Supplementary materials

To view the Supplementary Material for this article, please visit http://dx.doi.org/10.1017/S0016756814000077

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