



General palaeontology, systematics and evolution (Vertebrate palaeontology)

A peculiar anseriform (Aves: Anseriformes) from the Miocene of Gargano (Italy)



Un ansériforme particulier (Aves : Ansériformes) en provenance du Miocène du Gargano, Italie

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ABSTRACT

A new large representative of the Anseriformes, *Garganornis ballmanni* n. gen. et n. sp., from the Miocene of Gargano, Italy, is described from the distal end of a left tibiotarsus. *G. ballmanni* displays morphological features that are characteristic of the Anseriformes, but differs from all extant and fossil Anseriformes, as well as from taxa closely related to Anseriformes. *G. ballmanni* is characterized by a very wide and shallow fossa intercondylaris, a less pronounced difference in width of the lateral and medial condyle, reduced epicondylus, and a circular opening of the distal canal. *G. ballmanni* is larger than any living member of Anseriformes, and with an estimated body mass between 15.3 and 22.3 kg, it was most likely flightless. Although the observed similarities between *G. ballmanni* and basal taxa might indicate that *G. ballmanni* represents an insular relict of a stem lineage, it is considered more likely that *G. ballmanni* was a species of waterfowl highly adapted to a terrestrial lifestyle in an insular environment where mammalian carnivores are rare.

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RÉSUMÉ

Un nouveau grand représentant des ansériformes, *Garganornis ballmanni* n. gen. et n. sp., est décrit sur la base de l'extrémité distale d'un tibiotarse gauche dans le Gargano (Miocène, Italie). *G. ballmanni* présente des traits morphologiques qui sont caractéristiques des ansériformes, mais différent de tous les ansériformes actuels et fossiles, ainsi que des taxons étroitement liés aux ansériformes. *G. ballmanni* est caractérisé par une fosse antérieure intercondylienne large et peu profonde, une différence peu prononcée dans la largeur des condyles latéral et médial, des épicondyles réduits, et une ouverture circulaire du canal distal. *G. ballmanni* est plus grand que tous les ansériformes actuels, et, avec une masse estimée entre 15,3 et 22,3 kg, il était probablement incapable de voler. Bien que les similitudes observées entre *G. ballmanni* et les taxons de base puissent indiquer que *G. ballmanni* représente une relique insulaire d'une lignée primitive, il est considéré comme plus probable que *G. ballmanni* ait été une espèce d'oiseau aquatique très adaptée à un mode de vie terrestre, dans un environnement insulaire où les mammifères carnivores étaient rares.

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1. Introduction

Now firmly joined to the Italian mainland, the Gargano promontory (Fig. 1) once formed part of the Apulia platform and hosted a highly endemic insular fauna. Sediments from palaeokarst fissures have yielded extensive collections of Neogene and Pleistocene vertebrate remains (Abbazzi et al., 1996; Freudenthal, 1971, 1976; Pavia et al., 2012; Van der Geer et al., 2010). Although the timing and mode of colonization of the Apulia platform has been the subject of debate (see Freudenthal et al., 2013; Mazza and Rustioni, 2008; Van den Hoek Ostende et al., 2009), the Neogene assemblage, also known as the 'Mikrotia' fauna after the abundant endemic murid (Freudenthal, 2006), is now considered to be Tortonian in age (Freudenthal et al., 2013; Van den Hoek Ostende et al., 2009). It documents the arrival and evolution of an endemic fauna that, with the exception of the otter *Paralutra garganensis*, is devoid of mammalian carnivores and displays strong insular evolution. Examples of endemic lineages include the giant Gargano hedgehog *Deinogalerix*, the Gargano dormouse *Stertomys* and the deer-like ruminant *Hoplitomeryx* (Daams and Freudenthal, 1985; Freudenthal, 1972; Leinders, 1984; Masini and Fanfani, 2013; Van der Geer, 2008; Villier et al., 2013).

The Neogene fossil bird assemblage of Gargano was first described by Ballmann (1973, 1976), who identified 16 avian taxa, most of them endemic, in the orders Galliformes, Anseriformes, Accipitriformes, Strigiformes, Columbiformes, Apodiformes, Piciformes and Passeriformes. Göhlich and Pavia (2008) described the small phasianid *Palaeortyx volans*, the most abundant species

in the assemblage. Birds of prey were abundant and varied greatly in size, with the largest being the buteonine hawk *Garganoaetus freudenthali* Ballmann, 1973 (the size of a Golden Eagle) and the barn owl *Tyto gigantea* Ballmann, 1973 (larger than the Eurasian eagle owl *B. bubo* (Ballmann, 1976)). With mammalian carnivores being rare (note that *P. garganensis* is thought to have fed on shellfish (Willemssen, 1983)), birds filled the empty niche of predator (Ballmann, 1973, 1976). Recent studies by Pavia (2011, 2013) added several new taxa to the Gargano avifauna, including a species of *Calidris* and two new anatids, and brought the avifauna of Gargano to at least 26 taxa. Here, I describe a hitherto undescribed species of Anseriformes from the Miocene of Gargano that was discovered during a reorganisation of the Gargano collection at the Naturalis Biodiversity Center in Leiden, the Netherlands.

2. Material and methods

The specimen, a distal left tibiotarsus (RGM 443307) was compared to a number of extinct and extant Anseriformes (see Appendix) in the collections of the Naturalis Biodiversity Center (RMNH) in Leiden (the Netherlands), the British Museum of Natural History (BMNH) in London (UK), and the Smithsonian Institution's National Museum of Natural History (NMNH) in Washington, D.C. (USA). Comparisons to fossil species were mostly based on the literature. Measurements were taken with sliding calipers. Terminology follows Baumel and Witmer (1993), and Howard (1929) for structures not named in Baumel and Witmer. To estimate a body mass for this specimen, the minimum circumference of the tibiotarsus was estimated by wrapping a thin strap of paper around the tibiotarsus at the most proximal point and measuring the minimum circumference with sliding calipers calibrated to the nearest 0.05 mm. The minimum circumference was then log₁₀-transformed and body mass was estimated by using the least-squares linear regression for anseriform tibiotarsi as described by Iwaniuk et al. (2004).

3. Systematic Palaeontology

Class AVES Linnaeus, 1758
 Order ANSERIFORMES Wagler, 1831
 Family Insertae sedis
 GARGANORNIS n. gen.

Type species. *Garganornis ballmanni* n. sp.

Derivation of name. Masculine, after the Italian region Gargano where the quarries are located, and 'ornis', Greek for bird.

Diagnosis. Monospecific genus, as for species diagnosis. *Garganornis ballmanni* n. sp. (Fig. 2)

Derivation of name. 'ballmanni' refers to Peter Ballmann who was the first to describe the fossil avifauna of Gargano.

Holotype. Distal left tibiotarsus (RGM 443307), Fig. 2.

Diagnosis. A very large representative of the order Anseriformes characterized by the following unique combination of characters; central placement of the canalis



Fig. 1. Map of Italy and the location of Gargano.

Fig. 1. Carte de l'Italie et localisation du Gargano.

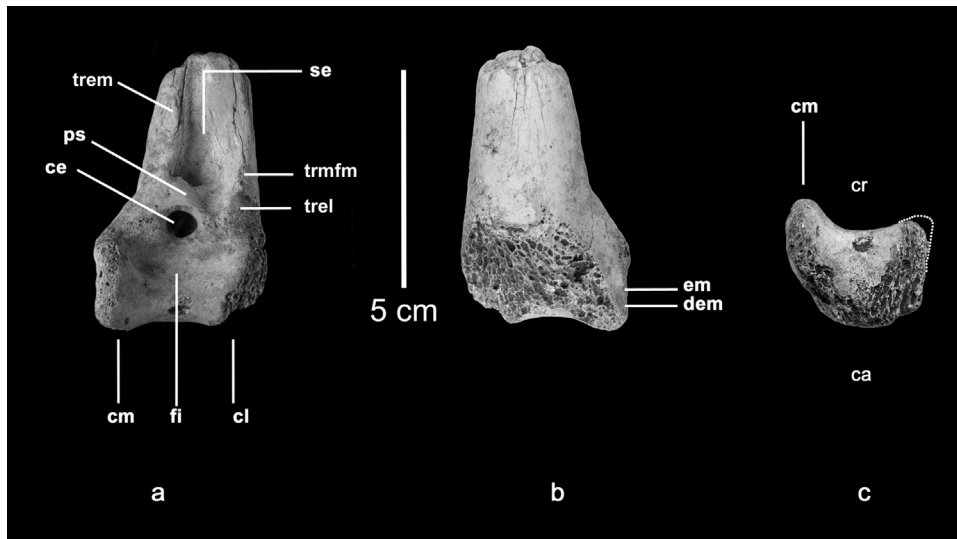


Fig. 2. *Garganornis ballmanni* n. gen. et n. sp., holotype, distal fragment of left tibiotarsus, in cranial (a), caudal (b) and distal view (c). Abbreviations: ca = caudal side; cr = cranial side; ce = canalis extensorius; cl = condylus lateralis; cm = condylus medialis; dem = depressio epicondylus medialis; em = epicondylus medialis; fi = fossa intercondylaris; ps = pons supratendineus; se = sulcus extensorius; trel = tuberositas retinaculum extensoris lateralis; trem = tuberositas retinaculum extensoris medialis; trmf = tuberculum retinaculi m. fibularis medialis.

Fig. 2. *Garganornis ballmanni* n. gen. et n. sp., holotype, fragment distal de tibiotarse gauche, en vues crâniale (a), caudale (b) et distale (c). Abréviations : ca = côté caudal ; cr = côté crânial ; ce = canalis extensorius ; cl = condylus lateralis ; cm = condylus medialis ; dem = depressio epicondylus medialis ; em = epicondylus medialis ; fi = fossa intercondylaris ; ps = pons supratendineus ; se = sulcus extensorius ; trel = tuberositas retinaculum extensoris lateralis ; trem : tuberositas retinaculum extensoris medialis ; trmf = tuberculum retinaculi m. fibularis medialis. Photos : E. Kruidenier.

Photos by E. Kruidenier.

extensorius, medially displaced condylus medialis, fossa intercondylaris very wide and shallow, distal opening of canalis extensorius circular, a less pronounced difference in width of the condylus lateralis and condylus medialis, condylus medialis projecting further cranially than condylus lateralis, a reduced epicondylus lateralis and a modestly developed epicondylus medialis, a reduced sulcus m. fibularis, a deep sulcus extensorius and the lateral half of pons supratendineus sunken.

Type locality. Posticchia 5 fissure filling, Gargano pedemountain belt (41.8° N, 15.4° E), Province of Foggia, Italy.

4. Description

The holotype of *Garganornis ballmanni* (RGM 443307, Fig. 2) consists of the distal end and part of the shaft of the left tibiotarsus. The bone surface is cream coloured with reddish stains. Overall, the bone has a heavy and stout appearance. Measurements: maximal length of fragment: 64.4 mm; maximal distal width: 37.1 mm; (proximodistal) height of tendinal bridge: 6.8 mm; minimum width of shaft: 21.51 mm; minimum depth of shaft: 15.8 mm.

The cortical bone wall is thick, ranging from 3–3.5 mm on the facies caudalis to 7–8 mm on the facies cranialis. In cross-section, the facies cranialis is flat and the facies caudalis is convex caudally. The sulcus extensorius (Fig. 2) is deep and located on the central axis of the shaft. The sulcus extensorius is medially bordered by a pronounced tuberositas retinaculum extensoris medialis, which slightly overhangs the sulcus. The pons supratendineus is high and attains a slightly medial position on the bone. Although its orientation is horizontal, the lateral half of the pons

supratendineus is sunken and forms a depression upon merging with the shaft. Disto-laterally of this depression lies the triangular tuberositas retinaculum extensoris lateralis. Proximal of the tuberositas retinaculum extensoris lateralis lies the tuberculum retinaculi m. fibularis medialis. The tuberculum retinaculi m. fibularis lateralis is hardly visible. Although there is very slight abrasion of the bone surface, it appears that the tuberculum retinaculi m. fibularis lateralis has not been very distinct. The canalis extensorius opens distally of the sulcus extensorius as a circular foramen centred immediately proximal to the fossa intercondylaris and at equal distances from either of the condyli. On the medial and lateral sides of the distal opening of the canalis extensorius lay the attachment sites for the medial and lateral crurae of the ligamentum meniscotibialis, with the medial point of attachment more pronounced than the lateral one. The fossa intercondylaris is very wide, approximately 2/3 of the maximal width across the condyli, and in distal view attains a relaxed U shape rather than a V shape. The condylus medialis is offset medially from the shaft. The caudal portions of both condyli are missing so that condylar shape and depth cannot be determined. Of the condylus lateralis also the cranial and distal portion are damaged. The epicondylus lateralis itself is eroded as well, but the depressio epicondylaris lateralis is still mostly intact. This suggests that only a limited part of the lateral side of the condylus lateralis is missing. The outline in distal view of the condylus lateralis is reconstructed in Fig. 2c. The condylus medialis is more intact, with only its caudal side missing. The epicondylus medialis is more pronounced, and the depressio epicondylus medialis is also deeper than the depressio epicondylus lateralis.

Table 1

Measurements (in mm) of *Garganornis ballmanni* n. gen. et n. sp. and selected Anseriform taxa. Note that the distal articulation is damaged in *G. ballmanni*, and distal width is underestimated.

Tableau 1

Mesures en millimètres de *Garganornis ballmanni* n. gen. et n. sp. et de taxons d'ansériformes sélectionnés. À noter que l'articulation distale est endommagée chez *G. ballmanni* et que la largeur distale est sous-estimée.

Species	Distal width	Width shaft	Depth shaft
<i>Garganornis ballmanni</i> RGM 443307 ^a	36.6	21.5	15.8
<i>Anhima cornuta</i>	20.1	10.9	7.8
<i>Chauna chavaria</i>	21	10.1	8
<i>Anas p. platyrhynchos</i> (n = 2)	9.2	4.5	3.5
<i>Branta leucopsis</i>	14.1	6.6	5.0
<i>Anser anser</i>	19.0	9.5	7.1
<i>Cygnus olor</i> (n = 2)	24.4	10.6	8.5
<i>Cygnus bewickii</i> (n = 2)	21.4	10.1	7.6
<i>Cygnus cygnus</i> (n = 2)	26.3	11.2	7.8
<i>Cnemionis calcitrans</i> (n = 4) ^a	35.9	19.4	15.3
<i>Cygnus falconeri</i> ^a	34.9	16.9	–

^a Denotes extinct species.

The impressio ligamentum collateralis medialis is prominent and extends proximally well up the shaft. Despite the damage, the width of the condyles is interpreted as the condylus lateralis being somewhat wider than the condylus medialis. In distal view (Fig. 2c), the condylus medialis projects further anteriorly than the (reconstructed) condylus lateralis. The facies caudalis bears very few distinctive features as the condyli lack the caudal portion.

5. Discussion

The distal left tibiotarsus described here represents a new genus and species of Anseriformes, *G. ballmanni*, based on distinct morphological characteristics. *G. ballmanni* represents the third, and largest, anseriform from the Miocene of Gargano, in addition to *Anas velox* and Anatidae indet (Pavia, 2013). Little is known regarding the origin of the Miocene Gargano avifauna, but there are indications that the Gargano avifauna is related to that of the Middle Miocene avifauna of La Grive-Saint-Alban in France. Ballmann (1973) considered the buteonine eagle *Garganoetus murivorus*, to be closely related to *Aquila delphinensis* of the La Grive avifauna. More recently, Göhlich and Pavia (2008) described a new species of phasianid from the Neogene of Gargano, *Palaeortyx volans*, which they considered to be closely related to *P. grivensis* from La Grive. Unfortunately, no species of anseriform is known from La Grive-Saint-Alban (Ballmann, 1969). *G. ballmanni* represents a large-bodied addition to the Miocene avifauna from Gargano. The tibiotarsus of *G. ballmanni* is 30% larger than that of the largest extant anseriform, *Cygnus olor* (Table 1). Based on the minimum circumference of the tibiotarsus fragment, the estimated body mass for *G. ballmanni* is 22.3 kg, which is much larger than that of *C. olor* (Dunning, 2008; Iwaniuk et al., 2010). Note that the minimum circumference of the fragment is not the minimum circumference of the bone itself. Assuming a minimum (conservative) circumference for

the bone of approximately 20% smaller than that of the fragment gives a body mass estimate of 15.3 kg, which is closer to, but still larger than, the range reported for *Cygnus olor* (9.2–14.3 kg, Dunning, 2008). No wing bones that could potentially belong to *G. ballmanni* have been found so far, but it is reasonable to assume that *G. ballmanni* led a mostly terrestrial lifestyle and may have had a limited ability to fly. The large size of *G. ballmanni* mirrors that of other Gargano birds, such as the hawk *Garganoetus murivorus* and the barn owl *Tyto gigantea* (Ballmann, 1973), and is most likely an adaptation to an insular environment where mammalian carnivores are rare or completely absent. Note that while insular birds of prey seem to increase in size and fill the empty niche of mammalian predator, insular waterfowl often increase in size and become major terrestrial herbivores. The most remarkable examples of gigantism in insular waterfowl are the Hawaiian waterfowl, i.e. the moa-nalo and giant Hawaii geese, which developed gigantism, flightlessness and terrestrial herbivory in the absence of mammalian herbivores (Paxinos et al., 2002). *G. ballmanni* might have followed a similar scenario that led to large body size and a lifestyle characterized by terrestrial herbivory.

5.1. Phylogenetic relationships

The medially deflected condylus medialis, the cranial projection of the condylus medialis, and the central placement of the canalis extensorius over the fossa intercondylaris of *G. ballmanni* n. gen. et n. sp. are considered synapomorphies of Anseriformes (Ericson, 1997; Livezey, 1986), and place *G. ballmanni* firmly in this group. However, *G. ballmanni* also displays characters that are reminiscent of the large-bodied extinct basal lineages of Dromornithidae, Gastornithidae and Presbyornithidae. Whereas Gastornithidae (Late Palaeocene to Middle Eocene of Europe and Early Eocene of North America (Mayr, 2009)) are considered a sister group to Anseriformes (Andors, 1992), Dromornithidae (Palaeogene and Neogene of Australia (Murray and Vickers-Rich, 2004)) and Presbyornithidae (Palaeogene of the New World as well as Mongolia and the London Clay (Kurochkin and Dyke, 2010; Mayr, 2009)) have been grouped within crown-group Anseriformes (Ericson, 1997; Livezey, 1997; Murray and Vickers-Rich, 2004). However, it has been pointed out that Presbyornithidae share morphological features with more basal groups (Elzanowski and Stidham, 2010) and might be outside Anseriformes. Upper Paleocene and Early Eocene *Gastornis* tibiotarsi from France have been described by Buffetaut (1997; 2008). *G. ballmanni* shares several features with *Gastornis*, such as a wide fossa intercondylaris, the circular opening of the distal canal, a deep sulcus extensorius and a pons supratendineus with a depression on the lateral end (Buffetaut, 2008) (Fig. 3a), but it differs from *Gastornis* in lacking the strong peroneal ridge (the sulcus m. fibularis) and having the distal opening of the canalis extensorius placed at equal distances from both condyles (a more medial position in *Gastornis*). The similarities between *Gastornis* and *G. ballmanni* are interesting, but the presence of Gastornithidae in Miocene Gargano is considered unlikely,

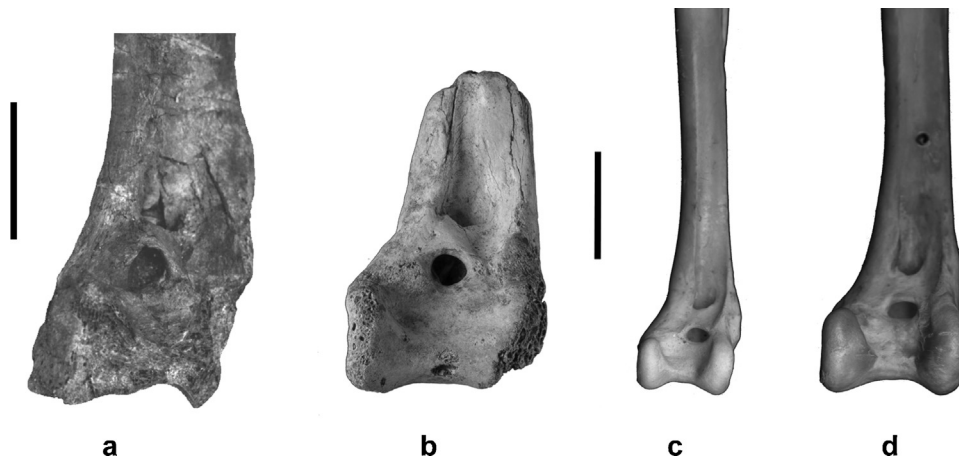


Fig. 3. Left tibiotarsi of selected anseriform taxa and *Garganornis ballmanni* n. gen. et n. sp. in cranial view. (a) *Gastornis parisiensis*, MDE-A18, Early Eocene of Saint-Papoul, Aude, France, reprinted with permission from Buffetaut, 2008; (b) *Garganornis ballmanni* n. gen. et n. sp. (c) *Branta canadensis*, NMNH 489759, (d) *Cygnus buccinator*, NMNH 432534. Scale bar for (a) 5 cm, scale bar (b–d) 2 cm.

Fig. 3. Tibiotarses gauches de taxa ansériformes et de *Garganornis ballmanni* n. gen. et n. sp. en vue crâniale. (a) *Gastornis parisiensis*, MDE-A18, Éocène inférieur de Saint-Papou, Aude, France, reproduit avec l'autorisation de Buffetaut, 2008; (b) *Garganornis ballmanni* n. gen. et n. sp.; (c) *Branta canadensis*, NMNH 489759; (d) *Cygnus buccinator*, NMNH 432534. Barre d'échelle pour (a) 5 cm, pour (b–d) 2 cm.

as there is no evidence for the survival of Palaeogene faunal elements in the Gargano fauna. Furthermore, this scenario would require Gargano to have been dry land since at least the Middle Eocene, which is unlikely in this tectonically active region. *G. ballmanni* shares with Presbyornithidae (based on the descriptions by Ericson (2000)) the medial thrust of the distal end, a pronounced tuberositas retinaculum extensorius medialis and a broad and steep pons supratendineus, a deep sulcus extensorius and a poorly developed epicondylus medialis and lateralis (although the epicondylus medialis is more distinct than the epicondylus lateralis in *G. ballmanni*), but *G. ballmanni* differs from Presbyornithidae in the absence of a well-marked sulcus m. fibularis with a foramen (present in Presbyornithidae) and a less pronounced difference in width of the condyli. Dromornithid tibiotarsi display the general anseriform bauplan with a medially displaced condylus medialis and a centrally placed distal opening of the canalis extensorius (Murray and Vickers-Rich, 2004). A more detailed study of the basal dromornithid *Barawertornis tedfordi* (Nguyen et al., 2010) shows a fossa intercondylaris that is deeper and narrower than in *G. ballmanni*. In addition, Nguyen et al. (2010) describe *B. tedfordi* as having condyli that are about equal in cranial extent, and the condylus medialis being wider than the condylus lateralis, which is in contrast to the character states observed in *G. ballmanni*.

Crown-group Anseriformes include the South American Anhimidae (screamers), the Anseranatidae (magpie geese) of Australia and New Guinea, and the globally distributed Anatidae (swans, geese and ducks) (Ericson, 1997; Hackett et al., 2008; Livezey, 1997; Worthy et al., 1997). Despite their global distribution and range of sizes and shapes, *G. ballmanni* differs from all extant Anseriformes by a significantly wider and shallower fossa intercondylaris, a less marked difference in width between the condylus medialis and condylus lateralis, and a circular distal opening

of the canalis extensorius. Both Anhimidae and Anseranatidae display distinct tuberculi retinacula m. fibularis medialis and lateralis, forming a clear sulcus m. fibularis, which is absent in *G. ballmanni*. Anhimidae also display characteristic skeletal pneumatisation (Alvarenga, 1999; O'Connor, 2004), but there is no sign of pneumatisation in *G. ballmanni*. Interestingly, within extant Anseriformes, *G. ballmanni* mostly resembles the Anserinae; they display a relatively wide fossa intercondylaris, and a less distinct sulcus m. fibularis (Fig. 3b–d). In addition, in cranial view, the medial side of the shaft that flares towards the medial condyle starts more proximally in Anserinae than in other groups.

Several fossil Anserinae have been described from the Late Eocene to the Pleistocene of Europe, but only a few taxa have the tibiotarsus preserved. The earliest representatives of Anatidae are the Romainvillinae from the Late Eocene to the early Late Oligocene (Lebedinsky, 1927; Mayr, 2008; Mayr and De Pietri, 2013). A large, goose-sized representative of the Romainvillinae from the Late Oligocene of France, *Saintandrea chenoides*, was described by Mayr and De Pietri (2013). The tibiotarsus of *S. chenoides* displays a distinct attachment for the distal fibula, absent in *G. ballmanni*, and a narrow fossa intercondylaris (wider in *G. ballmanni*). From the Lower Miocene of Germany comes *Cygnavus senckenbergi* Lambrecht, 1931, but this species is much smaller than *G. ballmanni* (width at the height of the pons supratendineus is 16 mm (Lambrecht, 1931)), versus 27.4 mm in *G. ballmanni*. The Early Miocene *Cygnopterus alphonsi* Cheneval, 1984, from Saint Gerand le Puy displays a very broad distal opening of the canalis extensorius, unlike *G. ballmanni*, and is smaller. *Cygnavus formosus*, from the Oligocene of Kazakhstan (Kurochkin, 1968), is smaller than *G. ballmanni*, has an elliptical distal opening of the canalis extensorius and a more narrow fossa intercondylaris. The Middle Pleistocene giant swan *Cygnus falconeri*, endemic to Malta and Sicily (Parker, 1867) is similar to

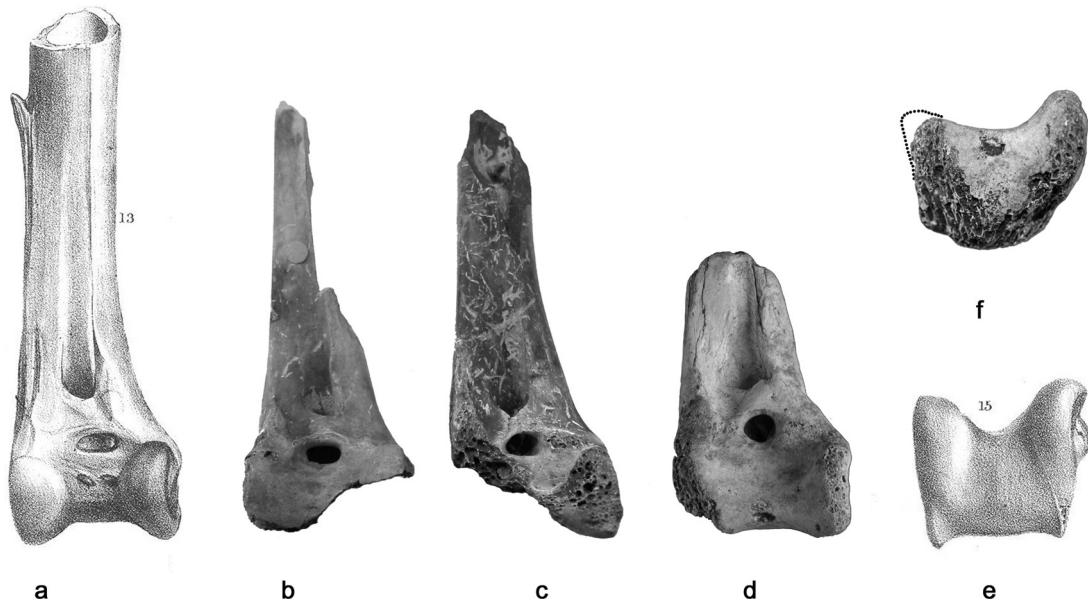


Fig. 4. Distal tibiotarsi of *Cygnus falconeri* from the Pleistocene of Malta and Sicily, and *Garganornis ballmanni* n. gen. et n. sp. from the Miocene of Gargano. (a) Right distal tibiotarsus, holotype, of *C. falconeri* as illustrated in Parker, 1867 (reprinted here with permission); right distal tibiotarsi of *C. falconeri*, (b) BMNH49323 and (c) BMNH49324; (d) *Garganornis ballmanni* n. gen. et n. sp. RGM 443307; (e) *C. falconeri*, holotype, in distal view as illustrated in Parker, 1867; (f) *Garganornis ballmanni* n. gen. et n. sp. RGM 443307 in distal view. Images are scaled to match in size. Note that (d) and (f) are mirror images from the original.

Fig. 4. Tibiotarses de *Cygnus falconeri* du Pléistocène de Malte et de Sicile et *Garganornis ballmanni* n. gen. et n. sp. du Miocène du Gargano. (a) Tibiotarse distal droit, holotype de *C. falconeri* tel qu'illustré in Parker, 1867 (reproduit ici avec autorisation) ; tibiotarses distaux droits de *C. falconeri* (b) BMNH49323 et (c) BMNH49324 ; (d) *Garganornis ballmanni* n. gen. et n. sp. RGM 443307 ; (e) *C. falconeri*, holotype en vue distale tel qu'illustré in Parker, 1867 ; (f) *Garganornis ballmanni* n. gen. et n. sp. RGM 443307 en vue distale. Les images sont ajustées pour être bien assorties en taille. À noter que (d) et (f) sont le reflet de l'original.

G. ballmanni in size (Table 1), but differs from the Gargano specimen in a number of morphological features; the distal opening of the canalis extensorius is oval in *C. falconeri* and is set more distally with respect to the medial condyle than in *G. ballmanni* (Fig. 4). In addition, the intercondylar fossa in *G. ballmanni* is much wider than in *C. falconeri*, which becomes evident in distal view (Fig. 4e–f). Interestingly, *G. ballmanni* also shares similarities with the fossil geese from the Hawaiian archipelago. The Big Island Goose *Branta rhuax* (Olson, 2013) and the moa-nalo *Thamnetochon chauliodous* are both large, flightless geese and display a relatively wide fossa intercondylaris (although less wide in *T. chauliodous*). *Branta rhuax* also displays a reduced difference in condylar width, similar to the condition in *G. ballmanni*. However, the tuberculum retinaculi m. fibularis lateralis is well developed in *B. rhuax* and *T. chauliodous*, and *B. rhuax* also displays a well-marked sulcus m. fibularis. A broad fossa intercondylaris and a reduced difference in condylar width were also observed in the extinct, flightless New Zealand goose *Cnemiornis calcitrans*.

6. Conclusion

G. ballmanni n. gen. et n. sp. displays morphological features that are characteristic for Anseriformes, but differs from all extant and fossil Anseriformes, as well as from taxa closely related to Anseriformes. Given the marked differences between *G. ballmanni* and related taxa, as well as the fact that important diagnostic features of the condyles are not preserved, I consider an “incertae sedis” position

most appropriate. It should be noted however, that insular evolution can result in morphologies that deviate from the ancestral state, and make it difficult to trace a taxon's ancestry. The observed similarities between *G. ballmanni* and basal taxa might indicate that *G. ballmanni* represents an insular relict of one of these basal lineages. Although insular environments can serve as refugia and preserve stem lineages, an alternative hypothesis considers *G. ballmanni* a species of waterfowl highly adapted to an insular environment, with a morphology that is interpreted as adaptations to a terrestrial lifestyle in an environment where mammalian carnivores are rare. Given similar adaptations in waterfowl from other islands and the highly insular nature of the Gargano fauna, I consider the latter scenario most likely. *G. ballmanni* thus represents an example of convergent evolution of waterfowl in island ecosystems.

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Appendix. List of specimens used in comparison.

Anhimidae *Chauna chavaria* MNMH 18996, *C. torquata* RMNH 3641, RMNH 6984, MNMH 635723; *Anhima cornuta* MNMH 18588.

Anseranatidae *Anseranas semipalmata* RMNH 25002, MNMH 347638, MNMH 621019.

Anatidae *Aix sponsa* MNMH 500362; *Alopothen aegyptiacus* MNMH 431687; *Amazonetta brasiliensis* MNMH 630177; *Anas p. platyrhynchos* RMNH 106153, RMNH 106154; *A. strepera* RMNH 86424; *Anser albifrons* MNMH 610517; *A. anser* RMNH 33–2, MNMH 290499; *A. caerulescens* MNMH 319918; *A. indicus* RMNH 7480; *Aythya fuligula* RMNH 9390, MNMH 432303; *A. ferina* MNMH 431534, 560588; *Branta b. bernicula* RMNH 86422, RMNH 86421, MNMH 553108; *B. canadensis* MNMH 555497, MNMH 489759; *B. leucopsis* RMNH 34–1, RMNH 34–2, RMNH 13357; *Bucephala clangula* MNMH 488592; *B. c. clangula* RMNH 90380; *B. islandica* MNMH 488596; *Cereopsis novaehollandia* no number (RMNH); *Clangula hyemalis* MNMH 561033; *Coscoroba coscoroba* no number (RMNH); *Cygnus atrata*, RMNH 1215, MNMH 345212; *C. bewickii* RMNH 80788, RMNH 104875; *C. buccinator* RMNH 104876, MNMH 432534; *C. cygnus* RMNH 86426, RMNH 104867; *C. olor* RMNH 9408, RMNH 104864, MNMH 344839; *Dendrocygna arcuata* RMNH 1659; *D. bicolor* RMNH 2056, MNMH 488132; *D. guttata* MNMH 560773; *Melanitta nigra* RMNH 11316; *Mergus merganser* RMNH 86431; *Neochen jubatus* MNMH 346907, MNMH 620513; *Netta rufina* MNMH 621199; *N. peposaca* MNMH 227348; *Nettapus coromandelianus* MNMH 318553; *N. auritus* MNMH 347388; *Oxyura dominica* MNMH 430928; *O. jamaicensis* MNMH 492433, 492491; *Somateria m. mollissima* RMNH 80999; *S. m. v-nigrum* MNMH 431986; *S. spectabilis* MNMH 620821; *Tachyeres brachypterus* RMNH 34414; *T. pteneres* MNMH 490930; *Tadorna tadorna* RMNH 86425, MNMH 432291; *T. variegata* MNMH 621375.

Phoenicopteridae *Phoenicopterus ruber* RMNH 106142; *P. chilensis* RMNH 6517.

Fossil species *Cnemionis calcitrans*, Pleistocene of New Zealand, BMNH A 2078, BMNH A 2080, BMNH A1561, BMNH A 2079; *Cygnus falconeri*, Pleistocene of Malta, BMNH49323, BMNH49324; *Branta rhuax*, Holocene of Hawaii, MNMH 560329; *Thambetochen chauliodous*, Holocene of Hawaii, MNMH 560328.

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