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**“Terror cranes” or peaceful plant-eaters:**
changing interpretations of the palaeobiology of gastornithid birds

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Abstract
Since the original description of a gastornithid in 1855, widely divergent hypotheses about the palaeobiology of these Early Tertiary giant birds have been put forward. Early interpretations, based on scanty material, often suggested aquatic habits. A faulty skeletal reconstruction by Lemoine in 1881 hindered the recognition of the close similarities between the European *Gastornis* and the North American *Diatryma*. After the description of a nearly complete skeleton from Wyoming in 1917, most reconstructions were based on it. The hypothesis of carnivorous gastornithids, on the model of the South American phorusrhacids, gained wide acceptance in the mid-20th century, and these giant birds were often considered as having competed with mammals. The alternative view of plant-eating gastornithids has gained ground since the 1990s, but their image as predators remains popular, partly on the basis of erroneous conceptions about their osteology. Contrary to what many reconstructions show, gastornithids had a short tarsometatarsus, a beak that was not hooked, and ungual phalanges that were more hoof-like than claw-like.

Keywords

Résumé
«Grues terrifiantes» ou paisibles végétariens: interprétations contradictoires de la paléobiologie des oiseaux gastornithidés.- Depuis la première description d’un gastornithidé en 1855, des hypothèses très divergentes ont été proposées au sujet de la paléobiologie de ces oiseaux géants du Paléogène. Les premières interprétations, fondées sur un matériel fragmentaire, suggéraient souvent des mœurs aquatiques. La reconstitution erronée publiée par Lemoine en 1881 empêcha de reconnaître les ressemblances étroites entre le *Gastornis* européen et le *Diatryma* nord-américain. Après la description d’un squelette presque complet venant du Wyoming en 1917, la plupart des reconstructions le prirent pour base. L’hypothèse de gastornithidés carnivores, sur le modèle des phorusrhacidés sud-américains, se répandit au milieu du XXe siècle, et ces oiseaux géants furent souvent considérés comme ayant été des concurrents des mammifères. La conception adverse suivant laquelle les gastornithidés se nourrissaient de végétaux a gagné du terrain depuis les années 1990, mais leur image de prédateurs demeure populaire, en partie à cause de conceptions erronées au sujet de leur ostéologie. Contrairement à ce que montrent nombre de reconstructions, les gastornithidés avaient un tarsometatarsus court, un bec qui n’était pas crochu et des phalanges unguéales ressemblant plus à des sabots qu’à des griffes.

Mots-clés

I. INTRODUCTION
Reconstructions of the giant bird *Gastornis* (frequently called *Diatryma*, a junior synonym) frequently feature in books and films about “prehistoric animals”, where it is usually depicted as a ferocious carnivore preying on the small mammals of the Early Tertiary. The fact that an alternative reconstruction of the palaeobiology of *Gastornis*, namely as a plant-eater, has also been put forward is often omitted, in favour of the far more spectacular interpretation as a “terror crane” (Kurtén, 1971). A review of the interpretations of the habits and diet of *Gastornis* since the first discoveries in the 1850s shows that interpretations have much varied over time, sometimes on the basis of erroneous reconstructions and doubtful comparisons. The purpose of the present paper is to critically examine these changing interpretations, from a historical point of view, as a basis for further investigations into the palaeobiology of *Gastornis*.

As first suggested by Coues (1884), and much more recently by Buffetaut (1997a, 2000, 2008), and as accepted by various authors (e.g. Mlîkovský, 2002; Mayr, 2009), *Diatryma* is herein considered as a junior synonym of *Gastornis*; both names are employed according to the way they have been used by previous authors.
II. THE EARLIEST INTERPRETATIONS

Gastornis remains were first discovered by the physicist Gaston Planté at Meudon, a western suburb of Paris, in 1855 (Buffetaut, 1997b). Although they were far from complete, consisting of an isolated tibiotarsus, to which a femur was soon added, they elicited much attention among the palaeontological community, because they indicated a very large bird of great geological antiquity (coming as they did from the basal Eocene, they were among the oldest bird remains known at that time). Speculations about the possible habits of Gastornis parisiensis were put forward in several of the papers that appeared in the 1850s about that giant bird. Whereas Valenciennes (1855) compared it with the albatross, Hébert (1855) considered that it was too heavy to have been able to fly. Prévost (1855) thought that it was as heavy as a horse, and able both to swim like a swan and to stand on one leg like a stork. The idea of a semi-aquatic Gastornis did not appeal to Owen (1856), who gave the first detailed and illustrated description of the tibiotarsus from Meudon; according to him it was more terrestrial than aquatic. Not surprisingly since they were based on the scanty original material from Meudon, the first interpretations of the habits of Gastornis were thus either vague or fanciful.

III. VICTOR LEMOINE’S RECONSTRUCTION

The first to propose a full skeletal reconstruction of Gastornis was Lemoine (1881). This was based on a number of bones from the Palaeocene of Cernay, near Reims in eastern France. Lemoine’s reconstruction showed a tall but rather slenderly built bird with a long neck, short wings and long legs (Fig. 1). This reconstruction was accepted by most authors for more than a century, until Martin (1992) showed that Lemoine had unwittingly incorporated in it skeletal elements belonging to various non-avian forms, including fishes and reptiles. Lemoine thought that the supposed wing bones (which were shown by Martin to be entirely non-avian) indicated a paddle-like limb suggesting aquatic habits. On the other hand, the tarsometatarsus was reconstructed by Lemoine (1878, 1881) as very long and slender, but, as noted by Martin (1992, p. 100): “The tarsometatarsus illustrated by Lemoine was enormously elongated by plaster restoration (Lemoine, 1878: pl. 3, figs. 1-3), and it includes fragments of a gastornithid femur and tibiotarsus”. Complete tarsometatarsi (Fig. 2) from Germany (Fischer, 1978) and France (Martin, 1992) have shown that European gastornithids, like their North American counterparts (see below) had short and broad tarsometatarsi. The erroneously elongated tarsometatarsus in Lemoine’s reconstruction may have influenced later reconstructions of gastornithids. Be that as it may, for a long time Lemoine’s erroneous reconstruction impeded the recognition of the very close similarities between European and North American gastornithids (Buffetaut, 1997b).

IV. DIATRYMA, AN AMERICAN GASTORNITHID

Cope (1876, 1877) described as Diatryma gigantea a fragmentary tarsometatarsus of a very large bird from the Early Eocene of New Mexico, and noted that its closest ally would probably turn out to be the European Gastornis. For several decades, however, the North American material contributed little to an understanding of gastornithid palaeobiology, because, although more fossils were discovered (Shufeldt, 1913), the available specimens were too fragmentary to provide much information about the osteology of the American giant bird. Shufeldt (1913) thought it was a huge ratite close
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to rheas, but admitted that many uncertainties remained about its anatomy. In addition, although Coues (1884) suggested that *Diatryma* and *Gastornis* were synonymous, possible affinities with the European giant bird were much disputed, and often rejected (Shufeldt, 1913), all the more easily that Lemoine’s faulty reconstruction was not questioned and obviously did not provide a reliable basis for comparisons (Buffetaut, 1997b).

V. THE SOUTH AMERICAN PHORUSRHACIDS
-A MODEL FOR GASTORNITHID PALAEOBIOLOGY?

Beginning in the late 1880s, palaeontological expeditions to Patagonia revealed that the South American continent had been inhabited during the Tertiary by giant flightless birds, the Phorusrhacidae, or Stereornithes, as they were often called (Moreno & Mercerat, 1891; Ameghino, 1895; Andrews, 1899). These birds attracted much attention among the international palaeontological community, notably because of their huge skulls (often described at the time as as big as that of a horse). Their large, sharply hooked beaks and talon-like ungual phalanges clearly indicated a carnivorous diet (Ameghino, 1895).

On the basis of size and of superficial similarities, possible affinities with *Gastornis* were sometimes mentioned. Lucas (1903, p. 556) suggested that *Diatryma* might be allied to the “Stereornithes”, basing his supposition on a comparison between the type of *Diatryma gigantea* and “an indifferent cast of *Brontornis*”. Interestingly, the sturdy tarsometatarsus of *Gastornis/Diatryma* does not resemble that of *Brontornis*, which is much more heavily built than other phorusrhacids and may not be a phorusrhacid at all (Agnolin, 2007). The idea of close relationships between gastornithids and phorusrhacids was eventually rejected by most authors (interestingly, it was recently revived by Bourdon & Cracraft, 2011). Nevertheless, the discovery of the Phorusrhacidae showed that very large carnivorous flightless birds, without any real equivalent in the modern world, had once existed, and this probably influenced later reconstructions of gastornithids, all the more so that the large beak of the latter appeared to be superficially similar to that of phorusrhacids. In many textbooks and popular publications, gastornithids and phorusrhacids are discussed together, thus suggesting analogies in biology and behaviour. However, they in fact differ in many points of their osteology, the phorusrhacids exhibiting various cursorial and predatory adaptations not seen in gastornithids (Fig. 3). Some commonly encountered inaccuracies in reconstructions of gastornithids (see below) may have been “borrowed” from features that are really present in phorusrhacids.

Fig. 2: A *Gastornis* tarsometatarsus from the Palaeocene of Bernu (eastern France) showing the real proportions of this relatively short and broad bone. Scale bar: 50 mm.
VI. THE *DIATRYMA* SKELETON FROM WYOMING

In 1916, a field party from the American Museum of Natural History discovered a nearly complete gastornithid skeleton in the Lower Eocene rocks of the Bighorn Basin of Wyoming. The specimen was described a year later as *Diatryma steini* by Matthew & Granger (1917). This find enormously increased our knowledge of the osteology of gastornithids and made possible the first well supported skeletal reconstruction of one of these birds. However, the reconstruction published by Matthew and Granger (Fig. 4) not unexpectedly was thoroughly different from the fanciful reconstruction of *Gastornis* published by Lemoine (1881). As noted by Buffetaut (1997b), this considerably delayed the recognition of the very close similarities (amounting to identity at the generic level) between the European *Gastornis* and the North American *Diatryma* (although Matthew and Granger suspected that Lemoine’s reconstruction possibly was at least partly incorrect). The reconstruction by Matthew and Granger showed a rather stockily built bird, with a huge beak, quite different from the more slender bird, with a smaller skull, envisioned by Lemoine. The tarsometatarsi of the skeleton from Wyoming were incomplete, only the proximal and distal ends being preserved, and interestingly Matthew and Granger reconstructed them with an exaggeratedly elongate shaft, just as Lemoine had done for *Gastornis* in 1881. No reason was given by Matthew and Granger for that reconstruction, and it can only be surmised that they were influenced by the elongate tarsometatarsals of various cursorial large birds. Although Matthew and Granger (1917) rejected any close affinities between phorusrhacids and *Diatryma* (which they thought had to be placed in an order of its own), they admitted that they shared parallel adaptations and that in particular the skulls were superficially alike (although they rightly noted that the beak of *Diatryma* lacks a decurved tip). Although they did not dwell much on the palaeobiology of *Diatryma*, they remarked (Matthew & Granger, 1917, p. 319) that it resembled *Phorushacos* “in size and proportions and was probably of similar habits”. What those habits were was not specified, but phorusrhacids were (and still are) generally considered as carnivorous.

Matthew & Granger (1917) also published a life reconstruction (by Erwin Christman) of *Diatryma steini* in an Eocene landscape (Fig. 5B), using the cassowary as a guide for the external characters (e.g. the plumage). This drawing served as a basis for many subsequent reconstructions. The giant bird was the only animal depicted and no clues were offered about the possible diet of *Diatryma*. In accordance with the skeletal reconstruction, the tarsometatarsus was unduly elongate.

VII. GASTORNITHIDS AS PREDATORS AND AS COMPETITORS OF MAMMALS

Matthew and Granger’s suggestion that *Diatryma* shared similar habits with phorusrhacids does suggest that they considered this giant bird as a carnivore, although they did not mention a specific diet. Heilmann (1926, p. 173) was among the first to explicitly interpret *Diatryma* as a predator, writing that “in all probability it lived on small reptiles and mammals, which it could easily overtake and kill at a blow with its heavy beak”. The concept of carnivorous gastornithids was subsequently accepted by a number of authors (e.g. Simpson, 1950; Storer, 1960; Kurtén, 1971; Gould, 1986).

The reconstruction of gastornithids as large predators then grew into the speculation that they had competed with mammals in the Early Tertiary. This was clearly expressed by Romer, beginning in the 1930s, in several of his influential books on vertebrate palaeontology.
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(Romer, 1954, 1966). The following quotation (Romer, 1954, p. 107) summarizes this viewpoint:

“Diatryma, a fossil wingless bird from Wyoming, was a contemporary of the earliest horses. The horse, at that time, was the size of a fox terrier; this bird was seven feet tall.

These giant early birds arouse one to speculation; their presence suggests some interesting possibilities – which never materialized. At the end of the Mesozoic, as we have seen, the great reptiles died off. The surface of the earth was open for conquest. As possible successors, there were two groups, the mammals – our own relatives – and the birds. The former group succeeded, but the presence of such forms as Diatryma shows that the birds were, at the beginning, their rivals. What would the earth be like to-day had the birds won and the mammals vanished? 

Although no predation is mentioned, the emphasis clearly is on the size discrepancy between the giant birds and the early horses. However, although this seems to have escaped Romer and many of those who followed him, small early horses were not necessarily typical of the whole mammalian environment of gastornithids. For instance, in many Early Eocene formations in Europe, North America and China, Gastornis occurs together with the pantodont Coryphodon, which was nearly the size of a hippopotamus. Nevertheless, the idea of gastornithids as competitors of Early Tertiary mammals was taken up by various authors (e.g. Colbert, 1945; Piveteau, 1951, 1955; Swinton, 1965; Beaumont, 1973; Desmond, 1975; Gould, 1986; Chatterjee, 1997). It was generally combined with the hypothesis of a carnivorous diet and soon became popularized by reconstructions showing those giant birds chasing small mammals (usually early horses). The whole concept was summarized by Kurtén (1971, p. 48-49), who described Diatryma and related forms as “terror cranes” and noted: “Towering over the mammals of its day, this giant bird was fast enough to outrun them all and powerful enough to kill any one of them. It is almost as if the ancient reptile lines was making a final bid for the supremacy on land; for birds, of course, are descended from reptiles, and are cousins to the dinosaurs and crocodiles”. According to Kay & Colbert (1965, p. 615), Diatryma was a large predatory bird, which “was able to prosper only so long as the meat-eating mammals remained relatively small”; once they became larger, they out-competed the giant birds. Interestingly, it was not until 1991 that an attempt was made to support the hypothesis of carnivorous gastornithids on the basis of sound biomechanical evidence. Witmer & Rose (1991, p. 95) argued that the safety factors in the construction of the skull of Diatryma were too high for a herbivore and that “the traditional hypothesis of Diatryma as a carnivorous bird accords as well or better with the data at hand”. They considered that the very large biting forces exerted by the jaws of that giant bird enabled it to crush bones, and reconstructed it as both an active predator and a scavenger (the scavenging hypothesis had already been put forward by Lanyon, 1963, and Fischer, 1978).

Fig. 4: A: Reconstruction of the skeleton of “Diatryma” based on skeleton AMNH 6169 from the Lower Eocene of Wyoming, after Matthew & Granger (1917). The reconstructed shafts of the tarsometatarsi (arrows) are too long. B: Corrected reconstruction with shorter metatarsi.
VIII. GASTORNITHIDS AS PLANT-EATERS

Witmer and Rose’s detailed biomechanical study was partly a response to Andors’s thesis on *Diatryma* (Andors, 1988; see also Andors, 1992), in which he reconstructed the giant bird as a graviportal herbivore (or more accurately a folivore), on the basis of various osteological features and comparisons with living birds with a similar beak shape such as the takahe from New Zealand. Andors’s hypothesis followed a suggestion by Watson (1976), and was to some extent supported by his classification of the Diatrymiformes as the sister-group of the Anseriformes, a group of plant-eating birds – thus somehow reviving Milne-Edwards’s idea that *Gastornis* was close to ducks (Milne-Edwards, 1867-1868). Curiously enough, the hypothesis of affinities between gastornithids and ducks was shared by some authors who considered these giant birds as carnivores, including Swinton (1965) and Desmond (1975, p. 156), the latter going so far as to mention “ostrich-sized geese” roaming the countryside in England and France during the Eocene.

The discussion about the habits, and more specifically the diet, of gastornithids is going on between tenants of carnivory and supporters of herbivory/folivory, and no consensus has yet been reached. However that may be, any serious discussion of the palaeobiology of these giant birds must be based on an accurate knowledge of their osteology. Previous palaeobiological interpretations and life reconstructions of gastornithids have too often been based on inaccurate representations of various elements of their skeleton. Some of these inaccuracies are discussed below.

IX. SOME FREQUENT INACCURACIES IN GASTORNITHID RECONSTRUCTIONS

As noted above, many reconstructions of the skeleton of gastornithids have suffered from various inaccuracies which in turn have sometimes led to flawed palaeobiological inferences. The worst mistakes were made by Lemoine (1881) and not only hampered the recognition of the very close similarities between the European and North American gastornithids, but also led to unwarranted palaeobiological conclusions, notably about the forelimb which was considered by Lemoine to be somewhat paddle-like and suggestive of aquatic habits. Later reconstructions, being mainly based on the fairly complete skeleton AMNH 6069, from Wyoming, originally described by Matthew and Granger (1917), were more reliable but nevertheless contained various errors (Fig. 6), which are discussed below.

Exaggerated length of the tarsometatarsus

Lemoine’s reconstructions of the tarsometatarsus of *Gastornis* showed a long, slender bone (Lemoine, 1878, 1881). Martin (1992) showed that the length of the
metatarsus in Lemoine’s reconstructions was artificially exaggerated by the incorporation of various elements that did not really belong to that bone. Presumably, Lemoine, who only had incomplete specimens at his disposal, was influenced by the long and slender tarsometatarsi of present-day ratites. On the basis of complete specimens from France (Fig. 2), Martin (1992) was able to show conclusively that the tarsometatarsus of *Gastornis* was short and broad – a conclusion already reached by Fischer (1978), based on material from the Geiseltal identified by him as *Diatryma* (Fig. 5A).

Interestingly, Matthew & Granger (1917), working on the skeleton from Wyoming in which the tarsometatarsi were incompletely preserved, chose to reconstruct these bones as relatively long and slender (Fig. 4). Writing a few years earlier, Shufeldt (1913) had been more prudent and noted that it could not be determined whether the tibiotarsus was long and slender, or short and thick as in some moas. Despite the fact that more complete tibiotarsi were described by Sinclair (1928 – as *Omorhamphus*, considered as a juvenile *Diatryma* by Andors, 1992) and by Troxell (1931), showing that that bone was indeed short and broad, the inaccurate skeletal reconstruction by Matthew & Granger (1917) continued to be reproduced in countless publications, with implications about the locomotion of gastornithids. For instance, Simpson (1950, p. 342) noted that “the phororhacoids in South America, *Diatryma* in North America, and *Gastornis* in Europe all had cursorial proportions” and were “probably running predators”. Curiously enough, although Andors (1988, 1992) correctly recognized that the tarsometatarsus as reconstructed by Matthew & Granger (1917) was too long, and published correct drawings of the pelvic limb, he reproduced the skeletal reconstruction by Matthew and Granger unchanged. While admitting that the tarsometatarsus of *Diatryma* was proportionately short, Witmer & Rose (1991, p. 116) considered that this feature was “simply plesiomorphic” and did not imply that this bird was graviportal. Their life reconstruction of *Diatryma* feeding on small mammals (Witmer & Rose, 1991, fig. 16) showed it with an unrealistically long tarsometatarsus.

Graviportal habits were suggested for the gastornithid from the Geiseltal (*“Diatryma geiselensis”*) by Fischer (1978), who rightly insisted on the relative shortness of the tarsometatarsus and produced a life reconstruction of the bird with relatively short, robust pelvic limbs (Fig. 5). This restoration is certainly closer to the truth than those showing gastornithids with long tarsometatarsi, but not enough attention has been paid to it, and reconstructions of long-limbed, cursorial-looking gastornithids are still common (e.g. Paul, 2002).

Whatever its phylogenetic significance, the shape and relative length of the tarsometatarsus are of obvious importance for a reconstruction of the habits of *Gastornis* and certainly deserve more research from a biomechanical point of view. Despite Witmer and Rose’s comments, the proportions of the pelvic limb of *Gastornis* place it among the graviportal rather than the cursorial forms, as defined by Storer (1960), as already noted by Andors (1992). From that point of view, contrary to Simpson’s (1950) assertion, gastornithids differ considerably from the Phorusrhacidae, which have long, slender legs with a long tarsometatarsus (with the exception of the robustly built *Brontornis*, but see Agnolin, 2007, about the possible position of that genus outside the Phorusrhacidae). Fischer (1978) compared *Gastornis* with short-limbed moas such as *Pachyornis* (a conclusion also reached by Andors, 1992) and this comparison may be more relevant than supposed but weakly supported analogies with phorusrhacids. However, the implications of limb proportions for the possible diet of *Gastornis* are not obvious: whereas Andors (1992) used the presumably graviportal locomotion of gastornithids as evidence for a herbivorous diet, Fischer (1978) considered that these heavy, non-cursorial birds were scavengers.

**Hook-shaped bill**

Life reconstructions of gastornithids (e.g. Swinton, 1965, pl. 7; Kurtén, 1971, fig. 7) frequently show them with a beak ending in a decurved hook, as in birds of prey. Whereas phorusrhacids clearly had an upper jaw with a strongly downward curving hook-shaped tip (Ameghino, 1895; Andrews, 1899 – see Fig. 3), highly suggestive
of carnivorous habits, the skull of *Gastornis* does not show such a bony structure (Fig. 4). The premaxilla has a triangular tip which is not markedly deflected ventrally (Matthew & Granger, 1917; Fischer, 1978), and in this regard resembles some of the Australian dromornithids, notably *Bullockornis* (Murray & Vickers-Rich, 2004) much more than the phorusrhacids (compare Fig. 3 and 4). The juvenile gastornithid described by Sinclair (1928) as *Omorhamphus* does show a premaxillary tip that is slightly curved, but not really hook-shaped. As noted by Witmer & Rose (1991), in some birds the horny rhamphotheca can increase the curvature of the beak, but in fact it mostly accentuates the shape of the premaxillary bone, and it seems unlikely that *Gastornis* possessed a strongly hook-shaped horny beak. However, as pointed out by Witmer & Rose (1991), some carnivorous birds, such as storks, do not have a hooked beak, and Fischer (1978) compared the shape of the beak of gastornithids with that of the carrion-eating crow (*Corvus crassirostris*), a scavenger in which the beak is not hooked. Therefore, reconstructions showing *Gastornis* with a phorusrhacid-like strongly hooked beak are probably not correct, but this in itself does not imply that it was herbivorous.

**Claw-like ungual phalanges**

Some life reconstructions (e.g. fig. 7 in Kurtén, 1971) show gastornithids with strongly curved, claw-like toes (Fig. 6). Kurtén’s reconstruction clearly implies that these talons were used by the bird to attack its prey (in his figure a small condylarth). In fact, unlike the phorusrhacids, which had hooked ungual phalanges very similar to those of raptors, with strong flexor tubercles (Ameghino, 1895), gastornithids had unguals that were not much curved (Fig. 7). Andors (1988, p. 253-254) describes them as “rather short, pointed, moderately decurved and destitute of prominent flexor tubercles; the unguals of digits II-IV (especially III) are broad and decidedly hoof-like, whereas the ungual of digit I is relatively slender. The morphology of the unguals of the anterior toes indicates that the foot of *Diatryma* was better suited for cursorial ground activity than for perching or for grasping prey”. Recently described footprints referred to gastornithids from the Early Eocene of Washington State, USA, do not indicate raptor-like claws (Mustoe et al., 2012). If gastornithids were indeed predators, they must have used their beak much more than their toes for the capture of prey, whereas in phorusrhacids both were certainly involved.

**X. CONCLUSIONS**

From this brief review, it appears that interpretations of gastornithid palaeobiology have frequently been influenced by inaccurate reconstructions, and that some of these interpretations have become entrenched in both scientific and popular literature, without being much questioned. In particular, once the idea of gastornithids as large predators feeding on small mammals, and more generally as competitors of mammals during the Early Tertiary, had been proposed during the first half of the 20th century (notably by Romer), it soon became considered as well established scientific truth and was widely disseminated in scientific papers, textbooks and popular publications (and more recently in films). The later hypothesis of herbivorous gastornithids, although it was supported by evidence that could not easily be dismissed (notably in Andors’s works) and has been favoured by various authors (e.g. Mayr, 2009), is not gaining acceptance easily, perhaps because it runs against conventional wisdom and is less spectacular than the image of giant birds tearing apart hapless mammals. At least, some authors now present both hypotheses (Feduccia, 1999; Paul, 2002; Wallace, 2004).

This is not to say that the matter has been definitively settled in favour of the herbivory (or folivory) of gastornithids and that tenants of a carnivorous diet are just clinging to an outdated concept. The question remains open, although it is clear that if gastornithids were predators, their adaptations to that mode of life were significantly different from those of other carnivorous giant birds such as phorusrhacids. Other options have been put forward, such as scavenging (Fischer, 1978), although it should be admitted that it is difficult to find instances of exclusive scavengers among living terrestrial tetrapods. Whether gastornithids fed on animals (alive or dead) or on plants, or possibly on both, remains undecided, and it is hoped that renewed investigations, based at least in part on new techniques (such as isotopic geochemistry) will shed light on that question. Whether gastornithids competed with mammals for “supremacy” on the continents in the...
Early Tertiary also is a moot point. Beyond the slightly anthropomorphic undertones of the question, it should be remembered that the giant birds may have competed with mammals just as well whether they were herbivores, omnivores, or carnivores.

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REFERENCES


Cope, E.D. (1877) - Report upon the extinct Vertebrata obtained in New Mexico by parties of the expedition of 1874. Reports upon United States geographical surveys west of the one hundredth meridian, 4(2): 1-370.


Moreno, F.P. & A. Mercera (1891) - Catálogo de los pájaros fósiles de la República Argentina conservados en el Museo de La Plata. Anales del Museo de La Plata, Paleontología Argentina, La Plata, 1: 1-68.


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