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3 **Two New Gypaetinae (Accipitridae, Aves) from the late Miocene of**
4 **Spain**
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Two New Gypaetinae (Accipitridae, Aves) from the late Miocene of Spain

Abstract

Only three monospecific genera of extant accipitrids –*Gypaetus*, *Neophron* and *Gypohierax*– have been grouped into the Gypaetinae vultures, which currently presents an Eurasian and African geographic distribution. The fossil record of these genera is meager and not older than the Pleistocene of both landmasses. A surprising Old World vulture radiation occurred in North America from the early Miocene to the late Pleistocene, with taxa more closely linked to Gypaetinae than to Aegyptiinae. More recently new fossil gypaetines have been described for the late Miocene of North America and China. Two new species assigned to genera *Gypaetus* and *Neophron* are described here, and their links with other related taxa are evaluated. The new specimens were found at two sites in the Cerro de los Batallones, a rich late Miocene paleontological complex located in the center of Spain.

Keywords: Avian systematics; Accipitriiformes; diurnal raptors; Neogene birds.

Introduction

Old World vultures were traditionally considered closely related (Livezey and Zusi, 2007), but are now classified into two distantly related groups, Aegyptiinae and Gypaetinae. The extant Gypaetinae includes three monospecific genera: *Gypaetus*, *Neophron* and *Gypohierax*, distributed across southern Europe, Africa and throughout Asia, east to Tibet and India (del Hoyo et al., 1994). They constitute a more basal and separate clade from the Aegyptiinae (Lerner and Mindell 2005; Lerner 2007), the other vultures within Accipitridae. Lerner and Mindell (2005) suggest that *Eutriorchis astur* (Sharpe, 1875), an eagle endemic to Madagascar, could be closely related to the Gypaetinae. The fossil record of the Accipitridae dates back to the late Eocene / early Oligocene (Mayr 2009), but the earliest evidence of Gypaetinae is considerably more modern (Mayr, 2017). Two new vultures referred to Gypaetinae have recently been reported from the late Miocene of North America and China. *Anchigyps voorhiesi* Zhang et al., 2012a, from Nebraska (USA), similar in size to *Neophron percnopterus* and to the congeneric species described here. *Mioneophron longirostris* Li et al., 2016, from the Gansu Province (China), has been described from a quite complete skeleton and related to the extant *Neophron percnopterus*. The finding of *Gypaetus barbatus* (Linnaeus, 1758) in the early Pleistocene of the Iberian Peninsula (Montoya et al. 1999, 2001; Mlíkovský 2002) is so far the oldest record of the genus in the Old World (Europe, Asia and Africa). *Gypaetus osseticus* Burchak-Abramovich, 1973, from the late Pleistocene of Tsona (also known as Bugas-Klde, Georgia), was considered *nomen nudum* by Brodkorb (1978). Fossil findings referred to *Neophron* come from many middle and late Pleistocene sites and have been assigned to the recent species *Neophron percnopterus* (Linnaeus, 1758) (Lambrecht 1933; Tyrberg 1998).

The Neogene of North America has yielded a substantial collection of fossils referred to Old World vultures, Aegyptiinae and Gypaetinae (Wetmore 1943; Rich 1977; Zhang et al. 2012a; Li et al. 2016, and references therein). *Neogyps errans* Miller, 1916, from the late Pleistocene of Rancho La Brea (California, USA), was closely related to *Gypaetus* because of its clear resemblance to that genus by Miller (1916). Six species of

Neophrontops have been described in North America, dating back from the early Miocene to the late Pleistocene (Brodkorb 1964; Olson and Rasmussen 2001). Also fossil bones from early Miocene and ~~to~~ early Pliocene localities of North America have each been attributed to species of the genus *Palaeoborus* (Cope 1874; Wetmore 1936; Miller and Compton 1939). The absence of *Neophron* and related forms prior to the Pleistocene in the Eurasian and African record has led to the suggestion that *Neophron* may have originated from a dispersal of *Neophrontops* from North America (Feduccia 1974). Due to the presence of specific anatomical features for prey capture, *Palaeoborus* and *Neogyps* were viewed of more eagle-like aspect than *Neophrontops* and the extant *Neophron* (Miller and Compton 1939).

The paleontological sites of Cerro de los Batallones, located in the south of Madrid, in the middle of Spain, were formed at the beginning of the late Miocene (Tortonian Age). The faunal context points to the biozone MN 10, with deposition ages of *circa* 9 Ma (Morales et al. 2008, Calvo et al. 2013). So far, in two of the sites, Batallones 1 and Batallones 3, more than one hundred fossils of birds belonging to about twelve species have been found. Most of them correspond to diurnal raptors. In these two paleontological sites, Only galliform birds have previously reported (Sánchez Marco 2006, 2021).

The avian assemblage recorded does not constitute a representative sample of the birds that populated the surrounding areas. Carrion birds are predominate predominant in these paleontological sites, which also happens with regard to mammals (Morales et al. 2008). Two new Gypaetinae vultures found in Cerro de los Batallones are described and analysed here.

Material and Methods

The osteological terminology follows to Baumel and Witmer (1993) and Howard (1980). The systematic classification follows Lerner and Mindell (2005), Griffiths et al. (2007) and recommendation of the IOC World Bird List, version 11.2 (Gill et al. 2021). The fossil bones are housed in the Museo Arqueológico Regional de Madrid, Spain, with the labels shown in this paper.

Institutional abbreviations: MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain. NMNH, Division of Birds, National Museum of Natural History, Smithsonian Institution, Washington, USA. CAM, Arturo Morales personal collection, Laboratorio de Arqueozología, Universidad Autónoma de Madrid, Spain. LMUM, Veterinary Faculty of the Ludwig Maximilians University of Munich, Germany.

Specimens of extant species used for comparisons: *Necrosyrtes monachus* (NMNH-18894, 291440, 291441, 291442, 291443), *Gypohierax angolensis* (NMNH-224820, 226143, 291078, 291316), *Neophron percnopterus* (CAM 2, CAM 3, MNCN 26843, NMNH-17835), *Milvus migrans* (NMNH-319228), *Gypaetus barbatus* (CAM 2, CAM 3, MNCN 23330, NMNH-17834, 345684), *Circaetus cinereus* (NMNH-430776), *Terathopius ecaudatus* (NMNH-17836, 289742, 292912, 319919), *Trigonoceps occidentalis* (NMNH-320859, 347358), *Torgos tracheliotus* (NMNH-19990, 320977, 321827, 347597), *Aegipytus monachus* (NMNH-289569, 428040, 614152), *Gyps africanus* (NMNH-431403, 587405), *Gyps fulvus* (NMNH-229051), *Gyps rueppellii* (NMNH-430178), *Gyps coprotheres* (NMNH-561314) and *Gyps himalayanus* (NMNH-19534), *Haliaeetus albicilla* (CAM 2, CAM 3, LMUM 2, LMUM 11), *Haliaeetus vocifer* (LMUM 3), *Haliaeetus leucocephalus* (LMUM 2, LMUM 3). No morphological or size differences have been observed between *Necrosyrtes monachus* and *Necrosyrtes*

m. pileatus. In consequence, the race *pileatus* has no relevance for this study, and we refer it as to *Necrosyrtes monachus*.

Systematic Paleontology

Accipitriformes Voous 1973

Accipitridae Vieillot 1816

Gypaetinae Vieillot 1816

Gypaetus Storr 1784

Gypaetus georgii n. sp.

Holotype: One complete left carpometacarpus (Bat 3.2012.437).

Referred specimens: Batallones 1 site: cranial end of coracoideum and scapula (B-1968), two right humeri (Bat 1.171, Bat 1.175), left radius (Bat 1.915), one proximal end and shaft of left radius (Bat 1.2286), left os carpi radiale (Bat 1.2008.35), two left carpometacarpi (Bat 1.2005.287, Bat 1.1403), two right phalanges proximalis digiti majoris (Bat 1.2008.6, Bat 1.2004.68), right tibiotarsus (Bat 1.2005.6), crushed left tibiotarsus and complete fibula (B-1970, not “in situ”). Batallones 3 site: right scapula (Bat 3.2008.616), proximal end of left radius (Bat 3.2007.130), right phalanx proximalis digiti majoris (Bat 3.2008.158), right tibiotarsus (Bat 3.2012.2591), crushed left tibiotarsus (Bat 3.2009.912).

Type locality: Batallones 3, Cerro de los Batallones, Torrejón de Velasco village, Madrid province, Spain.

Other locality: Batallones 1, Cerro de los Batallones, Torrejón de Velasco village, Madrid province, Spain. Biozone MN 10, early Tortonian, late Miocene (Morales et al. 2008, Calvo et al. 2013).

Stratotype: Upper zone of the “Intermediate Unit” (Morales et al. 1992, *sensu* Lomoschitz et al. 1985, Calvo et al. 2013), biozone MN 10, early Tortonian, late Miocene (Morales et al. 2008).

Etymology: Dedicated to Jorge Morales, a friend and paleontologist, who has conducted the works in the Batallones sites since their discovery. *Georgii* is the genitive of “Georgius” –the Latin for “Jorge”–.

Dimensions and figures: Table 1 and Figure 1.

Diagnosis: Differs from extant *Gypaetus barbatus* in: 1) smaller size (see Table 1); 2) coracoideum, processus procoracoideus large and curved medially and dorsally; 3) scapula, shorter and less developed acromion; 4) humerus, tuberculum dorsale not protruding from the line going between the caput humeri and the crista deltopectoralis; 5) epicondylus dorsalis scarcely developed, 6) more prominent processus flexorius; 7) radius, tuberculum bicipitale radii is closer to the facies articularis ulnaris in the new species than in the other vultures compared; 8) carpometacarpus, processus extensorius more horizontally oriented 9) tibiotarsus in distal view, more square-shaped distal end (vs. rectangular in *G. barbatus*).

Descriptions and comparisons

Coracoideum: The remains of this bone are in a poor state of preservation. The processus procoracoideus is large and curved medially and cranially, as in *Gyps*, *Aegyptius* and *Torgos*. In *Gypaetus*, *Neophron* and *Terathopius* the processus procoracoideus is scarcely developed as well as almost not curved. This trait is not observable in *Mioneophron longirostris*. In *Trigonoceps*, it is not curved at all. In *Gypaetus georgii* n. sp., the processus procoracoideus is larger than in *G. barbatus*. There are not remains of coracoids on which to take measures owing to their poor state of preservation. The size of this bone is considerable smaller than in *G. barbatus*.

Scapula: In cranial view, the triosseal surface of the acromion is less elongated (less developed dorso-cranially) than in any compared species. In this respect, *Trigonoceps*, *Gypaetus* and *Terathopius* show more elongated acromions than *Gyps*, *Aegyptius* and *Torgos*. The triosseal surface of the fossil scapula do not bear pneumatic foramens. This trait seems to be connected with the size of the specimen as the smaller species, *Trigonoceps occidentalis* (Burchell 1824) and *Terathopius ecaudatus* (Daudin 1800), likewise lack it. Nevertheless, the latter species has a large pneumatic area just in the dorsal surface of the acromion. In *Gypaetus*, *Torgos* and *Aegyptius* there is only a single foramen whereas in *Trigonoceps*, *Gyps* and in the fossil there is no pneumatization.

Humerus: Both humeri are crushed and in a bad state of preservation. They show the general aspect of the Old World vultures. The tuberculum dorsale is fairly separated from the head, a shared feature within extant Gypaetinae. The region of the processus flexorius is relatively more developed than in *Gyps*, *Aegyptius*, *Neophron* and even *G. barbatus*. In the extant Gypaetinae and in both new species described in this paper, the ventral condyle is larger and fairly more protruding distally than in *Neophrontops vetustus* (Rich 1977). In addition, the region of the flexor process and the entepicondylar prominence is more robust and rounded in *Neophron* and *Gypaetus*. A furrow that starts at the attachment of the latissimus dorsi posterioris and continues on the shaft towards the end of the crista deltopectoralis is very marked in the new species. It is present in Gypaetinae (Rich 1977), although not exclusive.

Radius: To a certain extent, size and general shape of the radius, including curvature and twisting of the diaphysis, are distinctive among accipitrids. The overall shape of the fossils is like that observed in other Old World vultures. The tuberculum bicipitale radii is closer to the facies articularis ulnaris in the new species than in the other vultures compared with. The area of the depressio ligamentosa and the facies articularis ulnaris is smooth in the fossil, as well as in *Terathopius* and *Gypaetus*. This region is deeper in the other species. The tuberculum bicipitale radii is closer to the facies articularis ulnaris than in *G. barbatus*. On the other extreme of the bone, the sulcus tendinosus is slightly marked out, as also in *Torgos* and *Aegyptius*. In *Torgos*, *Gypaetus*, *Aegyptius* and in the fossil the overall distal end protrudes distally more than in the rest of compared taxa.

Carpometacarpus: In the new species, on the ventral side of the proximal end there are two deep fossae, the fossa infratrochlearis (Baumel and Witmer 1993; internal ligamental fossa of Howard 1980) and the fovea carpalis cranialis, which is situated between the processus pisiformis and the base of the os metacarpale alulare. This

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3 pattern is only seen in *Torgos* and *Aegypius*. Likewise, at the base of the os metacarpale
4 alulare, but in dorsal view, the fossil presents a marked depression, deeper than in the
5 other taxa compared. One exclusive feature is the short distance between both edges of
6 the trochlea carpalis, in cranial as in ventral views. In Aegyptiinae, the os metacarpale
7 minus expands cranially considerably towards its junction with the os metacarpale
8 majus. This expansion is relatively broader in *G. georgii* n. sp. A character only shared
9 with *Torgos* is that the os metacarpale minus exceeds the os metacarpale majus distally.
10 The processus extensorius is more curved ventrally in the new species than in *G.*
11 *barbatus*.
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15 **Tibiotarsus:** The two proximal thirds of the fossil are crushed. Length and general
16 robustness are like in *Gypaetus barbatus* and *Trigonoceps occidentalis*. The cranial
17 edge of the crista cnemialis cranialis is round, like in *Gyps*, *Aegypius* and *Trigonoceps*,
18 not straight, like in the other taxa used for comparisons. The condylus medialis is round,
19 like in *Torgos*, *Gyps*, *Aegypius*, *Necrosyrtes*, *Terathopius*, *Trigonoceps*, *Haliaeetus*,
20 *Gypaetus*, *Neophron* and *Gypohierax*. Both distal condyles are less rounded in eagles.
21 In cranial aspect, the distal end of the fossil is quite symmetric with regard to its
22 longitudinal axe. This pattern is only observed in *Torgos tracheliotus* (Forster 1791).
23 Likewise, in distal view, the incisura intercondylaris is narrow, like in *Torgos*
24 *tracheliotus*, *Trigonoceps*, *Aegypius* and *Gyps*. It is much wider in *Gypaetus barbatus*.
25 The distal end, in distal view, offers a more rectangular shape in the accipitrids
26 compared, including *Gypaetus barbatus*, than in the fossil. The new species shows a
27 supratendinal bridge much more vertical than *Gypaetus barbatus*. In *Neophron* it is
28 practically horizontal. In *Anchigyps voorhiesi*, it is almost horizontal, but extraordinarily
29 wide (Zhang et al. 2012a), more than in extant Gypaetinae and Aegyptiinae. *Arikarornis*
30 *macdonaldi* Howard, 1966, was erected on one distal end of tibiotarsus. Neither the
31 description nor the figure of paper correspond to the morphology of this bone in the Old
32 World vultures. The remarkable inclination of the supratendinal bridge in *Arikarornis*
33 *macdonaldi* resembles that of *Gyps*, but the morphology of the rest of the bone is unlike
34 in Gypaetinae or Aegyptiinae.
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39 **Remarks:** All the bones of *Gypaetus georgii* n. sp. are smaller in size than in the *G.*
40 *barbatus* individuals to which they have been compared (Table 1). Forelimbs bones of
41 the new species are 10 to 20 % smaller, while the tibiotarsus is only 10 % shorter. This
42 estimate is conjectural since the size ratios would surely change if fossil and
43 comparative samples grew. In addition, we lack femora and tarsometatarsi to know if
44 the ratio between fore and hindlimbs has changed. As for the morphological features,
45 scarce differences have been found. *Neogyps errans*, from the Pleistocene of California,
46 is supported on the description of the tarsometatarsus. It bears morphological
47 resemblance to *Gypaetus barbatus*, and their sizes are similar, although *Neogyps* is
48 much less robust at its proximal end (Miller 1916).
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51 *Neophron* Savigny, 1809
52 *Neophron lolis* n. sp.

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55 **Holotype:** Complete right tarsometatarsus (Bat 1.3087).
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57 **Referred specimens:** Batallones 1 site: fragmentary cranium (Bat 1.2009.69), partially
58 crushed right humerus (Bat 1.59), almost complete left ulna (Bat 1.2004.209), proximal
59 end and shaft of right ulna (Bat 1.2002.247), two distal ends of right ulnae (Bat 1.3306,
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Bat 1.2006.128), right radius (Bat 1.6833), proximal end of left radius (Bat 1.3519), fragmentated right radius (Bat 1.3613), crushed distal end of right carpometacarpus (Bat 1.6835), part of proximal end of right carpometacarpus (Bat 1.2079), fragmentary right carpometacarpus (Bat 1.2002.5), complete pelvis (Bat 1.2004.92), fragmentary pelvis (Bat 1.2003.154), right femur very deteriorated (Bat 1.2006.297), distal end of left tarsometatarsus (Bat 1.216). Batallones 3 site: three fragmentary crania (Bat 3.2007.745, Bat 3.2008.329, Bat 3.2012.1432), medial part of left coracoideum (Bat 3.2009.1229), fragmentary right radius (Bat 3.2009.1190), proximal end of left radius (Bat 3.2008.301), distal end of right radius (Bat 3.2012.1216), deteriorated right carpometacarpus (Bat 3.2008.673), three right first alar phalanges digiti majoris (Bat 3.2007.518, Bat 3.2009.741, Bat 3.2012.5), right tarsometatarsus (Bat 3.2012.173), fragmentary right tarsometatarsus (Bat 3.2009.1397). Batallones 1 or 3 sites: incomplete left carpometacarpus (B-1969, not “in situ”)

Type locality: Batallones 1 site Cerro de los Batallones, Torrejón de Velasco village, Madrid province, Spain.

Other locality: Batallones 3 site , Cerro de los Batallones, Torrejón de Velasco village, Madrid province, Spain. Biozone MN 10, early Tortonian, late Miocene (Morales et al. 2008, Calvo et al. 2013).

Stratotype: Upper zone of the “Intermediate Unit” (Morales et al., 1992, *sensu* Lomoschitz et al., 1985, Calvo et al. 2013), biozone MN 10, early Tortonian, late Miocene (Morales et al., 2008).

Etymology: In honour of M. Dolores (‘Loli’) Soria, excellent person and a paleontologist who, in spite of a short life, became a reference for the study of the Spanish Tertiary. *Lolis* is the genitive of “Loli” (3rd. declension).

Dimensions and figures: Table 1 and Figures 2 and 3.

Diagnosis: Different morphologically from the other genera of Gypaetinae and Accipitridae compared. Differences with the extant *Neophron percnopterus* are more subtle. Differs from the extant *Neophron percnopterus* in: 1) cranium, slimmer and longer postorbital process; 2) os palatinum, more rounded angulus caudolateralis; 3) humerus, more distally protruding epicondylus ventralis; 4) pelvis, pubis completely merged with the ala ischii; 5) ischium wings are short and round; 6) tarsometatarsus, longer, though relatively slender (Table 1) The tarsometatarsus is likewise longer than in *Necrosyrtes* and *Mioneophron longirostris* (Table 1).

Descriptions and comparisons

An almost complete skeleton of a gypaetine has been recently named *Mioneophron longirostris* by Li et al. (2016). Although it preserves a remarkable amount of the bones, these are badly broken, many of the anatomical features have been lost or remain hidden in the slab matrix and the magnification of the figures is insufficient.

Cranium: Four crania, deformed and incomplete, have been unearthed. The rostrum maxillare is elongated and narrow, both dorsoventrally and laterally, and the nostrils are elongated horizontal slits, as in *Neophron percnopterus* and *Mioneophron longirostris*, and reaches a similar length (Table 1). On the contrary, a robust rostrum maxillare,

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3 broad dorsoventrally and hook-shaped, is common in Accipitridae, including *Gypaetus*
4 and *Gypohierax*. A rostrum as peculiar as this one also occurs in *Necrosyrtes* and
5 *Neophrontops americanus*. Two features distinguish the new species from its extant
6 congeneric form. In *Mioneophron longirostris*, the pre-narial portion of the rostrum
7 maxillare is longer than in *Neophron percnopterus* (Li et al. 2016, fig. 3a). In the new
8 species, it is proportionally similar. The postorbital process is far more slender and
9 longer in *Neophron lolis* n. sp. than in *Neophron percnopterus*. The angulus
10 caudolateralis of the os palatinum is more rounded in the specimens from Batallones
11 than in the latter species. The nares extend towards the end of the beak more in
12 *Neophron* (*N. percnopterus* and *N. lolis* n. sp.) than in *Mioneophron* (Li et al. 2016, fig.
13 3a).
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17 *Humerus*: The tuberculum dorsale is fairly developed and detached from the head, like
18 in *Gypaetus*. It is relatively larger than in *Aquila*, *Gyps*, *Aegypius*, *Hieraaetus* and
19 *Milvus*, and smaller than in *Pandion*. This tubercle is poorly developed in *Necrosyrtes*
20 and *Gypohierax*. The distal edge of the crista bicipitalis adopts a lobe-shaped form (Fig.
21 2), as in *Neophron*, *Necrosyrtes* and *Gypohierax*, which is more pronounced than in
22 *Aquila*, *Circaetus*, *Haliaeetus*, *Hieraaetus* and *Milvus*. This part of the edge of the crista
23 bicipitalis is not lobed in *Gypaetus barbatus* and *G. georgii* n. sp. The caput humeri is
24 large and protruding, like in both species of *Gypaetus*, *Neophron*, *Necrosyrtes* and
25 *Gypohierax*, and more developed than in *Mioneophron longirostris*. The ventral edge of
26 the crista bicipitalis is almost straight and parallel to the longitudinal axis of the bone.
27 This feature is shared with *Neophron*, both species of *Gypaetus*, *Aquila*, *Circaetus*,
28 *Haliaeetus*, *Hieraaetus* and *Milvus*, whereas it is not observed in *Necrosyrtes* and
29 *Gypohierax*. The distal margin of the crista bicipitalis is round and forms a marked step
30 with the shaft, as in *Neophron percnopterus*. This angle is less marked in *Gypaetus*
31 *barbatus* and even less in *M. longirostris* (Li et al (2016). The epicondylus dorsalis is
32 slightly developed in *Gyps*, *Necrosyrtes* and *Gypohierax*; it is larger in *Aegypius*,
33 *Aquila*, *Gypaetus*, *Haliaeetus*, *Hieraaetus* and in the fossil, whereas it is more
34 developed in *Neophron percnopterus*. In the fossil, in cranial view, the condylus
35 ventralis is very prominent with respect to the condylus dorsalis, which likewise is
36 observed in *Neophron*, *Gypohierax*, and in *Gypaetus* in a lesser extent. As in *Gypaetus*
37 *georgii* n. sp., one marked furrow that starts in the attachment of the m. latissimus dorsi
38 posterioris and continues on the shaft towards the end of the crista deltopectoralis is also
39 present in *Neophron lolis* n. sp. This furrow is present in Gypaetinae (Rich 1977),
40 although also in other accipitrids. The distal humerus on which *Neophrontops vetustus*
41 Wetmore, 1943, from the middle Miocene of Nebraska, was erected is similar in
42 morphology to *Neophron lolis* n. sp., although the epicondylus dorsalis is larger in the
43 latter species. The condylus ventralis is more robust and large in Batallones 1. The
44 flexor process is most acute in *N. vetustus*. Furthermore, the size of *N. vetustus* is
45 considerably lower than *Neophron lolis* n.sp. (Table 1). In turn, *N. vetustus* is only
46 slightly more than half as large than *Neophrontops dakotensis* Compton 1935, from the
47 early Pliocene of South Dakota (Howard 1966). In *Palaeoborus umbrosus*, from the
48 early Pliocene of New Mexico, the caput humeri is more developed and the edge of the
49 crista bicipitalis is less round than in *N. lolis* n. sp. The length of the humerus of
50 *Mioneophron longirostris* (see Table 1) is very small, both in absolute value and in its
51 proportion with ulna and radius. It may not be correct as the distal end of this bone was
52 manipulated by those who previously possessed the specimen. One of the specific
53 diagnostic traits of *Mioneophron longirostris* noted by Li et al. (2016) is a well-
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3 projected and globose caput humeri, although this is also seen in *N. percnopterus* and *N.*
4 *lolis* n. sp.

5 In summary, *Neophron lolis* n. sp. is overall similar in shape and size to the
6 extant *Neophron percnopterus*, with the following exceptions: (1) epicondylus dorsalis
7 is more distinctive in the extant species, and (2) the epicondylus ventralis protrudes
8 distally more in the fossil. As mentioned in the section on *Gypaetus*, what is known
9 about the *Neophrontops* humerus (its distal end) is nothing like that of *Gypaetus* and
10 *Neophron*.
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13 *Ulna*: Only one of the ulnae retains its proximal end. Although it is crushed, the well-
14 marked humero-ulnar depression is clearly visible, as in the extant Gypaetinae. The
15 tuberculum lig. collateralis ventralis is not distinctive, as in *N. percnopterus*. This
16 tuberculum is quite patent in *Gypaetus*, Aegyptiinae and *Anchigyps voorhiesi*. The early
17 Miocene *Palaeoborus rosatus* has a prominent and developed tuberculum carpale, as
18 seen in Aegyptiinae and Gypaetinae, but not in the other accipitrids. The characteristic
19 deep fossa radialis in Aegyptiinae (Manegold et al. 2014) is not observed in *P. rosatus*.
20 Also in this species, this fossa is shallower, as in Gypaetinae -including the two new
21 species reported in this work-, and is less marked in the other accipitrids. The carpal
22 tuberosity is more pointed and relatively larger in Gypaetinae and Aegyptiinae than in
23 the rest of Accipitridae. One such a robust carpal tuberosity is present in *N. lolis* n. sp.
24 and in *P. rosatus*. In fact, this tuberosity is more prominent in *N. lolis* n. sp. than in *N.*
25 *percnopterus*. The edge of the condylus dorsalis ulnae is more developed proximally in
26 the former than in the latter species. One of the features included in the diagnosis of
27 *Mioneophron longirostris* is a much longer ulna than tibiotarsus (ratio=1.45, Li et al.
28 2016). However, this same ratio is obtained in *Neophron percnopterus*. The length of
29 this bone in *Mioneophron longirostris* is similar to that of *Neophron lolis* n. sp. and *N.*
30 *percnopterus* (Table 1).
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35 *Radius*: In size and overall shape of the bone, including curvature and twisting of the
36 diaphysis, the fossil is almost indistinguishable from *Neophron percnopterus*, and is
37 very similar to *Gypohierax angolensis*. In the new species, the tuberculum aponeurosis
38 ventralis is less pronounced than in *N. percnopterus*, and looks alike in *G. angolensis*.
39 Morphological differences with *Necrosyrtes monachus* are sharpened. In particular, the
40 depressio ligamentosa on the distal end is smooth in the fossil and very deep in *N.*
41 *monachus*. Likewise, the fossil shares with these three living vultures a cotyla humeralis
42 round, one feature exclusive among the accipitrids compared.
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45 *Carpometacarpus*: The three carpometacarpi found are very damaged. Nevertheless,
46 some features can be seen. The proximal junction between the ossa metacarpi majus and
47 minus takes place relatively distally, as observed in Gypaetinae and Aegyptiinae. The
48 ventral edge of the proximal end of the trochlea carpalis is round, like in *Neophron*
49 *percnopterus*, *Gypohierax* and *Necrosyrtes*. In *Gypaetus barbatus* and *G. georgii* n. sp.,
50 this edge is flattened. *Necrosyrtes* presents a pneumatic fossa between the os
51 metacarpale minus and the fovea carpalis caudalis that *N. percnopterus*, *Gypohierax* and
52 the fossil do not.
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56 *Manus, phalanx proximalis digiti majoris*: This element in the new species is hardly
57 distinguishable in overall shape and size from *N. percnopterus*. In both taxa, the
58 proximal articular surface is triangular-like shaped whereas it is elongated in
59 *Necrosyrtes* and *Gypohierax*. *Neophron percnopterus* differs from the fossil because in
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cranial view this bone is straight in the former, and slightly curved dorsally in the new taxon.

Pelvis: It is similar in size and proportions to *N. percnopterus* (Figure 3). In lateral view, the ala ischii is shorter and more rounded in the new species than in *N. percnopterus*. The ilioschiatic, obturator and acetabulum foraminae are larger in the extant *Neophron*, but in the fossil the pubis is more robust and is fused with the ischium. The iliosynsacral sulcus is intermediate in width between *N. percnopterus* and *Mioneophron longirostris* (Li et al. 2016, fig. 4). Vertebrae of the caudal region of the synsacrum are higher in *N. percnopterus*.

Batallones, the trochlea metatarsi III is relatively strong and robust and its outline is nearly circular in lateral view, trait also observed in *G. barbatus*. In *Gypohierax*, this trochlea is relatively much smaller. The sulcus extensorius is shallow like in *Gyps* and *Aegyptius*, although not as smooth like in *Gypaetus*, *Neophron percnopterus* and *Necrosyrtes*. This sulcus is deep in *Gypohierax*, *Circaetus*, *Aquila*, *Haliaeetus* and *Hieraaetus*. Unlike in *G. barbatus*, the tuberositas musculi tibialis cranialis is little developed and is situated close to the foramina vascularia proximalia. The crista lateralis hypotarsi is very small, like in *Gypohierax* and *Neophron*. In distal view, the trochleae metatarsorum are aligned in *Gypohierax*, whereas they form a curve in the fossil, *Necrosyrtes*, *G. barbatus* and *N. percnopterus*. With regard to the other trochleae, the trochlea metatarsi III is small in *Gypohierax*, very large in *G. barbatus*, *Necrosyrtes*, and intermediate size in *N. percnopterus* and in the new species. The tarsometatarsus is larger than in the extant *Gypaetus G. barbatus*, *Neophron percnopterus*, *Gypohierax*. *Tarsometatarsus*: This bone is slender as in *Circaetus*, *Neophron*, *Necrosyrtes*, *Gypohierax* and *Anchigyps voorhiesi* (Table 1), not robust like in *Gyps*, *Aegyptius*, *Haliaeetus*, *Gypaetus*, and in some species of *Aquila*, as *A. chrysaetos* and *A. heliaca*. Size and robustness of the fossil are similar in the extant *Circaetus gallicus*. In most accipitrids trochlea metatarsi II protrudes distally from trochlea metatarsi III. On the contrary, trochlea III is far more protruding in half of the *Neophron percnopterus* specimens examined (n = 6), as well as in those of *N. lolis* n. sp., in *Gypaetus barbatus* (the tarsometatarsus of *Gypaetus georgii* n. sp. is not recorded) and in *Necrosyrtes*. Following the pattern of most Accipitridae, trochlea metatarsi II exceeds trochlea metatarsi III distally in *Neogyps*, *Neophrontops* (Miller 1916; Olson and Rasmussen 2001), *Anchigyps voorhiesi* (Zhang et al. 2012a) and *Gypohierax*. In the specimens from

angolensis and *Necrosyrtes monachus*. The tarsometatarsus of *Palaeoborus umbrosus* shows a more robust appearance than in *N. lolis* n. sp. In distal view, the trochleae describe a more curved line in *N. lolis* and *N. percnopterus* than in *P. umbrosus* and *P. howardae* (Storrs Olson, comm. pers. 2008).

Remarks: A more prominent distally metatarsal III is not autapomorphic within Gypaetinae because such a trait is present in *Necrosyrtes* and not in *Gypohierax*. However, this feature seem to be only seen in *Neophron* (*N. lolis* n. sp. included), *Gypaetus* and *Necrosyrtes* among accipitrids. The bones of the new species bear a greater general resemblance to the three living ~~vultures-gypaetines~~ vultures-gypaetines of small size: *Neophron-N. percnopterus*, *Necrosyrtes-N. monachus* and *Gypohierax-G. angolensis*. The sulcus extensorius tarsometatarsi is deep in more predatory accipitrids, meanwhile it is smooth in vultures and *Gypaetus*. In connection with this character, the facies subcutanea lateralis is wide and flat in hunting species, and curved in scavengers. These anatomical features may be ment *Neophron lolis* n. sp. had a more predatory behavior

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3 than its extant congeneric species. However, since the beak of the new species is similar
4 in size and robustness to that of the current *Neophron percnopterus*, it can be assumed
5 that the kinds of food consumed by *Neophron lolis* n. sp. and its strategies for accessing
6 it were not very different from those performed by the extant *Neophron-N.*
7 *percnopterus*.
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10 11 Discussion

12 The late Miocene paleontological complex of Cerro de los Batallones is singular for
13 having yielded a wide variety of avian bones, mainly of accipitriforms. Not all
14 specimens have been preserved in good condition, but the richness of the deposits
15 allows characterizing and describing a certain number of the implied taxa. Two diurnal
16 raptors and other species are pending description. The birds from these sites bear
17 marked morphological similarities with their living relatives, which is indicative of their
18 respective close phylogenetic affinities, contrasting with what happens with the
19 mammal taxas found. The finding of sympatric fossil vultures is not unusual (Zhang et
20 al. 2012b)
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23 Six species have been distinguished within *Neophrontops*. All of them are based
24 on scant and fragmentary remains, except *N. americanus*. An important differentiating
25 feature is size. *Neophrontops-N. dakotensis* (early/middle Pliocene) and *Neophrontops*
26 *N. vetustus* (middle Miocene) are each represented by a single distal end of humerus
27 (Compton 1935; Wetmore 1943). Both specimens differ only in size, the former being
28 almost twice as large as the latter one, and both are considerably smaller than
29 *Neophrontops-N. americanus* (early Miocene/late Pleistocene, Rich 1977). If the
30 paleospecies *N. americanus* had corresponded to one biological species, it would have
31 had an extraordinary vast existence. In the other extreme are two forms reaching similar
32 sizes, *N. slaughteri* (late Pliocene) and *N. vallecitoensis* (middle Pleistocene). *N.*
33 *americanus* reached intermediate dimensions (Wetmore 1943; Howard 1963; Feducia
34 1974; Rich 1977). From the above comparisons with the fossil bones from Batallones, it
35 follows that *Palaeoborus* and *Neophrontops* have anatomical features compatible with a
36 close relationships between them and to the *Gypaetus* and *Neophron* genera. However,
37 some of the characters observed in the humerus of *Neophrontops* and summarized by
38 Rich (1977)—such as a fossa m. brachialis triangular, the fossa pneumotricipitalis
39 ovoid-shaped with its tapering end dorsal, or sulcus transversus deep-, that it should
40 share with the rest of Gypaetinae, are neither exclusive to this group nor are they present
41 in all extant Gypaetinae. The finding of *Neophron* in the European Miocene reduces
42 support for the possibility that this genus had its origin in a stock of vultures from North
43 America. Furthermore, the shape of the tarsometatarsus and particularly the
44 arrangement of the trochlea metatarsi III with respect to the others trochleae not only
45 confers a more eagle-like appearance to *Palaeoborus* and *Neogyps* with respect to
46 *Neophrontops*, as noted by some authors (Miller and Crompton 1939), but also with
47 regard to *Gypaetus* and *Neophron*. The mandibular symphysis in *Anchigyps voorhiesi* is
48 strong and broad (Zhang et al. 2012a) which conflicts with the thin and slender aspect
49 that this region has in the extant Gypaetinae, *Mionephron longirostris* (Li et al. 2016),
50 *Neophrontops americanus* and surely in *Neophron lolis* n. sp., judging from its
51 maxillary jaws recovered—the mandible of *Gypaetus georgii* n. sp. is not preserved-.
52 The absence of pneumatic foramina at both ends of the ulna of *Anchigyps voorhiesi* and
53 regarded as a feature distinguishing Gypaetinae from Aegyptiinae, is also present in both
54 subfamilies (on the impressio brachialis, the incisura radialis, and the distal radial
55 depression). If the published humerus length (Li et al., 2016) is right, this bone was
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certainly very short, and would have consequences on the flight adaptations of this species.

As regards *Mioneophron longirostris*, the part of the rostrum maxillare that is exposed and the details of the pelvis, which preserves part of its integrity, undoubtedly belong to a gypaetine closely related to *Neophron*. It has been considered parsimonious to include the new species *Neophron lolis* n. sp. within the genus *Neophron* because the anatomical differences between *N. lolis* n. sp. and *N. percnopterus* do not seem to justify the naming of a new genus. Due to the poor state of preservation of the *Mioneophron-M. longirostris* specimen, it is difficult to assess the extent of the anatomical differences between *Mioneophron* and *Neophron*. Referring the new species to the genus *Mioneophron* because it has been described in the late Miocene and that there was no evidence of *Neophron* prior to the Pleistocene is out of consideration because taxonomic decisions have to be based only on intrinsic characteristics of the organisms. Although it would be expected that late Miocene finds should be assigned to genera other than the extant *Gypaetus* and *Neophron*, their respective morphological differences with these are subtle, insufficient to erect new genera.

The forelimb to hindlimb ratio is lower in both new raptors described here than in their extant congeners. Both *Gypaetus barbatus* and *Neophron percnopterus* perform gliding flight, and presumably the extinct forms did too. Being likely *Gypaetus georgii* n. sp. and *Neophron lolis* n. sp. worse fliers than their current close relatives, and since flight capability is subjected to maximum stress during migration, it is possible that the two new species were not migratory. The relative large size of the tarsometatarsus in *Neophron lolis* n. sp. could point to a more predatory behavior than its extant congeneric form. This would be strengthened if the femur and tibiotarsus, which have not been recovered, show similar proportions with *N. percnopterus*. Apart from what concerns its flight capability, the morphological features of *Gypaetus georgii* shows no evidence that such a species behaved very differently from the extant *Gypaetus barbatus*.

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Tables and Figure Captions

Table 1. Measurements (in mm) of bones of *Gypaetus georgii* n. sp. and *Neophron lolis* n. sp. compared with other extinct and extant Gypaetinae taxa.

Figure 1. *Gypaetus georgii* n. sp.: scapula, (a) dorsal view; carpometacarpus (holotype, Bat 3.2012.437), (b) ventral view; humerus, (e) caudal view; radius, (f) ventral view; tibiotarsus, (g) cranial view, (h) distal view. *Gypaetus barbatus*: carpometacarpus, (c) ventral view; humerus, (d) caudal view; tibiotarsus, (i) distal view. Abbreviations: ed – epicondylus dorsalis, ii – incisura intercondylaris, pe – processus extensorius. Scale bar: 50 mm.

Figure 2. *Neophron lolis* n. sp.: cranium, (a) dorsal view, (b) lateral view; tarsometatarsus (holotype, Bat 1.3087), (d) dorsal view; ulna, (f) dorsal view; humerus, (g) caudal view. *Neophron percnopterus*: cranium, (c) lateral view; tarsometatarsus, (e) dorsal view; humerus, (h) caudal view. Abbreviations: cb – crista bicipitalis, ev – epicondylus ventralis, n – nostrils, tm II – trochlea metatarsi II, tm III – trochlea metatarsi III. Scale bar: 50 mm.

Figure 3. Pelvis of *Neophron lolis* n. sp.: (a) dorsal view; (b) lateral view. Pelvis of *Neophron percnopterus*: (c) dorsal view; (d) lateral view. Abbreviations: is – iliosynsacral sulcus, iw – ala ischii. Scale bar: 50 mm.

Table 1. Measurements (in mm) of bones of *Gypaetus georgii* n. sp. and *Neophron lolis* n. sp. compared with other extinct and extant Gypaetinae taxa.

	Maximum length	Width of the proximal end	Width of the distal end	Width of the diaphysis at midpoint
<i>Gypaetus georgii</i> , n.sp.				
scapulae		21.8, 23.1		
humeri	ca. 190, 190.7	39.6	32.7, 35.5	
radii	214.5	9.6, 10.0	14.6	ca. 5.4
carpometacarpi	93.4 – 102.1 (3)	22.3 – 26.0 (3)	14.2, 16.0	5.9 – 6.9 (3)
phal. alar 1 dig. maj.	38.4, 38.9			
tibiotarsi	154.8	24.8	19.8, 20.6	
<i>Gypaetus barbatus</i>				
scapulae MNCN-23330, CAM-3, NMNH-17834, 345684		25.7 – 28.1 (4)		
humeri MNCN-23330, CAM-2, 3, NMNH-17834, 345684	215.0 – 236.6 (4)	40.9 – 43.8 (3)	34.5 – 40.0 (4)	15.8 – 17.9 (4)
radii MNCN-23330, NMNH-17834, 345684	233.0 – 254.7 (3)	10.7 – 11.7 (3)	17.2 – 18.1 (3)	5.9 – 6.0 (3)
carpometacarpi MNCN-23330, NMNH-17834, 345684	110.1 – 123.6 (3)	28.0 – 31.3 (3)	19.1	7.2 – 8.3 (3)
phal. alar 1 dig. maj. MNCN-23330	50.8			
tibiotarsi MNCN-23330, MNNH-17834, 345684	157.0 – 171.6 (3)	10.9 – 12.5 (3)	21.0 – 21.5 (3)	10.9 – 16.6 (3)
<i>Neophron lolis</i> n. sp.				
crania	> 95			
humeri	ca. 151.7	28.2	24.7	
ulnae	ca. 180.0		14.2 – 14.3 (3)	7.1, 8.4
radii	ca. 168.7	7.6 – 8.5 (4)	11.1 – 11.9 (4)	4.6 – 5.1 (5)
carpometacarpi	ca. 81.0	17.5		5.3
phal. alar 1 dig. maj.	34.7 – 37.0			
sacra	75.2, 77.0			
tarsometatarsi	86.9, 93.5	16.1, 16.2	17.2, 17.7	8.2, 8.3
<i>Neophron percnopterus</i>				
cranium MNCN-26843, CAM-2, 3, 10	96.4 – 106.3			

1					
2	humeri MNCN-26843,	118.8 – 151.6	29.9 – 31.5 (2)	25.1 – 25.7 (3)	10.6 – 11.6 (3)
3	CAM-2, 3	(2)			
4					
5	ulnae MNCN-26843,	175.5 – 179.0	16.9 – 17.5 (3)	14.6 – 14.7 (3)	8.0 – 8.5 (3)
6	CAM-2, 3	(3)			
7					
8	radii MNCN-26843,	168.2 – 171.9	7.7 – 8.2 (3)	12.1 – 12.9 (3)	3.9 – 5.4 (3)
9	CAM-2, 3	(3)			
10					
11	carpometacarpi MNCN-	76.7 – 83.3 (3)	19.6 – 21.2 (3)	12.0 – 12.7 (3)	5.0 – 5.3 (3)
12	26843, CAM-2, 3				
13	phal. alar 1 dig. maj.	33.5 – 36.1 (3)			
14	MNCN-26843, CAM-2,				
15	3				
16					
17	sacra MNCN-26843,	77.2, 86.7			
18	CAM-3				
19					
20	tibiotarsi MNCN-26843	129			
21					
22	tarsometatarsi MNCN-	76.7 – 83.5 (3)	16.4 – 17.1 (3)	16.9 – 17.9 (3)	7.3 – 8.1 (3)
23	26843, CAM-2, 3				
24					
25	<i>Gypohierax angolensis</i>				
26	humeri NMNH-226143,	140.2 – 145.6	26.2 – 28.2 (4)	21.9 – 23.9 (4)	
27	291316, 291078,	(4)			
28	224820				
29					
30	radii NMNH-226143,	150.1 – 155.5	6.8 – 8.1 (4)	9.7 – 10.7 (4)	3.4 – 4.1 (4)
31	291316, 291078,	(4)			
32	224820				
33					
34	carpometacarpi NMNH-		16.8 – 18.1 (4)		4.0 – 4.2 (4)
35	226143, 291316,				
36	291078, 224820				
37					
38	phal. alar 1 dig. maj.	28.3 – 29.6 (4)			
39	NMNH-226143,				
40	291316, 291078,				
41	224820				
42					
43	tarsometatarsi NMNH-	76.5 – 78.4 (4)	14.3 – 15.1 (4)	15.6 – 16.6 (4)	7.8 – 8.9 (4)
44	226143, 291316,				
45	291078, 224820				
46					
47	<i>Mioneophron</i>				
48	<i>longirostris</i>				
49	cranium	113.2			
50	humerus	146.0			
51	ulna	180.9			
52	radius	169.0			
53	carpometacarpus	82.0			
54	phal. alar 1 dig. maj.	33.5			
55	sacrum	84.8			
56	femur	80.4			
57	tibiotarsus	124.7			
58					
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2	tarsometatarsus	> 74.4			
3					
4					
5	<i>Necrosyrtes monachus</i>				
6	humeri NMNH-18894,	148.6 – 163.9	28.4 – 32.0 (5)	25.5 – 27.2 (5)	
7	291440, 291441,	(5)			
8	291442, 291443				
9					
10	radii NMNH-18894,	180.2 – 193.8	6.6 – 9.0 (5)	11.8 – 13.5 (5)	4.1 – 5.2 (5)
11	291440, 291441,	(5)			
12	291442, 291443				
13					
14	carpometacarpi NMNH-		20.3 – 22.1 (5)		5.0 – 6.3 (5)
15	18894, 291440, 291441,				
16	291442, 291443				
17	phal. alar 1 dig. maj.	32.2 – 37.0 (5)			
18	NMNH-18894, 291440,				
19	291441, 291442,				
20	291443				
21					
22	tarsometatarsi NMNH-	75.4 – 83.0 (5)	14.9 – 15.4 (5)	15.8 – 17.3 (5)	7.4 – 8.4 (5)
23	18894, 291440, 291441,				
24	291442, 291443				
25					
26					
27	<i>Anchigyps voorhiesi</i>				
28	ulna (Zhang et al.	127.5	15.5	12.4	7.1
29	2012)				
30	tibiotarsus (Zhang et al.	ca. 118.3		13.3	7.4
31	2012)				
32	tarsometatarsi (Zhang	84.5, 82.6	14.4, 13.9	15.8	6.5, 6.6
33	et al. 2012)				
34					
35					
36					
37					
38	<i>Neophrontops vetustus</i>				
39	humerus (Wetmore			17.1	
40	1943)				
41	humerus (taken on cast			19.2	
42	USNM 16814,				
43	unpublished)				
44					
45					
46					
47	<i>Neophrontops</i>				
48	<i>americanus</i>				
49	humerus (Howard	148			
50	1932)				
51	humeri (Rich 1977)	134 - 146			
52					
53					
54					
55	<i>Palaeoborus umbrosus</i>				
56	tibiotarsus (in Howard			16.0	
57	1966)				
58	tarsometatarsus (Cope			ca. 19	ca. 10
59	1874)				
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phal. alar 1 dig. maj. ca. 37
(Cope 1874)

Palaeoborus howardae

tarsometatarsus 20.4 9.7
(Wetmore 1936)

Neogyps errans

tibiotarsus (in Howard 18.0, 19.4, 20.8
1966)

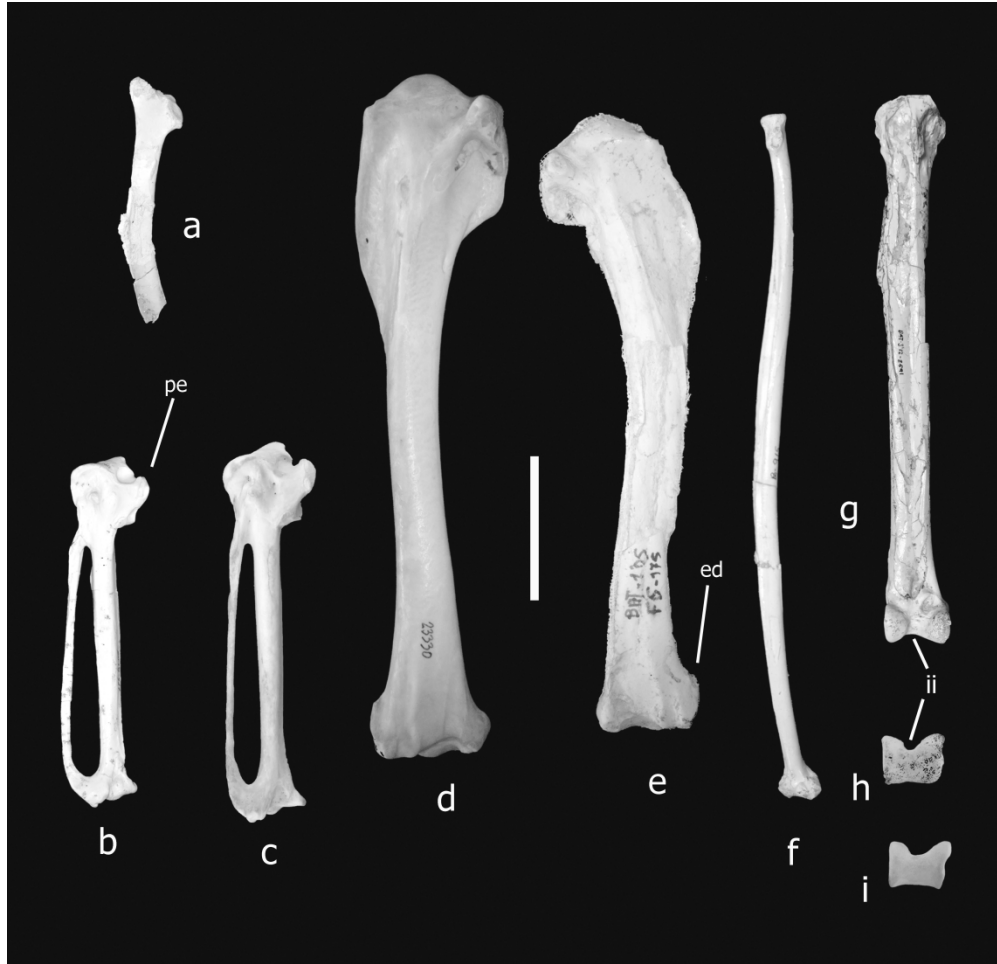


Figure 1. *Gypaetus georgii* n. sp.: scapula, (a) dorsal view; carpometacarpus (holotype, Bat 3.2012.437), (b) ventral view; humerus, (e) caudal view; radius, (f) ventral view; tibiotalus, (g) cranial view, (h), distal view. *Gypaetus barbatus*: carpometacarpus, (c) ventral view; humerus, (d) caudal view; tibiotalus, (i) distal view. Abbreviations: ed – epicondylus dorsalis, ii – incisura intercondylaris, pe – processus extensorius. Scale bar: 50 mm.

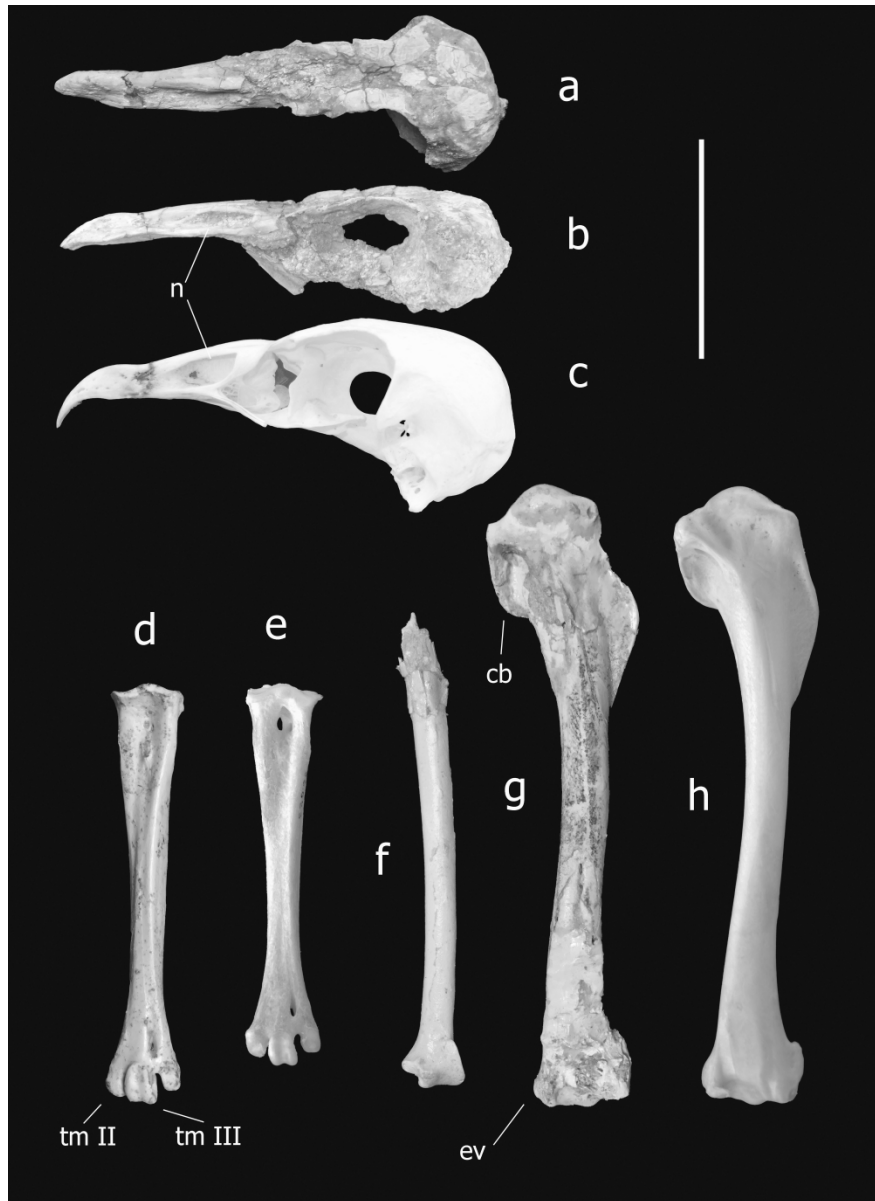


Figure 2. *Neophron lolis* n. sp.: cranium, (a) dorsal view, (b) lateral view; tarsometatarsus (holotype, Bat 1.3087), (d) dorsal view; ulna, (f) dorsal view; humerus, (g) caudal view. *Neophron percnopterus*: cranium, (c) lateral view; tarsometatarsus, (e) dorsal view; humerus, (h) caudal view. Abbreviations: cb – crista bicipitalis, ev – epicondylus ventralis, n – nostrils, tm II – trochlea metatarsi II, tm III – trochlea metatarsi III. Scale bar: 50 mm.

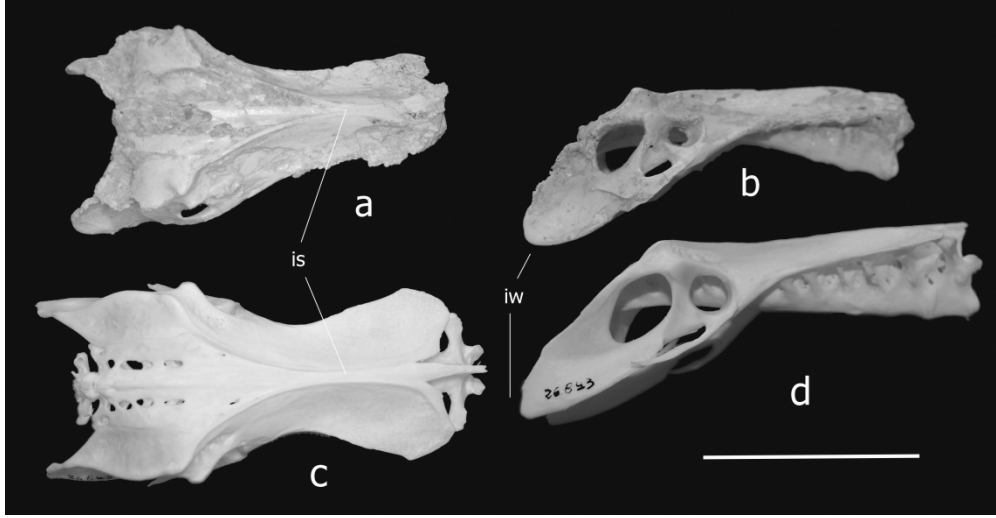


Figure 3. Pelvis of *Neophron lolis* n. sp.: (a) dorsal view; (b) lateral view. Pelvis of *Neophron percnopterus*: (c) dorsal view; (d) lateral view. Abbreviations: is – iliosynsacral sulcus, iw – ala ischii. Scale bar: 50 mm.