

## The oldest fossil record of *Buteo* (Aves, Accipitridae) from the Late Miocene of Italy and its evolutionary implications

Marco PAVIA\*, Simona CAVAGNA, Irene PELLEGRINO, Luca PELLEGRINO & Giorgio CARNEVALE

M. Pavia, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; marco.pavia@unito.it  
\*corresponding author

S. Cavagna, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; simona.cavagna@unito.it  
I. Pellegrino, Dipartimento di Scienze e Innovazione Tecnologica, Università del Piemonte Orientale, Viale Michel 11, I-15121 Alessandria, Italy; irene.pellegrino@uniupo.it

L. Pellegrino, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; lu.pellegrino@unito.it  
G. Carnevale, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; giorgio.carnevale@unito.it

**KEY WORDS** - Roddi, Accipitriformes, Messinian, paleornithology, phylogeny.

**ABSTRACT** - In this study the presence of *Buteo* sp. is documented from the Late Miocene (early Messinian MN 13) of Roddi, north-western Italy. The findings are based on an almost complete skeleton discovered within a 1.5-m-thick succession of laminated grey-brown marls, which have yielded numerous fish and plant remains. Despite the limited osteological information that can be obtained from this fossil, it exhibits some morphological characters that support its attribution to the extant genus *Buteo*, of which it represents the oldest confirmed record worldwide. It has been suggested that *Buteo* originated from a Neotropical ancestor, colonized Central and North America after the closure of the Panama Isthmus in the late Cenozoic, and reached Eurasia during the Pleistocene, while the Old World *Buteo* lineage evolved more recently, during the Late Pleistocene. The specimen from Roddi pushes back the divergence between the Old World and New World *Buteo* lineages by more than 6 Million years earlier than previously thought. Consequently, a revision of the phylogeny of the Buteoninae, including data from the fossil record, and its paleobiogeographical implications is recommended.

### INTRODUCTION

The Accipitridae is one of the families of diurnal raptors included in the order Accipitriformes together with Cathartidae, Pandionidae and Sagittariidae by Dickinson et al. (2013), or with Pandionidae and Sagittariidae by Del Hoyo et al. (2014), who consider Cathartidae as the sole family within Cathartiformes. Following Lerner & Mindell (2006), do Amaral et al. (2009) and Mindell et al. (2018), the accipitrid subfamily Buteoninae mainly includes New World taxa except for the cosmopolitan *Buteo*, and *Butastur*, whose four species currently occur in Asia and Africa (Winkler et al., 2020).

The fossil record of the Accipitridae dates back to the early Eocene of Egem in Belgium with a tarsometatarsus and two ungual phalanges attributed to Accipitridae by Mayr & Smith (2019). In addition, *Milvoides kemp* Harrison & Walker, 1979 was described based on a tarsometatarsus from the late Eocene of England, with a few other remains being known from Oligocene localities in Belgium and France (Harrison & Walker, 1979; Mayr, 2009, 2022; Mayr & Hurum, 2021). Most of the Paleogene fossil species have been described based on isolated bones, very few of them being known by the same skeletal elements. Because of the lack of shared skeletal elements, the affinities between these species cannot be determined and their attribution to a particular genus-level taxon is therefore questionable. More generally, the relationships of most of the Paleogene and Neogene accipitrids are poorly constrained owing to the fragmentary nature of their remains (Mayr, 2017) and the molecular analyses only recently provided a phylogenetic framework for the intrafamilial relationships of the Accipitridae (Lerner &

Mindell, 2006; Lerner et al., 2008; do Amaral et al., 2009; Mindell et al., 2018).

Within the Accipitridae, and the subfamily Buteoninae in particular, the oldest taxon tentatively referred to *Buteo* is *B. circooides* Kurockin, 1968 from the middle Oligocene of Mongolia; however, Mayr (2009, 2022) considered the attribution of those fragmentary remains as problematic. Some species of *Buteo* have been described from the Oligocene and Neogene of North America (Brodkorb, 1964; Cracraft, 1969), although their tentative assignment to *Buteo* was based on a superficial similarity with the extant species of *Buteo*, and the authors already recognized that there are some substantial morphological differences (see also Mayr & Perner, 2021). In addition, the synonymisation of *Geranoaetus* with *Buteo* proposed by Wetmore (1933) resulted in the attribution of at least nine extinct species from the Oligocene and Neogene of North America (Brodkorb, 1964) to the recent genus *Buteo*. The nine species listed by Brodkorb (1964) show similar morphological characters that could be plesiomorphic for most of the Accipitridae, thereby implying that their assignment to *Buteo* needs re-evaluation (see, e.g., Mayr, 2009, 2022).

Two species of *Buteo* have also been described from the Miocene of Europe, that is, *B. pusillus* Ballmann, 1969 and *B. spassovi* Boev & Kovachev, 1998 from the Middle Miocene of France and the Late Miocene of Bulgaria respectively (Ballmann, 1969; Boev & Kovachev, 1998).

The holotypic carpometacarpus of *Buteo pusillus* shows a number of differences from that of the recent species of *Buteo*; in particular, the facies articularis ulnocarpalis is concave and not flat, the small crest between the processus pisiformis and the trochlea carpalis

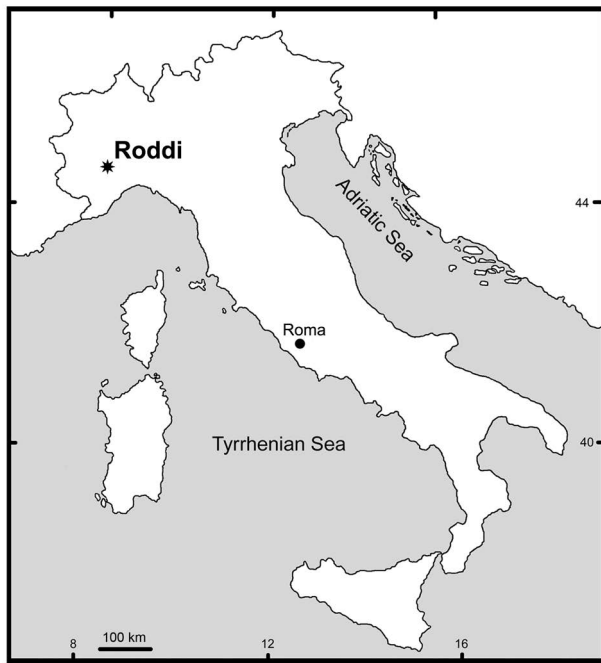


Fig. 1 - Sketch map of Italy showing the position of the fossil locality of Roddi (Cuneo, Italy).

is absent, the os metacarpalis alularis is extremely concave in dorsal view, and there is a small tuberculum below the processus pisiformis in ventral view. Although the holotype specimen has been properly described, the characters pointed out by Ballmann (1969) are not apomorphic for the genus *Buteo*, but more likely synapomorphic for various lineages among the Accipitridae. For those reasons, we consider the attribution of *B. pusillus* to the genus *Buteo* as questionable.

*Buteo spassovi* was described based on a nearly complete tibiotarsus (Boev & Kovachev, 1998). Its generic attribution is only tentative as the original description does not include any apomorphic character of the genus *Buteo* and the authors solely provided a differential diagnosis with modern and fossil species of *Buteo* and *Milvus*. In addition, the illustrations associated with the descriptive analysis are inadequate to understand the actual morphology of the holotypic tibiotarsus. For these reasons, also in the case of *B. spassovi*, the attribution to the genus *Buteo* is in need of a revisionary study and will be not considered hereafter. Therefore, based on our current knowledge, the reliable fossil record of the genus *Buteo* starts from the Pleistocene of the Old World (Mlíkovský, 2002), while its presence in the Oligocene and Neogene of Europe and North America should be necessarily re-examined.

The goal of this paper is to describe a nearly complete articulated accipitrid skeleton found in the Messinian (Late Miocene) locality of Roddi, in the vicinity of the city of Alba (Cuneo Province, north-western Italy) (Fig. 1).

#### GEOLOGICAL SETTING

The fossil described herein was found in 1985 during

the construction works carried out at the foothill of Roddi, a small village close to Alba (Fig. 1). The specimen was found, together with hundreds of extraordinarily well-preserved fossil fishes and leaves, including palm leaves that are more than 1 m long, in a 1.5-m-thick succession of laminated grey-brown marls alternating with fine sandy levels (Cavallo & Pavia, 1985). According to calcareous nannofossils (*Helicosphaera* cf. *sellii* [Bukry & Bramlette, 1969], *Reticulofenestra pseudoumbilicus* [Gartner, 1967]) and planktic foraminiferans (*Globorotalia humerosa* Takayanagi & Saito, 1962, *G. acostaensis acostaensis* Blow, 1959 and *G. praemargaritae* Catalano & Sprovieri, 1969), the Roddi section can be attributed to the lower Messinian (Gaudant et al., 2008), at 6.3 Million years (Ma). The paleontological content of the site has been cursorily described by Gaudant et al. (2008) and indicates a relatively shallow-water depositional environment, no more than 200 meters deep and not far from the coastline, as suggested by the consistent amount of very well-preserved plant remains (Cavallo & Pavia, 1985; Gaudant et al., 2008). The ichthyofaunal assemblage of Roddi was compared with that of other Late Miocene fish-bearing localities of the Piedmont Basin, i.e., Pecetto di Valenza (Gaudant et al., 2010) and the Tanaro River (Gaudant et al., 2007). All of these localities are characterized by abundant sardines and lanternfishes that represent the vast majority of the fish assemblage, suggesting a highly productive marine environment (Gaudant et al., 2008, 2010). At Roddi, this is confirmed by the abundant remains of calcareous phytoplankton associated to planktic and benthic foraminiferans, these latter also comprising species (e.g., *Bulimina elongata* d'Orbigny, 1846) adapted to exploit organic-rich substrates and eventually oxygen-poor conditions, which limited the activity of the scavengers and may have favoured the preservation of articulated vertebrate carcasses (Gaudant et al., 2008).

#### MATERIAL AND METHODS

The studied fossil is almost complete, in part and counterpart, with the main slab including the dorsal portion of the specimen (Fig. 2) and the counterpart showing its ventral portion (Fig. 3). After its discovery, the specimen was only preliminarily prepared and, unfortunately, coated with a solution of vinyl glue to preserve it. The analysis has been mostly carried out on the main part, as the counterpart is hardly informative, apart from the relatively well-preserved coracoids.

The specimen required matrix and glue removal before examination and was prepared using thin entomological needles. This is particularly true for small portions where the bones were still embedded in the sediment, such as the carpal joint of the left wing and the right pedal phalanges (Figs 4 and 5). In addition, the glue was removed from a few portions of the slab where feather imprints are preserved.

The morphological analyses have been performed using a Leica M205 stereomicroscope, while the analysis of the feather imprints has been performed with a JEOL JSM IT300LV scanning electron microscope (SEM; JEOL Limited, Tokyo, Japan).

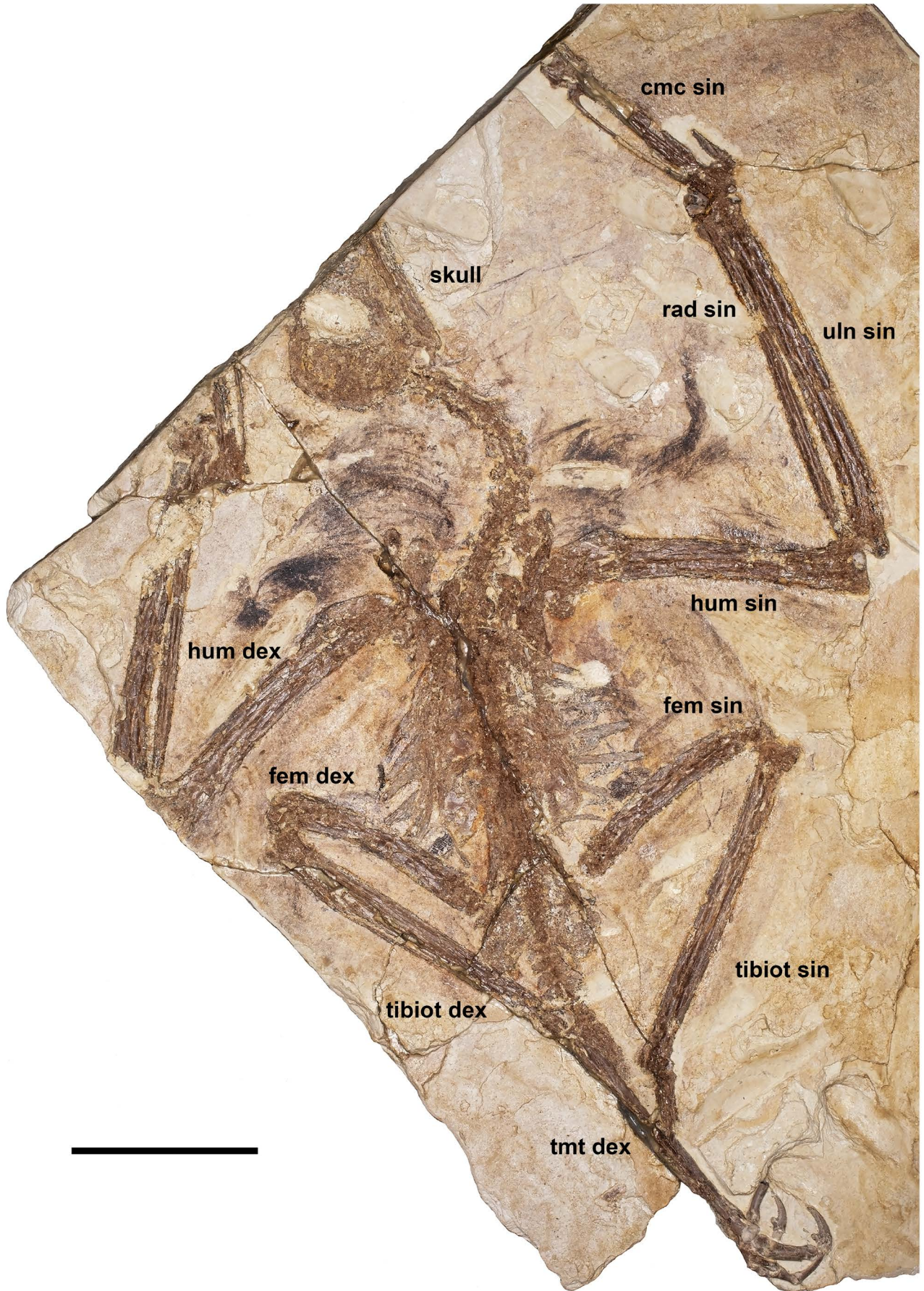


Fig. 2 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi, part. Cmc: carpometacarpus; rad: radius; uln: ulna; hum: humerus; fem: femur; tbiot: tibiotarsus; tmt: tarsometatarsus; dex: right; sin: left. Scale bar corresponds to 5 cm.

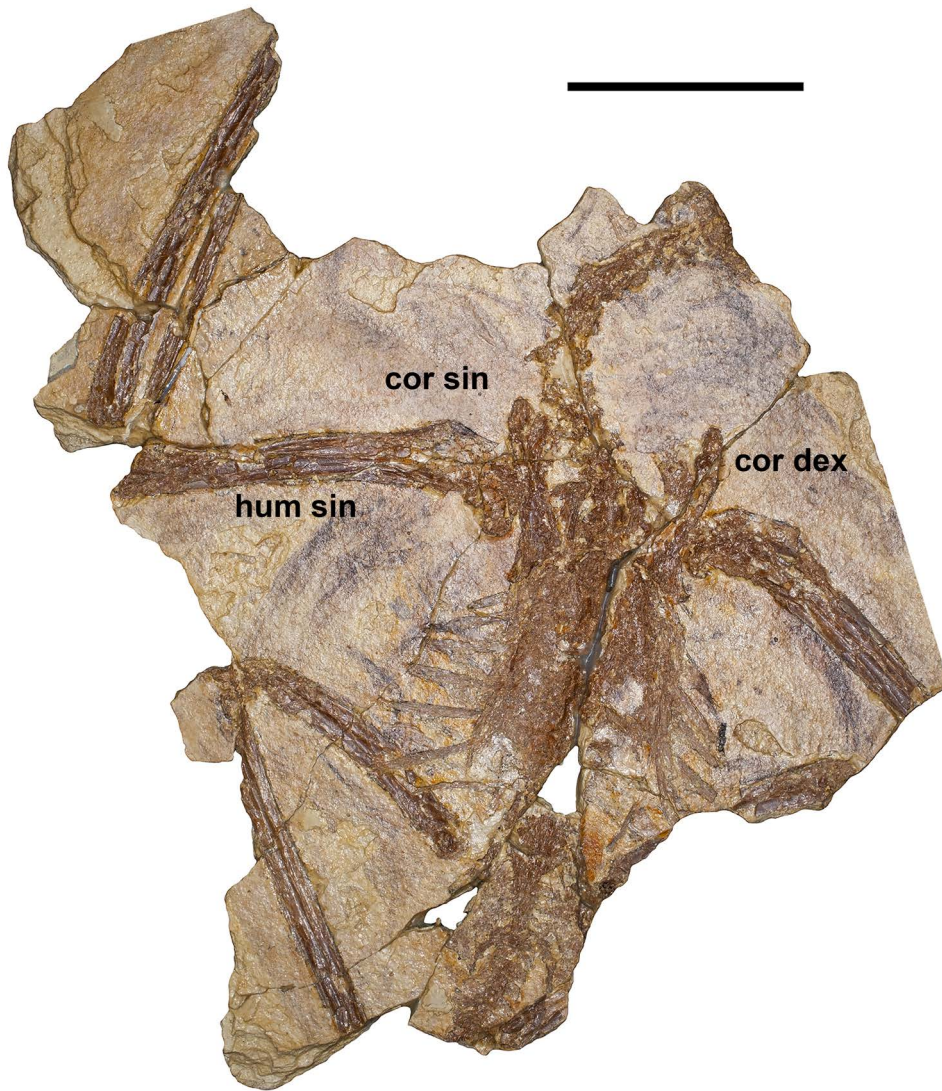


Fig. 3 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi, counterpart. Hum: humerus; cor: coracoid; dex: right; sin: left. Scale bar corresponds to 5 cm.

In order to estimate the relationships of the Old World *Buteo* species and their divergence time within the more recent Accipitridae and Buteoninae phylogenies (Lerner & Mindell, 2005; Lerner et al., 2008; do Amaral et al., 2009; Mindell et al., 2018), we performed a first investigation with a Bayesian analysis conducted in BEAST 1.10.4 (Drummond et al., 2012). We utilized a concatenated alignment of two mitochondrial genes (Cyt b of 1052bp and ND2 of 1016 bp), we selected sequences from 92 species of Accipitridae and three Accipitriiformes (*Pandion haliaetus* [Linnaeus, 1758], *Sagittarius serpentarius* [Miller, 1779], *Phalcoboenus megalopterus* [Meyen, 1834]) from Lerner & Mindell (2005) and Lerner et al. (2008).

For fossil calibration, we used the stem Pandionidae from the Middle Miocene of California (Becker, 1985), the oldest stem Accipitridae from the early Eocene of Belgium (54.5-50.5 Ma) (Mayr & Smith, 2019), the oldest representatives of the clade including, among others, Buteoninae and Aquilinae from the early Miocene (23-16 Ma) (Mayr, 2017), and the fossil from Roddi dated to the

early Messinian at 6.3 Ma. Analyses were run under the GTR + G + I, the best-fit substitution model estimated for each locus by PartitionFinder (Lanfear et al., 2012), using a Yule sampling priors, and an uncorrelated lognormal relaxed clock (Drummond et al., 2012). For these analyses, 20 billion of generations were run twice, sampled every 1000 generations, the first 10% of the generations were discarded as burn-in. The MCMC output was analyzed in Tracer version 1.7.1 to evaluate whether valid estimates of the posterior distribution of the parameters had been obtained. Trees were summarized using TreeAnnotator version 1.10.4, and were visualized in FigTree version 1.4.4 (Rambaut et al., 2018).

The fossil is housed in the collections of the Museo Civico Craveri di Storia Naturale di Bra, Cuneo, Italy (MCCB) with accession number MCCB 03740. Osteological terminology follows Baumel & Witmer (1993). The fossil was compared with recent skeletal material preserved in the Marco Pavia Ornithological Collection (MPOC) stored in the Dipartimento di Scienze della Terra of the Università degli Studi di Torino.

## SYSTEMATIC PALEONTOLOGY

Order ACCIPITRIFORMES Vieillot, 1816  
Family ACCIPITRIDAE Vigors, 1824

Genus *Buteo* Lacépède, 1799

*Buteo* sp.  
(Figs 2-8)

**Material** - A nearly complete skeleton (MCCB 03740), in part and counterpart, lacking part of the skull, the distal right wing, and the distal left foot.

**Measurements** - The measurements are in mm and indicate the greatest length of each measurable bone (\* indicates estimated values) - Right coracoid: 40.1; right humerus: 91.8; right radius: 102.0\*; right ulna: 110.1; right carpometacarpus: 52.5; right femur: 64.1; left femur: 62.3; right tibiotarsus: 94.5; left tibiotarsus: 92.8; left tarsometatarsus: 74.0\*; left phalanx 1 digit II: 5.3; left phalanx 2 digit II: 14.5\*; left phalanx 2 digit III: 7.8; left phalanx 3 digit III: 12.7; left phalanx 4 digit III: 11.7; left phalanx 1 digit IV: 6.3; left phalanx 2 digit IV: 4.6; left phalanx 3 digit 4: 4.0; left phalanx 4 digit IV: 10.4\*; left phalanx 5 digit IV: 9.4 (see also Tab. 1).

**Description** - The two slabs preserve the skeleton in unequal parts, as what is referred to as the main part (Fig. 2) contains the back portion of the specimen with almost all the preserved bones, while the counterpart (Fig. 3) is badly damaged, as some parts were lost during the excavation. As a consequence, the counterpart only shows the ventral portion of the specimen with the sternum and coracoids and portions of the main long bones. Overall, the specimen is almost complete as only a few parts are missing, particularly the rostral parts of the skull and mandible, part of the right wing (the distal humerus, proximal ulna and radius, part of the carpometacarpus and the wing phalanges), the distal half and all the pedal phalanges of the left leg, and a few phalanges of the right foot. The specimen in the main part is exposed in ventral view, lying on his back with the neck slightly curved rightward and the wings and legs almost symmetrically spread. On the other hand, in the counterpart the ventral portion of the specimen is exposed in dorsal view, with the morphology of the sternum hidden by bone fragments and the impressions of the viscera. All the bones are still articulated with each other, except for a few pedal phalanges, which are slightly displaced but still showing their original association. The wing bones are articulated with the slightly extended wings and the distal elements tilted frontally and partially displaced, especially the right carpometacarpus, resulting in the exposition of the cranial surfaces of the humeri, ventral sides of radius and ulna, and dorsal side of the carpometacarpus.

Almost all the bones are partially fragmented due to diagenetic compression and compaction, and the outer bone surfaces are commonly not exposed because the bones were split longitudinally along their main shafts during the opening of the two slabs. A few portions of the right wing and left foot were still embedded in the

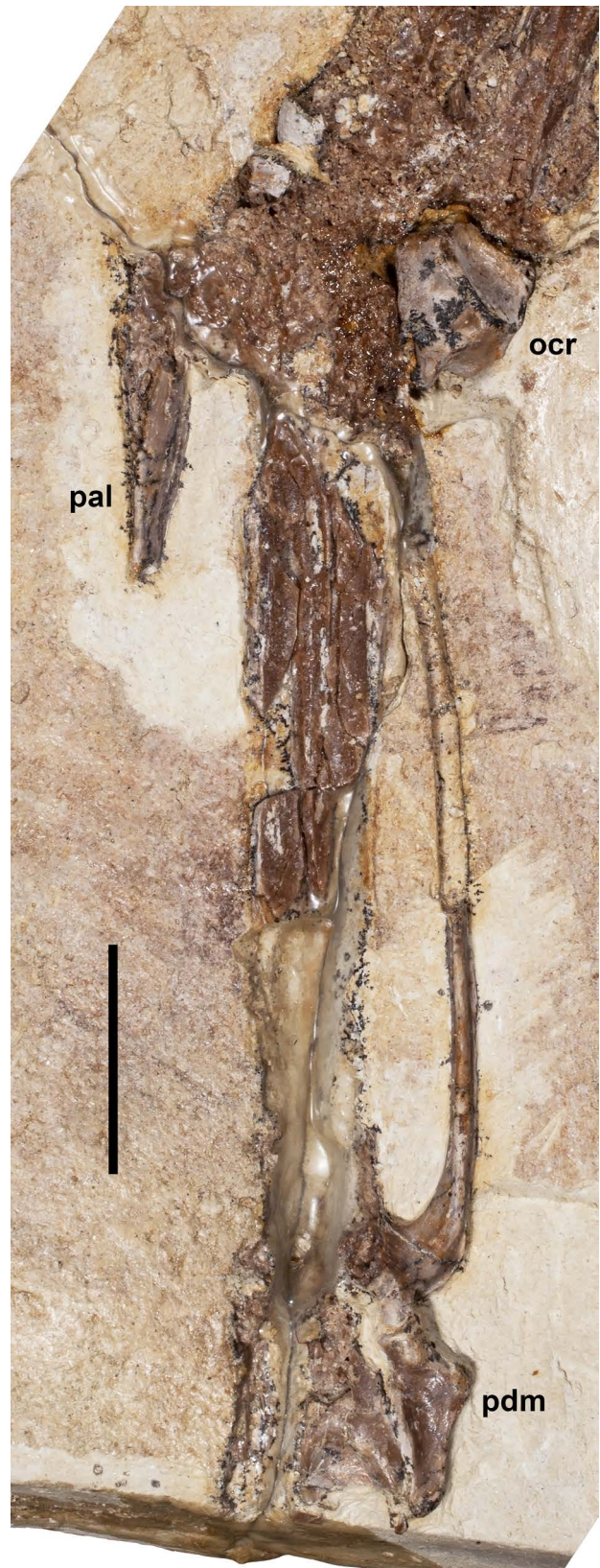


Fig. 4 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi. Left carpometacarpus with os carpi radiale (ocr), phalanx alularis (pal), and phalanx digit minoris (pdm) in anatomical position. Scale bar corresponds to 10 mm.

sedimentary matrix and the preparation allowed the examination of the distal part of the carpometacarpus

		Coracoid	Humerus	Radius	Ulna	Carpometacarpus	Femur	Tibiotarsus	Tarsometatarsus
<i>Pernis apivorus</i>	$\bar{X}$ GL	44.5	107.5	112.8	119.1	58.0	56.2	86.8	52.7
	(N)	(10)	(7)	(7)	(7)	(9)	(9)	(7)	(7)
	- Log	0	0	0	0	0	0	0	0
<i>Elanus caeruleus</i>	$\bar{X}$ GL	29.9	73.2	81.7	85.5	42.9	47.9	62.3	33.4
	(N)	(9)	(8)	(8)	(8)	(8)	(9)	(8)	(8)
	- Log	-0.17181	-0.16707	-0.14033	-0.1438	-0.13097	-0.06953	-0.14373	-0.19781
<i>Aviceda cuculoides</i>	$\bar{X}$ GL	34.4	76.6	81.5	85.6	41.3	42.8	62.1	34.3
	(N)	(3)	(3)	(3)	(3)	(3)	(3)	(3)	(3)
	- Log	-0.11141	-0.14716	-0.14108	-0.14337	-0.14783	-0.11906	-0.14498	-0.18633
<i>Circaetus gallicus</i>	$\bar{X}$ GL	60.1	164.1	185.1	193.2	85.0	81.9	127.4	91.1
	(N)	(6)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
	- Log	0.13076	0.183461	0.214987	0.209991	0.166119	0.163384	0.166779	0.237353
<i>Hieraaetus pennatus</i>	$\bar{X}$ GL	43.7	104.7	123.6	130.5	60.1	71.1	99.1	59.7
	(N)	(16)	(24)	(13)	(13)	(13)	(16)	(14)	(13)
	- Log	-0.00736	-0.0114	0.060734	0.039748	0.015558	0.101971	0.281803	0.053872
<i>Kaupifalco monogrammicus</i>	$\bar{X}$ GL	30.8	65.6	69.4	72.7	37.3	53.7	72.8	50.5
	(N)	(7)	(6)	(6)	(6)	(6)	(7)	(6)	(6)
	- Log	-0.15861	-0.21487	-0.21075	-0.21431	-0.19122	-0.02019	-0.07583	-0.019
<i>Accipiter gentilis</i>	$\bar{X}$ GL	45.2	92.9	96.5	103.8	56.7	78.4	105.6	77.7
	(N)	(29)	(25)	(25)	(26)	(25)	(28)	(26)	(25)
	- Log	0.007732	-0.06338	-0.06789	-0.05979	-0.00929	0.144212	0.085612	0.168286
<i>Circus aeruginosus</i>	$\bar{X}$ GL	43.8	106.5	118.5	124.1	64.5	72.9	110.1	87.1
	(N)	(9)	(6)	(6)	(6)	(6)	(7)	(6)	(6)
	- Log	-0.00583	-0.00437	0.021421	0.017756	0.046356	0.112761	0.103351	0.21764
<i>Circus cyaneus</i>	$\bar{X}$ GL	37.6	88.4	98.7	104.7	56.6	65.6	94.8	72.5
	(N)	(8)	(6)	(6)	(6)	(6)	(8)	(5)	(6)
	- Log	-0.0722	-0.08529	-0.05796	-0.056	-0.01023	0.067069	0.038686	0.138292
<i>Milvus milvus</i>	$\bar{X}$ GL	48.8	125.7	137.0	144.3	72.7	69.2	86.4	54.6
	(N)	(6)	(4)	(3)	(3)	(3)	(6)	(3)	(2)
	- Log	0.04045	0.067667	0.084196	0.08315	0.098305	0.09015	-0.00196	0.015544
<i>Milvus migrans</i>	$\bar{X}$ GL	44.9	117.0	129.6	137.47	68.0	64.6	84.1	54.6
	(N)	(14)	(10)	(10)	(10)	(10)	(11)	(10)	(8)
	- Log	0.004277	0.036456	0.060085	0.062192	0.069209	0.059945	-0.01328	0.015246
<i>Buteo lagopus</i>	$\bar{X}$ GL	47.2	113.2	125.0	132.1	68.5	79.6	102.9	69.5
	(N)	(10)	(8)	(8)	(8)	(8)	(7)	(8)	(8)
	- Log	0.025604	0.022169	0.044404	0.044846	0.072263	0.15067	0.074268	0.120017
<i>Buteo rufinus</i>	$\bar{X}$ GL	53.2	126.9	141.6	149.7	75.5	89.0	118.7	87.9
	(N)	(12)	(12)	(11)	(12)	(12)	(12)	(11)	(12)
	- Log	0.077942	0.071756	0.098675	0.099338	0.114728	0.199402	0.136079	0.222167
<i>Buteo buteo</i>	$\bar{X}$ GL	43.3	102.5	114.9	121.5	60.8	74.8	100.9	75.1
	(N)	(25)	(19)	(19)	(18)	(25)	(26)	(21)	(20)
	- Log	-0.01116	-0.02063	0.00809	0.008665	0.02019	0.123513	0.065629	0.153854
<b><i>Buteo</i> sp. RODDI</b>	<b>GL</b>	<b>40.1</b>	<b>91.8</b>	<b>102.0</b>	<b>110.1</b>	<b>52.5</b>	<b>64.1</b>	<b>94.5</b>	<b>74.0</b>
	<b>- Log</b>	<b>-0.04483</b>	<b>-0.06874</b>	<b>-0.05678</b>	<b>-0.03423</b>	<b>-0.04327</b>	<b>0.056693</b>	<b>0.037127</b>	<b>0.147186</b>

Tab. 1 - Measurements (in mm) of the greatest length (GL) of the major long bones of *Buteo* sp. from Roddi compared with the mean values of the same bones of selected Accipitridae species, and the values of the log differences (- Log) with *Pernis apivorus*, selected as standard in Fig. 9.

with the phalanx digiti minori, the os carpi radiale (Fig. 4), the proximal ulna of the left wing, and almost all the pedal phalanges (Fig. 5).

The preserved part of the skull consists of its posterior part showing a rounded outline and the orbital area partially covered by the matrix. Due to poor preservation, it is not possible to recognize any detail except for the arcus jugalis, occurring above the mandible, and the

processus mandibularis of the os quadratum. The mandible has a linear outline and ends with a rounded morphology and a small fenestra. Some of the rings of the trachea are still preserved in anatomical position and visible below the skull (Fig. 6). The vertebral column is recognizable, especially in the main slab, and the vertebrae are clearly identifiable, especially the cervical and the upper thoracic trait, while the lower thoracic trait is concealed. The ribs

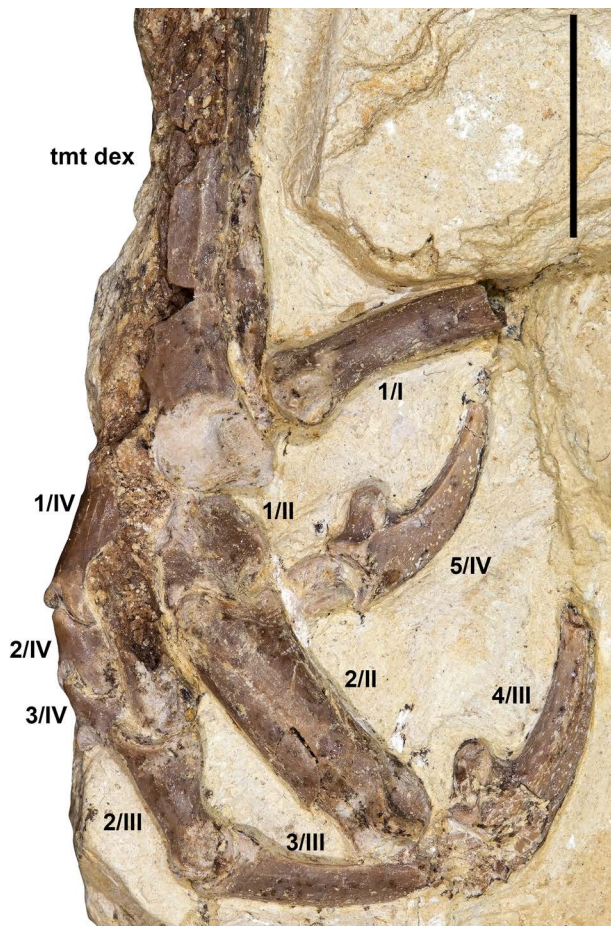


Fig. 5 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi. Right distal tarsometatarsus (tmt) with the pedal phalanges of the digits I-IV. Scale bar corresponds to 10 mm.

are clearly visible in both slabs with the uncinat processes well preserved; in the counterpart the sternal ribs are embedded and aligned almost parallel to the vertebral column. The pelvis is crushed longitudinally, likely along the crista dorsolaterali ilii, making the dorsal outline well recognizable in the part. The pelvis is quite narrow with a rounded and laterally extended margo iliolateralis. The ala praecetabularis ilii is not visible, but the distal outline of ilium is concave. No foramina intertransversaria are visible. In the counterpart the impressions of the alae ischii are clearly visible, as well as the processus terminalis ischia. Only the distal part of the synsacrum is preserved with the extremitas caudalis synsacri and the vertebrae caudales, of which the processus transversi are clearly identifiable. The caudal vertebrae are visible in both slabs, with the corpi vertebrae and the pygostyle preserved in the main part and their impressions including those of the processus transversus also in the counterpart. The pygostyle is elongated, but no other morphological details are visible as it is dorsoventrally preserved. The coracoids are mostly preserved in the counterpart. The left coracoid is partially embedded in the matrix and slightly tilted dorsolaterally with the rounded processus acrocoracoideus clearly recognizable together with the processus lateralis. The right coracoid is preserved dorsoventrally being mostly not acrocoracoideus, still

embedded in the sedimentary matrix. The outline of the processus acrocoracoideus is recognizable together with the lateral outline of the facies articularis humeralis. The area of the processus procoracoideus and the processus lateralis is preserved with the cranial part of the scapula. The furcula is broken and its original shape is no longer recognizable, although the two processus acromialis are visible between the coracoids. The sternum is preserved in the counterpart, but its dorsal morphology is completely concealed by bone fragments and impressions of the viscera. The left humerus is relatively elongate and slightly curved, with the dorsal outline of the crista deltopectoralis characterized by a pointed process in its distal half and by a depression close to this process, which is visible in the counterpart. There is a single tuberculum supracondylaris dorsalis. The condylus ulnaris is the only preserved portion of the distal end, but it is incomplete. The radius and ulna are heavily crushed and only a portion of the cotyla ventralis and olecranon can be recognized, together with the tuberculum ligament collateralis ventralis, which is smooth. The preparation revealed the complete os carpi radiale, still in anatomical position, showing its caudal side. The os carpi ulnare is not recognizable. The carpometacarpus is completely preserved, although its proximal end is crushed, and part of the distal end was partially embedded in the matrix or covered by the glue. The preparation and the removal of the glue revealed the morphology of the sulcus interosseus and the presence of an almost uncrushed phalanx digit minoris, with a longitudinal crest along the entire bone. Only the proximal part of the first phalanx digit majoris is preserved although heavily crushed. Both the femora are complete and lateromedially compressed, hence their morphology was largely altered by diagenetic compression. These bones are preserved in their anatomical position, being disarticulated from the pelvis. In particular, in the counterpart, the section of the caput femori is recognizable. Both tibiotarsi are preserved in the main slab, with the left one being lateromedially exposed with only a small part of the distal end not crushed, while the right one is craniocaudally associated with the respective fibula. Unfortunately, the main slab is broken along the right tibiotarsus and tarsometatarsus and was badly restored just after its



Fig. 6 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi. Detail of the trachea with some of the preserved rings. Scale bar corresponds to 1 mm.

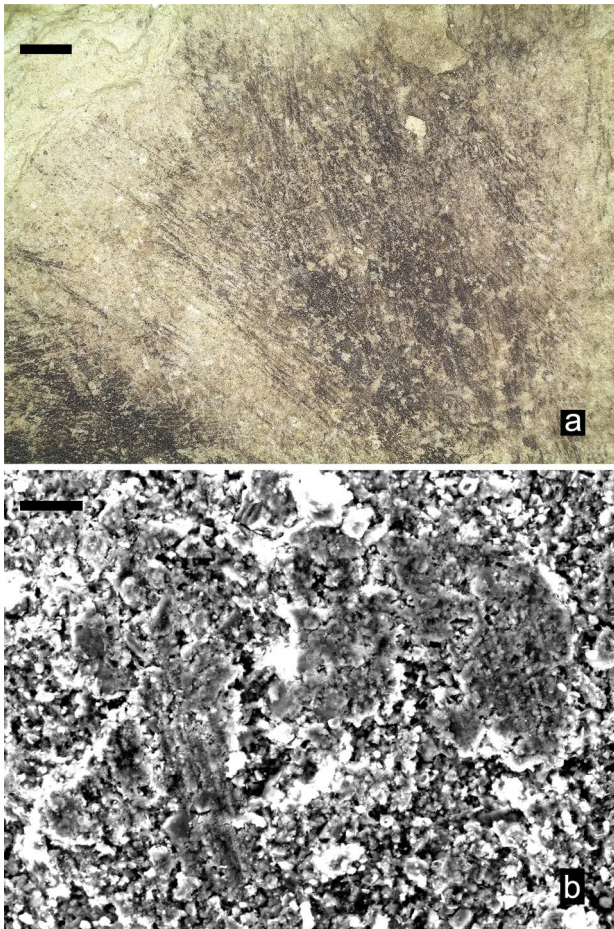


Fig. 7 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi. a) View of the feather imprints on the right side of the neck. Scale bar corresponds to 1 mm. b) Detail of the same area (SEM image) with the impressions of the barbules still evident. Scale bar corresponds to 20  $\mu$ m.

discovery, thereby preventing the observation of additional anatomical details and preparation of the surfaces of the bones, especially the articulation between the right tibiotarsus and tarsometatarsus. The right tarsometatarsus is complete and the bone surface locally well preserved. Only the trochlea metatarsi I is preserved with the fovea ligament collateralis visible. The left tarsometatarsus was probably complete but is now broken about 19 mm distally from the proximal end. The right pedal phalanges are partially preserved. All the recognizable pedal phalanges are complete and partially connected to each other and to the tarsometatarsus, except for the left phalanx 1 digit I, which is only partially preserved.

What appear to be impressions of soft tissues are visible along the left femur and tibiotarsus, including two black rounded masses preserved in the main slab along the femurs. Soft tissues are preserved in the abdominal cavity, although no organs or other soft structures are clearly recognizable.

Around the body and the neck in both part and counterpart, numerous feather imprints are preserved as a thin dark organic-rich film (Fig. 7a). Surprisingly, no traces of the larger wing feathers (primaries, secondaries and wing coverts) and of the rectrices are present. The

preserved feathers are concentrated mainly around the neck and the axillaries. A detailed analysis of the slab surface where feather imprints are located using both optical microscope and scanning electron microscope reveals the preservation of part of the original feather structure with the impression of the barbules (Fig. 7b).

*Comparisons* - The fossil clearly represents a member of the Accipitriformes due to the general morphology of the wing and leg bones, and of the pedal phalanges. It can be assigned to the Accipitridae because of the elongated tarsometatarsus, which excludes any attribution to the Pandionidae and Cathartidae, being at the same time not so elongated as in the Sagittariidae.

The morphology of certain skeletal elements is partially altered by the taphonomic and diagenetic processes as well as by the excavation procedure. Nevertheless, some morphological details can be observed and are useful for the phylogenetic assignment of the fossil. In particular, the os carpi radiale (Fig. 8) shows: 1) the sulcus for the tendon of musculus ulnometacarpalis ventralis that is very marked; 2) the sulcus for the tendon of musculus extensor carpi radialis that is dorsally rather than proximodorsally situated; 3) the cranial surface of the bone that bears a marked fossa and is proximally slanting. These three characters conform to the derived morphology described by Mayr (2014, p. 429) as characteristic of the os carpi radiale of the accipitrid lineages Harpiinae, Circinae, Melieraxinae, Accipitrinae, Milvinae, Haliaeetinae, Buteoninae, and Aquilinae, thereby excluding the Elaninae, Perninae, Circaetinae and all the Old World vultures. The radial carpal bone of the fossil is furthermore 4) fully consistent with that of the Buteoninae in caudal view by having the symmetrical sides of the notch for tendon of musculus ulnometacarpalis ventralis and a relatively small tuberculum distal to the crest dividing the facies articularis radialis from the facies articularis ulnaris; 5) the distoventral projection in caudal view (Mayr, 2014, fig. 1c) is more pointed ventrally, like in *Buteo*, and not distally bent as in *Hieraaetus*; 6) the proximal outline of the facies articularis radialis in caudal view shows a point in the middle as in *Buteo*, whereas in *Hieraaetus* this outline is gently curved, bearing a small bulge; 7) the facies articularis ulnaris on the caudal side of the os carpi radiale is as deep as in *Buteo*, while it is shallower in *Hieraaetus*; 8) the proximal outline of the sulcus for the tendon of musculus extensor carpi radialis is curved in caudal view (Mayr, 2014, fig. 1c), almost forming a right angle between the dorsal and the proximal parts of the sulcus as in *Buteo*, while it is not as marked as in *Circus* or straight as in *Hieraaetus*, where it is 45° proximally oriented with respect to the ventral/dorsal axis of the bone; 9) the sulcus for the tendon of the musculus extensor carpi radialis is proximally pointed as in *Buteo* and not smooth as in *Hieraaetus* (see also character 4 above). In addition, 10) on the distal carpometacarpus the synostosis metacarpalis distalis is similar to *Buteo* (it is not as wide as in *Accipiter* and not as narrow as in *Hieraaetus*); 11) the small tuberculum in the synostosis metacarpalis distalis that is characteristic of *Circus* is absent; 12) the articulation with phalanx digiti minoris is not as protruding distally as in *Accipiter*; 13) the first



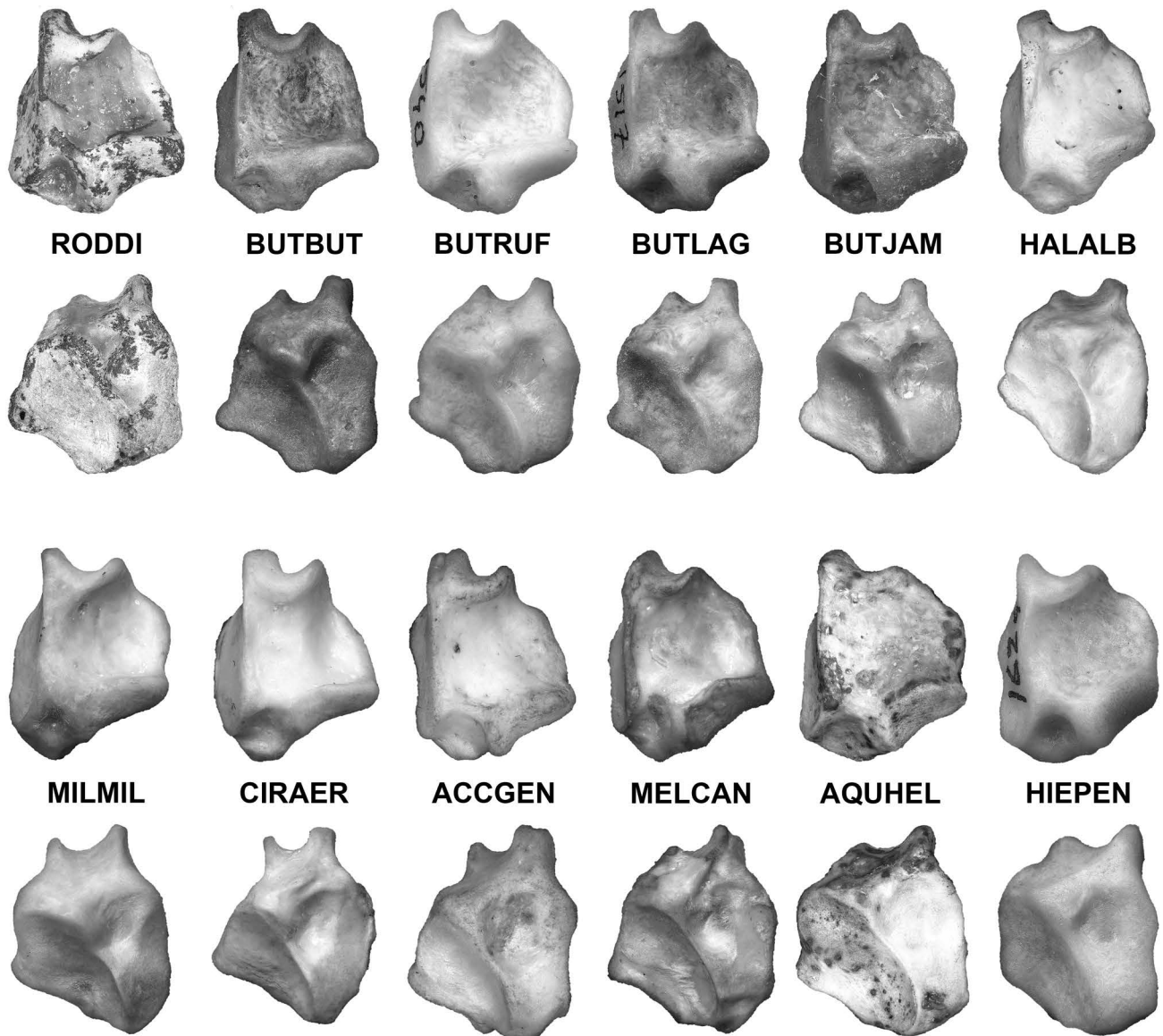


Fig. 8 - *Buteo* sp., MCCB 03740, from the Late Miocene of Roddi. Left os carpi radiale compared with those of other *Buteo* species and selected species of the Accipitridae lineages related to the Buteoninae. The upper row for each taxon shows the cranial view, while the lower row shows caudal view. BUTBUT, *Buteo buteo* (MPOC 1665); BUTRUF, *Buteo rufinus* (MPOC 1540); BUTLAG, *Buteo lagopus* (MPOC 1517); BUTJAM, *Buteo jamaicensis* (Gmelin, 1788) (MPOC 1121); HALALB, *Haliaeetus albicilla* (Linnaeus, 1758) (MPOC 1494); MILMIL, *Milvus milvus* (Linnaeus, 1758) (MPOC 300); CIRAER, *Circus aeruginosus* (Linnaeus, 1758) (MPOC 739); ACCGEN, *Accipiter gentilis* (Linnaeus, 1758) (MPOC 1700); MELCAN, *Melierax canorus* (Risilachi, 1799) (MPOC 2318); AQUHEL, *Aquila heliaca* Savigny, 1809 (MPOC 716); HIEPEN, *Hieraaetus pennatus* (Gmelin, 1788) (MPOC 1624). Specimens are not to scale.

and second phalanges of the pedal digit II are separated (Fig 5), allowing to exclude all the members of Milvinae and Haliaeetinae; 14) the pedal phalanges are also not extremely elongated as in the bird-feeding *Accipiter* or weak as in the hymenopteran-eating *Pernis*; 15) the second phalanx of the pedal digit III are robust and stout as in *Buteo* and not as elongated as in *Accipiter*, weak as in *Circus* or extremely stout as in *Hieraaetus*.

The limb proportions of the Roddi specimen indicate a mid-sized Accipitridae with no extreme elongation of the wings and legs compared to the rest of the body (Tab. 1). These proportions are strongly reminiscent of those of aerial generalist among accipitrids (*Buteo*, *Aquila*, *Hieraaetus*) rather than those of the more specialized

taxa, like *Accipiter*, *Circus* or *Milvus*. In particular, the ratio between the various bones and between wings and legs of the Roddi specimen is consistent with the genus *Buteo*, in particular with the Palearctic species *Buteo buteo* (Linnaeus, 1758) and *Buteo rufinus* (Cretzschmar, 1829), whereas it differs from the Holarctic *Buteo lagopus* (Pontoppidan, 1763) and other accipitrid genera (Fig. 9).

Therefore, it is reasonable to conclude that the detailed morphological analysis of the skeletal remains suggests that the specimen from Roddi documented herein can be referred to the extant genus *Buteo*. The poor preservation of certain skeletal structures, especially the epiphysis of the long bones, prevents any species-level attribution, including the possibility of the description of a new taxon.

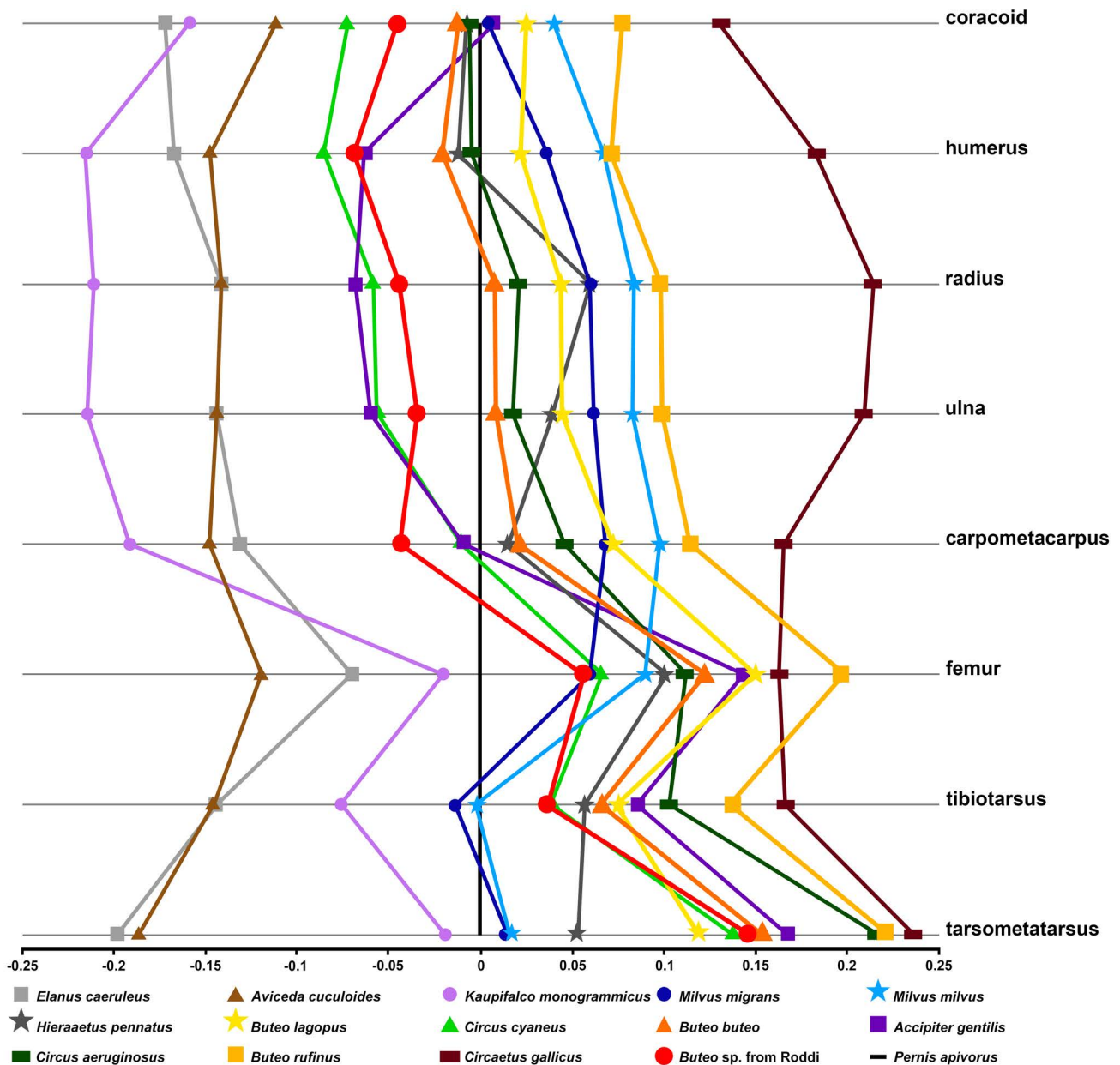


Fig. 9 - Simpson's Log-Ratio diagram comparing the dimensions of the long bones of *Buteo* sp. from Roddi (MCCB 03740) with those of *B. buteo*, *B. rufinus*, *B. lagopus*, *Elanus caeruleus* (Desfontaines, 1789), *Aviceda cuculoides* (Swainson, 1837), *Kaupifalco monogrammicus* (Temminck, 1824), *Milvus milvus*, *M. migrans* (Boddaert, 1783), *Hieraetus pennatus*, *Circus cyaneus* (Linnaeus, 1766), *C. aeruginosus*, *Accipiter gentilis*, and *Circaetus gallicus* (Gmelin, 1788). *Pernis apivorus* (Linnaeus, 1758) is selected as standard.

DISCUSSION

The *Buteo* specimen discovered at Roddi represents the oldest confirmed fossil that can be referred to this genus, providing new insights about the evolutionary history of the genus *Buteo* and, more generally, of the subfamily Buteoninae. The morphological features that can be observed in the specimen are indicative of a close affinity to the Palearctic species *Buteo buteo* and *B. rufinus*, with broad implications in our knowledge of the evolutionary history of the genus *Buteo* within the Buteoninae.

The Accipitridae, and the Buteoninae in particular, have been the subject of several phylogenetic studies, based on molecular or integrated approaches (Lerner &

Mindell, 2005; Griffith et al., 2007; Lerner et al., 2008; do Amaral et al., 2009; Mindell et al., 2018). In addition, phylogenetic analyses have been carried out on the genus *Buteo* or on the relationships between Western Palearctic species (Riesling et al., 2003; Jowers et al., 2019). All of these studies agree with a Neotropical origin of the genus *Buteo*, a colonization of Central and North America between 7.7 and 3.3 Ma related to the closing of the Panama Isthmus, while the Old World group of *Buteo* species originated after a dispersal event from North America during the Pleistocene (do Amaral et al., 2009). This framework is consistent with the assumption that the Old World *Buteo* species form a monophyletic group representing the most recent radiation within the genus

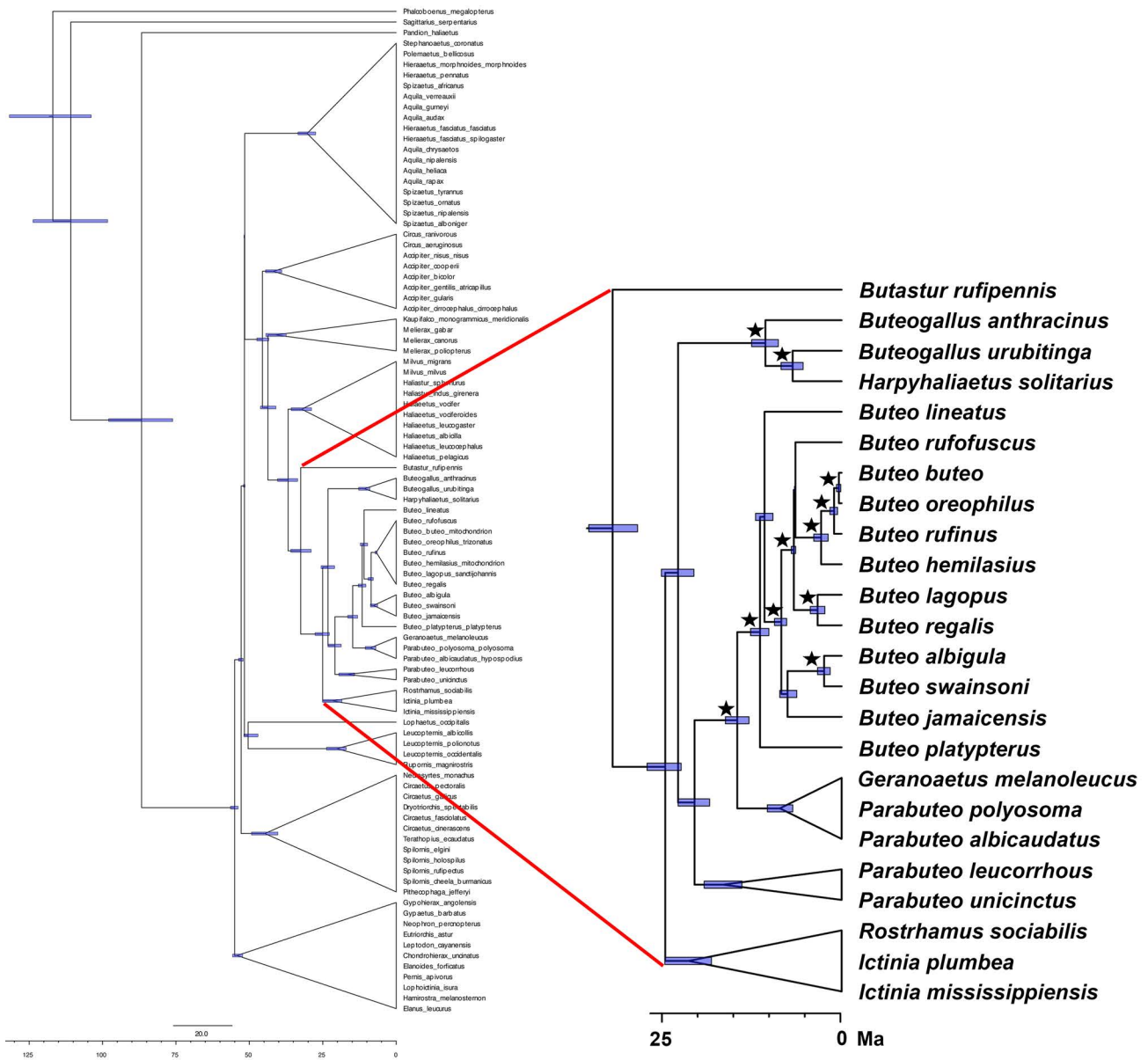


Fig. 10 - Bayesian chronogram inferred using BEAST (time scale in Ma) based on concatenated mitochondrial dataset (Cytb and ND2). Error bars represent 95% HPD intervals. Stars indicate nodes supported by posterior probabilities  $P \geq 0.95$ .

(Riesling et al., 2003). However, the relationships between the Old World *Buteo* species, i.e., the most derived clade following do Amaral et al. (2009, fig. 3), are less well resolved than those among the rest of the examined taxa.

As pointed out above, the Buteoninae lack any unambiguous evidence in the pre-Pleistocene fossil record (Mayr, 2017), with negative implications for our understanding of the divergence times of the various lineages, especially the more basal nodes (do Amaral et al., 2009, fig. 4). A recent analysis of the Palearctic species of *Buteo* (Jowers et al., 2019) indicates a very recent split between *Buteo buteo*, *B. hemilasius* Temminck & Schlegel, 1845 and *B. rufinus*, as also confirmed by the phylogenetic analyses of the whole subfamily (do Amaral et al., 2009).

The fossil described herein has a clear impact on the reconstruction of the evolution of the genus *Buteo*, in

particular the Old World lineage, and of the Buteoninae in general, since the specimen from Roddi predates the first occurrence of the Palearctic clade of *Buteo* by ca. 6 Ma compared to what previously hypothesized using molecular data (do Amaral et al., 2009; Mindell et al., 2018; Jowers et al., 2019). The use of the Roddi specimen as a calibration point in the phylogeny of the Accipitridae pushes back in time the separations between the various lineages of this genus. In particular, the time-calibrated analyses estimated the split between the Old and New World clades of *Buteo* at 6.633 Ma (6.501-6.964 95% HDP), with the African taxa included in the former (Fig. 10). Further analyses using an integrative approach with sequence data, morphology, and biogeographic data could help to clarify the origin and evolutionary history of the genus *Buteo*. It is nevertheless evident that the presence of a *Buteo* species with clear affinities to the Palearctic

taxa in the Late Miocene of Italy clearly contrasts the hypothesis of a late Middle Pleistocene-Late Pleistocene origin of the Palearctic clade of *Buteo* (including *B. buteo*, *B. rufinus*, and *B. hemilasius*) (Jowers et al., 2019), as also confirmed by the presence of *Buteo buteo* and *B. rufinus* in the Middle Pleistocene European fossil record around 400 ky and 125 ky, respectively (Tyrberg, 2008).

The fossil from Roddi might also suggest an opposite scenario for the evolutionary history of the genus *Buteo* within the Buteoninae, with the presence of an Old World ancestor in the Eurasiatic lineage of *Buteo* dating back to the Late Miocene and a successive colonization of the Nearctic via Beringia and later colonisation of South America. This hypothesis would be consistent with the lack of confirmed *Buteo* remains in the pre-Pleistocene American fossil record.

### CONCLUSIONS

The almost complete, articulated skeleton of *Buteo* sp. from the Late Miocene of Roddi represents the oldest remain of Accipitridae found in Italy and one of the few complete bird skeletons in the entire Italian fossil vertebrate record. Unfortunately, the preservation is not fully adequate to allow for an identification at the species level. Nevertheless, the specimen is greatly significant since it represents the oldest unambiguous record of the genus *Buteo* worldwide and its affinities to the Old World lineage of *Buteo* species pushes back its divergence more than 6 Ma earlier than previously hypothesized (do Amaral et al., 2009; Mindell et al., 2018). The specimen described herein might support an Eurasian origin of the genus *Buteo*, a subsequent Neogene spread into North America and, finally, a colonisation of the whole American continent. The relationships of the Accipitridae within the Accipitriformes are currently regarded as well resolved (Mindell et al., 2018), with the Buteoninae as part of a large clade that includes most of the extant species together with the Aquilinae and Accipitrinae, and the phylogenetic relationships within the Buteoninae being also well resolved. However, the specimen described herein provides evidence of a different scenario in the evolution of the genus *Buteo* (do Amaral et al., 2009; Mindell et al., 2018), revealing the necessity of a complete revision of the Buteoninae phylogeny, which should take into account also the fossil record and its biogeographic significance. This specimen also confirms the relevance of improving our knowledge of the Neogene fossil record of the Piedmont region, as this area was characterized by a unique condition in the Italian scenario, both in the marine and continental domains, as testified by its remarkable fossils (e.g., Colombero et al., 2014, 2017; Pavia et al., 2022 and references therein).

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### REFERENCES

- Ballmann P. (1969). Les oiseaux miocenes de La Grive St. Alban (Isere). *Geobios*, 2: 157-204.
- Baumel J.J. & Witmer L.M. (1993). Osteologia. In Baumel J.J. (ed.), Handbook of Avian Anatomy: Nomina Anatomica Avium. Second Edition. Publications of the Nuttall Ornithological Club, 23, Cambridge MA: 45-132.
- Becker J.J. (1985). *Pandion lovensis*, a new species of osprey from the late Miocene of Florida. *Proceedings of the Biological Society of Washington*, 98: 314-320.
- Blow W.H. (1959). Age, correlation, and biostratigraphy of the upper Tocuyo (San Lorenzo) and Pozon Formations, eastern Falcon, Venezuela. *Bulletins of American Paleontology*, 39: 67-251.
- Boddaert M. (1783). Table des planches enluminées d'histoire naturelle de M. D'Aubenton. Avec les denominations de MM de Buffon, Brisson, Edwards, Linnæus et Latham. Précédé d'une notice des principaux ouvrages zoologiques enluminés. 67 pp. Utrecht.
- Boev Z. & Kovachev D. (1998). *Buteo spassovi* sp. n. - a Late Miocene Buzzard (Accipitridae, Aves) from SW Bulgaria. *Geologica Balcanica*, 29: 25-129.
- Brodkorb P. (1964). Catalogue of fossil birds. Part 2 (Anseriformes through Galliformes). *Bulletin of the Florida State Museum, Biological Sciences*, 8: 195-355.
- Bukry D. & Bramlette M.N. (1969). Some new and stratigraphically useful calcareous nannofossils of the Cenozoic. *Tulane Studies in Geology*, 7: 131-142.
- Catalano R. & Sprovieri R. (1969). Stratigrafia e micropaleontologia dell'intervallo tripolaceo di torrente Rossi (Enna). *Atti della Accademia Gioenia di Scienze Naturali in Catania*, 1: 513-527.
- Cavallo O. & Pavia G. (1985). Un nuovo giacimento fossilifero nel Messiniano inferiore di Roddi d'Alba. *Alba Pompeia*, 4: 85-87.
- Colombero S., Alba D.M., D'Amico C., Delfino M., Esu D., Giuntelli P., Harzhauser M., Mazza P.P.A., Mosca M., Neubauer T.A., Pavia G., Pavia M., Villa A. & Carnevale G. (2017). Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleogeological and paleoclimatological implications. *Palaeontologia Electronica*, 20.1.10A: 1-66.
- Colombero S., Angelone C., Bonelli E., Carnevale G., Cavallo O., Delfino M., Giuntelli P., Mazza P., Pavia G., Pavia M. & Repetto G. (2014). The upper Messinian assemblages of fossil vertebrate remains of Verduno (NW Italy): Another brick for a latest Miocene bridge across the Mediterranean. *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, 272: 287-324.
- Cracraft J. (1969). Notes on fossil hawks (Accipitridae). *The Auk*, 86: 353-354.
- Cretzschmar J. (1829). Atlas zu der Reise im nordlichen Afrika von Eduard Ruppell. 141 pp. Gedruckt und in Commission bei Hein Ludl. Brunner, Frankfurt Am Main.
- Del Hoyo J., Collar N.J., Christie D.A., Elliot A. & Fishpool L.D.C. (2014). Illustrated Checklist of the Birds of the World. Vol. 1: Non-Passerines. 903 pp. Lynx Editions, Barcelona.
- Desfontaines R.L. (1789). Mémoire sur quelques nouvelles espèces d'oiseaux des cotes de Barbaire. *Mémoires de l'Académie Royale Paris*, 1787: 496-505.
- Dickinson E.C. & Christidis L. (eds) (2014). The Howard and Moore complete checklist of the birds of the world, 4th Edition, vol. 1. Non-Passerines. 461 pp. Aves Press, Eastbourne.
- do Amaral F.R., Sheldon F.H., Gamauf A., Haring E., Riesing M., Silveira L.F. & Wajntal A. (2009). Patterns and processes of

- diversification in a widespread and ecologically diverse avian group, the buteonine hawks (Aves, Accipitridae). *Molecular Phylogenetics and Evolution*, 53: 703-715.
- Drummond A.J., Suchard M.A., Xie D. & Rambaut A. (2012). Bayesian phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, 29: 1969-1973.
- Gartner S. (1967). Calcareous nannofossils from Neogene of Trinidad, Jamaica, and Gulf of Mexico. *University of Kansas Paleontological Contributions, Papers*, 29: 1-7.
- Gaudant J., Cavallo O., Courme-Rault M.D., Fornaciari E. & Lauriat-Rage A. (2008). Paléontologie du gisement de poissons fossiles du Messinien préévaporitique de Roddi, près d'Alba (Piémont, Italie). *Rivista Piemontese di Storia Naturale*, 29: 3-60.
- Gaudant J., Cavallo O., Courme-Rault M.D., Fornaciari E., Lauriat-Rage A., Lapparent F. & Merle D. (2007). Paléontologie des marnes tortoniennes affleurant dans le lit du Tanaro, près d'Alba (Piémont, Italie). *Rivista Piemontese di Storia Naturale*, 28: 3-51.
- Gaudant J., Courme-Rault M.D., Fornaciari E. & Fourtanier E. (2010). The Upper Miocene fossil fish locality of Pecetto di Valenza (Piedmont, Italy): a multidisciplinary approach. *Bollettino della Società Paleontologica Italiana*, 49: 203-225.
- Gmelin J.F. (1788). In Linnaeus C. (1788). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tomus I, Part 1. Editio decima tertia, aucta, reformata. 500 pp. Beer, Lipsiae.
- Griffiths C.S., Barrowclough G.F., Groth J.G. & Mertz L.A. (2007). Phylogeny, diversity, and classification of the Accipitridae based on DNA sequences of the RAG-1 exon. *Journal of Avian Biology*, 38: 587-602.
- Harrison C.J.O. & Walker C.A. (1979). Birds of the British Middle Eocene. *Tertiary Research Special Papers*, 5: 19-27.
- Jowers M.J., Sánchez-Ramírez S., Lopes S., Karyakinc I., Dombrowski V., Qinba A., Valkenburg T., Onofre N., Ferrand N., Beja P., Palma L. & Godinho R. (2019). Unravelling population processes over the Late Pleistocene driving contemporary genetic divergence in Palearctic buzzards. *Molecular Phylogenetics and Evolution*, 134: 269-281.
- Kurochkin E.N. (1968). Fossil remains of birds from Mongolia. *Ornitologija*, 9: 323-330. [in Russian]
- Lacépède B.G.É. de la V. (1799). Tableaux des divisions, sous-divisions, ordres et genres des mammifères. In Discours d'Ouverture et de Clôture du Cours d'Histoire Naturelle, l'An VII de la République; et Tableaux Méthodiques des Mammifères et des Oiseaux. 57 pp. Plassan, Paris.
- Lanfear R., Calcott B., Ho S.Y.W. & Guindon S. (2012). PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, 29: 1695-1701.
- Lerner H.R.L., Klaver M.C. & Mindell D.P. (2008). Molecular Phylogenetics of the Buteonine Birds of Prey (Accipitridae). *The Auk*, 125: 304-315.
- Lerner H.R.L. & Mindell D.P. (2005). Phylogeny of eagles, Old World vultures, and other Accipitridae based on nuclear and mitochondrial DNA. *Molecular Phylogenetics and Evolution*, 37: 327-346.
- Linnaeus C. (1758). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Tenth Edition. 824 pp. Laurentii Salvii, Stockholm.
- Linnaeus C. (1766). *Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis*. Twelfth Edition. 532 pp. Laurentii Salvii, Stockholm.
- Mayr G. (2009). *Paleogene Fossil Birds*. 262 pp. Springer, Heidelberg.
- Mayr G. (2014). Comparative morphology of the radial carpal bone of neornithine birds and the phylogenetic significance of character variation. *Zoomorphology*, 133: 425-434.
- Mayr G. (2017). *Avian Evolution: The Fossil Record of Birds and its Paleobiological Significance*. 293 pp. Wiley-Blackwell, Chichester.
- Mayr G. (2022). *Paleogene fossil birds*, 2<sup>nd</sup> edition. 239 pp. Springer, Cham, Switzerland.
- Mayr G. & Hurum J.H. (2021). A tiny, long-legged raptor from the early Oligocene of Poland may be the earliest bird-eating diurnal bird of prey. *Science of Nature*, 107: 48.
- Mayr G. & Perner T. (2021). A new species of diurnal birds of prey from the late Eocene of Wyoming (USA) – one of the earliest New World records of the Accipitridae (hawks, eagles, and allies). *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 297: 205-215.
- Mayr G. & Smith T. (2019). A diverse bird assemblage from the Ypresian of Belgium furthers knowledge of early Eocene avifaunas of the North Sea Basin. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 291: 253-281.
- Meyen F.J.F. (1834). Reise um die erde ausgeführt auf dem Königlich preussischen Seehandlungs-Schiffe Prinzess Louise commandirt von Capitain W. Wendt in den Jahren 1830, 1831 und 1832. *Nova acta physico-medica Academiae Caesareae Leopoldino-Carolinae Naturae Curiosum*, Suppl. 16: 1-493.
- Miller J.F. (1779). *Icones animalium et plantarum*. Part 5. 140 pp. London.
- Mindell D.P., Fuchs J. & Johnson J.A. (2018). Phylogeny, taxonomy, and geographic diversity of diurnal raptors: Falconiformes, Accipitriformes, and Cathartiformes. In Sarasola J., Grande J. & Negro J. (eds), *Birds of Prey*. Springer, Cham: 3-32.
- Mlikovsky J. (2002). *Cenozoic Birds of the World*. Part I: Europe. 406 pp. Ninox Press, Praha.
- Orbigny A.D. d' (1846). *Foraminifères fossiles du bassin tertiaire de Vienne*. 312 pp. Gide et Comp Libraires Editeurs, Paris.
- Pavia G., Dulai A., Festa A., Gennari R., Pavia M. & Carnevale G. (2022). Palaeontology of the Upper Pliocene marine deposits of Rio Vaccaruzza, Villalvernia (Piedmont, NW Italy). *Rivista Italiana di Paleontologia e Stratigrafia*, 128: 129-210.
- Pontoppidan E. (1763). *Den danske atlas eller kongeriget Dannemark, med dets naturlige egenskaber, elementer, indbyggere, vaexter, dyr og andre affodninger, dets gamle tildrageiser of naervaerene omstaendigheder i alle provintzer, staeeder, kirker, slotte of herregaarde* (Den Danske Atlas). Vol. 1. 723 pp. Royal University Printer, Copenhagen.
- Rambaut A., Drummond A., Xie D., Baele G. & Suchard M. (2018). Posterior summarisation in Bayesian phylogenetics using Tracer 1.7. *Systematic Biology*, 67: 901-904.
- Riesing M.J., Kruckenhauser L., Gamauf A. & Haring E. (2003). Molecular phylogeny of the genus *Buteo* (Aves: Accipitridae) based on mitochondrial marker sequences. *Molecular Phylogenetics and Evolution*, 27: 328-342.
- Rislachi G. (1799). De Falcone Canoro. In Thunberg C.P. (ed.), *Dissertationes Academiae Upsaliae Habitaе*, Volume tertium: 264-272.
- Savigny L. (1809). *Description de L'Egypte. Oiseaux. Haute Egypte*. 339 pp. Lechevalier, Paris.
- Swainson W. (1837). *The natural history of birds of Western Africa*. 246 pp. Lizards, Edimburgh.
- Takayanagi Y. & Saito T. (1962). Planktonic foraminifera from the Nobori formation, Shikoku, Japan. *Science Reports of the Tohoku University, Series 2 (Geology)*, 2: 67-105.
- Temminck C.J. (1824). *Livraison 53*. In Temminck C.J. & Laugier M. (eds), *Nouveau recueil de planches coloriées d'oiseaux, pour cliac de suite et de eliacal aux planches enluminées de Buffon*. 314 pp. Levrault, Dufour et d'Ocagne, Paris.
- Temminck C.J. & Schlegel H. (1845-1850). *Descriptions des oiseaux observes au Japon par les voyageurs hollandaise*. 141 pp. Arnz et Soc., Leiden.
- Tyrberg T. (1998). *Pleistocene birds of the Palearctic: a catalogue*. 720 pp. Publications of the Nuttall Ornithological Club No. 27, Cambridge.

Vieillot L.J.P. (1816). Analyse d'une nouvelle ornithologie élémentaire. 70 pp. Deterville, Paris.

Vigors N.A. (1824). Sketches in ornithology; or observations on the leading affinities of some of the more extensive groups of birds. On the groups of the Falconidae. *Zoological Journal*, 1: 308-346.

Wetmore A. (1933). An Oligocene eagle from Wyoming. *Smithson Miscellaneous Collection*, 87: 1-9.

Winkler D.W., Billerman S.M. & Lovette I.J. (2020). Hawks, Eagles, and Kites (Accipitridae), version 1.0. In Billerman S.M., Keeney

B.K., Rodewald P.G. & Schulenberg T.S. (eds), *Birds of the World*. Cornell Lab of Ornithology, Ithaca, NY, USA.

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