

Connecting Europe and Asia: The Neogene birds of Bulgaria and their paleoenvironmental and paleornithogeographical significance

Zlatozar N. Boev

National Museum of Natural History – Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd. 1000 Sofia, Bulgaria;
e-mails: boev@nmnhs.com, zlatozarboev@gmail.com

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Abstract. Seventeen Neogene avian localities are documented in Bulgaria, including 12 Miocene and 5 Pliocene sites, distributed across lowland and semi-mountainous regions of both Northern and Southern Bulgaria. The known avifauna comprises 24 taxa, including three new genera – *Euroceros* (ground hornbill), *Balcanas* (dabbling duck), and *Eremarida* (lark) – and 11 new species, highlighting the previously underestimated diversity of Neogene birds in Southeastern Europe.

In addition to its taxonomic significance, the Bulgarian Neogene avifauna provides important insights into paleornithogeographic patterns in the Eastern Paratethys region. The composition of these assemblages indicates faunal affinities with both Western Eurasian and, to a lesser extent, Asian provinces, supporting the role of the Balkan region as a biogeographic corridor during the Neogene.

In a broader context, Bulgarian fossil birds represent a small but non-negligible fraction of the global Neogene avifauna, accounting for approximately 1.0% of known taxa. Their stratigraphic distribution and taxonomic composition, however, suggest that the region preserves key evidence for avian dispersal and diversification in Southeastern Europe. These findings emphasize the importance of the Balkan Peninsula as an underexplored area with significant potential for refining Neogene avian paleobiogeography.

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INTRODUCTION

Following the most recent revision of the boundary between the Neogene and the Quaternary (Gibbard *et al.*, 2010), concepts regarding the extent of the Quaternary have changed significantly, also affecting interpretations of the Pliocene.

Over the past three decades, significant paleornithological discoveries have been made in Bulgaria. These include the first European records of hornbills, fossil snake eagles, and Neogene pheasants, as well as the first records in the country of ostriches, peafowls, swans, dabbling ducks, falcons, larks, and other taxa. Although still limited, this evidence pro-

vides important insights into the Neogene terrestrial faunas of the Balkan Peninsula and Southeastern Europe.

To date, information on the Neogene avifauna of Bulgaria remains scattered. Relevant studies have been published across multiple countries, including Austria, Bulgaria, the Czech Republic, France, the Netherlands, Poland, Russia, Turkey, and the United States. The present study aims, for the first time, to provide a comprehensive synthesis of all available data on Neogene paleozoological localities in Bulgaria, together with the avian taxa identified therein.

During the past three decades, several summaries of Neogene birds in Bulgaria have been pub-

lished: Boev (1996) reported 8 localities; Boev (2002a), 9; Boev (2007a), 11; and Boev (2011a), 13. In addition, Boev (2005) documented 83 avian bone remains, while further reviews were presented in Boev (1999, 2018). Over time, these syntheses have become partly outdated, necessitating an updated and comprehensive review based on recently accumulated data.

In recent decades, some previously reported taxa have been revised, and new Neogene avian localities have been discovered. This underscores the need for a revised and expanded synthesis of the available information.

The study collects all known Neogene Bulgarian bird localities, summarizes their taxonomic composition and paleoecological characteristics, and assesses the paleobiogeographic significance of Bulgarian fossil birds from the Neogene.

MATERIAL AND METHODS

Neogene bird remains have so far been recorded from 17 localities (Fig. 1; Table 1) in both Northern (north of the Balkan Mountains) and Southern Bulgaria. Most have been studied and published, although several remain under investigation.

For each locality, data are provided on geographic position, approximate altitude, geological age, excavation history (including years and leaders), and relevant references (Table 1). The small number of findings at the moment does not allow any representative statistical analysis.

The general habitat preferences of the recorded taxa are inferred from the ecological characteristics of their closest living relatives, following Harrison (1982).

Abbreviations: Mya – million years ago; nr – near; P. – province; v. – village

RESULTS AND DISCUSSION

Seventeen Neogene avian localities are recognized in Bulgaria, including 12 Miocene and 5 Pliocene sites. They are distributed across both lowland and semi-mountainous regions of the country.

A total of 24 avian taxa have been identified (APPENDIX). Approximately one-quarter represent aquatic or water-associated species, including swans, geese, ducks, cormorants, gulls, and flamingos. Forest-dwelling birds, such as capercaillies, peacocks, and hawks, are comparatively rare, comprising roughly one-eighth of the recorded taxa.

The highest species richness is recorded at the Late Miocene locality of Hadzhidimovo (five taxa), followed by Hrabarsko, Dorkovo, and Muselievo (three taxa each).

Savannah–steppe birds

The highest avian diversity is associated with open landscapes. These assemblages include ostriches, ground hornbills, buzzards, falcons, snake eagles, ptarmigans, and larks, collectively representing nearly half of the identified Neogene avifauna of Bulgaria.

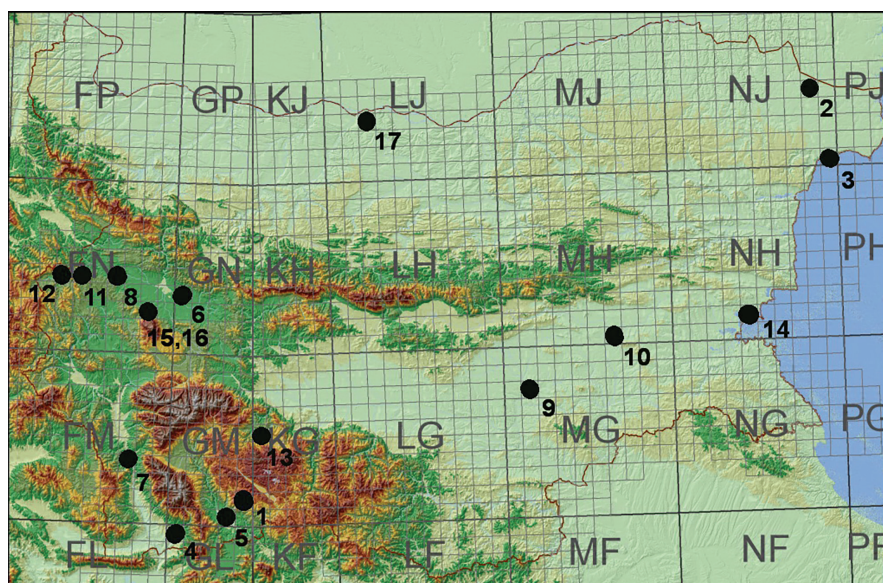


Fig. 1. Miocene avian localities in Bulgaria. (Numbers correspond to those of Table 1).

Table 1
Localities of Miocene avian bone remains in Bulgaria

No.	Locality	Province	Altitude a.s.l. (m)	Age	Years and leaders of excavations	Reference
1.	Satovcha	nr. Satovcha v. (Blagoevgrad P.)	1029	Middle Miocene (Middle Badenian); ~14.2–13.8 Mya	1960s; Emanuil Palamarev; 2019; Vladimir Bozukov	Vatsev and Pirumova (1983)
2.	Kardam	nr. Kardam v. (Dobrich P.)	198	Middle Miocene (Konkian), MN 5–8; 12.5–10.5 Mya	1950s unknown drilling workers	Jones and Simmons (1997)
3.	Balchik	nr. town of Balchik (Dobrich P.)	199	Late Miocene (Late Sarmatian); 11.6–9.0 Mya	ca. 2005; unknown	Nikolov (1985)
4.	Kalimantsi	nr. Kalimantsi v. (Blagoevgrad P.)	433	Late Miocene (Middle Turolian); 8.7–7.4 Mya	1980s; Dimitar Kovachev	Spasov <i>et al.</i> (2006)
5.	Hadzhidimovo	nr. town of Hadzhidimovo (Blagoevgrad P.)	500	Late Miocene (Turolian = Late Meotian), end of MN 11 – beginning of the MN 12 zone; ca. 7.5 Mya)	1980s; Dimitar Kovachev	Spasov (2002)
6.	Kremikovtsi	nr. Kremikovtsi (Sofia City P.)	946	Late Miocene, MN 12–13; 7.5–5.3 Mya	1995; Nikolay Spasov	Angelova and Yaneva (1998)
7.	Gorna Sushitsa	nr. Gorna Sushitsa v. (Blagoevgrad P.)	554	Late Miocene (Middle Turolian), 7.36 Mya	2006; joint Bulgarian- French team	Spasov <i>et al.</i> (2019)
8.	Hrabarsko	nr. Hrabarsko v., Coal Mine “Plamak “ (Sofia P.)	672	Late Miocene (Middle- Late Pontian); 7.2–5.3 Mya	1960s; unknown mine workers	Kamenov and Koyumdzhieva (1983)
9.	Troyanovo	nr. Troyanovo v., Coal mine “Troyanovo – 1” (Stara Zagora P.)	105	Late Miocene (Pontian – Pontian-Dacian); 7.2–5.3 Mya		Kamenov and Panov (1976)
10.	Azmaka	nr. town of Chirpan (Stara Zagora P.)	168	Late Miocene (Middle Turolian), ca. 7 Mya	Petar Popdimitrov; 1985–2005	Popov (1993); Spasov <i>et al.</i> (2012)
11.	Yalbotina	Coal mine “Beli Breg” nr. Yalbotina v. (Sofia P.)	675	Late Miocene (Maeotian- Pontian), MN13–14; 6 Mya	Dimiter Ivanov, 2010	Boev (2011a)
12.	Stanyantsi	Coal mine “Sveti Stefan” (“Stanyantsi”) nr. Stanyantsi v. (Sofia P.)	735	Late Miocene (Portaerrian – Early Bosphorian); 5.8–5.35 Mya	2012; Madeline Böhme	Böhme <i>et al.</i> (2013)
13.	Dorkovo	nr. Dorkovo v. (Pazardzhik P.)	852	Late Pliocene (Ruscinian), MN 14; 5.4–3.4 Mya	1983–1985; N. Spasov & H. Thomas	Thomas <i>et al.</i> (1986)
14.	Sarafovo	nr. former Sarafovo v. (pr. Sarafovo neigh- borhood, Burgas City; Burgas P.)	10	Early Pliocene; 5.33– 2.58 Mya	ca. 1971; Władysław Karaszewski	Jakubowski and Karaszewski (1972)
15.	Sofia – 1	Lozenets neighbor- hood, Sofia City	600	Early Pliocene (Ruscinian), MN 14; 5 Mya	1890–1930, Rafail Popov	Popov <i>et al.</i> (1921); Boev (1992)
16.	Sofia – 2	Lozenets neighbor- hood, Sofia City	610	Early Pliocene (Ruscinian), MN 14; 5 Mya	1995, unknown	Boev (2000a)
17.	Muselievo	nr. Muselievo v. (Pleven P.)	35	Late Pliocene (2nd half of the Middle Ruscinian), MN 15; 3.3–3.1 Mya	1989–1990; Vassil Popov	Popov and Delchev (1997)

Four ostrich localities (Hadzhidimovo, Kalimantsi, Sarafovo, and Stanyantsi) document the presence of Hipparion fauna, corresponding to the Iranian–Turanian savannah biome during the Late Miocene. Fossil remains include both skeletal material of *Struthio karatheodoris* (Boev, 2007b; Boev *et al.*, 2008; Boev and Spassov, 2009) and eggshell fragments (Jakubowski and Karaszewski, 1972; Böhme *et al.*, 2013). All known localities of the species so far outline its peri-Aegean range (Fig. 2). Later summaries of Cenozoic ostriches (Mikhailov and Zelenkov, 2020) suggest the coexistence in Bulgaria at that time of not only two species, but also two genera (*Struthio* and *Pachystruthio*) of ostriches. It has already been shown that the Black Sea region was part of the range of *Pachystruthio* (Zelenkov *et al.*, 2019).

The first European record of hornbills (Bucerotidae) is represented by *Euroceros bulgaricus*, a new genus of ground hornbills (Bucorvini), indicating a broader Late Miocene distribution of Bucerotidae across Africa, Europe, and Asia (Boev, 2007c; Boev and Kovachev, 2007). The modern range of this family is limited to sub-Saharan Africa and the Indo-Malayan zoogeographic region (Fig. 3). Neogene finds of representatives of the tribe Bucorvini from southern Bulgaria and northern Morocco prove the widespread dis-

tribution of savannah landscapes in the peri-Mediterranean region at least towards the end of the Miocene.

The genus *Buteo* is represented by *Buteo spassovi*, one of the earliest records of this lineage in the Western Palearctic (Boev and Kovachev, 1998; Boev, 2022). During the Neogene, the distribution of buzzards of the genus *Buteo* is documented by finds in southern Europe (Fig. 4).

Similarly, the Late Miocene species *Circaetus rhodopensis* represents the earliest known fossil snake eagle worldwide (Boev, 2012a).

The Late Miocene species *Falco bulgaricus* indicates that the divergence of the genus *Falco* into the ‘tinnunculus’ and ‘cherrug’ groups occurred no later than the Late Pliocene. The ‘tinnunculus’ group is of older origin and had already diversified by the late Miocene. The falcon from Hadzhidimovo, Bulgaria, described as a new species, provides further support for this conclusion (Boev, 2011b). Like the buzzards, the Neogene finds of falcons of the genus *Falco* are localized in Southern, and especially in Southeastern Europe (Fig. 5).

Early Pliocene records of *Lagopus* rank among the oldest occurrences of the genus (Boev, 2001, 2002b), although the first finds of this genus originate from the peri-Carpathian region of Hungary and Poland (Boev, 2002b; Mlíkovský, 2002).

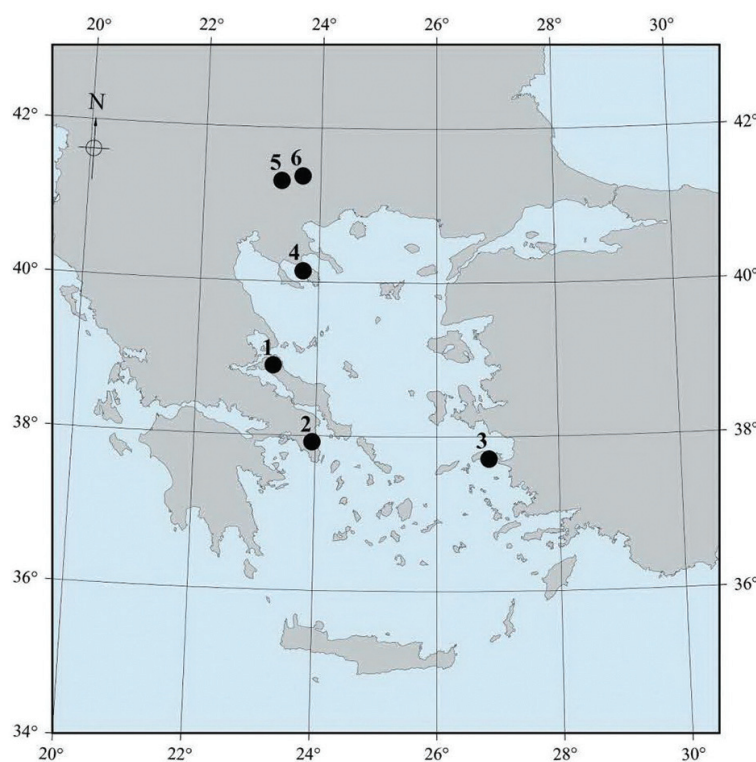


Fig. 2. Geographical distribution of *Struthio karatheodoris* in Europe in the Miocene: 1, Kerassia; 2, Pikermi; 3, Samos; 4, Nikiti – 2 (Greece); 5, Kalimantsi; 6, Hadzhidimovo – 2 (Bulgaria) (after Kampouridis *et al.*, 2021).

Small Phasianidae from Dorkovo likely inhabited open grassland environments dominated by Poaceae (Boev, 1998).

Despite the Miocene radiation of passerines, only two lark taxa have been identified, including the new genus *Eremarida*, interpreted as an inhabitant of arid open landscapes (Boev, 2012b, c).

Both species of larks (*Melanocorypha serdicensis* and *Eremarida xerophila*) are inhabitants of open savanna-steppe expanses, which do not exist today in this part of the Balkan Peninsula.

Woodland birds

The occurrence of *Tetrao rhodopensis* indicates a forested or wooded savannah environment dominated by straight-tusked mastodon (*Anancus arvernensis*) (Thomas *et al.*, 1986; Boev, 1998). The Bulgarian remains of *T. rhodopensis* from the Ruscinian locality of Dorkovo represent the oldest known record of the genus *Tetrao* to date (Boev, 2002b). The

capercaillie lineage within *Tetrao* is regarded as an indicator of forested environments. *Tetrao* lineage is well documented in the Central Europe and the peri-Carpatian region (Jánossy, 1974, 1976).

The associated fauna at this site further supports the presence of such habitats, likely in the form of open parkland forest or wooded savanna (Boev, 1998).

The Late Miocene species *Phasianus bulgaricus* represents the earliest Neogene record of true pheasants in Europe (Boev, 2020a).

Phasianus etuliensis and *Pavo moldavicus*, identified from Pliocene finds from a region adjacent to Bulgaria (southern Moldova; Bocheński and Kurochkin, 1987), are today synonymized with *Pavo bravardi* (Mlíkovský, 2002).

The presence of *Pavo bravardi* suggests a wider distribution of peafowl (Pavonini) in the Balkans during the Late Neogene (Boev and Koufos, 2000; Boev, 2001) (Fig. 6). The modern range of peafowl spans the Afrotropical and Indo-Malayan

Fig. 3. Present range of Bucerotidae (after Kemp, 2001) and the localities of its fossil (Neogene) record: Beni-Mellal, Late Miocene, Morocco (Brunet, 1971) (1) and Hadzhidimovo, Late Miocene, Bulgaria (2) (after Boev and Kovachev, 2007).



Fig. 4. Geographical distribution of g. *Buteo* in Europe in the Miocene: (1) Grive-Saint-Alban (Isère – SE France; after Ballmann *et al.*, 1969); (2) Hadzhidimovo (Blagoevgrad Province – SW Bulgaria; after Boev and Kovachev, 1998); (3) Roddi (Cuneo – NW Italy; after Pavia *et al.*, 2022).



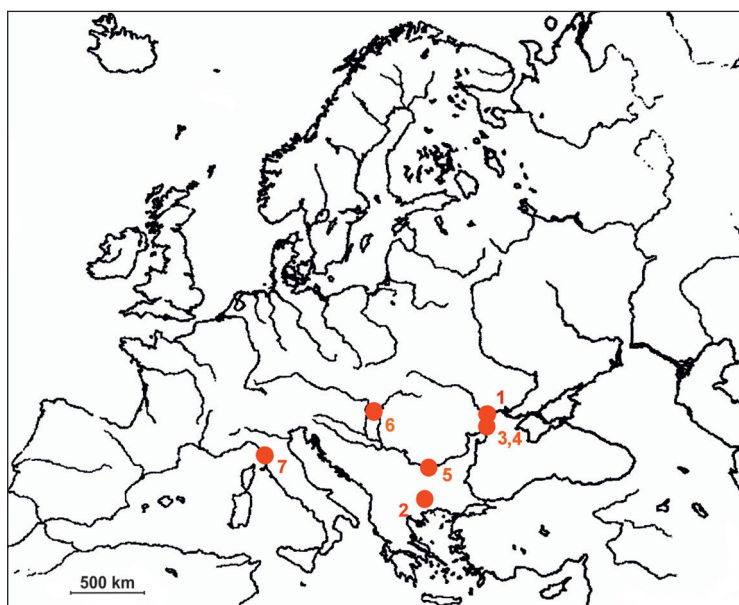


Fig. 5. Distribution of genus *Falco* during the Neogene in Europe: (1) *Falco medius* Umanskaja, 1981 – Chebotarevka, Southern Ukraine, Late Miocene (Umanskaja, 1981); (2) *Falco bulgaricus* Boev, 2011 – Hadzhidimovo, Southern Bulgaria, Late Miocene (Boev, 2011b); (3) *Falco umanskajae* Sobolev, 2003 – Krizhanovka (Odessa region), Southern Ukraine, Late Pliocene (Sobolev, 2003); (4) *Falco* sp. – Odessa Catacombs, Southern Ukraine, Early Pliocene (Vojinstvensky, 1967); (5) *Falco* sp. (size of *F. peregrinus*) – Muselievo, Northern Bulgaria, Early Pliocene (Boev, 2001); (6) *Falco* sp. – Beremend 11, Southern Hungary, Late Pliocene (Jánossy, 1986); (7) *Falco* sp. – Orciano Pisano, Tuscany, Central Italy, Middle Pliocene (Ghelardoni *et al.*, 1968)

zoogeographical regions. Like hornbills and ostriches, it is an example of the large-scale Afro-Asian disjunction that occurred at the end of the Tertiary (Müller, 1974). Ostriches existed in Asia until the middle of 20th century, and their disappearance from this continent is a late Holocene phenomenon.

Passerines are represented by a single family, Sturnidae, including the newly described genus *Dobrostrurnus*. These fossils rank among the oldest known birds from Bulgaria, dated to 12.5–10.5 Mya (Boev, 2020b).

The Satovcha locality has yielded only fossil feathers rather than skeletal remains, likely belonging to at least two species. Numerous plant fossils, including trees and shrubs, have also been recovered from the site (Bozukov *et al.*, 2023). The feather evidence suggests that these birds inhabited forested habitats in that region in the Middle Miocene (Boev and Bozukov, 2021).

Aquatic birds

The first formally described Neogene birds from Bulgaria, *Phalacrocorax serdicensis* and *Anser thraceiensis*, were reported relatively recently (Burchak-Abramovich and Nikolov, 1984), although

earlier undocumented finds date back to the early 20th century (Popov *et al.*, 1921; Boev, 1992).

The presence of the dabbling duck *Balcanas pliocaenica* indicates large, slow-moving freshwater bodies in a wooded savannah environment (Boev, 1998). The swan *Cygnus verae* further supports the existence of a substantial Pliocene lake in the Sofia Basin (Boev, 2000a). After Kouzov *et al.* (2024) “*Cygnus verae* from the early Pliocene of Bulgaria appears as transitional form between the subgenus *Cygnus* and *Olor*.” (p. 3). If this is so, the importance of the Bulgarian find from Sofia greatly increases.

A small dabbling duck from Kremikovtsi represents one of the earliest Miocene records of Anatini in Europe (Boev, 2020c). An almost complete gull skeleton from Hrabarsko suggests the presence of a large inland water body during the Early Miocene (Boev, 2000b).

CONCLUSIONS

Seventeen Neogene bird localities are currently known in Bulgaria, comprising 12 Miocene and 5 Pliocene sites distributed across diverse landscapes. A total of 24 taxa, including three genera and 11 species new to science, have been identified, rep-

representing approximately 0.36% of all known fossil bird species and 1.0% of all known Neogene bird taxa worldwide. The fossil record of Neogene birds is extremely rich and includes over a thousand described species, with the number continuing to grow with new discoveries (Mayr, 2017).

The Bulgarian Neogene avifauna includes several taxa that are currently absent from Europe, such as ostriches, peafowls, and ground hornbills, whose modern distribution is restricted to the Afrotropical and Indomalayan zoogeographic regions (Boev, 2008). Their presence in the Bulgarian Neogene provides further evidence for the coexistence of open savanna-steppe and forest environments during this period.

The Balkan region, particularly its southern parts, functioned as a transitional biogeographic zone connecting Eurasian and Afro-Asian faunal elements within the former Irano-Turanian paleobiogeographic province (Akhani *et al.*, 2013).

The Neogene avifauna of Bulgaria, as currently known and considered part of the Southeastern European Neogene avifauna, also shows strong similarities to that of the neighboring inland Pericarpinian region (Kessler, 2014, 2019).

Climatic changes during the Late Miocene and Pliocene led to increasing aridity and the expansion of grasslands, facilitating faunal dispersal between regions. Subsequent climatic changes caused range contractions, ultimately giving rise to the modern distribution patterns observed today.

Despite its relatively low taxonomic diversity, the Bulgarian Neogene avifauna is fully consistent with that known from neighboring Balkan countries (Greece and Romania), as well as from several

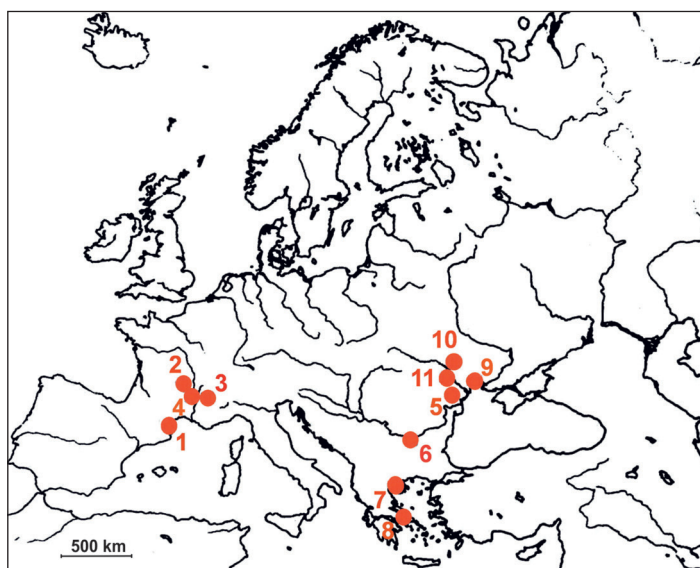
countries of the Black Sea region (Ukraine, Moldova, and Georgia) and the Pericarpinian region (Poland, Hungary, and the Czech Republic). Its most distinctive feature so far is the discovery of hornbills in the Late Miocene of southern Bulgaria. The geographically closest fossil occurrence of the family Bucerotidae outside its modern range is known from the Atlas Mountains of Morocco (Boev and Kovachev, 2007). This provides another example among birds of the post-Miocene (post-Pliocene) Afro-Indomalayan disjunction in the geographic ranges of numerous terrestrial vertebrate taxa.

From the paleontological materials collected so far, it can be concluded that there is a certain disproportionate representation of the different metric classes of birds. It is obvious that small (especially passerine) birds are underrepresented in the studied materials. Conversely, large species with better chances of fossilization of their remains are better represented. This is a universal pattern, which is also present here. Therefore, the peculiarities of taphonomy should not affect the conclusions about the paleoecological situation in individual localities. However, this is an inevitable risk due to the specific fragmentation of the paleontological record.

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Fig. 6. Geographical distribution of g. *Pavo* in Europe: *Pavo bravardi*: 1 – Serrat-d'en-Vacquer; 2 – Arde'; 3 – Saint-Vallier; 4 – Seneze (France); 5 – Lucheshti (Moldova); 6 – Muselievo (Bulgaria); 7 – Megalo Emvolon (Greece); *Pavo aesculapi*: 8 – Piskermi (Greece); 9 – Odessa; 10 – Novoelisavetovka (Ukraine); 11 – Kolkotova Balka (Moldova) (after Boev and Koufos, 2000).



APPENDIX. SYSTEMATIC LIST OF THE AVIAN TAXA FROM THE NEOGENE LOCALITIES OF BULGARIA

No.	Taxon	Authority	Locality	Age	Habitat
Struthioniformes					
1	<i>Struthio karatheodoris</i>	Forsyth Major, 1888	Kalimantsi; Hadzhidimovo	Late Miocene	Savanah
2	<i>Struthioniformes</i> indeterminate	–	Sarafovo	Early Pliocene	Savanah
3	<i>Struthio</i> sp.	–	Stanyantsi	Late Miocene	Savanah
Bucerotiformes					
4	<i>Euroceros bulgaricus</i>	Boev and Kovachev, 2007	Hadzhidimovo	Late Miocene	Savanah
Anseriformes					
5	<i>Cygnus verae</i>	Boev, 2000a	Sofia (locality 2)	Early Pliocene	Aquatic (freshwater lake/river)
6	<i>Anser thraceiensis</i>	Burchak-Abramovich and Nikolov, 1984	Troyanovo	Late Miocene	Aquatic (freshwater lake/river)
7	<i>Balcanas pliocaenica</i>	Boev, 1998	Dorkovo	Late Pliocene	Aquatic (freshwater lake/river)
Suliformes					
8	<i>Phalacrocorax serdicensis</i>	Burchak-Abramovich and Nikolov, 1984	Hrabarsko	Late Miocene	Aquatic (freshwater lake/river)
Falconiformes					
9	<i>Falco bulgaricus</i>	Boev, 2011b	Hadzhidimovo	Late Miocene	Svannah
10	<i>Falco</i> sp. (<i>cherrug</i> group)	–	Muselievo	Late Pliocene	Rocky openland
Galliformes					
11	<i>Tetrao rhodopensis</i>	Boev, 1998	Dorkovo	Late Pliocene	Forest
12	<i>Lagopus</i> aff. <i>atavus</i>	Jánossy, 1974	Muselievo	Late Pliocene	Forested savannah
13	<i>Pavo bravardi</i>	Gervais, 1849	Muselievo	Late Pliocene	Riparian wood
14	<i>Perdicinae</i> genus indeterminate	–	Dorkovo	Late Pliocene	Grassy openland
15	<i>Perdicinae</i> genus indeterminate	–	Stanyantsi	Late Miocene	Grassy openland
Accipitriformes					
16	<i>Circaetus rhodopensis</i>	Boev, 2012a	Hadzhidimovo	Late Miocene	Svannah
17	<i>Buteo spassovi</i>	Boev, 1998	Hadzhidimovo	Late Miocene	Svannah
18	<i>Accipiter</i> sp. (<i>gentilis</i> group)	–	Muselievo	Late Pliocene	Forest
Charadriiformes					
19	<i>Larinae</i> genus indeterminate	–	Hrabarsko	Late Miocene	Aquatic (lacustrine, marine)
Phoenicopteriformes					
20	<i>Phoenicopteridae</i> genus indeterminate	–	Balchik	Late Miocene	Aquatic (lacustrine, marine)
Passeriformes					
21	<i>Melanocorypha serdicensis</i>	Boev, 2012b	Hrabarsko	Late Miocene	Steppe
22	<i>Eremarida xerophila</i>	Boev, 2012b	Hrabarsko	Late Miocene	Steppe
23	<i>Passeriformes</i> family indeterminate	–	Yalbotina	Late Miocene	–
Neognathae					
24	<i>Neognathae</i> order indeterminate	–			–

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