

# First record of ostriches (Aves, Struthioniformes, Struthionidae) from the late Miocene of Bulgaria with taxonomic and zoogeographic discussion

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Boev Z. & Spassov N. 2009. — First record of ostriches (Aves, Struthioniformes, Struthionidae) from the late Miocene of Bulgaria with taxonomic and zoogeographic discussion. *Geodiversitas* 31 (3): 493-507.

## ABSTRACT

We describe two new fossils, the distal end of a right tarsometatarsus and a proximal pedal phalanx of the left third toe, from two sites in southwestern Bulgaria: Kalimantsi (middle Turolian) and Hadzhidimovo-2 (MN 11/12 boundary). These specimens are compared to Neogene-Quaternary ostriches, and are referred to *Struthio* cf. *karatheodoris*. A general overview of Neogene-Quaternary ostrich specimens, a taxonomic discussion of late Miocene Eurasian struthionid taxa, and the ecological and zoogeographic implications of the new specimens are presented.

## RÉSUMÉ

*Premières découvertes d'autruches (Aves, Struthioniformes, Struthionidae) du Miocène supérieur de Bulgarie et discussion taxonomique et zoogéographique.*

Deux vestiges du membre postérieur, l'extrémité distale d'un tarsométatarsaire droit et une phalange proximale du troisième doigt gauche, provenant de deux gisements de la Bulgarie du sud-ouest: Kalimantsi (niveaux du Turolien moyen) et Hadzhidimovo-2 (limite MN 11/12) sont décrits et rapportés à *Struthio* cf. *karatheodoris*. Nous présentons une revue des restes fossiles d'autruches du Néogène au Quaternaire, ainsi qu'une discussion sur leurs implications écologique et paléogéographique.

## KEY WORDS

Aves,  
Struthioniformes,  
Struthionidae,  
*Struthio karatheodoris*,  
taxonomy,  
palaeoecology,  
palaeogeography,  
Bulgaria,  
late Miocene.

## MOTS CLÉS

Aves,  
Struthioniformes,  
Struthionidae,  
*Struthio karatheodoris*,  
taxonomie,  
paléoécologie,  
paléogéographie,  
Bulgarie,  
Miocène supérieur.

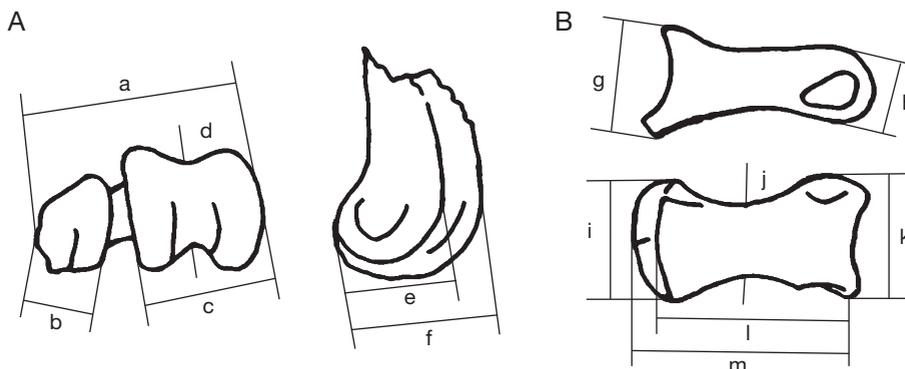


FIG. 1. — Measurements of distal tmt. and phal. 1 dig. 3 ped. in *Struthio* spp. (used in Table 1): **A**, tmt. dex. dist.: **a**, maximum width of distal epiphysis; **b**, width of tr. tmt 4; **c**, width of tr. tmt 3; **d**, minimum diameter of tr. mt. 3; **e**, diameter of tr. tmt 4; **f**, diameter of tr. tmt 3; **B**, phal. 1 dig. 3 ped. sin.: **g**, maximum height of facies articularis prox.; **h**, maximum height of dist. end; **i**, maximum width of facies articularis prox.; **j**, minimum width of (body of the) phal.; **k**, maximum width of dist. end; **l**, dorsal length of ph.; **m**, ventral length of phal.

## INTRODUCTION

Ratite birds have not been recorded so far from the fossil record of Bulgaria, despite the presence of the genus *Struthio* Linnaeus, 1758 in geographically neighbouring and nearby countries (Greece, Turkey, Hungary, Ukraine, Moldova, Russia, Georgia) (Mlíkovský 2002). However, the taxonomy of the osteological and oological remains of the European struthionids remains complicated. Recent discovery of *Struthio* remains from two Bulgarian Late Neogene localities provides an opportunity to discuss the Turolian history of the genus in southeastern Europe.

## MATERIAL AND METHODS

The new fossil material has been compared with specimens of recent ostriches (collections of the Fossil and Recent Birds Department, NMNHS) and with measurement data and illustrations from the scientific literature (Table 1; Fig. 1). We follow the osteological terminology of Baumel & Witmer (1993) and the biostratigraphy of Mein (1990).

## ABBREVIATIONS

### Anatomical abbreviations

ad. adult individual;

dex. dextra;  
dig. digitis;  
dist. distalis;  
ped. pedis;  
phal. phalanx;  
prox. proximal;  
tmt. tarsometatarsus;  
tr. mt. trochlea metatarsi;  
sin. sinistra.

### Other abbreviations

HD Hadzhidimovo (given as Hadjidimovo by Spassov [2002] and Spassov *et al.* [2006]);  
KM Kalimantsi (given as KAL by Spassov [2002] and Spassov *et al.* [2006]);  
NMNHS National Museum of Natural History, Bulgarian Academy of Sciences, Sofia.

## THE NEOGENE FOSSIL RECORD OF THE STRUTHIONIDAE

Burchak-Abramovich (1953a) listed 26 fossil and subfossil taxa of *Struthio* from Eurasia and northern Africa. Eight of these taxa (*S. novorossicus* Aleksejev, 1915; *S. brachydactylus* Burchak-Abramovich, 1939; *Palaeostruthio sternatus* Burchak-Abramovich, 1939; *S. chersonensis* Brandt, 1885; and three *Struthio* spp. from Novoemetovka, Il'inka/Ilynka, Snigirevka/Snegurovka, and Pavlodar) are from the late Miocene of the North Peri-Pontic region and eastern Kazakhstan. Of these taxa, only *S. novorossicus* and *S. brachydactylus* may represent valid species

TABLE 1. — Measurements (in mm) of the distal tmt. and phal. 1 dig. ped. 3 of *Struthio* spp. (see Figure 1). Measurements explanations: *S. karatheodoris* – Pikermi, all (except measurement “h”) from Bachmayer & Zapfe (1962), measurement “h” from photograph; *S. brachydactylus* 408/359 – from Burchak-Abramovich (1953a); *S. brachydactylus* – 1 from Burchak-Abramovich (1949), we reversed the measurements of “j” and “k”, which were apparently erroneously reversed in Burchak-Abramovich (1949), measurement “l” from photograph (Burchak-Abramovich 1949: fig. 4); *S. brachydactylus* – 2, from Burchak-Abramovich (1953: table 9, 146); *S. brachydactylus* – 3, from photograph (Burchak-Abramovich 1967: fig. 5); *S. asiaticus*, from Burchak-Abramovich (1953: table 9); *S. pannonicus* – Kislang, from Kretzoi (1955); *S. novorossicus* 1560 and 1561, from Aleksejev (1915); *S. orlovi* 6-4, from Kurochkin & Lungu (1970); *Struthio* sp. – Maragha, from Mecquenem (1925); *Struthio* sp. (Odessa catacombs, 5011, dated as MN 15), from Burchak-Abramovich (1953a: table 8); *S. camelus* – 1, this and the next eight specimens from Burchak-Abramovich (1953a: table 9).

| Species   | tmt. |      |      |      |      |      | phal. |      |      |      |      |      |       |
|---|------|------|------|------|------|------|-------|------|------|------|------|------|-------|
|   | a    | b    | c    | d    | e    | f    | g     | h    | i    | j    | k    | l    | m     |
| <b>Fossil</b>   |      |      |      |      |      |      |       |      |      |      |      |      |       |
| <i>S. cf. karatheodoris</i> ad. NMNHS 16371 – KM (Bulgaria) | 65.3 | 19.0 | 42.4 | 28.4 | 32.4 | 40.5 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. cf. karatheodoris</i> ad. NMNHS 16372 – HD (Bulgaria) | –    | –    | –    | –    | –    | –    | 49.6  | 33.7 | 49.6 | 31.2 | 47.4 | 89.3 | 92.0  |
| <i>S. karatheodoris</i> – Pikermi                           | –    | –    | –    | –    | –    | –    | 50.0  | 35.3 | 48.0 | 28.5 | 44.0 | 85.8 | 83.4  |
| <i>S. brachydactylus</i> 408/359                            | –    | –    | 40.0 | 37.0 | –    | 45.0 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. brachydactylus</i> – 1                                | –    | –    | –    | –    | –    | –    | –     | –    | 40.0 | 25.0 | 39.5 | 69.7 | 77.0  |
| <i>S. brachydactylus</i> – 2                                | –    | –    | –    | –    | –    | –    | 45.0  | –    | 40.0 | 25.0 | 39.5 | 70.0 | 70.0  |
| <i>S. brachydactylus</i> – 3                                | –    | –    | –    | –    | –    | –    | –     | –    | 37.3 | 22.7 | 36.0 | 69.3 | –     |
| <i>S. asiaticus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 41.9 | 25.0 | –    | –    | –     |
| <i>S. pannonicus</i> – Kislang                              | –    | –    | –    | –    | –    | –    | –     | –    | 56.0 | –    | 55.0 | –    | 110.0 |
| <i>S. novorossicus</i> 1560                                 | –    | –    | –    | –    | 48.3 | 77.0 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. novorossicus</i> 1561                                 | –    | –    | –    | –    | 42.5 | 62.5 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. orlovi</i> 6-4  | –    | –    | 40.0 | –    | –    | –    | –     | –    | –    | –    | –    | –    | –     |
| <i>Struthio</i> sp. – Maragha                               | –    | –    | –    | –    | –    | –    | –     | –    | –    | 29.0 | 45.0 | –    | –     |
| <i>Struthio</i> sp. (Odessa catacombs, 5011)                | 71.0 | 19.0 | 46.0 | –    | –    | 59.0 | –     | –    | –    | –    | –    | –    | –     |
| <b>Recent</b>   |      |      |      |      |      |      |       |      |      |      |      |      |       |
| <i>S. camelus</i> ad. NMNHS 2/2001                          | 54.0 | 14.9 | 37.4 | 34.7 | 28.6 | 43.4 | 44.8  | 25.4 | 38.0 | 21.2 | 35.6 | 92.0 | 91.3  |
| <i>S. camelus</i> ad. NMNHS 3/2003                          | 60.8 | 19.3 | 38.3 | 33.8 | 32.6 | 41.5 | 44.0  | 28.5 | 40.0 | 22.1 | 37.4 | 84.1 | 84.0  |
| <i>S. camelus</i> ad. NMNHS 4/2003                          | 60.2 | 17.4 | 38.3 | 34.6 | 28.8 | 41.0 | 42.8  | 29.0 | 40.8 | 23.8 | 39.2 | 88.2 | 89.3  |
| <i>S. camelus</i> ad. NMNHS 5/2003                          | 60.2 | 16.3 | 37.9 | 34.4 | 26.6 | 40.9 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. camelus</i> ad. NMNHS 6/2003                          | 59.4 | 15.7 | 37.2 | 33.8 | 26.0 | 37.3 | –     | –    | –    | –    | –    | –    | –     |
| <i>S. camelus</i> – 1                                       | –    | –    | –    | –    | –    | –    | –     | –    | 43.6 | –    | –    | 92.0 | 90.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 42.0 | –    | –    | 91.0 | 91.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 38.0 | –    | –    | 82.0 | 80.0  |
| <i>S. camelus australis</i>                                 | –    | –    | –    | –    | –    | –    | –     | –    | 40.0 | –    | –    | 86.0 | 86.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 42.0 | –    | –    | –    | 86.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 45.0 | –    | –    | 92.0 | 90.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 40.0 | –    | –    | 89.0 | 89.0  |
| <i>S. camelus molybdophanes</i>                             | –    | –    | –    | –    | –    | –    | –     | –    | 38.0 | –    | –    | 77.0 | 77.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 40.0 | –    | –    | 78.0 | 80.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 39.0 | –    | –    | 82.0 | 82.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 43.0 | –    | –    | 93.0 | 89.0  |
| <i>S. camelus</i>   | –    | –    | –    | –    | –    | –    | –     | –    | 38.0 | –    | –    | 74.0 | 75.0  |

(see below). Burchak-Abramovich (1953b; 1967) considered that southern Ukraine was the centre of speciation for Struthioniformes, and that both large and small ostrich species coexisted until the end of the Pliocene.

Brodkorb (1963: 197) listed six fossil species of *Struthio*: *S. asiaticus* Milne-Edwards, 1871 from the Pliocene (Siwalik series) of India (recently also reported from the late Pliocene of Ahl al Oughlam, Morocco; Mourer-Chauviré & Geraads 2008); *S. chersonensis* (Brandt, 1873) from the Upper Miocene (Turolian) of Greece (Brodkorb [1963] interpreted this site as lower Pliocene [Pannonian]), Ukraine, Kazakhstan and Egypt; *S. wimani* Lowe, 1931 of the lower Pliocene (*Hipparion*-fauna) of China, and the lower Pliocene (Ertemte stage) of Mongolia; *S. pannonicus* Kretzoi, 1953 from the latest Pliocene of Hungary (Brodkorb [1963] interpreted the Kisláng locality as lower Pleistocene [Upper Calabrian]); *S. oldawayi* Lowe, 1933 from the Villafranchian (Olduvai series) of Tanzania; and *S. anderssoni* Lowe, 1931 from the upper Pleistocene (Sanmen series, Fenho stage) of China. *Struthio anderssoni* has also recently been reported from Buryatia, Russia (Tyrberg 2005).

Kurochkin & Lungu (1970) described the species *S. orlovi*; considered that all of the Old World ostrich species (including *S. karatheodoris* Forsyth Major, 1888), with the exception of *S. orlovi* and *S. brachydactylus*, were synonyms of *S. asiaticus*; and interpreted this last species as the direct ancestor of *S. camelus*, a view also followed by Olson (1985). However, Mourer-Chauviré & Geraads (2008) noted that some of these synonymized taxa are 50% larger than the recent ostrich.

Mihaylov & Kurochkin (1988) considered that only two ostrich species existed in the Asian Neogene-Pleistocene: *S. asiaticus* and *S. transcasicus* Burchak-Abramovich & Vekua, 1971. They referred *S. wimani* and *S. anderssoni* to *S. asiaticus*, and suggested that *S. asiaticus* had a chronostratigraphic distribution from the upper Miocene to the Pleistocene (and into the Holocene of northern China and Mongolia).

A lower Miocene ostrich (*S. coppensi*) has been described by Mourer-Chauviré *et al.* (1996a) from Namibia. It is the oldest known *Struthio* species,

dated *c.* 20 Ma. New specimens of a late Middle Miocene ostrich (*c.* 14 Ma) were recently discovered in Kenya (Leonard *et al.* 2006). The oldest ostrich remains from Eurasia date to the middle Miocene of Çandir, Turkey (*c.* 12 Ma) (Mourer-Chauviré *et al.* 1996b).

Bocheński (1997) considered that the European record includes three species of *Struthio*: *S. chersonensis* (including *S. pannonicus*, synonymised by Mlíkovský [2002]) from the late Miocene of Greece and Ukraine (Bocheński [1997] erroneously dated these sites as lower Pliocene); *S. brachydactylus* (early Turolian; Grebeniki, Ukraine) (Burchak-Abramovich [1939] originally dated this site as lower Pliocene); and *S. orlovi* (late Miocene, Vallesian; Varnitsa, Moldova). Bocheński (1997) did not consider *S. karatheodoris*.

Tyrberg (1998) listed four species of *Struthio* from the Pleistocene of the Palearctic: *S. camelus* (Algeria, Egypt, Jordan, Mongolia, Russia); *S. pannonicus* (Hungary); *S. anderssoni* (China); and *S. dmanisensis* Burchak-Abramovich & Vekua, 1990 (Georgia).

Two other “ootaxa”, *Struthiolithus adzalycensis* Roshchin, 1962 and *Struthiolithus alexejevi* Roshchin, 1962, were not discussed by Bocheński (1997) or Tyrberg (1998). These were both described on the basis of eggshells from southern Ukraine, from Late Pontian and Sarmatian deposits respectively (Roshchin 1962).

The most recent study, by Mlíkovský (2002), recognised only two species of *Struthio*, *S. chersonensis* and *S. karatheodoris*, from the European fossil record. Mlíkovský (2002) considered that in Europe, *S. chersonensis* was present in the late Miocene (MN 9-13) of Ukraine, Moldova and Greece; the early Pliocene (MN 14-15) of Ukraine; the late Pliocene (MN 16-18) of Moldova, Ukraine, Russia and Hungary; and the (?) early Pleistocene (MQ 1a) of Russia. Eggshells referred to *S. chersonensis* are also recorded from Kalgan, northern China (Eastman 1898), and Neumayer (1990: 27) suggested that *S. chersonensis* was distributed from southern Russia to northern China “probably [in the] Pleistocene times”. Andersson (1923) listed 29 eggs from 18 localities of China, all referred to *S. chersonensis*. However, it seems doubtful that a single taxon persisted from

the Vallesian to the Pleistocene. Mlíkovský (2002: 62) considered that it was likely that *S. karatheodoris* from the late Miocene (Turolian) from Samos Island (Greece) “is identical with some or all of the Mio-Pliocene ostriches described from Siwalik Hills in NW India and adjacent parts of Pakistan”, i.e. it could be referred to *Struthio asiaticus*.

It also should be mentioned the remains of *Struthio* sp. from Çalta (Central Anatolia, Turkey) of Pliocene (MN 15 Zone). They belonged “to a young individual” and compared to modern ostrich was “much larger” (Janoo & Sen 1998: 340).

*Struthio transcausicus* from the upper Pliocene of Georgia was described on the basis of a synsacrum. This species is larger than *S. wimani* (i.e. *S. asiaticus* after Mihaylov & Kurochkin 1988), *S. brachydactylus*, *S. karatheodoris*, and *S. camelus* (Burchak-Abramovich & Vekua 1971). Because of the lack of comparable skeletal elements, *S. dmanisensis* and *S. transcausicus* could not be compared to the much older Bulgarian material.

*Struthio barbarus* Arambourg, 1979 from the Ain Boucherit (Algeria, Villafranchian) is “slightly larger than *S. camelus*” (Janoo & Sen 1988: 349). Arambourg (1979: 139) noted that this species is “of large size, mainly characterized by the more robust and heavily built legs, in comparison to *S. camelus*”. Mourer-Chauviré & Geraads (2008) also note that specimens of *S. barbarus* are 20% larger than recent (male) ostriches.

*Struthio dmanisensis* from the lower Pleistocene of Georgia was described on the basis of a femur, which is larger and stouter than that of *S. camelus* and is similar to *S. pannonicus* (Burchak-Abramovich & Vekua 1990).

In addition, Pleistocene records of *Struthio* sp. not identified to species level have been reported from Azerbaijan (Burchak-Abramovich 1966), Algeria, China, Lebanon, Russia, Tunisia, Egypt, Morocco, Israel, Jordan, Saudi Arabia, Syria (Tyrberg 1998) and India (Sahni *et al.* 1990). Fossil (Pleistocene) remains of *S. camelus* are known from South Africa, Algeria, Morocco, Egypt, Israel, Saudi Arabia, Jordan, Ukraine, Russia (including Transbaikalia, Krasnodar Region and Buryatia), Azerbaijan, Turkmenistan, Tadjikistan, Mongolia and China (Burchak-

Abramovich 1962; Brodkorb 1963; Olson 1985; Tyrberg 1998, 2005).

*Struthio kakesiensis* Harrison & Msuya, 2005 has recently been described from the late Pliocene (c. 4.5-3.6 Ma) of Laetoli, Tanzania, on the basis of numerous eggshells. It is believed this species was chronologically directly replaced by *S. camelus*, which appeared at c. 3.6-3.8 Ma (Harrison & Msuya 2005). *Struthio kakesiensis* can be excluded from our discussion (below) due to the lack of skeletal remains and this considerable chronostratigraphic difference in age.

*Struthio karingarabensis* (c. 6.5-4.2 Ma), described from eggshells from the late Miocene-early Pliocene of southwestern and southeastern Africa can also be excluded from further comparisons. This species is older than *S. kakesiensis* (Harrison & Msuya 2005); however, Harrison & Msuya did not exclude possible temporal overlap of these species, and the coexistence with *S. daberasensis*, another oospecies from Namibia, has also been suggested by Senut (2000). Bibi *et al.* (2006) recognised *S. daberasensis* and *S. kakesiensis* as valid taxa which coexisted in the Pliocene with the recent *S. camelus*.

*Struthio oshanaï* Sauer, 1966 is also based on eggshells from the Kalahari (southwestern Africa) and dated as Upper Tertiary or lower/middle Pleistocene (Sauer 1966). More recently, this ootaxon has been separated from *Struthio* under the name *Namornis oshanaï* and re-dated as Pliocene in age (Bibi *et al.* 2006).

Finally, we accept four species as valid for the late Miocene of Europe and Asia:

1. *Struthio karatheodoris* Forsyth Major, 1888, a robust form from the south Balkans and the Middle East, including Samos, Pikermi and probably also Maragha (several specimens from the late Miocene of Siwaliks, Pakistan, probably belong to this species). The smaller *S. asiaticus* Milne-Edwards, 1871 from India and *S. pannonicus* Kretzoi, 1953 from central Europe, both from the Plio-Pleistocene, are too recent in age to be referred to *S. karatheodoris*.
2. *Struthio novorossicus* Alekseev, 1915 from the Turolian of the northern Peri-Pontic area

(Novo-Elizavetovka, Odessa region), described from three fragments of distal tarsometatarsus. This is the largest species of *Struthio* known so far, and displays morphological differences from *S. karatheodoris*. *Palaeostruthio sternatus* Burchak-Abramovich, 1939, described from a very large sternum from Grebeniki, Ukraine, may be a junior synonym of *S. novorossicus*.

3. *Struthio brachydactylus* Burchak-Abramovich, 1939 (see Burchak-Abramovich 1939, 1949; Mlíkovský 2002), another species from the northern Peri-Pontic area and also known from Grebeniki, differs in its higher degree of monodactyly and its significantly smaller size compared to the species mentioned above.
4. *Struthio orlovi* Kurochkin & Lungu, 1970. This relatively small Peri-Pontic form (synonymised by Mlíkovský 2002 with *S. chersonensis*) may also represent a valid species. It is Vallesian in age, and could be the oldest of the Eurasian late Miocene *Struthio* species. Kurochkin & Lungu (1970) demonstrated clear morphological differences between *S. orlovi* and *S. brachydactylus*, which are otherwise comparable in size.

As stated above, recent taxonomic revisions have typically interpreted all Neogene specimens from the northern Peri-Pontic region (sometimes even including all Neogene specimens from the Balkans and eastern Europe) as being synonymous with *S. chersonensis*. The type specimen eggshell of *S. chersonensis* (Brandt 1885), as well as some eggshells from China (Anderson 1923), are much larger than those of *S. camelus* (Kretzoi 1955). The size of the holotype eggshell is actually close to that of *S. novorossicus*, but the lack of comparative studies, as well as the lack of any data on individual and population-level variability of fossil *Struthio* eggshells, leaves the possible synonymy of *S. novorossicus* with *S. chersonensis* unclear. Specimens from the northern Peri-Pontic area referred to *S. chersonensis* may in fact represent more than one species. As *S. chersonensis* is described from eggshell remains only, its affinities with the numerous skeletal specimens remains unclear and practically impossible to investigate. We therefore prefer to restrict the name *S. chersonensis* to the holotype only, and this name may be interpreted as a *nomen dubium*.

## SYSTEMATIC PALEONTOLOGY

Order STRUTHIONIFORMES Latham, 1790

Family STRUTHIONIDAE Vigors, 1825

Genus *Struthio* Linnaeus, 1758

### *Struthio* cf. *karatheodoris*

Forsyth Major, 1888

TYPE MATERIAL. — Holotype femur, from Samos 1. Said to be in the Barbey collection (Lambrecht 1933: 100); present location unknown (Mlíkovský 2002).

TYPE HORIZON. — Late Miocene (MN 11) (Mlíkovský 2002).

TYPE LOCALITY. — Samos 1, Samos Island (southeastern Greece).

NEW DIAGNOSIS. — Fossil late Miocene ostrich of large size, only smaller than *S. novorossicus*, more bipedal, with better developed fourth toe; more robust pedal phal. in comparison to *S. camelus*.

OTHER MATERIAL EXAMINED. — Kalimantsi: tmt. dex. dist. (epiphysis, complete articular end) ad., NMNHS 16371 (Fig. 2); from the middle Turolian of the fossiliferous area near Kalimantsi village (Blagoevgrad Region, 43.17°N, 27.44°E; UTM grid: NH 59; c. 300 m a.s.l.). — Hadzhdimovo: phal. 1 dig. 3 ped. sin. (almost complete) ad., NMNHS 16372 (Fig. 2); from the base of the middle Turolian or the early-middle Turolian boundary at Tumbichkite (HD-2), near the town of Hadzhdimovo (Blagoevgrad Region, 41.30°N, 23.52°E; UTM grid: GM 30; 500 m a.s.l.). Both sites represent the richest Bulgarian localities of the so-called “*Hipparion*-fauna”. The two specimens are morphometrically similar to each other, and their relatively close chronostratigraphic position indicates that they are referable to the same fossil species.

Both specimens were collected in the 1980's by D. Kovachev.

LOCALITIES. — The fossiliferous area around Kalimantsi village in the Middle Struma basin covers a large region (c. 6 km<sup>2</sup>) of late Miocene deposits including more than 10 known fossil mammal localities (labelled KM sites). Recent biostratigraphic revision demonstrates that all KM sites are of Turolian age. KM-1, belonging to the newly established Gradishte lithocomplex, is likely to yield a fauna of early Turolian age, while other KM faunas (referred to the Strumyani Genetic Lithocomplex) are considered to belong to the middle Turolian (Tzankov *et al.* 2005; Spassov *et al.* 2006). The middle Turolian fauna of KM is presented by c. 10 different localities, which are faunally dominated by *Gazella* sp., *Cremohipparion*

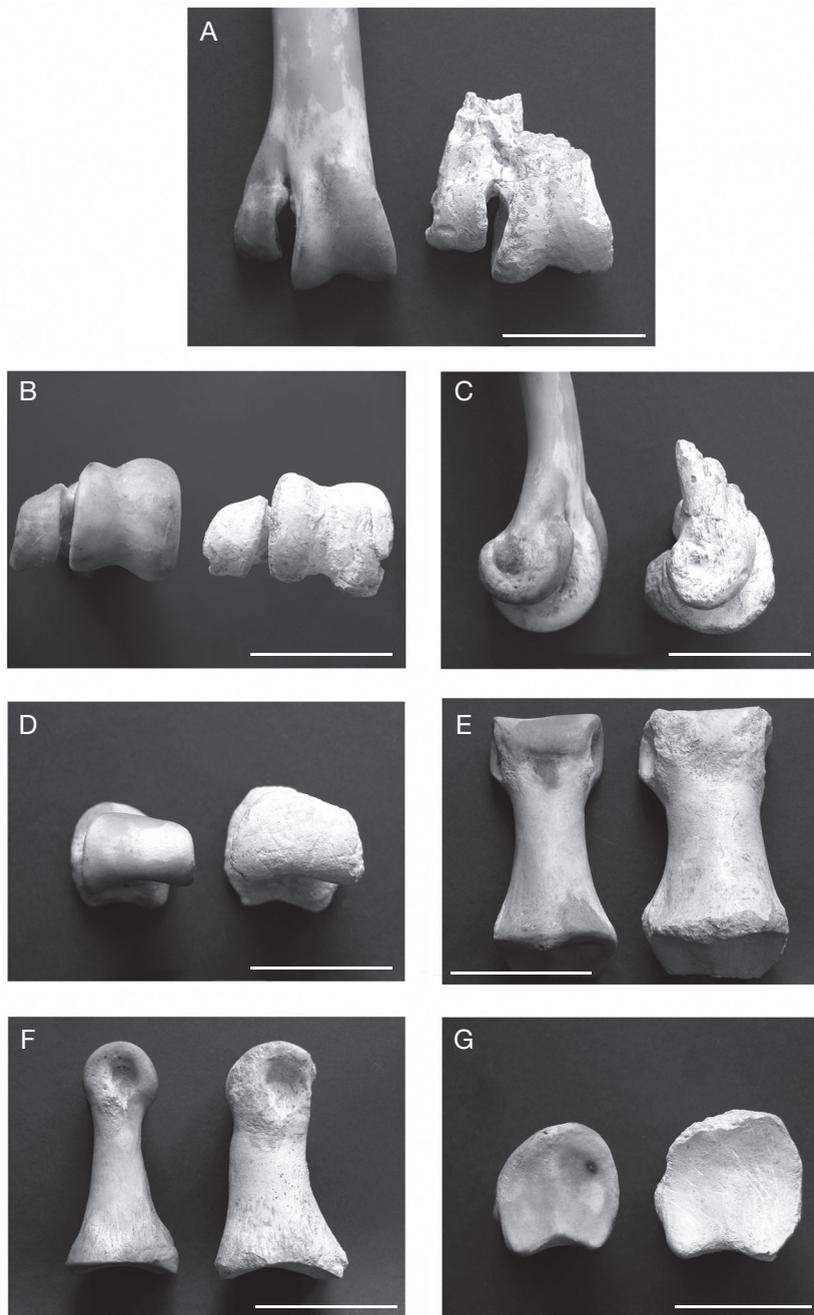


FIG. 2. — *Struthio* cf. *karatheodoris* (Sk, right) in comparison to *S. camelus* (Sc, left): **A-C**, tmt. dex. dist. ad., Sk (NMNHS 16371), middle Turolian near Kalimantsi village (Blagoevgrad Region, southwestern Bulgaria) and Sc (NMNHS 6/2006); **A**, cranial view; **B**, distal view; **C**, lateral view; **D-G**, phal. 1 dig. 3 ped. sin. ad., Sk (NMNHS 16372), middle Turolian or early-middle Turolian boundary near Hadzhidimovo (Blagoevgrad Region, southwestern Bulgaria) and Sc (NMNHS 4/2006); **D**, distal view; **E**, dorsal view; **F**, medial view; **G**, proximal view. Photographs: Asen Ignatov. Scale bars: 5 cm.

*mediterraneum* (Roth & Wagner, 1855) and *Hippotherium brachypus* (Hensel, 1862), and which also contain *Tragoportax* cf. *amalthaea*, *Palaeoreas lindermayeri* (Wagner, 1848), *Helladotherium duvernoyi* (Gaudry & Lartet, 1856), *Boblinia attica* (Gaudry & Lartet, 1856), *Adcrocuta eximia* (Roth & Wagner, 1854), *Mesopithecus pentelicus* Wagner, 1839, and other species (Spassov *et al.* 2006). NMNHS 16371 comes from horizons of middle Turolian age and is probably slightly younger than NMNHS 16372.

Hadzhidimovo is a late Miocene site with three fossil vertebrate localities: HD-1, HD-2 (Tumbichkite) and HD-3. The main locality, HD-1 (from which more than 30 mammal species have been reported), is dated to the MN 11/12 boundary (Spassov 2002). The other two localities could be of slightly different age; HD-2 is several tens of metres higher than the level of HD-1. The fauna of the locality consists of *Gazella* sp., *Palaeoreas lindermayeri*, *Tragoportax rugosifrons* (Schlosser, 1904), *Helladotherium duvernoyi*, *Hipparion/Cremohipparion* spp. (probably *H. brachypus* and *C. mediterraneum*), *Ancylotherium pentelicum* (Gaudry & Lartet, 1856), *Deinotherium gigantissimum* Stefanescu, 1892 and *Choerolophodon pentelici* (Gaudry & Lartet, 1856). The occurrence of *P. lindermayeri* and *C. pentelici* further suggests that HD-2 is younger than HD-1 (Geraads *et al.* 2003; Markov 2004).

## COMPARISON AND DISCUSSION

We first compare the Bulgarian material with struthionid taxa from the Turolian of the Greco-Iranian (*sensu* Bonis *et al.* 1992) zoogeographic province and the late Miocene of the northern Peri-Pontic area, including: 1) *S. chersonensis* *sensu lato* [*S. novorosicus* group]; 2) *S. karatheodoris* [*S. asiaticus* group]; 3) *S. brachydactylus*; and 4) *S. orlovi*. Available taxonomic and stratigraphic data and biogeographic distribution data suggest that these are the most suitable taxa for comparison (Fig. 3).

### COMPARISON WITH *STRUTHIO ORLOVI*

The Vallesian *S. orlovi* was described from two distal fragments of tibiotarsi dex. and a distal fragment of left tmt. (tr. metatarsi tertii) (Kurochkin & Lungu 1970). These authors determined that *S. orlovi* was “less massive” than *S. asiaticus*, *S. brachydactylus* or *S. camelus*: “in relation to the size of the block of digit III, *S. orlovi* is the smaller ostrich in comparison to Meotian *S. brachydactylus*, *Struthio* sp. from Kuyal’nik [...] and recent *S. camelus*” (Kurochkin & Lungu 1970: 123).

This species has generally been considered to be smaller than *S. camelus* and indeed than any other fossil ostrich (Olson 1985), but Mourer-Chauviré *et al.* (1996a) considered that it was comparable in size to recent ostriches, an opinion that seems more reliable (Table 1). The width of its tr. mt. III is 40.0 mm, while this measurement in recent *S. camelus* lies within the range 37.2–38.3 mm based on specimens from the NMNHS collection ( $n = 5$ ; Table 1), and 36.0–42.4 mm based on specimens from the Muséum national d’Histoire naturelle, Paris and the Natural History Museum, Lyon collections ( $n = 14$ ; Mourer-Chauviré *in litt.*). However, the pedal bones of *S. orlovi* are smaller and more graceful than in Bulgarian *S. camelus* specimens, and the fossa tendinea on the inner surface of tr. mt. tertii of NMNHS 16371 seems deeper in *S. camelus* than in *S. orlovi*.

### COMPARISON WITH *STRUTHIO BRACHYDACTYLUS*

*Struthio brachydactylus* from Grebeniki (MN 11) is slightly smaller or comparable in size to *S. camelus* but is heavily built, with a relatively shorter and somewhat more robust posterior phal. (Burchak-Abramovich 1949: 142–143; Kurochkin & Lungu 1970; Mourer-Chauviré *et al.* 1996a). NMNHS 16372 could not be referred to *S. brachydactylus* because of its proportional differences: the phal. 1 dig. 3 ped. has a much thicker body. According to Burchak-Abramovich (1967), *S. brachydactylus* is much more monodactyl than the recent (more didactyl) *S. camelus*. The third toe bears the main supporting function of its foot, and the fourth toe is reduced in comparison to that of *S. camelus*.

*Struthio brachydactylus* is more monodactyl than NMNHS 16371 (see Burchak-Abramovich 1953a: table XII, 193). The axis of its tr. mt. 4 is much less parallel to tr. mt. 3 than in the Bulgarian specimen. A similar condition is also shown by the so-called “Odessa ostrich” (*Struthio* sp.; Burchak-Abramovich 1953a: table III, 175). Phal. 1 dig. 3 of *S. brachydactylus* is considerably smaller than in NMNHS 16372 according to the measurements provided by Burchak-Abramovich (1953a: table XIII, 195) (Table 1); some of its dimensions differ by up to 20%, and are not suggestive of conspecificity.

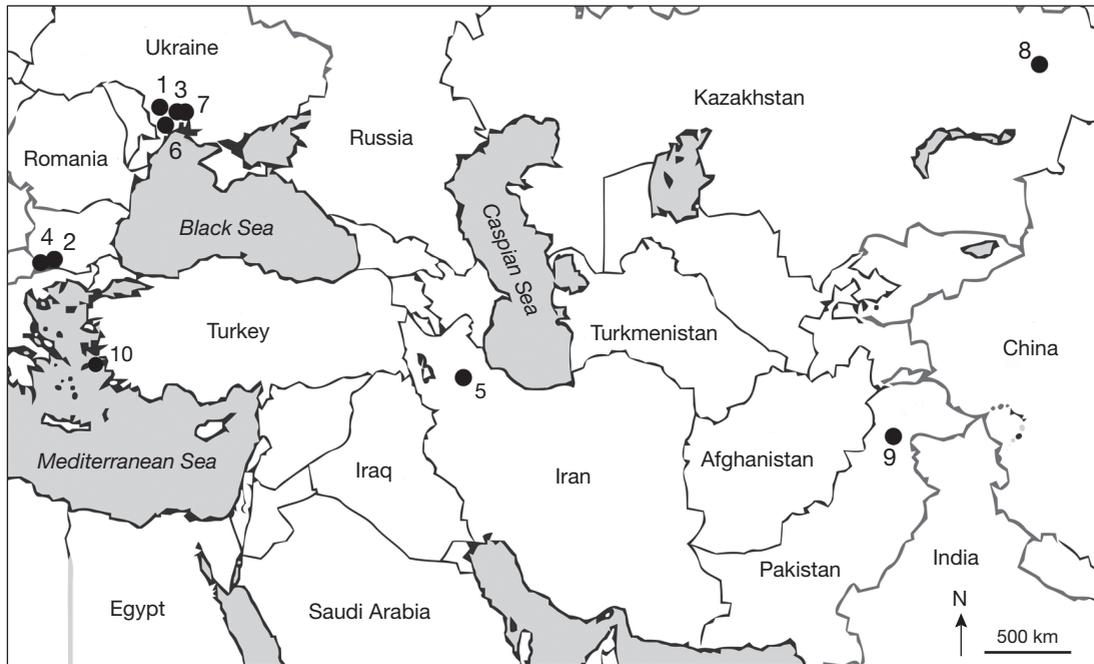


FIG. 3. — Distribution of *Struthio* spp. in the late Miocene: 1, Grebeniki, Ukraine; 2, HD, Bulgaria; 3, Novoelizavetovka (Novo-elizavetovka), Ukraine; 4, KM, Bulgaria; 5, Maragha, Iran; 6, Il'inka and Snigirevka, Ukraine; 7, Nova Emetivka (Novaya Emetovka), Ukraine; 8, Pavlodar, Kazakhstan; 9, Siwalik, Pakistan; 10, Samos, Greece.

#### COMPARISON WITH *STRUTHIO NOVOROSSICUS*

The Bulgarian specimens show more slender morphology and smaller size in comparison to *S. novorossicus* from the north Peri-Pontic area. *Struthio novorossicus* also differs by its large size from *S. camelus* and *S. asiaticus* (Table 1; Burchak-Abramovich 1953a), and its systematic status remains unclear. It is associated with the so-called “Pikermian fauna” (Aleksejev 1915). Aleksejev (1915: fig. 55) showed significant differences in the morphology of the distal tarsometatarsal epiphysis in *S. novorossicus* compared with other struthionids. Incisura intertrochlearis lateralis in plantar view is wider in *S. novorossicus* and its edges are more parallel than in NMNHS 16371. The angle between tr. mt. III and tr. mt. IV is almost twice as large as in NMNHS 16371.

The eggshell volume of *S. camelus* is only 68.6% that of *S. chersonensis* (type specimen, after measurement data in Eastman 1898:133), and is 88.2% as large according to linear dimensions (type specimen,

after measurement data in Andersson 1923: 70). As we have restricted the name *S. chersonensis* only to the type eggshell, it is not necessary to compare the Bulgarian specimens with this species; however, the eggshell of *S. chersonensis* (which possibly represents *S. novorossicus*) could be expected to be larger in size than eggshell from the Bulgarian struthionids based on other measurement correlations.

#### COMPARISON WITH *STRUTHIO KARATHEODORIS*

*Struthio karatheodoris* has been described from a femur, sternum and synsacrum from Meotian deposits on Samos Island, which were lost during the Second World War (Janoo & Sen 1998) (Fig. 3). Direct comparison with the Bulgarian specimens was therefore not possible. This species has been described as “of larger size than the recent ostrich” (Mecquenem 1926: 54) or of the “dimension of the largest individuals of *Struthio camelus*, and differing slightly [morphologically]” (Forsyth Major

1888: 1181); however, this differential diagnosis is insufficient for meaningful taxonomic comparison. More recently, Bachmayer & Zapfe (1962) referred a tibiotarsus dist. dex., 3 dist. phal. ped. (2 dex. and 1 sin.) and a phal. 1 dig. 3 ped. sin. from the late Miocene of Pikermi to *S. karatheodoris*.

Bachmayer & Zapfe (1962: plate III, fig. 5a-c) show several morphological differences between the Pikermian specimen of *S. karatheodoris* and NMNHS 16372. The Bulgarian specimen has a stouter body of the phal. The proximal articular surface in medial view is relatively smaller (measurement “g”) towards the diameter of the distal end (measurement “h”) and the base of the body of the phal. at the distal articular (“trochlear”) part. The shape of the tendon concavity on the medial surface is also different. It is more or less teardrop-shaped in NMNHS 16372, and round (circle-like) in *S. karatheodoris*. Both dorsal and ventral views of the phal. show that *S. karatheodoris* is slightly more gracile. However, the morphology and dimensions of the Bulgarian specimens otherwise correspond closely to the available material of *S. karatheodoris*, and these differences could be individual or sexual, given that the range of intraspecific variation in large cursorial birds is close to that of large terrestrial mammals.

Given that 1) *S. karatheodoris* and NMNHS 16372 differ significantly both in size and morphology from *S. novorossicus*; and 2) NMNHS 16371 is much more similar to *S. karatheodoris* than to *S. novorossicus*, the Bulgarian material is assigned to *S. cf. karatheodoris*. This provides additional support for the hypothesis that *S. novorossicus* and *S. karatheodoris* represent two distinct species.

#### STRUTHIO SP. FROM MARAGHA

*Struthio* sp. from the early Turolian of Maragha is “an ostrich of very large size” (Mecquenem 1926: 54; Table 1), which we also consider to be conspecific with *S. karatheodoris*. The phal. 1 dig. 3 of the Maraghan ostrich is slender and longer than that of *S. brachydactylus* (Burchak-Abramovich 1953a: 67). The phal. 1 dig. 3 ped. dex. figured by Mecquenem (1926: fig. 15) shows considerable morphological similarity to NMNHS 16372. Lesser width of the diaphysis of phal. 1 dig. 3 ped. of *Struthio* sp. from Maragha is 29.0 mm (Mecquenem 1926,

see Burchak-Abramovich 1953a: 67). The same measurement (Table 1, measurement “j”) of the Bulgarian specimen is 31.2 mm, exceeding the size of the Maragha ostrich by 7%.

#### STRUTHIO SP. FROM KUYAL'NIK

*Struthio* sp. from the Turolian of Kuyal'nik (Odessa Region, Ukraine) was reported to be smaller than *S. camelus* by Burchak-Abramovich (1953a), but our data (Table 1) indicate that the so-called “Kuyal'nik Ostrich” was larger, or at least comparable in size to recent *S. camelus*, and was larger than the fossil ostrich specimens from Bulgaria.

#### STRUTHIO SP. (“ODESSA OSTRICH”)

According to Burchak-Abramovich (1953a: 141, table 8), the so-called “Odessa Ostrich” differs considerably from *S. brachydactylus* in proportions of the distal tmt. (Table 1, measurements “c”, “d”, “f”). The distal tmt. of the “Odessa Ostrich”, as figured by Burchak-Abramovich (1967: fig. 3), differs strongly from NMNHS 16371 by the relatively smaller tr. mt. 2 and the much more transverse orientation of its axis towards the axis of tr. mt. 3, possibly indicating less well-developed bidactyly in the Ukrainian taxon.

#### COMPARISON WITH OTHER STRUTHIO TAXA

*Struthio coppensi* from the lower Miocene of Namibia is of “smaller size and different proportions, which indicate a more gracile appearance” (Mourer-Chauviré *et al.* 1996a: 325).

*Struthio asiaticus* from the Siwalik Hills has a relatively short and thick posterior phal. (Mourer-Chauviré *et al.* 1996a), and has been interpreted as being “in direct relation with *S. karatheodoris*”, possibly representing its direct descendant (Martin 1903: 209). However, Burchak-Abramovich (1953a: 57) considered that that distal tmt. of *S. asiaticus* does not differ either dimensionally or morphologically from that of recent *S. camelus*, and that phal. 1 dig. 3 of *S. asiaticus* is much closer to *S. camelus* than that of *S. brachydactylus*. Burchak-Abramovich concluded that *S. asiaticus* is “a relatively not-large ostrich” (p. 96), possibly the size of *S. brachydactylus*, *S. anderssoni*, *S. mongolicus*, and *Struthio* spp. from Emetovka and Kuyal'nitskiy Liman, Odessa

Region. *Struthio asiaticus* can therefore be excluded from comparison with the Bulgarian material on the basis of size alone. Furthermore, Mourer-Chauviré & Geraads (2008: 172) stated that in all fossil ostriches referred to *S. asiaticus* by Kurochkin & Lungu (1970) as well as some other taxa (*S. dmanisensis*), “the ratio between proximal width and minimum width of shaft [of phal. prox. dig. 3] is comprised between 1.57 and 1.68, whereas in the recent *S. camelus* it varies from 1.68 to 1.92”. This ratio in NMNHS 16372 is 1.589, which further refers it to the group of the larger fossil ostrich species.

#### COMPARISON WITH *STRUTHIO CAMELUS*

The phal. 1 dig. 3 ped. sin. ad. of *S. camelus* is much more slender than in NMNHS 16372. Its thickness in the middle of the phal. (measurement “j”) is smaller by almost one third (29.2%). On the other hand, the length of the phal. of *S. camelus* (measurement “m”) reaches up to 91.3% of NMNHS 16372. The distal tmt. of *S. camelus*, in addition to its significantly smaller dimensions, differs from NMNHS 16371 by the relatively more proximal position of tr. mt. 4 (Fig. 2), indicating that the KM struthionid probably had a more developed fourth toe and showed stronger didactyly than the recent ostrich. For this reason, the incisura intertrochlearis lateralis of NMNHS 16371 is almost twice as narrow (Fig. 2).

Cramp & Simmons (1977) showed that individual metrical variability of tarsus length in *S. camelus* reaches up to 15.1%, and up to 16.1% in *S. c. syriacus*. Body weight may also vary from 90 to 130 kg, i.e. variation of more than 30% (Brown 1982). Such considerable metrical variability in the body dimensions of ostriches warns that careful interpretation of qualitative morphological characters is required when considering potential taxonomic variation in the group, and that considering only quantitative morphological dimensions is likely to be unreliable.

#### PALEOECOLOGICAL IMPLICATIONS

Recent *Struthio camelus* is a typical inhabitant of continental semi-desert and desert regions (Folch

1992). It prefers open areas with xerophytic vegetation (Burchak-Abramovich 1953b). In the Pliocene this species was widespread in North Africa, western Asia, and southern Europe. In Iran, Beludzhan, China and Transbaikalia, *S. camelus* survived into the Holocene, presumably because of constant environmental conditions in these regions throughout the Pliocene and Quaternary. Late Miocene ostriches probably had similar environmental requirements and were inhabitants of the open shrublands.

The dominance of open woodlands (park-type forests) in HD-1 is suggested by the analysis of both mammalian megafauna (Spassov 2002), and avifauna (Boev & Kovachev 2007), and the faunal composition of Tumbichkite (HD-2) indicates a similar landscape. However, the middle Turolian KM faunal complex possesses ecological characteristics suggestive of a continuation of the landscape opening (Spassov *et al.* 2006), including: *Hipparion* skull and teeth morphology adapted for grazing (Hristova & Kovachev 2005); the lack of forested specialists present in HD-1, such as tapirs and cervids; and the faunal dominance of *Ceratotherium* among the rhinocerotids (D. Geraads, N. Spassov, D. Kovachev unpublished data). Multi-proxy analysis combining dental microwear and stable isotope profiles in bovid tooth enamel (based on data from KM, MN 12, and HD) also suggests that the Turolian of southwestern Bulgaria was dominated by open wooded landscapes where C<sub>3</sub> graminoids grew in abundance among a diverse herbaceous layer. Microwear data suggest that bushes and open shrublands were more widespread in the vegetation at KM than at HD-1 (Merceron *et al.* 2006). We conclude that the occurrence of an ostrich species as a member of the megafauna of the middle Turolian localities of HD-2 and KM strongly supports the existence of open spaces as a characteristic component of a mosaic open woodland-park type forest landscape in this part of the Pikermian biome (*sensu* Solounias *et al.* 1999) of the Balkan-Iranian (Bonis *et al.* 1992; Spassov *et al.* 2006) late Miocene paleogeographical province. The presence of ostriches in this region during the middle Turolian also supports the hypothesis that the surrounding mountains developed through very fast and geologically recent elevation, probably during the last 1-2 Ma (Tzankov *et al.* 2005).

## ZOOGEOGRAPHIC IMPLICATIONS

As summarized by Mlíkovský (1996: 801), all Tertiary records of the genus *Struthio* in Europe “are confined to its southeastern parts. It is possible that *Struthio* has never reached western Europe”. Davitashvili (1969) listed 31 localities and 71 complete eggs of ostriches from China. Ostrich remains are also numerous in Mongolia, Transbaikalia and Iran. Burned ostrich eggs used as vessels are found in the Late Paleolithic (Chellean-Acheulian) in the Atlas Mountains of northern Africa (Makeev 1963). *Struthio camelus* survived in the Ukraine and Moldova until the beginning of the Pleistocene (Burchak-Abramovich 1953a, b). Pleistocene and Holocene records of *S. camelus* are known from Algeria, the Arabian Peninsula, Buryatia, and Inner Mongolia (Brodkorb 1963).

Late Miocene European ostrich findings are restricted to the northern Peri-Pontic region, Greece and Bulgaria (Fig. 3). In spite of the fact that the Balkans and the northern Pontic region show several faunal similarities in the late Miocene, the Bulgarian Turolian ostrich specimens are much closer to those from Pikermi and Samos. They therefore provide further support for the existence of faunal and environmental similarities across a larger geographical region from the Balkans to Iran and Afghanistan, the so-called Southeast European-Southwest Asian “superprovince” *sensu* Bernor *et al.* (1996) or the Greco-Iranian (i.e. Balkan-Iranian) province *sensu* Bonis *et al.* (1992), during that period.

It has been suggested that the Balkan area was separated by sea from Asia Minor at the beginning of the late Miocene (Rögl 1999). However, the taxonomic similarity of ostriches from Samos, Pikermi, HD and KM, and their difference from contemporary material from the north Peri-Pontic area (Novo-Elizabetovka and Grebenniki), supports the existence of an intensive land contact between the Balkan and Asia Minor areas during a time-interval related to the Turolian. We suggest that such a land bridge could have started to play a significant role in faunal exchange of terrestrial animals of the Balkan-Iranian zoogeographic province in the second half of the early Turolian and the middle Turolian. In the same time the “northern”

faunal route (via the northern Peri-Pontic area) was apparently more important for faunal migrations during the Vallesian and possibly also the beginning of the Turolian.

## CONCLUSION

The occurrence of the genus *Struthio* in the Bulgarian Neogene is not surprising, as it is present at a series of localities in neighbouring countries as part of the so-called “*Hipparion*” fauna, in which ostriches were one of the characteristic faunal elements.

The new Bulgarian remains from HD-2 and KM help to clarify the diversity and relationships of Late Neogene ostriches of the Peri-Pontic region. Taxonomic and stratigraphic analyses show that 1) two Turolian ostrich species, *S. novorosicus* and *S. brachydactylus*, are known from the northern Pontic region, with a further species *S. chersonensis* restricted to the type egg shell; and 2) a different species, *S. karatheodoris*, is known from the western and southern Pontic region and southwestern Asia. This conclusion provides support for including the northern Pontic region within the Turolian Balkan-Iranian zoogeographic province, but as a separate sub-province. It also supports the existence of an important southern route for faunal exchange through the Balkans and Asia Minor in the Turolian after the first half of the Early Turolian.

The presence of ostriches as a component of the megafauna of the middle Turolian localities of HD-Tumbichkite and KM also supports the existence of open spaces as a characteristic element of the mosaic open woodland-park type forest landscape (Spassov 2002) in the western Pontic/northeastern Mediterranean part of the Pikermian biome (*sensu* Solounias *et al.* 1999) of the Balkan-Iranian late Miocene zoogeographic province.

## Acknowledgements

We thank Dr Mourer-Chauviré (Université Claude Bernard, Lyon 1 – Centre des Sciences de la Terre), Dr Evgeny Kurochkin (Paleontological Institute, Russian Academy of Sciences, Moscow), and Dr Denis Geraads (Centre national de la Recherche

scientifique, Paris) for copies of some publications, and three reviewers for their critical reviews of the manuscript. We are grateful to Dr Mourer-Chauviré for providing measurements of recent ostriches, and to Dr Samuel Turvey (Institute of Zoology, Zoological Society of London) for the correction of English text and some remarks on the manuscript.

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*Submitted on 2 September 2007;  
accepted on 24 April 2009.*