

Pigeons, sandgrouse, cuckoos, nightjars, rollers, bee-eaters, kingfishers and swifts in the European fossil avifauna and their osteological characteristics

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Abstract In the article, the author describes the presence of fossil records of the pigeons (Ord. Columbiformes, Fam. Columbidae), sandgrouse (Ord. Pteroclidiformes, Fam. Pteroclidiidae), cuckoos (Ord. Cuculiformes, Fam. Cuculidae), nightjars (Ord. Caprimulgiformes, Fam. Caprimulgidae), rollers (Ord. Coraciiformes, Fam. Coraciidae), bee-eaters (Ord. Coraciiformes, Fam. Meropidae), (Ord. Coraciiformes, Fam. Upupidae), kingfishers (Ord. Coraciiformes, Fam. Alcedinidae) and swifts (Ord. Apodiformes, Fam. Apodidae) in Europe, particularly the Carpathian Basin, during the Tertiary and Quaternary, as well as their osteological characteristics. These orders generally contain a small number of species in Europe, most of them consisting of thermophilic, migratory species. Their fossil and subfossil remains provide precious information about the climatic conditions of their respective areas of origin.

The text is supplemented by 15 figures and 2 tables.

Keywords: Carpathian Basin, Tertiary, Quaternary, avian fauna

Összefoglalás A tanulmányban a szerző bemutatja a galambok, pusztai tyúkok, kakukkok, lappantyúk, szalatkóták, gyurgyalagok, jégmadarak és sarlósfejűk jelentősét a harmad- és negyedidőszak európai, benne a Kárpát-medencei fosszilis madárvilágban, és ismerteti csonttani jellegzetességeiket. A kevés európai fajjal rendelkező rendek többségükben melegkedvelő, vonuló fajokat foglalnak magukban, így maradványai a lelőhelyeik éghajlatára nézve is értékes információkat szolgáltatnak. Csonttani jellegzetességeik eltérőek.

A szöveget 15 ábra és 2 táblázat egészíti ki.

Kulcsszavak: Kárpát-medence, harmadidőszak, negyedidőszak, madár fauna

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Introduction

These orders and families are usually represented by merely a few species amongst the European fossilized and recent avian fauna, but are also representative of certain dry land habitats considering their lifestyles, diets and nesting habits.

Most of them are insectivorous, thus are only present as summer guests in Europe, but as such, they provide a reference point regarding climate characteristics of the respective eras to which their remains belong.

Their skeletal remains are typically easy to distinguish from species of other orders. In the following, we will describe these characteristics, and illustrate them on plates. For every discussed skeletal part, the anatomical terminology (after: Lambrecht 1933, Ballmann 1976, Baumel *et al.* 1979, Gilbert *et al.* 1981, Jánossy 1985, Kessler 2013) and method of measurement (von den Driesch 1976, Gál 2002, Kessler 2013) of the bone is given. Arrows indicate the morphological characteristics (*Figure 1*) and the method of measurement (*Figure 2*).

According to skeletal parts, their characteristics are the following:

1. *Mandibula* (*Figure 3*)

a. the tip of the beak is:

- very short: *Columba*, *Streptopelia*, *Syrhaptes*;
- short: *Cuculus*;
- long: *Coracias*, *Merops*;
- very long: *Alcedo*, *Upupa*;

b. the recess between the stems is:

- ovoid: *Coracias*, *Syrhaptes*;
- ovoid, with recess in the middle: *Alcedo*, *Cuculus*, *Merops*;
- pointed: *Columba*, *Streptopelia*, *Upupa*;

c. the stem is:

- very long: *Columba*, *Streptopelia*, *Syrhaptes*;
- long: *Alcedo*, *Coracias*, *Merops*, *Upupa*;
- with spur: *Cuculus*;

2. *Coracoideum* (*Figure 4*)

a. the *processus acrocoracoidalis* is:

- rounded: *Alcedo*, *Caprimulgus*, *Coracias*, *Upupa*;
- hooks: *Columba*, *Merops*, *Streptopelia*, *Syrrhaptes*;
- cut-off: *Apus*, *Cuculus*;

b. the *processus procoracoidalis* is:

- missing: *Caprimulgus*;
- mixed with a *processus acrocoracoidalis*: *Alcedo*, *Upupa*;
- long: *Cuculus*, *Syrrhaptes*;
- short: *Apus*, *Columba*, *Coracias*, *Merops*, *Streptopelia*;

c. the medial end of the sternal part is:

- short and pointed: *Upupa*;
- long and pointed: *Caprimulgus*, *Merops*, *Syrrhaptes*;
- cut-off and pointed: *Alcedo*;
- short and rounded: *Apus*, *Cuculus*;
- long and rounded: *Columba*, *Coracias*, *Streptopelia*;

d. the lateral end of the sternal part:

- curves downward sharply: *Apus*, *Upupa*;
- curves upward: *Columba*, *Coracias*, *Merops*, *Streptopelia*;
- cut-off straight: *Caprimulgus*;

- straight: *Cuculus*, *Syrrhaptes*;
- rounded: *Alcedo*;

3. *Scapula* (Figure 5)

a. the lateral projection is:

- cone-shaped: *Apus*, *Coracias*, *Merops*, *Streptopelia*;
 - rounded: *Alcedo*, *Columba*, *Upupa*;
 - cut-off end: *Caprimulgus*, *Cuculus*;
- b. the dorsal projection is:
- cone-shaped: *Apus*, *Columba*, *Streptopelia*;
 - rounded: *Caprimulgus*, *Coracias*, *Cuculus*;
 - forked: *Alcedo*, *Merops*, *Upupa*;

4. *Humerus* (Figure 6–7)

a. the *crista biccipitalis* is:

- rounded: *Caprimulgus*, *Columba*, *Coracias*, *Merops*, *Streptopelia*, *Upupa*;
- cone-shaped: *Alcedo*, *Cuculus*, *Syrrhaptes*;
- cut-off: *Apus*;

b. the *crista pectoralis* is:

- rounded: *Alcedo*, *Caprimulgus*, *Coracias*, *Cuculus*;
- cone-shaped: *Merops*, *Syrrhaptes*, *Upupa*;
- curves downward: *Columba*, *Streptopelia*;
- cut-off end: *Apus*;

c. the *processus supracondylaris dorsalis* is:

- rounded: *Caprimulgus*, *Merops*;
- slightly protruding cone shape: *Coracias*, *Cuculus*;
- missed: *Alcedo*, *Apus*, *Columba*, *Streptopelia*, *Syrrhaptes*, *Upupa*;

d. the *processus flexorius* is:

- cone-shaped: *Columba*, *Coracias*, *Cuculus*;
- rounded: *Alcedo*, *Apus*, *Caprimulgus*, *Merops*, *Streptopelia*, *Upupa*, *Syrrhaptes*;

5. *Ulna* (Figure 8–9)

a. the *olecranon* is:

- pointed cone: *Alcedo*, *Apus*, *Caprimulgus*, *Coracias*, *Merops*, *Upupa*, *Syrrhaptes*;
- blunt cone: *Columba*, *Cuculus*, *Streptopelia*;

b. the *cotyla dorsalis* is:

- blunt cone: *Alcedo*, *Apus*, *Caprimulgus*, *Columba*, *Coracias*, *Cuculus*, *Merops*, *Streptopelia*, *Syrrhaptes*, *Upupa*;

c. the *tuberculum carpale* is:

- rounded: *Alcedo*, *Apus*, *Merops*, *Streptopelia*;
- pointed cone: *Syrrhaptes*;
- blunt cone: *Caprimulgus*, *Columba*, *Coracias*, *Cuculus*, *Upupa*;

6. *Radius (Figure 10)*

a. the *corpus radii* is:

- slightly curved: *Alcedo, Caprimulgus, Coracias, Merops, Upupa*;
- straight: *Apus, Columba, Cuculus, Streptopelia, Syrrhaptes*;
- c. *tuberculum aponeurosis ventralis*:
- pointening: *Apus, Caprimulgus, Cuculus, Upupa*;
- blunted: *Alcedo, Coracias, Columba, Merops, Streptopelia, Syrrhaptes*;
- d. *tuberculum aponeurosis dorsalis*:
- pointening: *Upupa*;
- with double point: *Apus*;
- rounded: *Alcedo, Columba, Merops, Streptopelia, Syrrhaptes*;
- curved: *Caprimulgus, Coracias, Cuculus*;

7. *Carpometacarpus (Figure 11)*

a. the *spatium intermetacarpalis* is:

- narrow: *Apus*;
- large: *Columba, Streptopelia, Syrrhaptes*;
- very broad: *Cuculus, Upupa*;
- medium wide: *Alcedo, Caprimulgus, Coracias, Merops*;

b. the *facies articularis digitii majoris* is:

- straight: *Apus, Caprimulgus, Syrrhaptes*;
- oblique cone shaped: *Columba, Coracias, Cuculus, Streptopelia, Upupa*;
- with protruding end: *Alcedo, Merops*;
- c. the *distal end of the metacarpus majoris* is:
- pointed cone shape: *Apus*;
- blunt cone: *Caprimulgus, Columba, Cuculus, Streptopelia, Syrrhaptes*;
- rounded: *Alcedo, Coracias, Merops, Upupa*;

8. *Phalanx proximalis digitii majoris (Figure 12)*

a. the proximal end is:

- wavy: *Alcedo*;
- straight: *Merops, Upupa*;
- rounded: *Apus, Caprimulgus*;
- oblique: *Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes*;
- b. the distal end is:
- rounded: *Cuculus, Merops*;
- protruding: *Alcedo, Apus, Columba, Caprimulgus, Coracias, Streptopelia, Syrrhaptes*;
- protruding dorsal: *Upupa*;
- c. the dorsal side is:
- rounded: *Caprimulgus, Columba, Coracias, Merops, Streptopelia, Syrrhaptes*;
- wavy: *Alcedo, Cuculus*;
- straight: *Upupa*;
- oblique: *Apus*;

9. *Femur* (Figure 13)

a. the *trochanter femoris* is

– protruding: *Caprimulgus, Columba, Streptopelia, Syrrhaptes*;

– not protruding: *Alcedo, Apus, Coracias, Cuculus, Merops, Upupa*;

The morphological homogeneity is significant in the case of this skeletal part.

10. *Tibiotarsus* (Figure 14)

a. the *crista fibularis* is:

– well-developed: *Alcedo, Apus, Columba, Coracias, Streptopelia, Upupa*;

– undeveloped: *Caprimulgus, Cuculus, Merops, Syrrhaptes*;

b. the *incisura intercondylaris* is:

– deep: *Alcedo, Apus*;

– medium developed: *Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes*;

– poorly developed: *Merops, Upupa*;

Homogeneity is significant in the case of this skeletal part.

11. *Tarsometatarsus* (Figure 15)

a. the *corpus metatarsi* is:

– narrow: *Upupa*;

– medium thick and straight: *Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes*;

– thick, short and straight: *Alcedo, Apus*;

– thick and curved: *Merops*;

b. the *trochlea metatarsi II.* is:

– pointed: *Apus, Cuculus, Merops, Upupa*;

– rounded: *Alcedo, Caprimulgus, Columba, Coracias, Streptopelia, Syrrhaptes*;

c. the *trochlea metatarsi III.* is:

– protruding: *Apus, Merops, Upupa*;

– not protruding: *Alcedo, Caprimulgus, Columba, Coracias, Cuculus, Streptopelia, Syrrhaptes*;

d. the *trochlea metatarsi IV.* is:

– semicircular: *Merops, Streptopelia*;

– cone shape: *Apus, Syrrhaptes, Upupa*;

– protruding: *Alcedo, Caprimulgus, Columba, Coracias, Cuculus*;

This bone is the most typical skeletal part of these orders. Figure 2. helps understand the size charts (Table 1–2).

Systematics

The presence of fossil species in Europe and the occurrence of recent genera and species at sites of the Carpathian Basin and Europe, and symbols for fossilized species from the Carpathian Basin are as follows:

Abbreviations: **Q1-Q2** – Lower Pleistocene; **Q3 (Q3/I-Q3/II)** – Middle Pleistocene; **Q4/I** – Upper Pleistocene; **Q4/II** – Holocene; † – extinct/fossil species.

Ord. Columbiformes (Latham, 1790)

Fam. Columbidae (Illiger, 1811)

Representatives of the family are only known since the early Miocene across Europe. Their oldest occurrences are *Columba omnisanctorum* Ballmann, 1976 and *C. pisana* Portis, 1889 from the early and middle Pliocene of Italy (MN 14-15, MN 15-16) (Portis 1889, Ballmann 1976).

Pigeons are only known on the recent genus level from the Neogene of Europe: *Columba* sp. from Vărsec, Bulgaria and Sandalja, Croatia (MN 17).

– *Columba* (Linnaeus, 1758)

– *Columba livia* (Gmelin, 1789)

Q1: Beremend 17 (Hungary) (Jánossy 1992, 1996); **Q4/I:** Velika pec na Lipi (Croatia) (Malez-Bačić 1979, V. Malez 1984,); **Q4/II:** Legény Cave (Hungary) (Lambrecht 1913); from the Quaternary of Europe: **Q1-2:** France, Italy; **Q3:** Azerbaijan, Croatia, France, Georgia, Greece, Russia, Ukraine; **Q4:** Austria, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Montenegro, Portugal, Russia, Spain, Ukrajne, United Kingdom (Tyrberg 1998).

– *Columba palumbus* (Linnaeus, 1758)

MN 16: Betfia 13 (Romania) (Kessler 1975, Gál 2002); **Q2:** Nagyharsány Hill 1–4 (Hungary) (Lambrecht 1916, 1933, Jánossy 1979a); **Q3/I:** Hundsheim (Austria) (Jánossy 1971, 1974); **Q4/I:** Bajót, Baits Cave (Jánossy 1979b); Bajót, Jankovich Cave (Lambrecht 1933, Jánossy 1979a); Budapest, Remetehegy Shelter Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979a, 1986); Cserépfalu, Subalyuk Cave (Jánossy 1979a); Pilisszántó, I. Shelter Cave (Lambrecht 1915, 1933, Jánossy 1979a, 1986); Tatabánya, Szelim Cave (Jánossy 1979a); Barbó, Lambrecht Kálmán Cave (Jánossy 1979a) (all in Hungary); Körösmart (Rápa, Romania) (Jánossy in Hamar & Csák 1969, Kessler 1974, Gál 2002); **Q4/II:** Bajcsa Castle (Gál 2002); Balatonkeresztúr, Réti-Dűlő (Gál 2007a); Balatonszemes, Bagódomb (Gál 2004, 2007a); Bodajk, Rigólyuk (Kordos 1984); Debrecen, Nyulas (Gál 2007b); Ecsegfalva 23 (Pike-Tay *et al.* 2004, Gál 2007b); Felsőtárkány, Petényi Cave (Jánossy 1979a); Jósavafő, Musztáng Cave (Kessler 2009); Röszke, Ludvár (Jánossy 1985, Gál 2004, 2007b); Tác, Fövénypuszta (Jánossy 1979a, 1979b); Tác-Gorsium (Bökonyi 1984, Jánossy 1985); Tiszaszölös, Domaháza-puszta (Gál 2007b); Visegrád Castle (Bökonyi & Jánossy 1965, Jánossy 1979a (all in Hungary); Parác (Parça) (Kessler & Gál 1997, Gál 2004), Remetelórév, Bólyikő Cave (Piatra Boiului) (Kessler 1982); Szegyestel, Drăcoiaia Cave (Sighiștel) (Kessler 1982); Vársonkolyos, Izbındış Cave (Şuncuiuş) (Kessler 1977, Gál 2002) (all in

Romania); from the Quaternary of Europe: **Q3:** Austria, France, Greece, Italy, Spain, United Kingdom; **Q4:** Austria, Belgium, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Moldova, Montenegro, Poland, Portugal, Romania, Russia, Spain, Switzerland, Ukraine, United Kingdom (Tyrberg 1998).

– ***Columba oenas* (Linnaeus, 1758)**

Q4/I: Hollókő (Jánossy & Vörös 1979, Jánossy 1980); Kőszeg (Lambrecht 1912, 1915, 1933) (all in Hungary); **Q4/II:** Remetelórév, Bólyikő Cave (Piatra Boiului) (Kessler 1982); Révi Caves (Vadu Crișului) (Kessler 1982) (all in Romania); Teufelslucken (Austria) (Soergel 1966); from the Quaternary of Europe: **Q1-2:** Greece; **Q3:** France, Greece, Spain; **Q4:** Austria, France, Greece, Italy, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– ***Columba* sp. foss. indet.**

MN 15: Beremend 26 (Kessler 2010); **MN 15:** Csarnóta 2 (all in Hungary) (Jánossy 1979a: as *Columba livia*);

– ***Columba* sp.**

Q4/II: Körösbánlak Cave (Bálnaca) (Kessler 1982); Révi Caves (Vadu Crisului, all in Romania) (Kessler 1982).

– ***Streptopelia* (Linnaeus, 1758)**

– ***Streptopelia turtur* (Linnaeus, 1758)**

Q4/II: Legény Cave (Hungary) (Lambrecht 1913); Szegyestel, Drăcoiaia Cave (Sighiștel, Romania) (Kessler 1982); from the Quaternary of Europe: **Q3:** Italy; **Q4:** Austria, Czech Republic, France, Italy, Spain, Ukraine (Tyrberg 1998).

– ***Columbidae* gen. et sp. foss. indet.**

From the middle Miocene of Mátraszólós 2 (MN 7/8), it was identified to the family level based on the distal fragment of a *tibiotarsus* (Kessler & Hír 2012).

The distal *tibiotarsus* fragment, that had an abraded *condylus*, resembles Columbidae in its main characteristics, but differs from recent *Columba* and *Streptopelia* genera, and shows more similarities with the latter. Its size reflects this as well.

Fam. Pteroclidae (Bonaparte, 1831)

Sandgrouse species live in the semi-arid regions of Southern Eurasia and Africa.

Their presence among remains from the Miocene of the Carpathian Basin is somewhat surprising, but they are quite frequently found in the Paleogene and Neogene of the western part of the continent. The bone found in Mátraszólós may as well come from a migrating specimen.

Their earliest finds come from the Eocene and Oligocene of France (*Archaeoganga pinguis* Mourer-Chauviré, 1992; *A. validus*, *A. larvatus* Milne-Edwards, 1892), as well as the Miocene (*Leptoganga sepultus* Milne-Edwards, 1892; *Gerandia calcaria* Milne-Edwards, 1867). They are not known from earlier sediments. Recent species are known since the Quaternary.

– **Pteroclidae gen. et sp. foss. indet.**

Site and era: The middle Miocene of Mátraszólós 1 (MN 7/8) identified from a distal *phalanx* (Kessler 2010).

Typical distal *phalanx* of a sandgrouse:

– ***Syrrhaptes paradoxus* (Pallas, 1773)**

Q4/I: Pilisszántó I. Shelter Cave (Hungary) (Lambrecht 1915, 1933, Jánossy 1979a, 1986); from the Quaternary of Europe: **Q4:** Czech Republic (Tyrberg 1998).

– ***Pterocles alchata* (Linnaeus, 1766)**

Only **Q4:** from Italy (Tyrberg 1998).

Ord. Cuculiformes (Wagler, 1830)

Fam. Cuculidae (Vigors, 1825)

Cuculidae can be found in the temperate and tropical territories of every continent, apart from the Antarctic, in open, grassy areas, among bushes, or trees.

Their earliest appearance is known from the Eocene represented by the species *Parvicululus minor* Harrison & Walker, 1977, described from sites of Burnham-on-Crouch, England (MP 8-9, London Clay) (Harrison & Walker 1977, Harrison 1982), as well as Condé-en Brie, France (MP 8–9) (Mayr & Mourer-Chauviré 2005) from *tarsometatarsus* respectively, as well as from the Eocene and Oligocene of France (*Dynamopterus velox* Milne-Edwards, 1892; *D. boulei* Gailard, 1939), the Eocene of the USA (*Eocucculus cherpinae* Chandler, 1999), this species was also found in the Oligocene of France. *Neococcyx mccorquodalei* Weigel, 1963 from the Oligocene of France. *Veflintonpris meini* Ballmann, 1969 from the Miocene of Germany. From the Miocene of Hungary *Cuculus pannonicus* Kessler, 2010 (from the late Miocene of Polgárdi 4 (MN 13) and the late Pliocene of Beremend 15 (MN 16) was described (Kessler 2010), while from the early Pliocene of Csarnóta 2, (MN 15) *C. csarnotanus* was described (Jánossy 1979b). The latter is smaller than the recent European cuckoo, but is a morphologically identical species, while the former is a new species larger than the recent European cuckoo and differs in several morphological characteristics. Representatives of the family are already present in the middle Miocene of Mátraszólós I, identified as Cuculidae gent. et sp., from a distal phalanx not identifiable from more recent times (Kessler 2010).

The genus was not found elsewhere in the Neogene of Europe. The recent species is known from the lower Pleistocene of Spain (Quibas, Q1) and Czech Republic (Stránská Skála, Q2) outside of the Carpathian Basin. Materials from the Carpathian Basin is thus unique from this era.

– ***Cuculus canorus* Linnaeus, 758**

Q3/II: Uppony 6 (Hungary) (Jánossy 1979a); **Q4/I:** Merkenstein (Austria) (Wettstein & Mühlhofer 1938); Pilisszántó I., Shelter Cave (Lambrecht 1915, 1933, Jánossy 1979a, 1986); Tatabánya, Kálvária Cave nr. 4 (all in Hungary) (Gál 2004, 2005); **Q4/II:** Szegyestel, Drăcoiaia Cave (Sighiștel, Romania) (Kessler 1982); Teufelslucken (Austria) (Soergel 1966); from the Quaternary outside the Carpathian Basin **Q3:** Czech Republic, France, Germany; **Q4:** Austria, Czech Republic, France, Italy, Spain (Tyrberg 1998).

Ord. Caprimulgiformes (Ridgway, 1881)

Fam. Caprimulgidae (Vigors, 1825)

The order of Caprimulgiformes contains families Steatornithidae, Podargidae, Nyctibiidae, Caprimulgidae and Aegothelidae. They are present on every continent apart from the frigid zones.

The earliest signs of the Caprimulgidae family come from the Eocene of Great Britain, France, Germany and North America (*Eocypselus rowei* Klepsa, et al. 2013; *Fluvioviridiavis platyrhamphus* Mayr and Daniels, 2001 from the USA; *Eurofluviridavis robustipes* Mayr, 2005, *Paraprefica kelleri* and *P. major* Mayr, 1999 from Germany; as well as *Archaeotrogon venustus* Milne-Edwards, 1892, *A. nocturnus* Mlíkovský, 2002, *Euronyctibius kurochkinii* Mourer-Chauviré, 1989 and *Ventivorus ravei* Mourer-Chauviré, 1989 from the Eocene and Oligocene of France), while recent genera are only known from the Quaternary.

– ***Caprimulgus* (Linnaeus, 1758)**

– ***Caprimulgus europaeus* (Linnaeus, 1758) / *Caprimulgus* † *capeki* Jánossy, 1977**

Site and era: **Q1:** Betfia 2, 9 (Romania) (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1977, Gál 2002, Mlíkovský 2002); **Q4/I:** Tatabánya, Kálvária Cave nr. 4 (Hungary) (Gál 2004, 2005);

W. Čapek described the subspecies *Caprimulgus europaeus* † *fossilis* from the material gathered by Kormos T., modified by Jánossy D. as species *C. capeki*. The European nightjar is only known from the early Pleistocene of Europe from Stránská Skála, Czech Republic (**Q2**), and is not too common in the middle and upper Pleistocene either. **Q3:** France, Italy; **Q4:** Croatia, Georgia, Italy, Russia, United Kingdom (Tyrberg 1998).

– ***Caprimulgus ruficollis* (Temminck, 1820)**

The recent species is known outside the Carpathian Basin: **Q3:** France; **Q4:** France (Tyrberg 1998).

Ord. Apodiformes (Peters, 1940)

Their earliest finds come from the Eocene of Great Britain, *Primapus lacki* Harrison and Walker, 1975; from the Eocene of Denmark: *Scaniacypselus wardi* Harrison and Walker, 1984; from the Eocene of Germany: *S. szarskii* Peters, 1985; *Hassiavis laticauda* Mayr, 1998; from the Eocene and Oligocene of France: *Cypselavus gallicus* Gaillard, 1908; *Procyphelooides ignotus* Milne-Edwards, 1871, *P. mourerchauvirae* Mlíkovský, 2002. Recent genera are present from the Miocene. *Apus gailardi* Ennouchi, 1930 is known from the Miocene of France, *A. wetmorei* Ballmann, 1976 from the Pliocene of Italy and Bulgaria, *A. baranensis* Jánossy, 1977 from the Pliocene of Hungary, while *Chaetura baconica* Jánossy, 1977 is known from the Miocene of Hungary. Recent species are known since the Quaternary.

Fam. Apodidae Olphe-Galliard, 1887

– ***Apus* Scopoli, 1777**

– ***Apus* † *baranensis* (Jánossy, 1977) / *Apus* † *wetmorei* (Ballmann, 1976)**

Site and era: Polgárdi 4, upper Miocene (MN 13) (Kessler 2010); Csarnóta 2, lower Pliocene (MN 15) (Kessler 2010); Beremend 5 (Jánossy 1977); Osztramos 20 (Kessler 2010); upper Pliocene (MN 16) (all in Hungary);

It is a fossil species that has typical characteristics of common swifts, but is smaller than recent species. According to its dimensions, Mlíkovský defines it as belonging to the species *Apus wetmorei* Ballmann, 1976, described from the late Pliocene of Italy. Bones identified from Csarnóta 2 (MN 15), but mainly from Polgárdi (MN 13), indicate an even smaller

species than in Italy, furthermore they predate it as well. Our opinion is that the two species are not identical.

The genus is only known from the middle Miocene of France in Europe, apart from the Carpathian Basin. Recent species are only known from the early Pleistocene.

– *Apus apus* (Linnaeus, 1758) / *Apus apus* † *palapus* (Jánossy, 1974)

Q2: Kövesvárad (Hungary) (Kessler 2010); **Q3/I:** Hundsheim (Austria) (Jánossy 1974); Tarkő 1 (Jánossy 1977); **Q4/I:** Hámor, Puskaporos (Lambrecht 1912, 1916, 1933, Jánossy 1986); Szilvásvárad, Istállóskő Cave (Jánossy 1986); **Q4/II:** Felsőtárkány, Petényi Cave (Jánossy 1977) (all in Hungary). From outside the Carpathian Basin, **Q3:** Czech Republic, France, Italy, Russia, Ukraine; **Q4:** Austria, Bulgaria, Czech Republic, France, Germany, Greece, Italy, Poland, Romania, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

The new subspecies was described by Jánossy from the middle Pleistocene find with dimensions matching that of the recent species, and is probably right to be classified into the recent type.

– *Apus melba* (Linnaeus, 1758) / *Apus* † *submelba* (Jánossy, 1972)

Q3/I: Tarkő 2, 3, 4 (Jánossy 1972, 1977); **Q3/II:** Uppony 6 (Jánossy 1977); **Q4/I:** Cserépfalu, Subalyuk Cave (Jánossy 1977) (all in Hungary); outside the Carpathian Basin **Q3:** France, Italy; **Q4:** Bulgaria, France, Georgia, Greece, Poland, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

Jánossy describes the material from Tarkő as a more massive, robust species than the recent one, but their dimensions do not differ significantly from the upper values measured in recent specimens. In the absence of morphological characteristics, Mlikovský (2002) classified it as belonging to the recent species.

– *Apus pallidus* (Shelley, 1855)

Outside the Carpathian Basin, it is known from the middle Pleistocene (**Q3**) of France (Tyrberg 1998).

– *Chaetura* (Stephen, 1826)

– *Chaetura* † *baconica* (Jánossy, 1977)

Site and era: Sümeg, Polgárdi 4, upper Miocene (MN 11-12, MN 13) (Jánossy 1977); Bere-mend 26, lower Pliocene (MN 15) (all in Hungary) (Kessler 2010);

The fossil species is only known from the Carpathian Basin, as well as the genus from across Europe.

Common swifts are migrating, insectivorous birds with rather typical morphology and lifestyle. Other members of the order live in tropical areas. They spend most of their lives airborne, they only land to nest on ledges of cliffs and rock walls. Although they are quite swift fliers, they might fall prey in the daytime to falcons and in the nighttime to owls.

Ord. Coraciiformes (Forbes, 1884)

Fam. Meropidae (Vigors, 1825)

European bee-eaters are typical migrating birds of warm climates, feeding on hymenopterans. They nest in cavities carved into walls of clay and loess. While they have quite conspicuous feathers and live in groups, thus can relatively easily fall prey to predators, we rarely come across their fossilized remains.

– *Merops* (Linnaeus, 1758)

– *Merops* † *radobojensis* (Meyer, 1865)

Site and era: Radoboj, middle Miocene (MN 7) (Croatia) (von Meyer 1865, Mlíkovský 1997); Rudabánya, upper Miocene (MN 9) (Hungary) (Kessler 2010). It was originally described as *Fringilla radobojensis* (von Meyer 1865) and Mlíkovský redefined it.

– *Merops apiaster* (Linnaeus, 1758)

Q3/I: Hundsheim (Austria) (Jánossy 1974); the recent species has also been reported from the late Pleistocene (**Q4**) of France (Tyrberg 1998).

– *Merops* sp. foss. indet.

Q1: Betfia 9 (Romania) (Gál 2002).

– *Meropiidae* gen. et sp. foss. indet.

MN 6: Kőalja 2 (Subpiatra 2, Romania) (Kessler & Venczel 2009).

Fam. Coraciidae (Vigors), 1825

Rollers are insectivorous with conspicuous feathers, due to this they are migrating summer guests, approximately the size of pigeons. They nest on trees, but live in more open areas. Most of the species live in warm climates.

Representatives of other genera of the family are missing from the Neogene of Europe and extinct genera are known from the Eocene of France (Montmartre, Quercy) and Germany (Messel), represented by the taxa *Cryptornis antiquus* Milne-Edwards, 1871; *Geronopterus alatus* Milne-Edwards, 1892; *G. milneedwardsi* Mayr et Mourer-Chauviré, 2000, as well as *Eocoracias brachyptera* Mayr et Mourer-Chauviré, 2000 (Milne-Edwards 1869–1871, Mayr & Mourer-Chauviré 2000, Mlíkovský 2002). From the Eocene of USA, *Primo-bucco kistneri* Feduccia, 1973; *Uintornis lucaris* Mars, 1872; *Eobucco brodkorbi* Feduccia and Martin, 1976 were reported.

– *Coracias* (Linnaeus, 1758)

– *Coracias garrulus* (Linnaeus, 1758)

Q4/II: Ecsegfalva (Hungary) (Pike-Tay *et al.* 2004, Gál 2007b);

– *Eurystomus* (Vieillot, 1816)

– *Eurystomus* † *beremendensis* (Kessler, 2010)

Described from the early Pliocene of Beremend 26 (MN 15) (Hungary), based on the proximal segment of a *metacarpus* and 2 distal *phalanges* (Beremend, BKAH) (Kessler 2010). It is larger than either the recent species or the find from Betfia.

– *Eurystomus* sp. foss. indet.

Q1: Betfia 2, 9 (Romania), (Gál 2002).

Finds differ from characteristics of the recent *Coracias garrulus*, but match those of the other genus living in Southern Europe and Africa. Fossilized *Eurystomus* finds are only known from Beremend 26 and Betfia 9, while the recent *Coracias garrulus* species is only known from the early Pleistocene of Ukraine (Tarchankut, **Q1**) (Vojinststven'skyj 1967).

Fam. Upupidae Bonaparte

Hoopoes also belong to the group of birds mainly widespread in tropical regions. They are summer guests of the Carpathian Basin, feed on insects and larvae, and nest in tree burrows close to the ground. We rarely come across them among fossilized material.

The family only has two extinct species from the Quaternary: *Upupa antaios* Olson, 1975 from Saint Helena and *U. phoeniculoides* from Austria and Hungary. The recent species is known since the Quaternary.

- *Upupa* (Linnaeus, 1758)

- *Upupa* † *phoeniculoides* (Jánossy, 1974)

Site and era: upper Pliocene of Beremend 38 (MN 16) (Hungary) (Kessler 2010); Hundsheim, middle Pleistocene (**Q3/I**) (Austria) (Jánossy 1974).

The find shows intermediate characteristics between *Upupa epops* and *Phoeniculus purpureus*. The newer find from Beremend (Kessler 2010), as well as the fact that the recent species is only known from more current material, just like the genus *Upupa* (lower Miocene, Czech Republic, MN 3, the find has only been identified to the genus level), both support the validity of the fossilized species.

The genus is known from the upper Miocene of Czech Republic (*Upupa* sp. – Merkur, MN 3) (Mlikovský 2002), then from the middle Pleistocene of France and Spain.

- *Upupa epops* (Linnaeus, 1758)

Q4/II: Kevélynyergi-zsomboly (Hungary) (Kessler 2009). From outside the Carpathian Basin: **Q3:** France, Spain; **Q4:** France, Germany, Poland, Spain, Ukraine (Tyrberg 1998).

Fam. Alcedinidae (Vigors, 1825)

Kingfishers are widespread in the tropical regions.

Recent *Halcyon* species are only known from the upper Pleistocene of Israel and China from the Palearctic region, while *Alcedo atthis* is only known from the late Pleistocene of Great Britain, Israel and France. Their earliest known extinct representatives are the *Halcyornis toliapicus* Koenig, 1825 from the Eocene of England and the *Quasisyndactylus longibrachis* Mayr, 2004 from the Eocene of Germany, although their classification is debated.

- *Halcyon* (Swainson, 1821)

- *Halcyon* † sp. foss. indet.

Site and era: Lucsia Cave, middle Pleistocene (**Q3/I**), (Romania) (Gál 2002);

- *Alcedo atthis* (Linnaeus, 1758)

From Europe outside of the Carpathian Basin it is known from upper Pleistocene sites of France and Great Britain (Tyrberg 1998).

Palaeoecological conclusions

Representatives of the orders and families listed and discussed are typically rarely found among fossilized material, except for pigeons. One reason for this is that they are not present in large numbers even in the recent fauna, and another is that despite their conspicuously colored feathers, they rarely fall prey to predators, especially to owls, to whom we would

be able to attribute the accumulation and fossilization of remains due to their pellets. The presented material contains members of two genera that are missing not only from the Carpathian Basin but also most of Europe, apart from the Mediterranean region.

The presence of representatives of the genera *Eurystomus*, but mainly *Halcyon*, in the middle Pleistocene of the Carpathian Basin indicates the climate characteristics of the time, which may have been much milder than those of today, especially since the Lucsia Cave is located on the eastern edge of the Transylvanian mountain chain.

Acknowledgements

The author wishes to express his deep gratitude to Mihály Gasparik for access to the recent bird bone collection in the Natural History Museum of Hungary, to József Vuts and Lóránd Abos for the language revision.

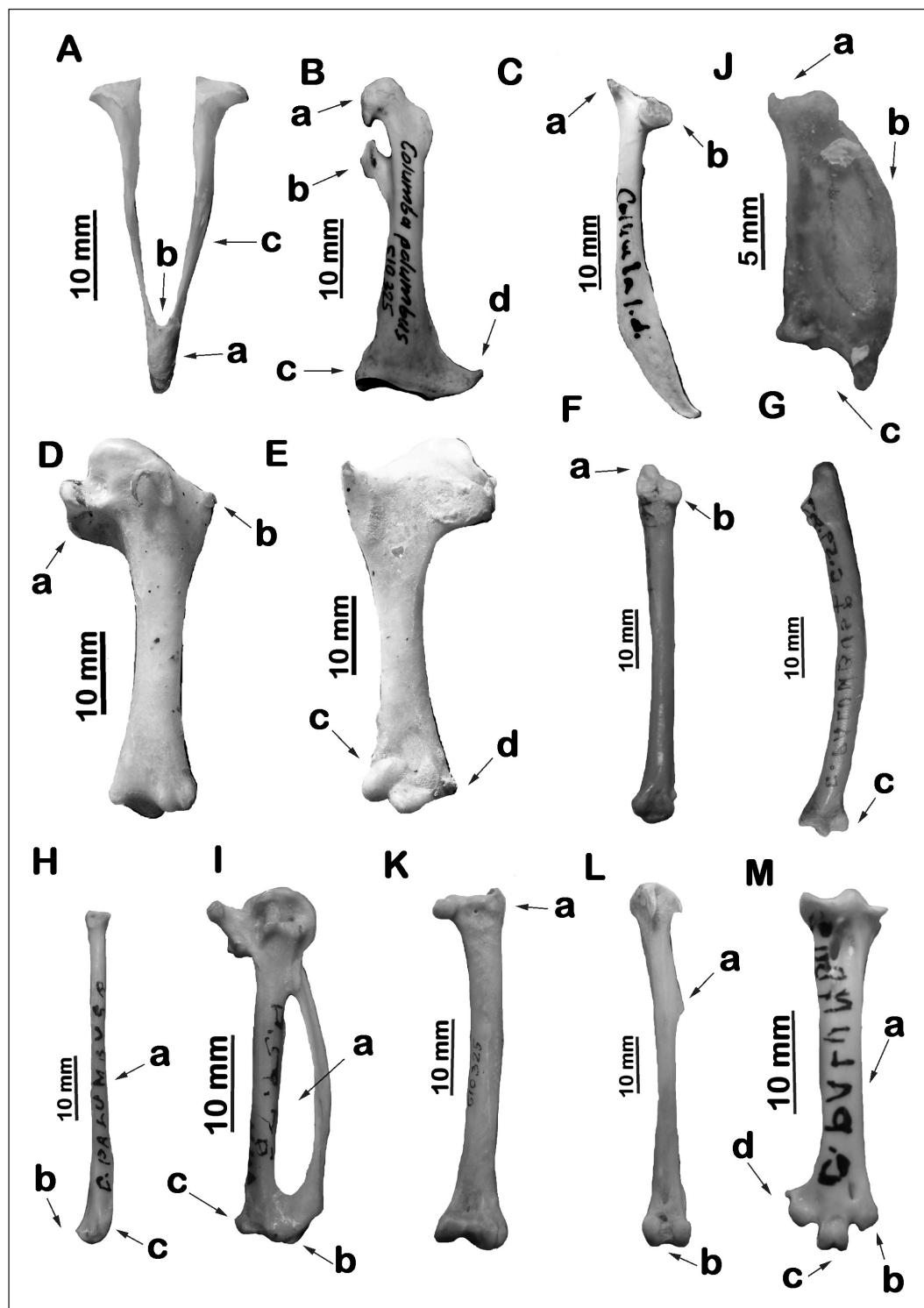
Figure 1. Columba palumbus Linnaeus, 1758 osteology characters:

- A. *Mandibula* – a. the tip of the beak; b. the recess between the stems; c. the stem;
- B. *Coracoideum* – a. *processus acrocoracoidalis*; b. *processus procoracoidalis*; c. the medial end of the sternal part; d. the lateral end of the sternal part;
- C. *Scapula* – a. *acromion*; b. *processus articularis humeralis*;
- D, E. *Humerus* – a. *crista bicipitalis*; b. *crista deltopectoralis*; c. *processus supracondylaris dorsalis*; d. *epicondylus ventralis*;
- F, G. *Ulna* – a. *olecranon*; b. *apophysis glenoidalis interna*; c. *tuberculum carpale*;
- H. *Radius* – a. *corpus radii*; b. *tuberculum aponeurosis ventrale*; c. *tuberculum aponeurosis dorsale*;
- I. *Carpometacarpus* – a. *spatium intermetacarpale*; b. *facies articularis digitalis major*; c. the distal end of the *metacarpus major*;
- J. *Phalanx proximalis digiti majoris* – a. proximal end; b. distal end; c. the dorsal side;
- K. *Femur* – a. *trochanter femoris*;
- L. *Tibiotarsus* – a. *crista fibularis*; b. *incisura intercondylaris*;
- M. *Tarsometatarsus* – a. *corpus metatarsi*; b. *trochlea metatarsi II*; c. *trochlea metatarsi III*; d. *trochlea metatarsi IV*.

1. ábra

Columba palumbus Linnaeus, 1758 csonttani jellegek:

- A. Alsó állkapocs – a. a csőrhegy jellege; b. a két szár közti mélyedés jellege; c. a szár;
- B. Hollócsőrcsont – a. *processus acrocoracoidalis*; b. *processus procoracoidalis*; c. a mellcsonti rész mediális vége; d. a mellcsonti rész laterális vége;
- C. Lapocka – a. *acromion*; b. *processus articularis humeralis*;
- D, E. Felkarcson – a. *crista bicipitalis*; b. *crista deltopectoralis*; c. *processus supracondylaris dorsalis*; d. *epicondylus ventralis*;
- F, G. Singcsont – a. *olecranon*; b. *apophysis glenoidalis interna*; c. *tuberculum carpale*;
- H. Orsócsont – a. *corpus radii*; b. *tuberculum aponeurosis ventrale*; c. *tuberculum aponeurosis dorsale*;
- I. Kézközépcson – a. *spatium intermetacarpale*; b. *facies articularis digitalis major*; c. a *metacarpus major* disztális vége;
- J. A nagy (középső) kézujj első ujjperce – a. proximális vég; b. disztális vég; c. *dorsalis* oldal;
- K. Combcsont – a. *trochanter femoris*;
- L. Lábszárcsont – a. *crista fibularis*; b. *incisura intercondylaris*;
- M. Csüd – a. *corpus metatarsi*; b. *trochlea metatarsi II*; c. *trochlea metatarsi III*; d. *trochlea metatarsi IV*.



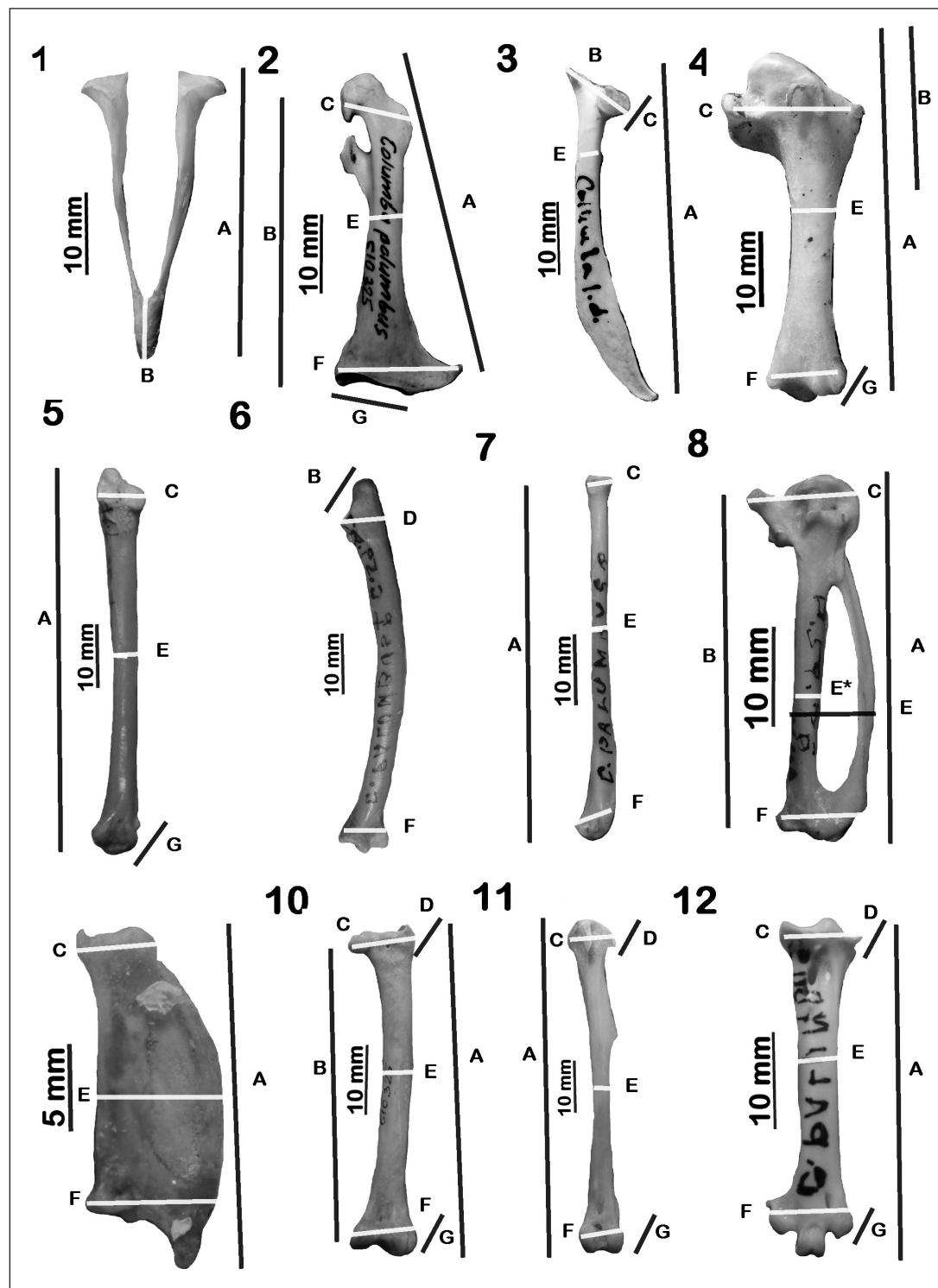


Figure 2. Measurements methods of bones:

1. *Mandibula*: A. total length; B. partial length (length of apex);
2. *Coracoideum*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; F. total breadth of the distal end; G. partial breadth of the distal end;
3. *Scapula*: A. total length; C. breadth of the proximal end; E. breadth of the corpus;
4. *Humerus*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
- 5-6. *Ulna*: A. total length; B. length of the proximal epiphysis; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
7. *Radius*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end;
8. *Carpometacarpus*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; E1: breadth of the *metacarpus majus*; F. breadth of the distal end;
9. *Phalanx proximalis digiti majoris*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end;
10. *Femur*: A. total length; B. partial length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
11. *Tibiotarsus*: A. total length; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
12. *Tarsometatarsus*: A. total length; C. breadth of the proximal end; D. thickness of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end

2. ábra Csontok mérési mintái:

1. Alsó állkapocs: A. teljes hossz; B. a csőr hegy hossza;
2. Hollócsőrcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
3. Lapockacsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége;
4. Felkarcson: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
- 5-6. Singcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. proximális vég átlós szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
7. Orsócsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;
8. Kézközépcson: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; E1: a *metacarpus majus* vastagsága; F. a disztális vég szélessége;
9. Kézujjperc (II. ujj, 1. perc): A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;
10. Combcson: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
11. Lábszárcsont: A. teljes hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
12. Csüd: A. teljes hossz; C. proximális vég szélessége; D. proximális vég vastagsága; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága

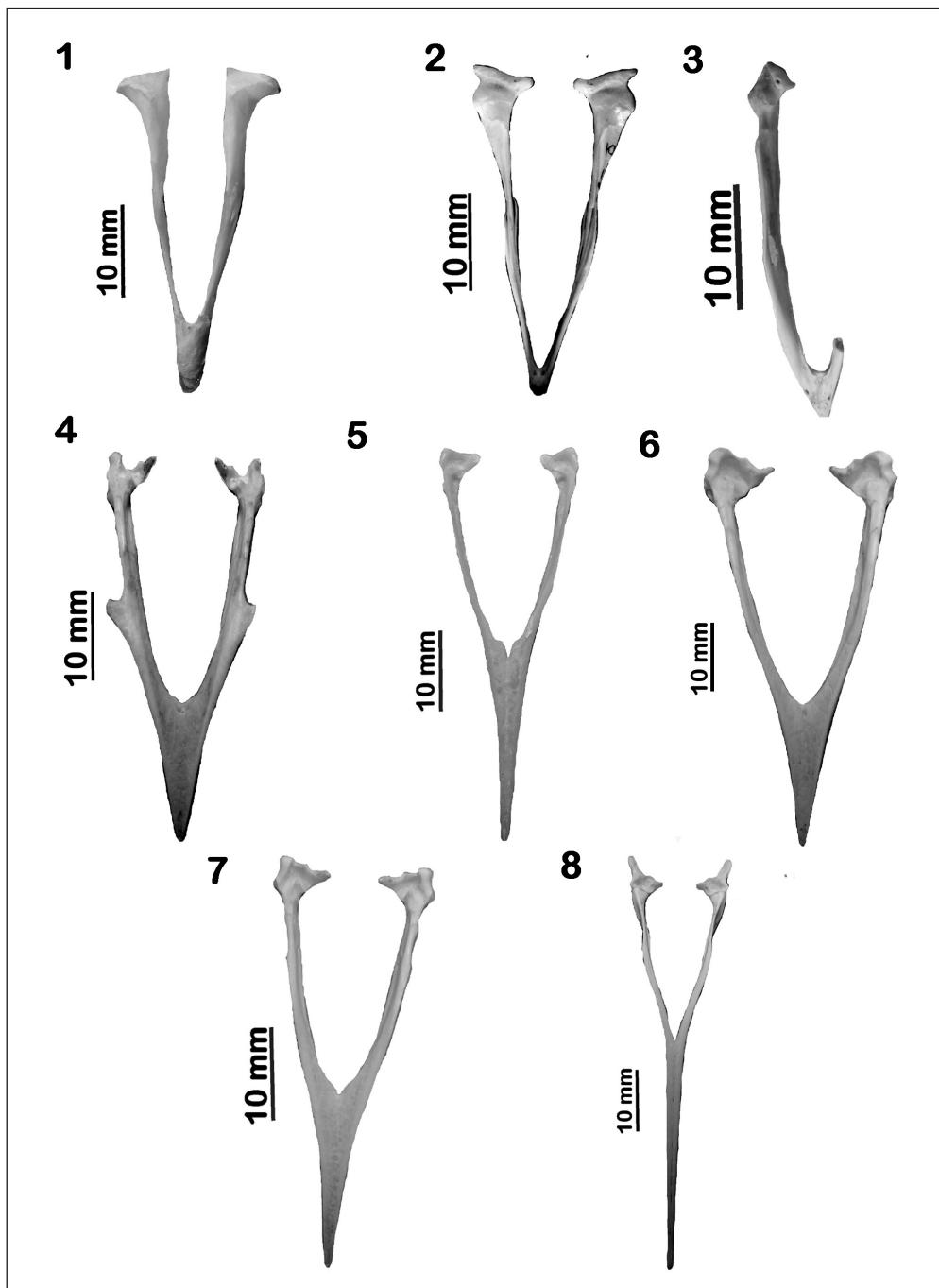


Figure 3. Mandibula – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Alcedo atthis*; 6. *Coracias garrulus*; 7. *Merops apiaster*; 8. *Upupa epops*

3. ábra Alsó állkapocs – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Alcedo atthis*; 6. *Coracias garrulus*; 7. *Merops apiaster*; 8. *Upupa epops*

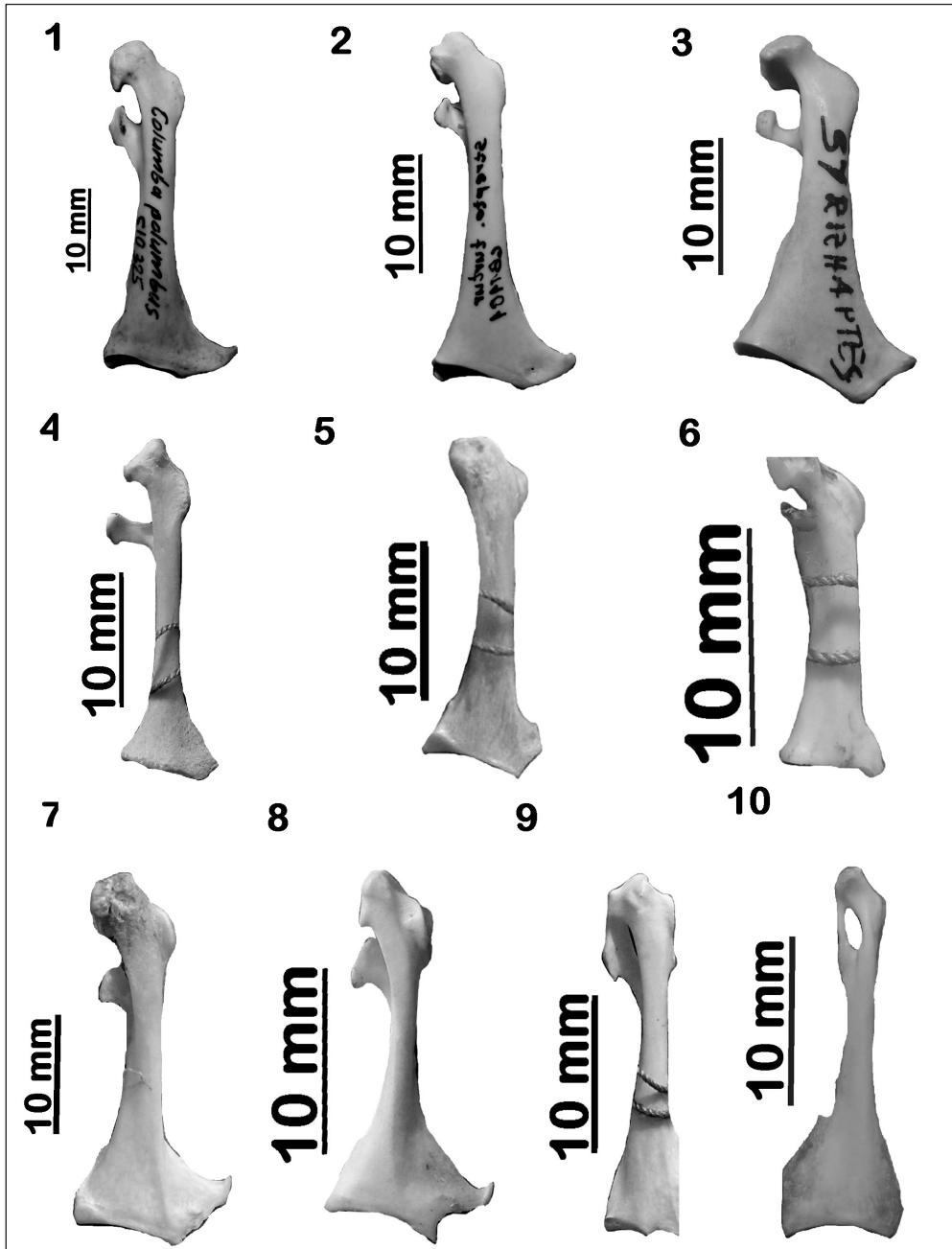


Figure 4. Left coracoideum (ventral surface) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

4. ábra Bal oldali hollócsőrcsont (hasi oldal) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

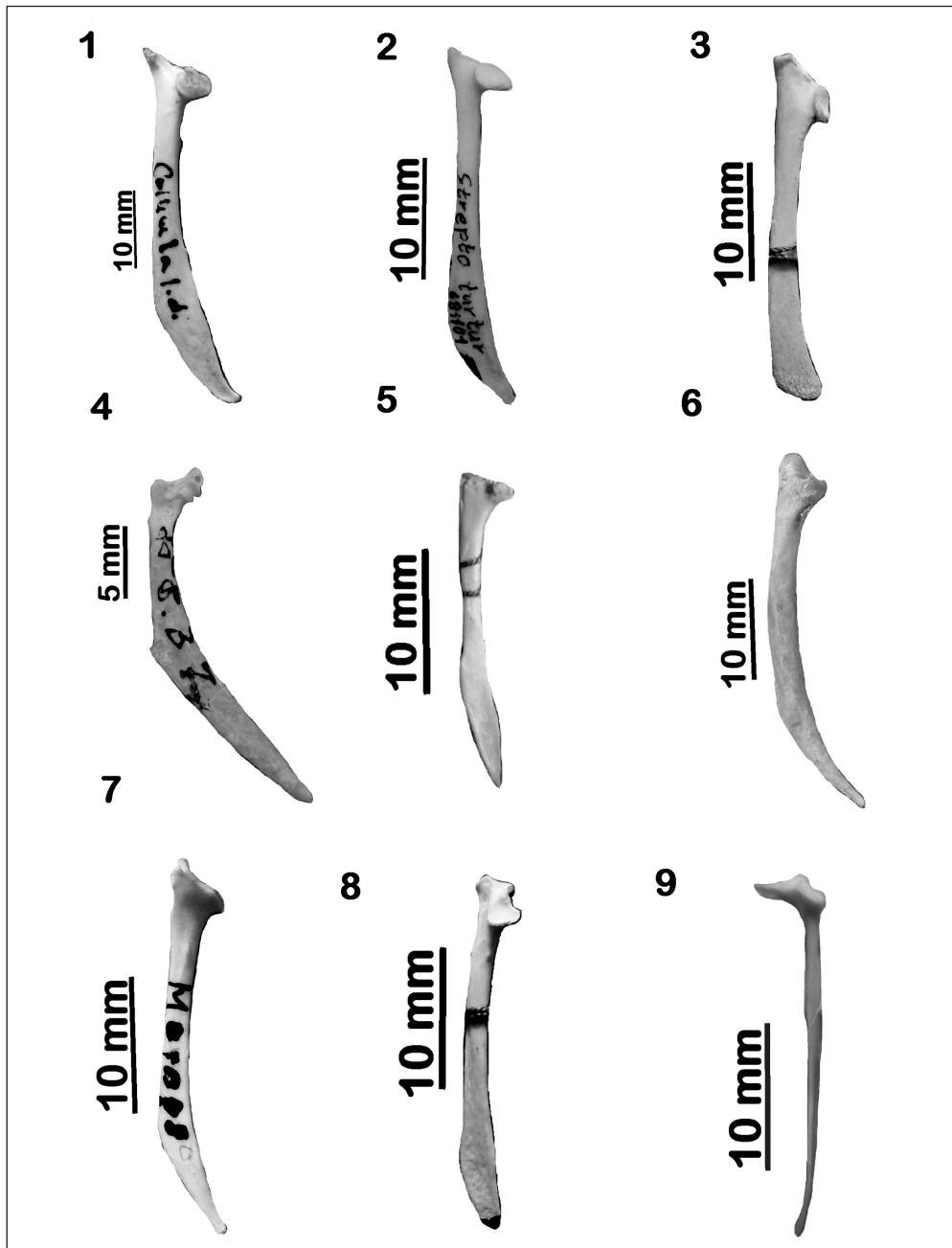


Figure 5. Right scapula (medial surface) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Cuculus canorus*; 4. *Caprimulgus europaeus*; 5. *Apus apus*; 6. *Coracias garrulus*; 7. *Merops apiaster*; 8. *Upupa epops*; 9. *Alcedo atthis*

5. ábra Jobb oldali lapocka csont (mediális oldal) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Cuculus canorus*; 4. *Caprimulgus europaeus*; 5. *Apus apus*; 6. *Coracias garrulus*; 7. *Merops apiaster*; 8. *Upupa epops*; 9. *Alcedo atthis*

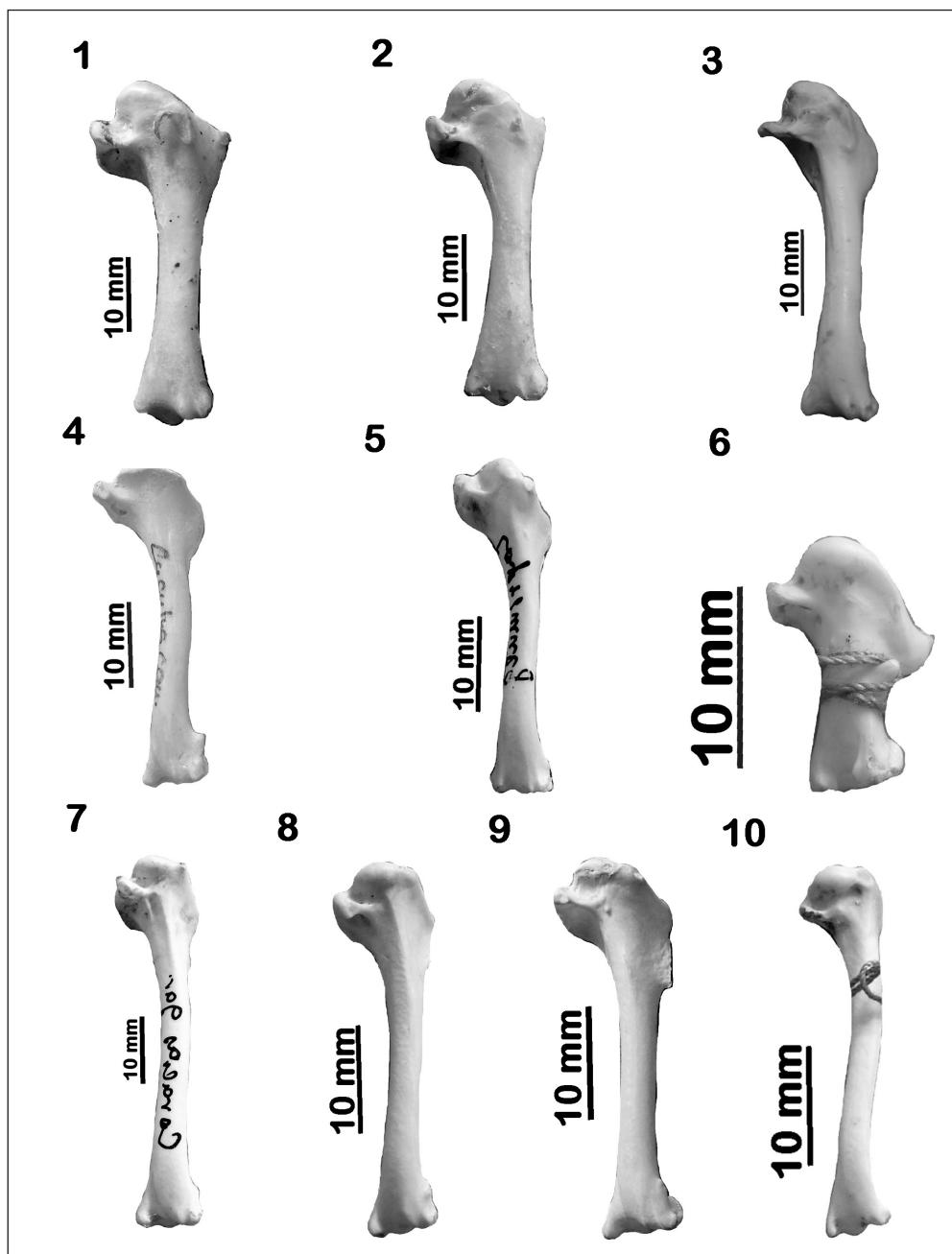


Figure 6. Right humerus (caudal surface) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

6. ábra Jobb oldali felkarcsont (palmáris oldal) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

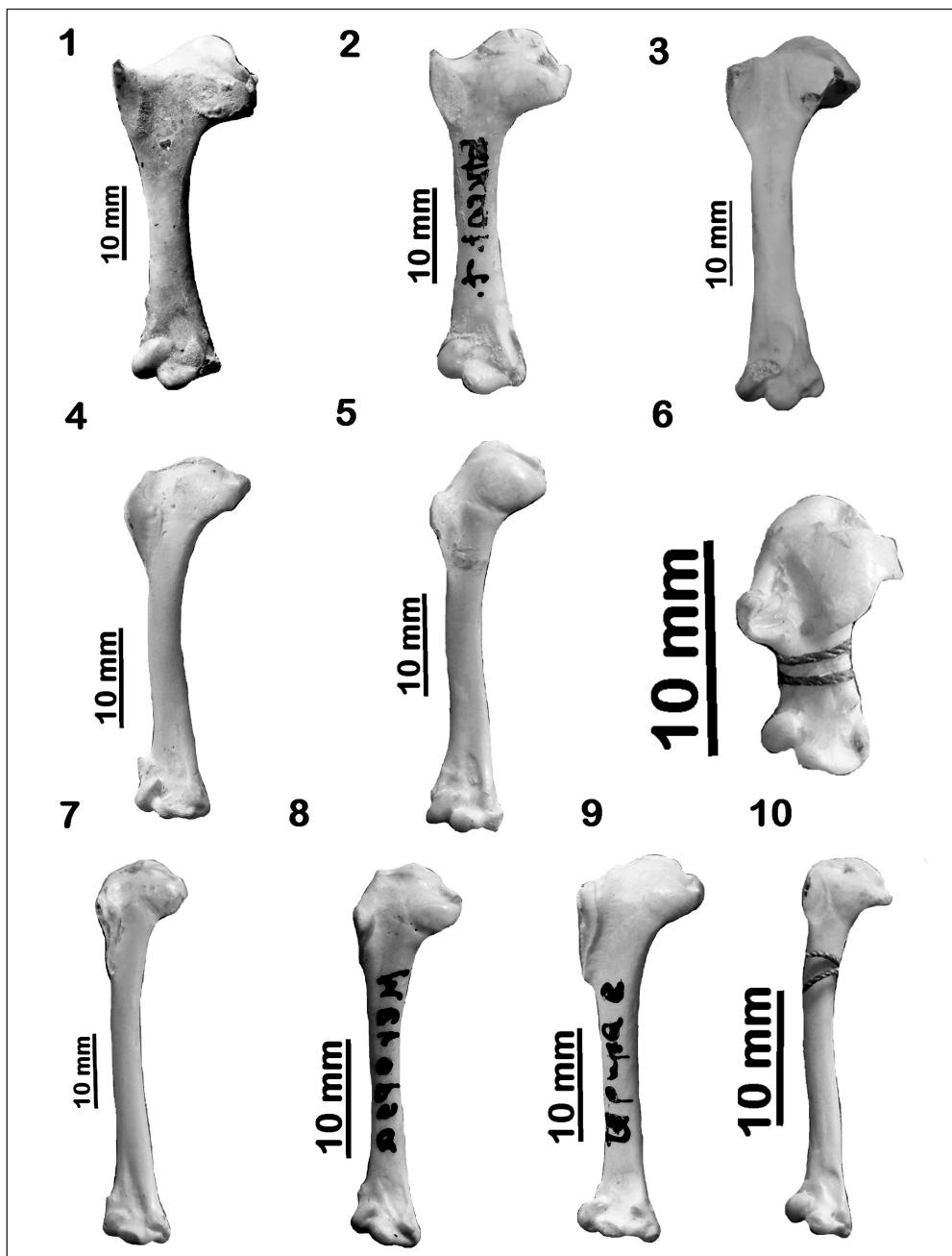


Figure 7. Right humerus (cranial surface) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

7. ábra Jobb oldali felkarcsont (dorzális oldal) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

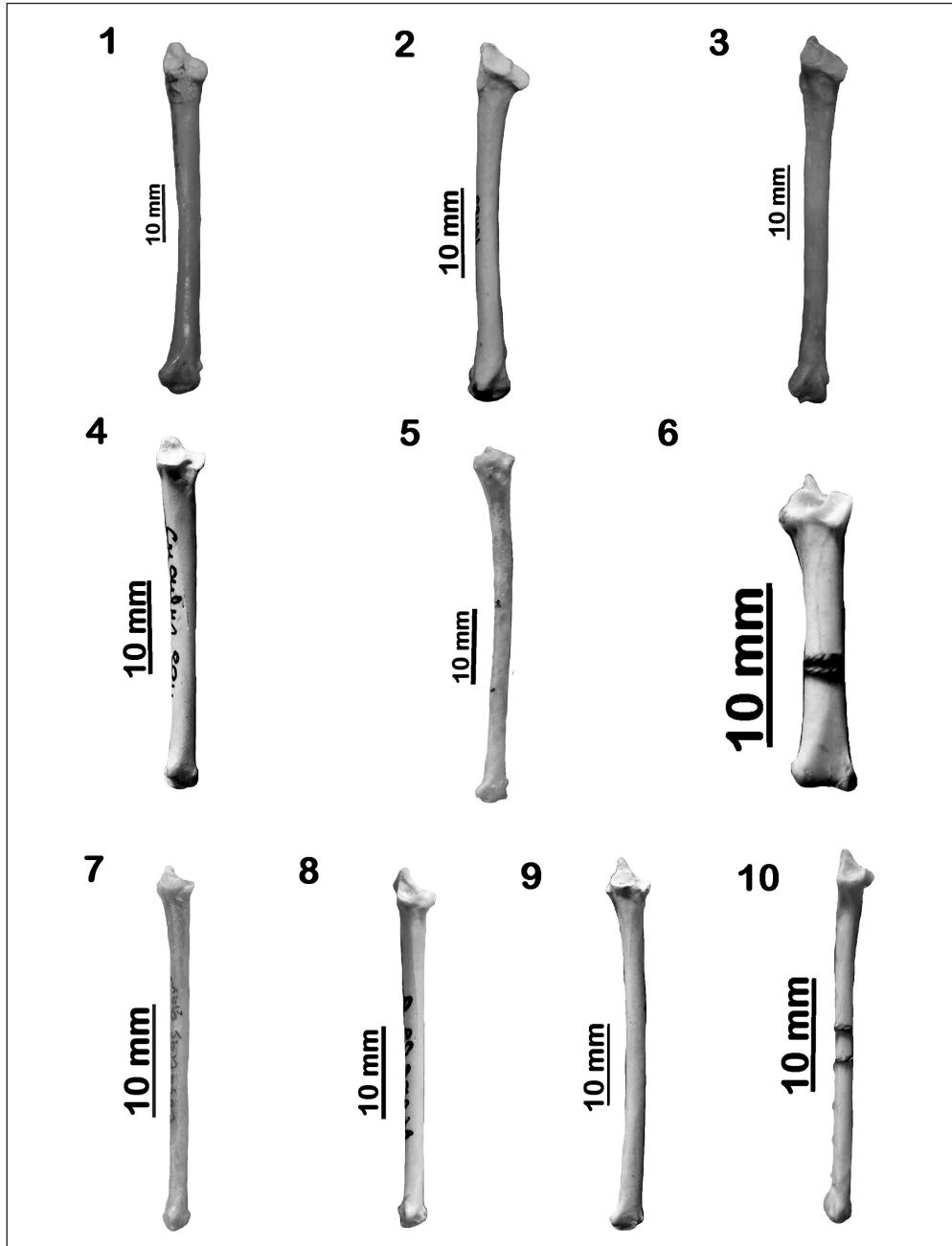


Figure 8. Left ulna (ventral aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

8. ábra Bal oldali singcsont (hasi nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

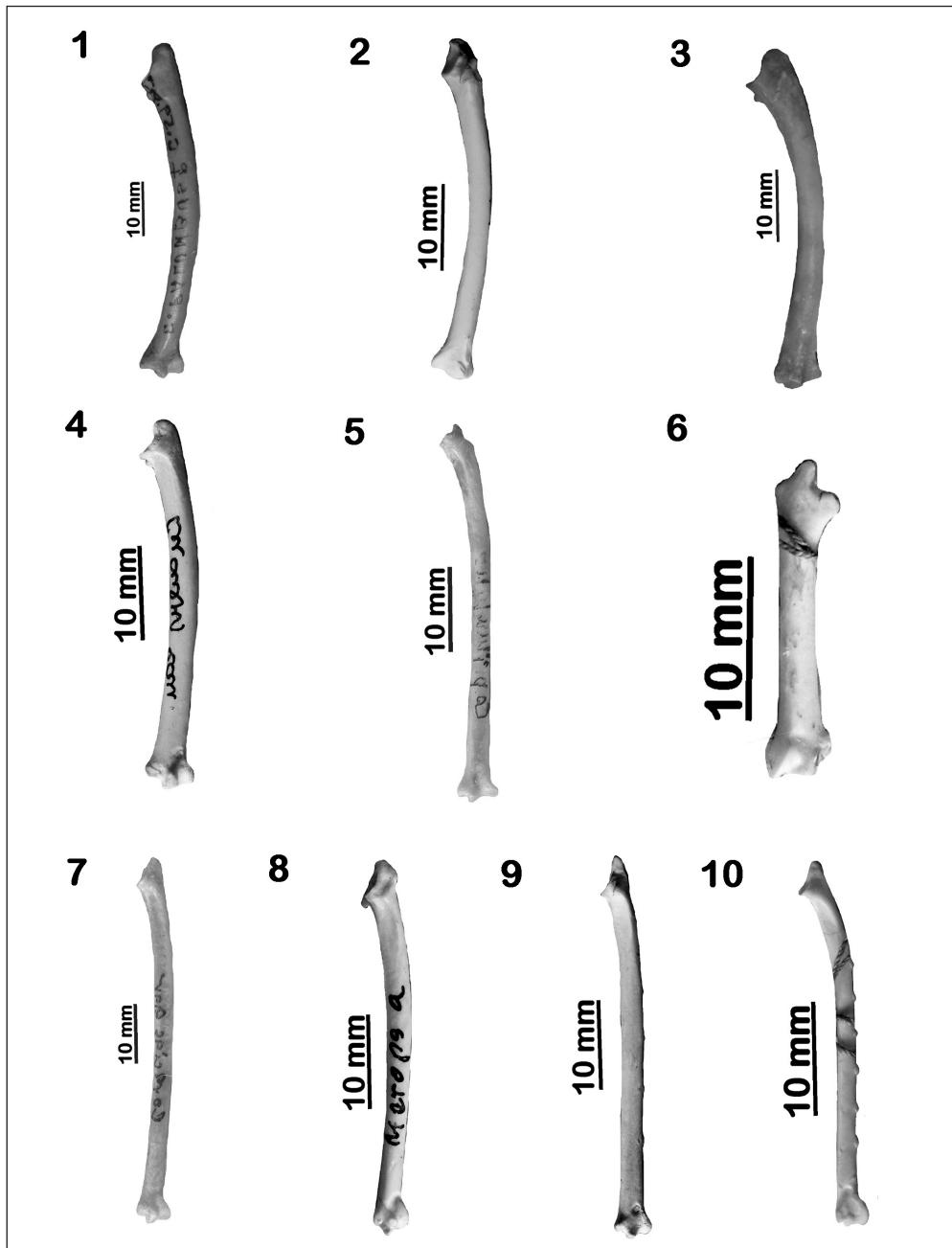


Figure 9. Left ulna (dorsal aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

9. ábra Bal oldali singcsont (háti nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

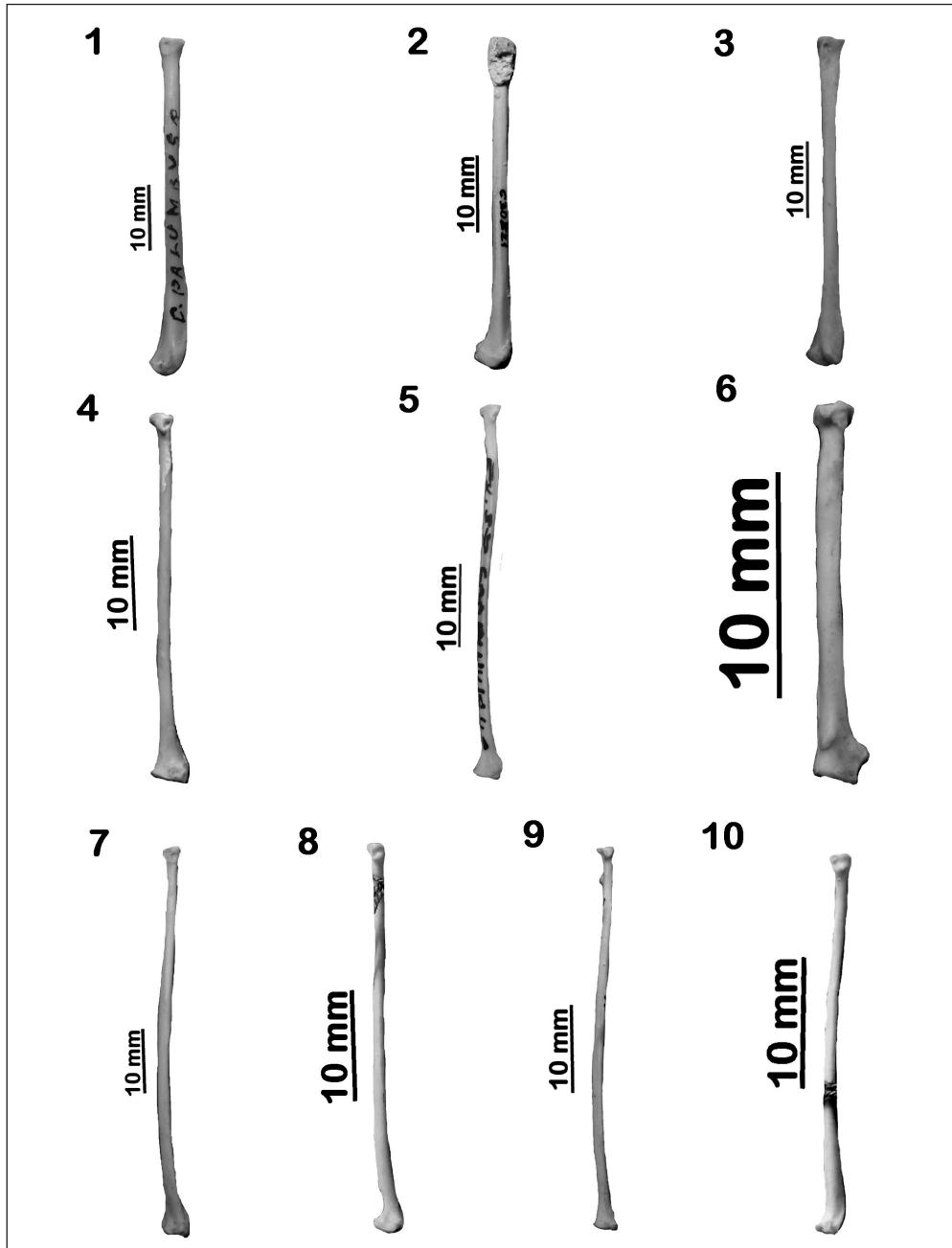


Figure 10. Left radius (dorsal aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

10. ábra Bal oldali orsócsont (háti nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

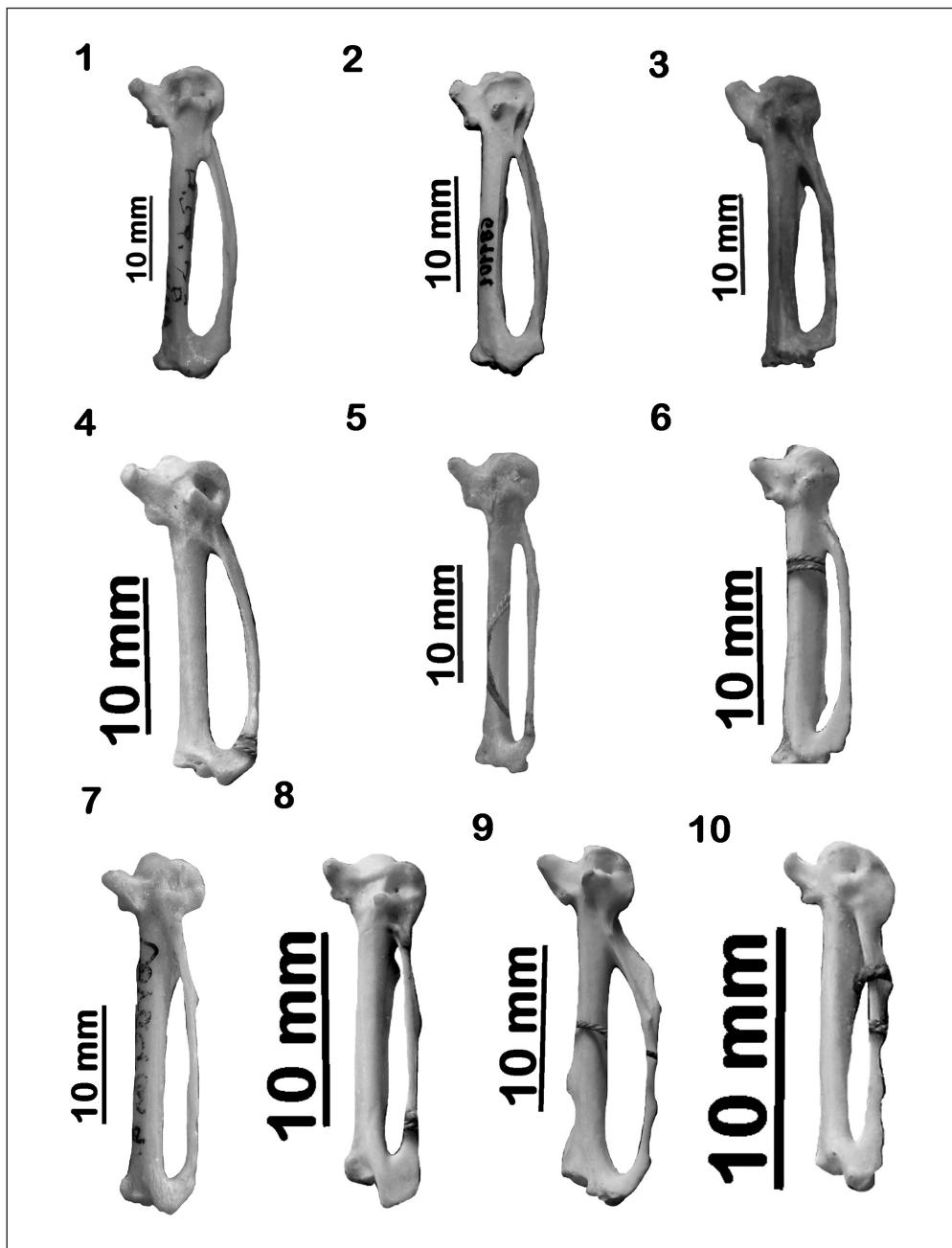


Figure 11. Left carpometacarpus (ventral aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

11. ábra Bal oldali kézközépcsontról (hasi nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

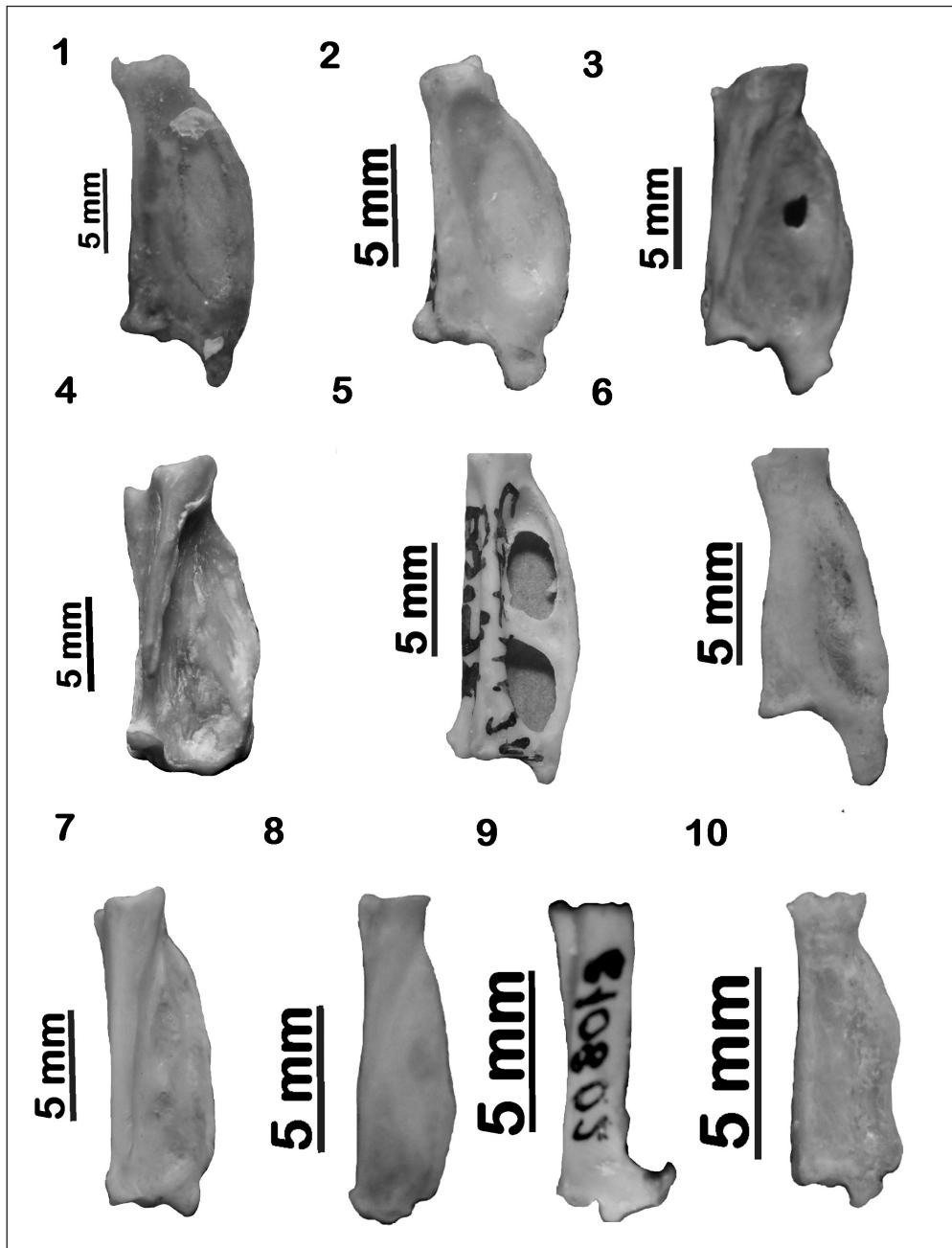


Figure 12. Left phalanx proximalis digiti majoris (ventral aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*
12. ábra Bal oldali kézujjperc (l. ujjperc, 2. ujj, hasi nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

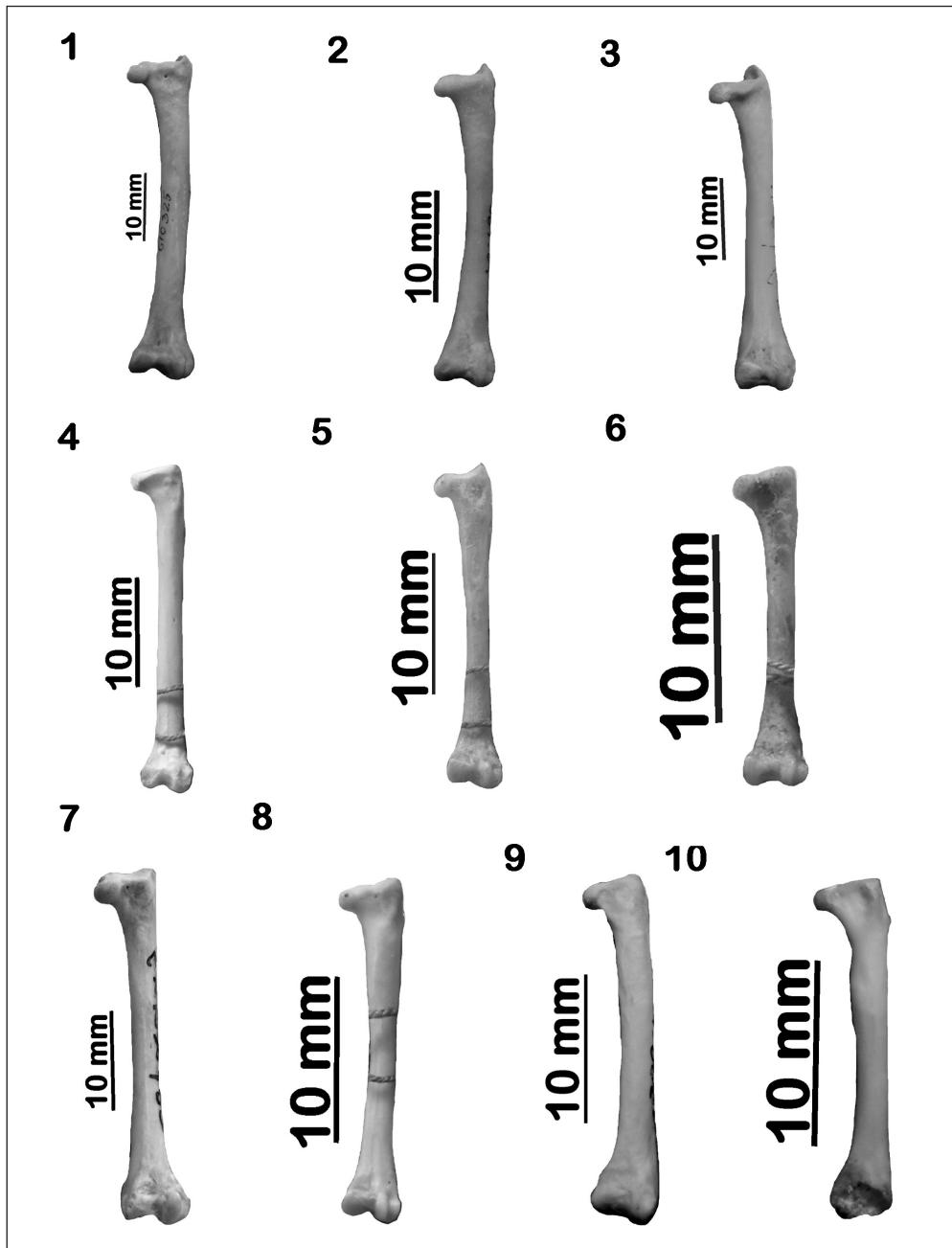


Figure 13. Right femur (caudal aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

13. ábra Jobb oldali combcsont (háti nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

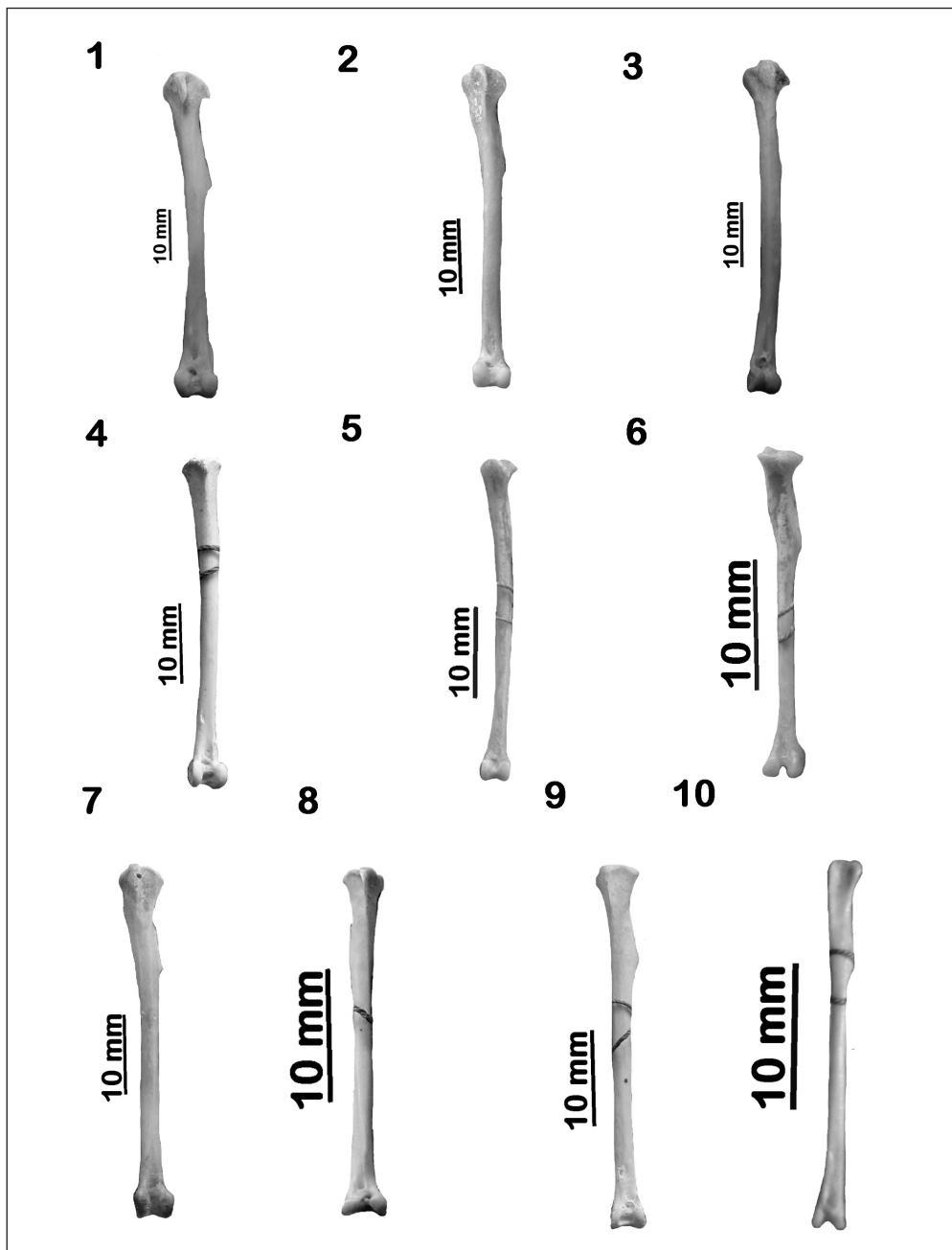


Figure 14. Left tibiotarsus (cranial aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

14. ábra Bal oldali lábszárcsont (hasi nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

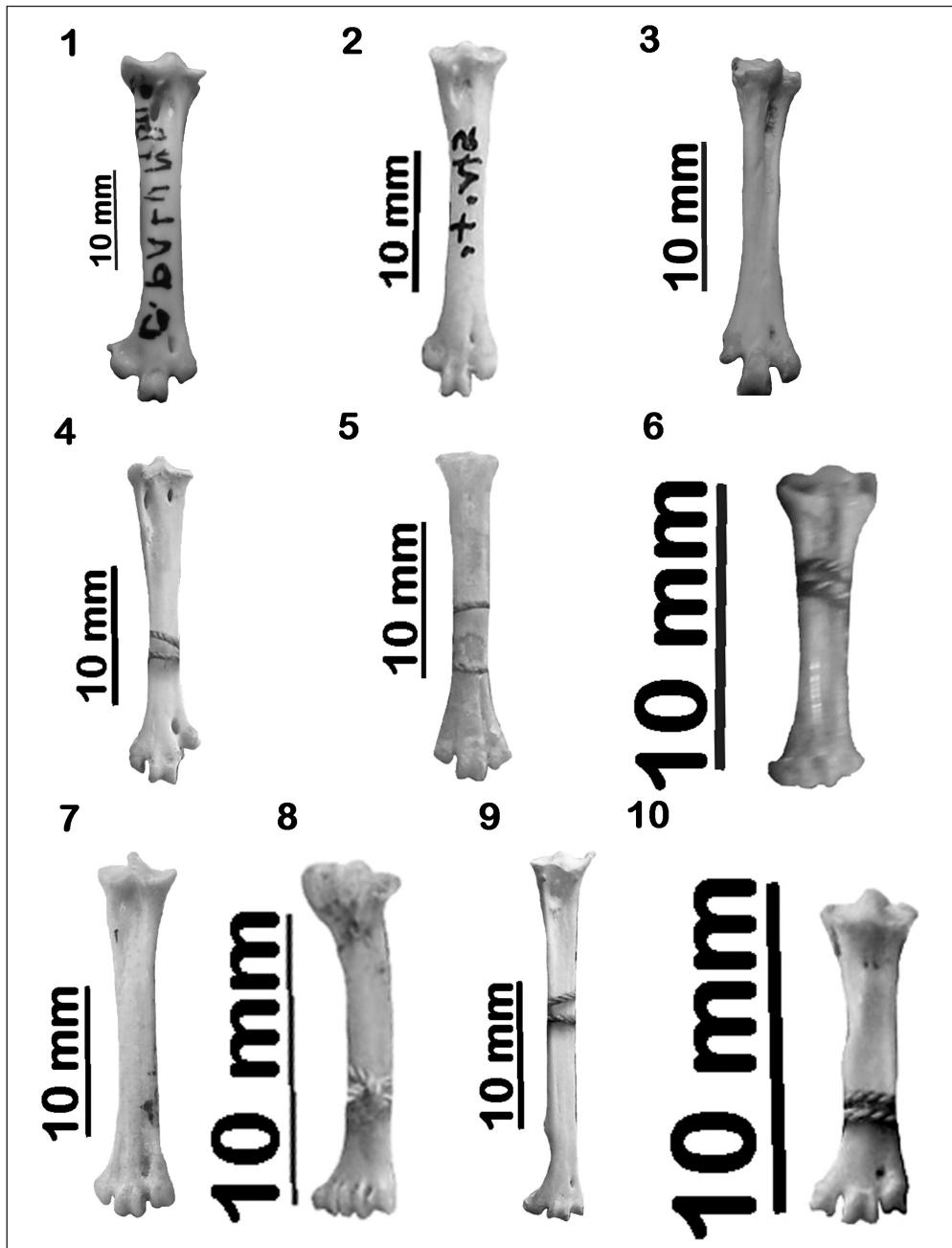


Figure 15. Left tarsometatarsus (dorsal aspect) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

15. ábra Bal oldali csüd (háti nézet) – 1. *Columba palumbus*; 2. *Streptopelia turtur*; 3. *Syrrhaptes paradoxus*; 4. *Cuculus canorus*; 5. *Caprimulgus europaeus*; 6. *Apus apus*; 7. *Coracias garrulus*; 8. *Merops apiaster*; 9. *Upupa epops*; 10. *Alcedo atthis*

Table 1.; 1. táblázat

Bones	<i>Columba palumbus</i>	<i>Columba livia</i>	<i>Columba oenas</i>	<i>Streptopelia tutur</i>	<i>Streptopelia decaocto</i>	<i>Syrrhaptes paradoxus</i>	<i>Cuculus canorus</i>	<i>Caprimulgus europeus</i>	<i>Apus apus</i>	<i>Coracias garrulus</i>	<i>Merops apiaster</i>	<i>Alcedo atthis</i>	<i>Upupa epops</i>
Mandibula													
A	44.35			30.91		28.00	41.30		57.00	45.00	49.51	65.50	
B	9.12		3.53		4.20	19.70			20.00	19.50	24.50	36.00	
Coracoid													
A	43.50	36.14-37.30	32.86	26.00	29.50	29.47	25.30	19.60	14.30	29.90	20.90	21.30	21.80
B	40.00	34.58-35.70	30.79	25.20	28.30	26.30	23.90	18.20	13.10	27.10	19.20	21.00	21.00
C	5.00	4.07-6.09	4.69	3.60	4.60	3.60	4.00	3.90	3.40	4.30	3.20	1.90	4.00
D	6.20	6.01-7.60	6.14	5.00	6.90	5.25	6.50	4.60	3.80	6.10	4.50	2.40	4.50
E	4.80	3.81-4.10	3.18	2.70	3.00	3.75	1.40	2.00	1.90	2.90	1.20	1.60	1.30
F	17.00	13.65-15.40	13.56	10.70	12.00	12.36	8.20	6.90	12.80	9.10	5.80	7.00	
G	11.00	9.76-10.30	9.00	6.80	8.40	10.56	6.90	5.90	4.50	8.50	6.20	5.80	5.20
Scapula													
A	53.64	42.00-46.10	37.10	31.20	37.40	43.23	26.90	25.80	24.00	38.00	26.30	23.00	26.40
B	10.90	9.60-10.30	8.59	7.00	8.8	9.72	6.50	6.00	4.10	6.30	4.20	5.00	4.60
C	5.00	4.11-5.20	3.78	3.50	4.10	4.07	3.20	3.00	2.40	3.00	2.20	3.50	2.60
D	3.90		3.80	3.11		3.20	3.07						
E	3.40		3.34	3.07	2.40	2.80	2.89	1.80	1.50	1.20	3.00	1.80	1.80
Humerus													
A	52.00-53.92	48.00	42.74	36.00	37.90	43.51	37.50	35.60	12.40	53.20	31.00	25.70	34.20
B	20.00	20.00	15.34	13.60	13.60	17.01	12.60	13.60	7.90	13.20	9.50	6.10	13.60
C	21.00	18.10	13.20	14.10	14.00	12.62	12.60	9.00	6.40	11.10	8.90	6.00	11.00
E	6.50	5.40	5.29	4.10	4.50	4.47	3.40	3.00	3.70	3.90	2.50	2.00	3.20
F	12.20	11.00	10.12	7.60	8.90	9.44	8.40	6.70	5.00	9.60	5.80	4.80	8.00
G			4.70	6.46	3.40	3.90	6.07	3.10	2.40	3.50	2.30	2.00	2.90
Ulna													
A	61.27	54.40-56.10	48.67	42.70	45.00	47.52	39.00	47.50	19.30	64.30	38.70	32.00	45.90
B	8.70	6.88-7.80	6.52	6.00	6.50	6.57	4.90	3.20	3.50	6.10	4.20	3.40	5.00
C	8.00		6.84	6.37	8.00	8.30	6.13	6.20	5.00	3.70	7.30	5.10	3.40
E	4.50	4.00	3.60	2.80	3.10	3.96	2.00	2.10	2.40	3.20	1.90	1.90	2.20
F	8.00	7.01-7.80	6.41	5.80	6.00	6.84	5.20	5.00	4.10	6.20	3.80	3.00	4.50

Table 2.; 2. táblázat

	Bones	<i>Columba palumbus</i>	<i>Columba livia</i>	<i>Columba oenas</i>	<i>Streptopelia turtrur</i>	<i>Streptopelia decaoctor</i>	<i>Syrrhaptes paradoxus</i>	<i>Cuculus canorus</i>	<i>Caprimulgus europeus</i>	<i>Apus apus</i>	<i>Coracias garrulus</i>	<i>Merops apiaster</i>	<i>Alcedo atthis</i>	<i>Upupa epops</i>
G		5.35-6.50	5.46	5.10	5.20	6.07	3.80	3.80	3.70	5.00	3.10	2.10	3.10	
Radius														
A	54.17	49.44-51.80	43.59	38.20	40.50	42.90	37.80	45.80	18.00	61.00	35.80	29.80	42.00	
C	4.80	4.53-4.90	4.10	3.70	3.70	4.21	3.00	3.00	1.90	4.00	2.40	2.00	2.50	
E	3.00	2.50-2.62	2.08	1.70	1.90	2.08	1.50	1.40	1.00	2.00	1.20	0.90	1.20	
F	5.70	5.18-5.50	4.29	4.00	4.00	4.80	3.90	3.20	2.40	4.60	2.90	4.50	2.30	
Carpometacarpus														
A	38.18	34.79-35.00	30.04	26.50	27.00	28.09	21.30	26.00	21.30	29.50	18.50	13.30	21.00	
B	34.50	32.53-32.80	28.67	24.50	25.50	25.90	19.00	24.60	20.20	27.20	16.60	11.80	19.00	
C	11.20	9.38-10.00	8.47	7.50	7.50	9.14	6.80	7.20	5.90	8.70	5.40	4.00	5.60	
E	8.30		7.00	6.78	6.00	6.00	6.85	5.20	4.50	4.40	5.20	3.20	2.70	5.50
E*	3.40	2.79-3.70	2.41	2.80	3.10	2.50	3.00	2.40	2.30	3.00	1.80	1.30	2.00	
F	7.00	6.03-6.20	5.77	5.00	5.40	5.46	5.00	5.00	4.00	5.40	4.10	2.70	5.50	
G	3.93-4.40	3.78	3.50	3.20	3.96	3.30	3.30	3.30	3.00	3.50	2.10	1.60	2.20	
Phalanx alae														
A	20.00		21.00	15.10	14.30	17.00	23.30	14.00	13.20	15.00	11.00	6.90	9.80	
C	3.50	4.00	4.50	3.00	5.00	4.40	3.00	3.00	3.00	4.00	2.70	1.70	2.20	
E	7.00		7.20	5.00	6.30	7.00	5.00	4.70	5.00	5.00	3.00	2.20	1.70	
F	8.70	7.00		6.00	6.20	6.00	4.50	4.40	5.00	4.00	2.20	1.80	3.40	
Femur														
A	45.54	40.91-43.00	35.68	29.00	32.70	39.39	28.30	22.40	16.80	31.20	19.20	21.00	24.40	
B	43.20	38.42-40.80	33.90	27.00	31.20	36.24	27.50	21.20	16.40	30.10	18.50	19.60	23.00	
C	9.20	8.64-8.90	7.59	5.40	5.40	8.28	4.80	4.00	3.50	6.00	3.60	3.00	4.80	
D		5.90-6.00	5.96		4.80	7.34	3.70	3.10	2.40	4.80	2.70		3.70	
E	4.10	4.00	3.14	2.30	2.80	3.44	2.10	1.40	1.40	2.40	1.50	1.70	2.20	
F	8.80	7.53-8.00	6.55	5.50	5.80	7.04	4.80	3.80	3.60	5.70	3.40	3.00	4.40	
G	6.70	5.35		4.70	6.10	4.00	3.20	2.80	5.00	2.70			3.80	
Tibiotarsus														
A	65.57	57.68-62.20	49.60	42.30	43.40	50.27	37.70	32.40	25.30	43.50	25.30	25.80	37.10	
C	9.30	9.57-10.20	7.87	5.80	6.80	8.55	5.50	4.00	3.80	5.40	3.40	2.80	4.70	
D		6.68-7.00	5.54	4.80	5.00	6.27	4.00	3.80	3.20	4.70	2.90	2.50	3.40	

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