

Evolution of Corvids and their Presence in the Neogene and the Quaternary in the Carpathian Basin

Jenő (Eugen) KESSLER

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Abstract: Corvids are the largest songbirds in Europe. They are known in the avian fauna of Europe from the Miocene, the beginning of the Neogene, and are currently represented by 11 species. Due to their size, they occur more frequently among fossilized material than other types of songbirds, and thus have been examined to the largest extent. In the current article, we present their known evolution and their fossilized taxa in Europe and examine the osteology of extant species.

Keywords: Corvidae, Neogene, Quaternary, Europe, Carpathian Basin, osteology

Összefoglalás: A varjúfélék a legnagyobb termetű, Európában is elterjedt énekesmadarak. A kontinens madárfaunájában a neogén elejétől, a miocénből ismertek, és jelenleg 11 fajjal vannak képviselve. Termetük következtében gyakrabban előfordulnak a fosszilis anyagban, mint a többi énekesmadár típus, és ennek következtében nagyobb mértékben is tanulmányozták őket. Jelen tanulmányban bemutatjuk az ismert európai evolúciójukat és fosszilis taxonjaikat, és foglalkozunk a recens fajok csonttánával is.

Kulcsszavak: Corvidae, neogén, negyedidőszak, Európa, Kárpát-medence, csonttan

Department of Paleontology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary, e-mail: kessler_jeno@yahoo.com

Introduction

About half of the current avian species – if not more – consists of songbirds, which are distributed all around the world apart from Antarctica with a large number of specimens. Despite this fact, we know little of their origins and evolution. They supposedly formed in the ancient continent of Gondwana, but their fossilized remains in the Palearctic and Nearctic are only known from the Neogene, and even those only in small numbers. Recently, however, their research received a boost, and thus the number of identified and described taxa and new fossil species increased (Kessler 2013a, 2013b, 2015).

The families of the order Corvidae are an exception to this, and due to their larger size, they were always in the focus of interest of paleornithologists. Most songbird species had been described during the past two centuries from this family. During their classification, we follow the Brodkorb type of systematics, since those that are based on DNA data (Sibley & Ahlquits 1990, Monroe & Sibley 1993, Jarvis *et al.* 2014) cannot be used in case of fossils in the absence of comparative molecular material, and other types of systematics classify solely based

on appearance and feathers, excluding skeletons that can be examined within the framework of paleontology (e.g. Clements 1974, Cramp 1998, Dickinson & Christidis 2014).

Brodkorb (1978) distinguishes two subfamilies within the family:

- Garbulinae (Bole, 1825) to which he only classifies Nearctic taxa (*Miocitta*, *Protocitta*, *Hetocitta*) from the Neogene and Quaternary of North America. Examples of this are †*Miocitta galbreathy* (Brodkorb 1972) (from the Miocene of Colorado), †*Protocitta ayax* Brodkorb, 1972 (from the Pliocene of Kansas and Texas), †*P. dixi* (Brodkorb 1957) (from the Pleistocene of Florida and Texas), †*Henocitta brodkorbi* Holman 1959 (from the Pleistocene of Florida);
- *Corvinae* (Bonaparte 1831), where the Palearctic species belong. Brodkorb mentions the following species from outside Europe: *Corvus* †*wetmorei* (Brodkorb, 1959) (from the Pleistocene of Bahama), *C.* †*pumilis* (Wetmore, 1920) (from the Quaternary of Puerto Rico and the Virgin Islands), *C.* †*moriolum* (Forbes, 1892) (from the Quaternary of the Chatham Islands). Apart from the Corvidae finds, crow remains were recently described from the Miocene of North America (Olson & Rasmussen 2001) report the taxon *Corvus* aff *ossifragus* (Wilson, 1812) from the site at Lee Creek Mine, based on a *tibiotarsus* find. We discuss fossil corvids of the western Palearctic and the Carpathian Basin in the systematic section after the osteology chapter.

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

A – total lengths; B – partial lengths; C – breadth of proximal epiphysis; C1 – partial breadth of proximal epiphysis; D – thickness of proximal epiphysis; E – breadth of diaphysis; E1 – partial breadth of diaphysis; F – breadth of distal epiphysis; G – thickness of distal epiphysis; H – height of distal epiphysis.

Osteology of Corvids

Anatomical terminology (after: Milne-Edwards 1868, Fürbringer 1888, Lambrecht 1933, Ballmann 1966, Mourer-Chauviré 1975, Baumel *et al.* 1979, Gilbert *et al.* 1981, Cheneval 1983, Jánossy 1985, Solti 1996, Tomek & Bochenski 2000, Kessler 2013a) (*Figure 1*).

Method of measurement: (after: von den Driesch 1976, Gál 2002, Kessler 2013b) (*Figure 2*).

A = TL – total length;

B = PL – partial length;

C = Bp – breadth of the proximal end;

C1 = partial breadth of the proximal end;

D = partial length of the proximal end;

E = Sc – breadth of the corpus;

E1 = partial breadth of the corpus;

F = Bd – breadth of the distal end;

G = thickness of the distal end;

H = height of the distal end.

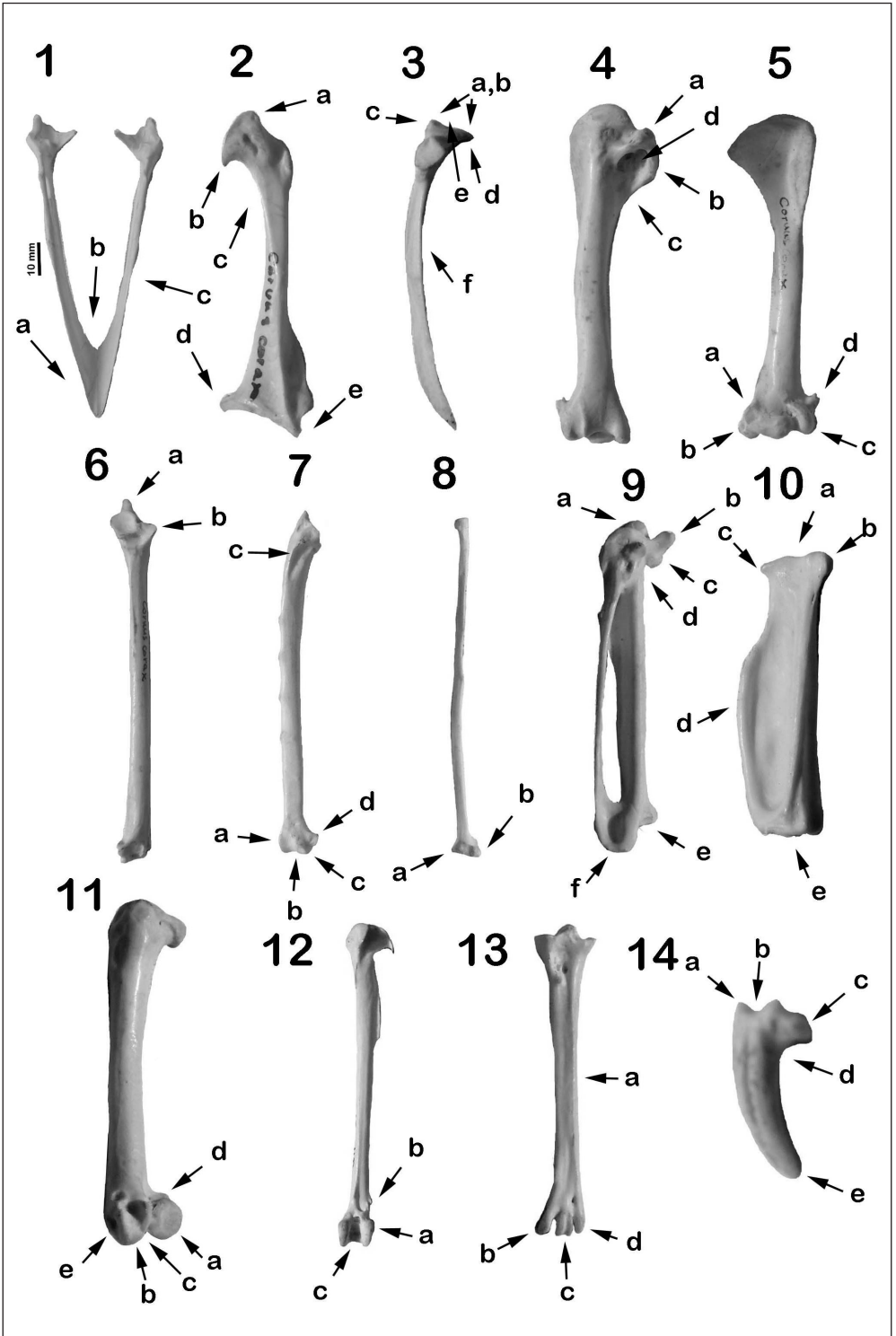


Figure 1. *Corvus corax* Linnaeus, 1758 osteology characters:

1. *Mandibula*: a. the pointed end of the *rostrum mandibulae*; b. the immersed part of the *rostrum*; c. the *ramus mandibulae, pars symphysialis*;
2. *Coracoideum*: a. the *processus acroracoidalis*; b. the *processus procoracoidalis*; c. the *sulcus musculi supracoracoideus*; d. the *angulus medialis*; e. the *processus lateralis*;
3. *Scapula*: a. the dorsal branch of the *acromion*; b. the lateral branch of the *acromion*; c. the pit between the branches of the *acromion*; d. the *corpus scapulae*;
4. *Humerus, epiphysis proximalis*: a. the *tuberculum ventrale*; b. the *crista bicipitalis*; c. the edge between *crista bicipitalis* and *corpus humeri*; d. the *fossa pneumotricipitalis*;
5. *Humerus, epiphysis distalis*: a. the *tuberculum supracondylare ventrale*; b. the *processus flexorius*; c. the *condylus dorsalis*; d. the *processus supracondylaris dorsalis*;
6. *Ulna, epiphysis proximalis*: a. the *olecranon*; b. the *cotyla dorsalis*; c. the *impressio brachialis*;
7. *Ulna, epiphysis distalis*: a. the *condylus dorsalis ulnaris*; b. the *sulcus intercondylaris*; c. the *condylus ventralis ulnaris*; d. the *tuberculum carpale*;
8. *Radius*: a. the *tuberculum aponeurosis ventrale*; b. the *tuberculum aponeurosis dorsale*;
9. *Carpometacarpus*: a. the *trochlea carpalis*; b. the *processus extensorius*; c. the *processus alularis*; d. the *fovea subalularis*; e. the *protuberantia metacarpale majus*; f. the *facies articularis digitale minor*;
10. *Phalanx proximalis digiti majoris*: a. the *margo proximalis*; b. the *tuberculum ventralis*; c. the *tuberculum dorsalis*; d. the *margo dorsalis*; e. the *margo distalis*;
11. *Femur, epiphysis distalis*: a. the *condylus medialis*; b. the *condylus lateralis*; c. the *sulcus intercondylaris*; d. the *epicondylus medialis*; e. the *epicondylus lateralis*;
12. *Tibiotarsus, epiphysis distalis*: a. the *epicondylus lateralis*; b. the *tuberculum retinaculum musculi fibularis*; c. the *incisura intercondylaris*;
13. *Tarsometatarsus, epiphysis distalis*: a. the *margo medialis*; b. the *trochlea metatarsi II.*; c. the *trochlea metatarsi III.*; d. the *trochlea metatarsi IV.*;
14. *Phalanx unguis*: a. the *tuberculum extensorium*; b. the *cotyla articularis*; c. the *tuberculum flexorium*; d. the curvature of the *margo plantaris*; e. the *apex phalangis*

1. *ábra Corvus corax* Linnaeus, 1758 csonttani jellegek:

1. Alsó állkapocs: a. a *rostrum mandibulae* hegye; b. bemélyedés a *rostrum*-on; c. *ramus mandibulae, pars symphysialis*;
2. Hollócsőrcsont: a. *processus acroracoidalis*; b. *processus procoracoidalis*; c. *sulcus musculi supracoracoideus*; d. *angulus medialis*; e. *processus lateralis*;
3. Lapocka: a. az *acromion* dorzális ága; b. az *acromion* oldalsó ága; c. az *acromion* ágai közti bemélyedés alakja; d. *corpus scapulae*;
4. Felkarcsont, proximális vég: a. *tuberculum ventrale*; b. *crista bicipitalis*; c. a *crista bicipitalis* és a *corpus humeri* közti él jellege; d. *fossa pneumotricipitalis*;
5. Felkarcsont, disztális vég: a. *tuberculum supracondylare ventrale*; b. *processus flexorius*; c. *condylus dorsalis*; d. *processus supracondylaris dorsalis*;
6. Singcsont proximális vég: a. *olecranon*; b. *cotyla dorsalis*; c. *impressio brachialis*;
7. Singcsont disztális vég: a. *condylus dorsalis ulnaris*; b. *sulcus intercondylaris*; c. *condylus ventralis ulnaris*; d. *tuberculum carpale*;
8. Orsócsont: a. *tuberculum aponeurosis ventrale*; b. *tuberculum aponeurosis dorsale*;
9. Kézközépcsont: a. *trochlea carpalis*; b. *processus extensorius*; c. *processus alularis*; d. *fovea subalularis*; e. *protuberantia metacarpale majus*; f. *facies articularis digitale minor*;
10. A nagy kézujj első ujjperce: a. *margo proximalis*; b. *tuberculum ventralis*; c. *tuberculum dorsalis*; d. *margo dorsalis*; e. *margo distalis*;
11. Combcsont, disztális vég: a. *condylus medialis*; b. *condylus lateralis*; c. *sulcus intercondylaris*; d. *epicondylus medialis*; e. *epicondylus lateralis*;
12. Lábszárcsont, disztális vég: a. *epicondylus lateralis*; b. *tuberculum retinaculum musculi fibularis*; c. *incisura intercondylaris*;
13. Csüd, disztális vég: a. *margo medialis*; b. *trochlea metatarsi II.*; c. *trochlea metatarsi III.*; d. *trochlea metatarsi IV.*;
14. Karomcsont: a. *tuberculum extensorium*; b. *cotyla articularis*; c. *tuberculum flexorium*; d. a *margo plantaris* íve; e. *apex phalangis*

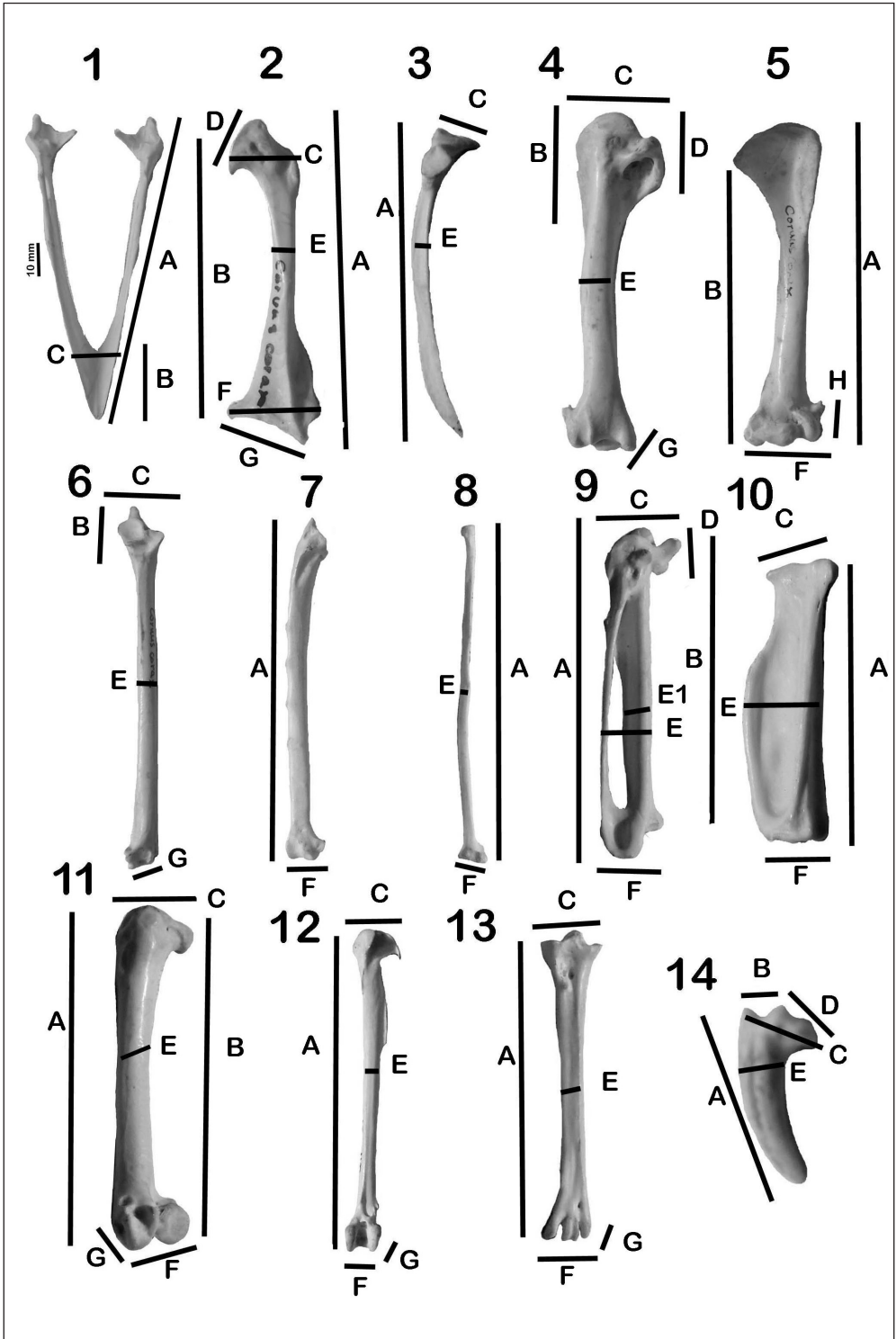


Figure 2. Measurements methods of bones:

1. *Mandibula*: A. total length; B. length of the *rostrum*; C. breadth of the *rostrum*;
2. *Coracoideum*: A. total length; B. partial length; C. length of the *processus procoracoidalis*; D. breadth of the corpus and *processus procoracoidalis*; 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;
- 4-5. *Humerus*: A. total length; B. partial length 1; C. breadth of the proximal end; D. partial length 2; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end; H. height of the distal end;
- 6-7. *Ulna*: A. total length; B. length of the proximal epiphysis; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
8. *Radius*: A. total length; F. breadth of the distal end;
9. *Carpometacarpus*: A. total length; B. partial length; C. breadth of the proximal end; D. length of the *processus extensorius*; E. breadth of the corpus; E1: breadth of the *metacarpus majus*; F. breadth of the distal end;
10. *Phalanx proximalis digiti majoris*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end;
11. *Femur*: A. total length; B. partial length 1.; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
12. *Tibiotarsus*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
13. *Tarsometatarsus*: A. total length; C. breadth of the proximal end; E. breadth of the corpus; F. breadth of the distal end; G. thickness of the distal end;
14. *Phalanx ungularis*: A. total length; B. length of the *cotyla articularis*; C. breadth of the proximal end; D. length of the *tuberculum flexorium*; E. breadth of the corpus

2. ábra A csontok mérési mintái:

1. Alsó állkapocs: A. teljes hossz; B. a csőr vég hossza; C. a csőrvég szélessége;
2. Hollócsőr csont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég részleges szélessége;
3. Lapockacsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége;
- 4-5. Felkarcsont: A. teljes hossz; B. részleges hossz 1.; C. proximális vég szélessége; D. részleges hossz 2.; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága; disztális vég magassága;
- 6-7. Singcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
8. Orsócsont: A. teljes hossz; F. a disztális vég szélessége;
9. Kéz középcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; D. a *processus flexorius* hossza; E. a test szélessége; E1: a *metacarpus majus* vastagsága; F. a disztális vég szélessége;
10. Kézujjperc (II. ujj, 1. perc): A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége;
11. Combcsont: A. teljes hossz; B. részleges hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
12. Lábszárcsont: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
13. Csüd: A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége; G. a disztális vég vastagsága;
14. karomcsont: A. teljes hossz; B. ízületi vápa hossza; C. proximális vég szélessége; D. a *processus flexorius* szélessége; E. a test szélessége

1. Mandibula (Figure 3)**1.a the pointed end of the rostrum mandibulae:**

- medium long and medium width: *Corvus*, *Garrulus*, *Pica*;
- long and narrow: *Pyrrhocorax*;
- long and medium width: *Nucifraga*;

1.b the immersed part of the rostrum:

- narrow semicircular: *Pyrrhocorax*;
- pointed: *Corvus frugilegus*;
- ovoid: *Corvus corax*, *C. corone*, *C. monedula*, *Pica*;
- semi-circle with small recess: *Garrulus*;
- wide semi-circle: *Nucifraga*;

1.c the form of the ramus mandibulae:

- short: *Nucifraga*;
- long and medium wide: *Corvus*, *Garrulus*, *Pica*;
- long and narrow: *Pyrrhocorax*;

2. Coracoideum (Figure 4)**2.a the processus acrocoracoideus (tuberculum brachiale):**

- curved and pointed: *Corvus corax*, *C. monedula*, *Garrulus*, *Pica*, *Pyrrhocorax*;
- narrow and pointed: *Nucifraga*;
- strongly curved and pointed: *Corvus corone*, *C. frugilegus*;

2.b the acrocoracoideum:

- semicircular: *Corvus corone*, *Pyrrhocorax graculus*;
- wide cone-shaped: *Corvus monedula*, *Pica*, *Pyrrhocorax pyrrhocorax*;
- asymmetric cone-shaped: *Corvus corax*, *C. frugilegus*;
- small pointed cone-shaped: *Garrulus*;
- small bunted cone-shaped: *Nucifraga*;

2.c the sulcus musculi supracoracoidei:

- symmetrically semicircular: *Corvus*, *Garrulus*, *Pyrrhocorax*;
- flattened: *Nucifraga*, *Pica*;

2.d the angulus medialis:

- pointed: *Garrulus*, *Nucifraga*;
- pointed and curved: *Pyrrhocorax graculus*;
- protruding: *Corvus monedula*, *Pyrrhocorax pyrrhocorax*;
- truncated: *Corvus corax*, *C. corone*, *C. frugilegus*, *Pica*;

2.e the processus lateralis:

- semicircular-shaped: *Corvus frugilegus*, *Garrulus*, *Nucifraga*, *Pica*;
- symmetric truncated: *Corvus corone*, *Pyrrhocorax graculus*;
- asymmetric truncated: *Corvus corax*, *C. monedula*, *Pyrrhocorax pyrrhocorax*;

3. Scapula (Figure 5)**3.a the length of the branches of acromion:**

- symmetrically (equal): *Nucifraga*, *Pica*;
- asymmetrically (unequal): *Corvus*, *Garrulus*, *Pyrrhocorax*;

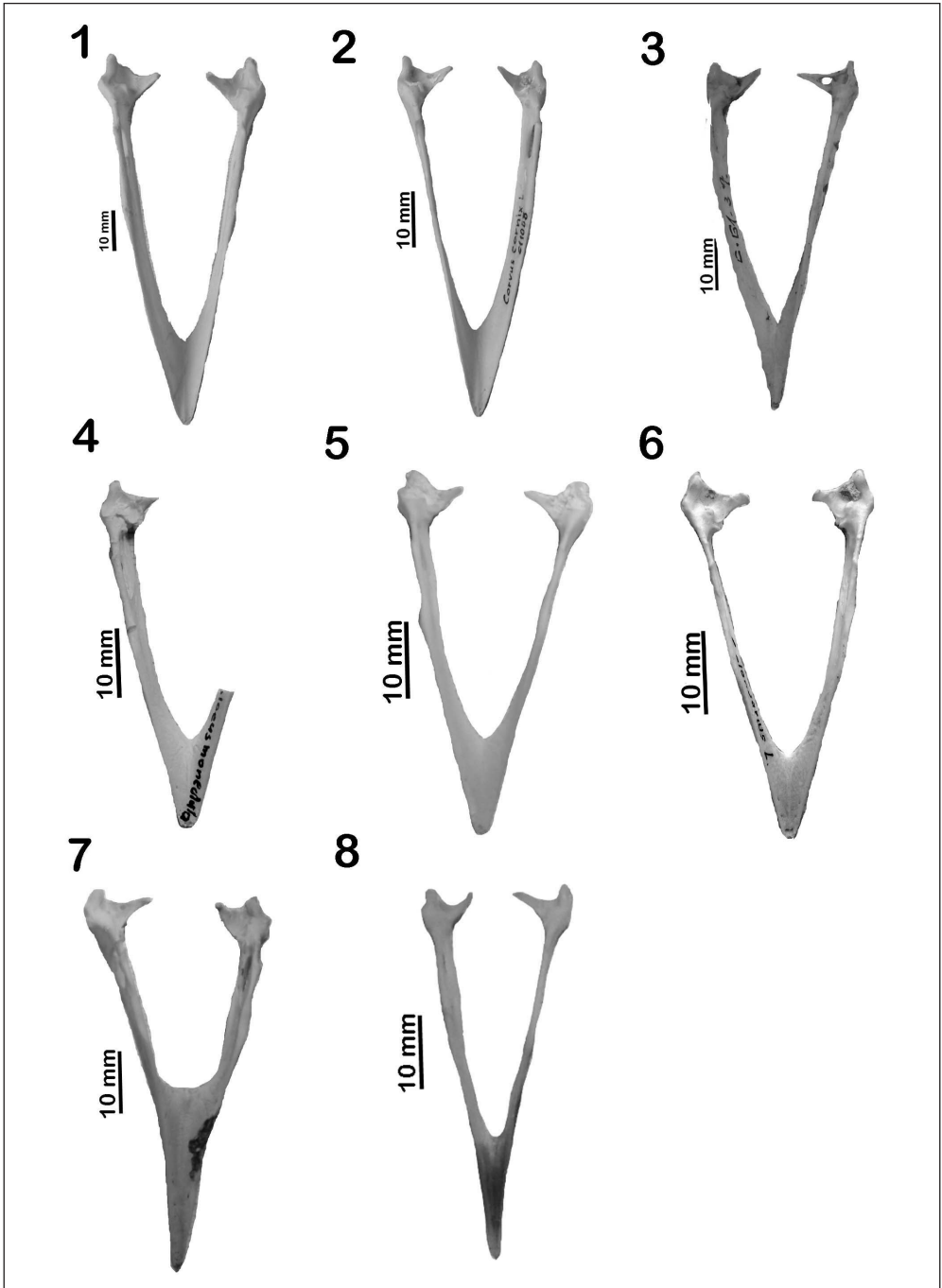


Figure 3. Mandibula (dorsal surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*
 3. ábra Alsó állkapocs (háti nézet): 1. *Corvus corax*; 2. *corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*

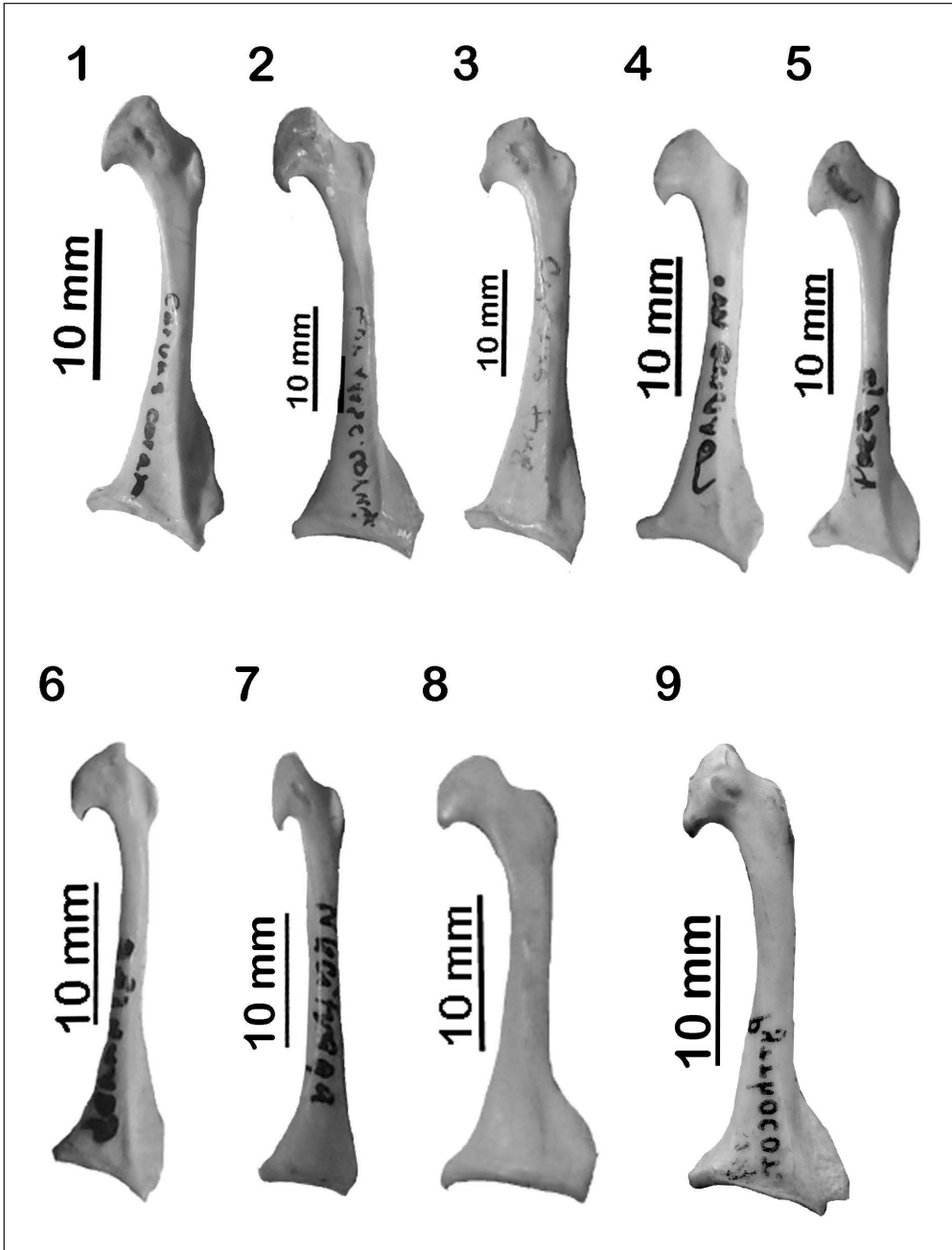


Figure 4. Left coracoideum (ventral surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

4. ábra Bal oldali hollócsőrscsont (hasi oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

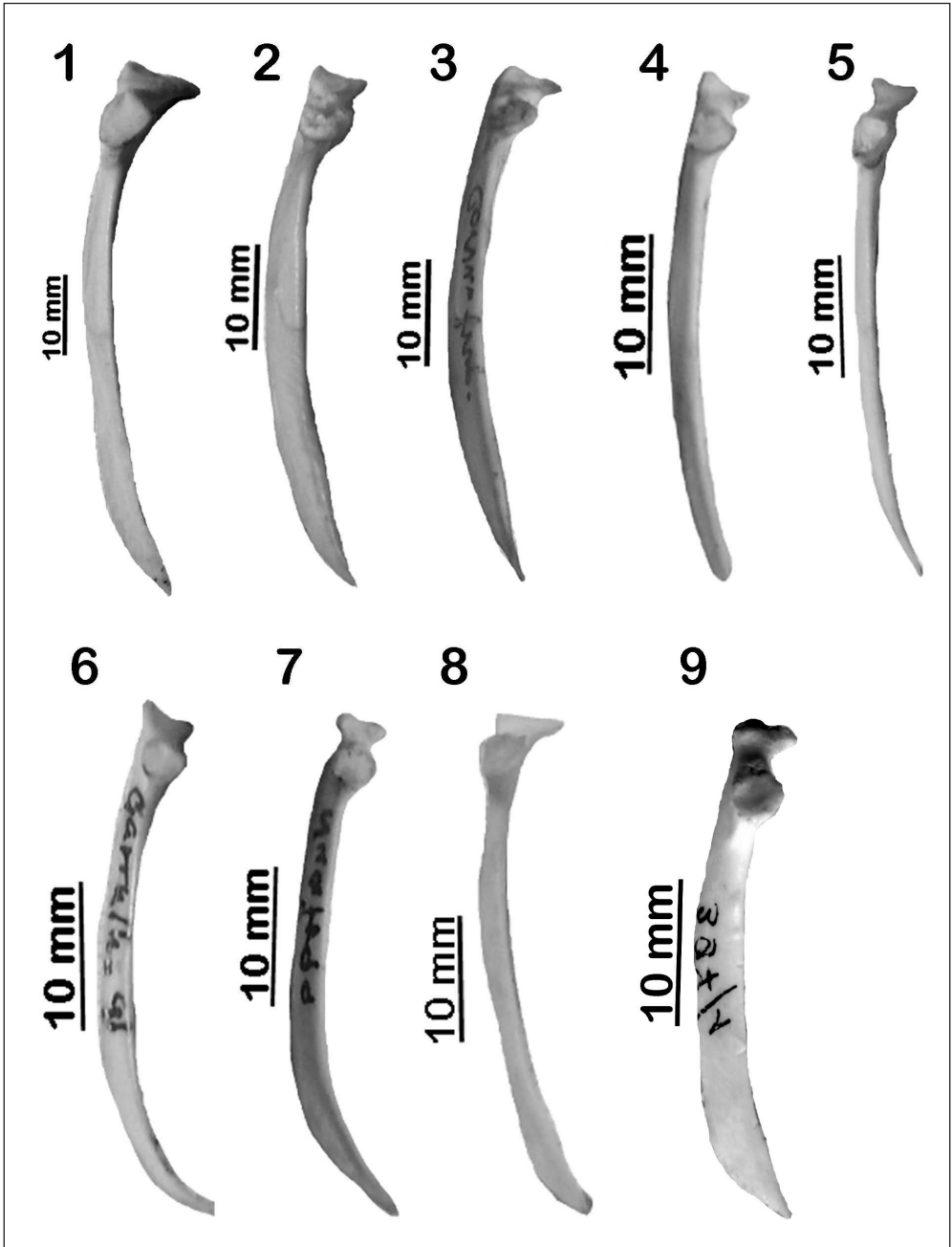


Figure 5. Right scapula (medial surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

5. ábra
Jobb oldali lapocka csont (mediális oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

3.b the shape of the branches of acromion:

- symmetrically (equal): *Nucifraga*, *Pica*, *Pyrrhonorax graculus*;
- asymmetrically (unequal): *Corvus*, *Garrulus*, *Pyrrhonorax pyrrhonorax*;

3.c the apex dorsalis (dorsal branch):

- short and blunted: *Corvus frugilegus*, *Pyrrhonorax pyrrhonorax*;
- short and pointed: *Corvus corax*, *C. corone*, *Pyrrhonorax graculus*;
- long and blunted: *Corvus monedula*, *Nucifraga*, *Pica*;
- long and pointed: *Garrulus*;

3.d the apex lateralis (lateral branch):

- short and blunted: *Garrulus*;
- short and pointed: *Corvus corone*, *C. monedula*;
- long and blunted: *Nucifraga*, *Pica*, *Pyrrhonorax pyrrhonorax*;
- long and pointed: *Corvus corax*, *C. frugilegus*, *Pyrrhonorax graculus*;

3.e the pit between the branches:

- shallow and symmetrical: *Corvus corone*, *C. monedula*, *Nucifraga*, *Pica*, *Pyrrhonorax pyrrhonorax*;
- shallow and unsymmetrical: *Corvus corax*, *C. frugilegus*, *Garrulus*;
- straight: *Pyrrhonorax graculus*;

3.f the shape of corpus:

- curved: *Garrulus*, *Nucifraga*;
- very wide: *Pyrrhonorax pyrrhonorax*;
- wide: *Corvus cornix*; *C. frugilegus*;
- moderately wide: *Corvus corax*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pyrrhonorax graculus*;
- narrow: *Pica*;

4. Humerus (proximal epiphysis) (Figure 6)**4.a the tuberculum ventrale:**

- strongly protruding: *Corvus*, *Pyrrhonorax graculus*;
- poorly protruding: *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhonorax pyrrhonorax*;

4.b the projection of the crista bicipitalis:

- prominent and rounded: *Garrulus*;
- truncated: *Pica*, *Pyrrhonorax graculus*;
- rounded and not prominent: *Corvus*, *Nucifraga*, *Pyrrhonorax pyrrhonorax*;

4.c the distal edge of the crista bicipitalis:

- flatly curved: *Corvus corone*, *C. frugilegus*, *C. monedula*, *Nucifraga*;
- strongly curved: *Corvus corax*, *Garrulus*, *Pica*, *Pyrrhonorax pyrrhonorax*;
- straight: *Pyrrhonorax graculus*;

4.d the fossa pneumotricipitalis:

- split: *Corvus*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhonorax*;

5. Humerus (distal epiphysis) (Figure 7)**5.a the tuberculum supracondylare ventrale:**

- protuberant: *Corvus corax*;

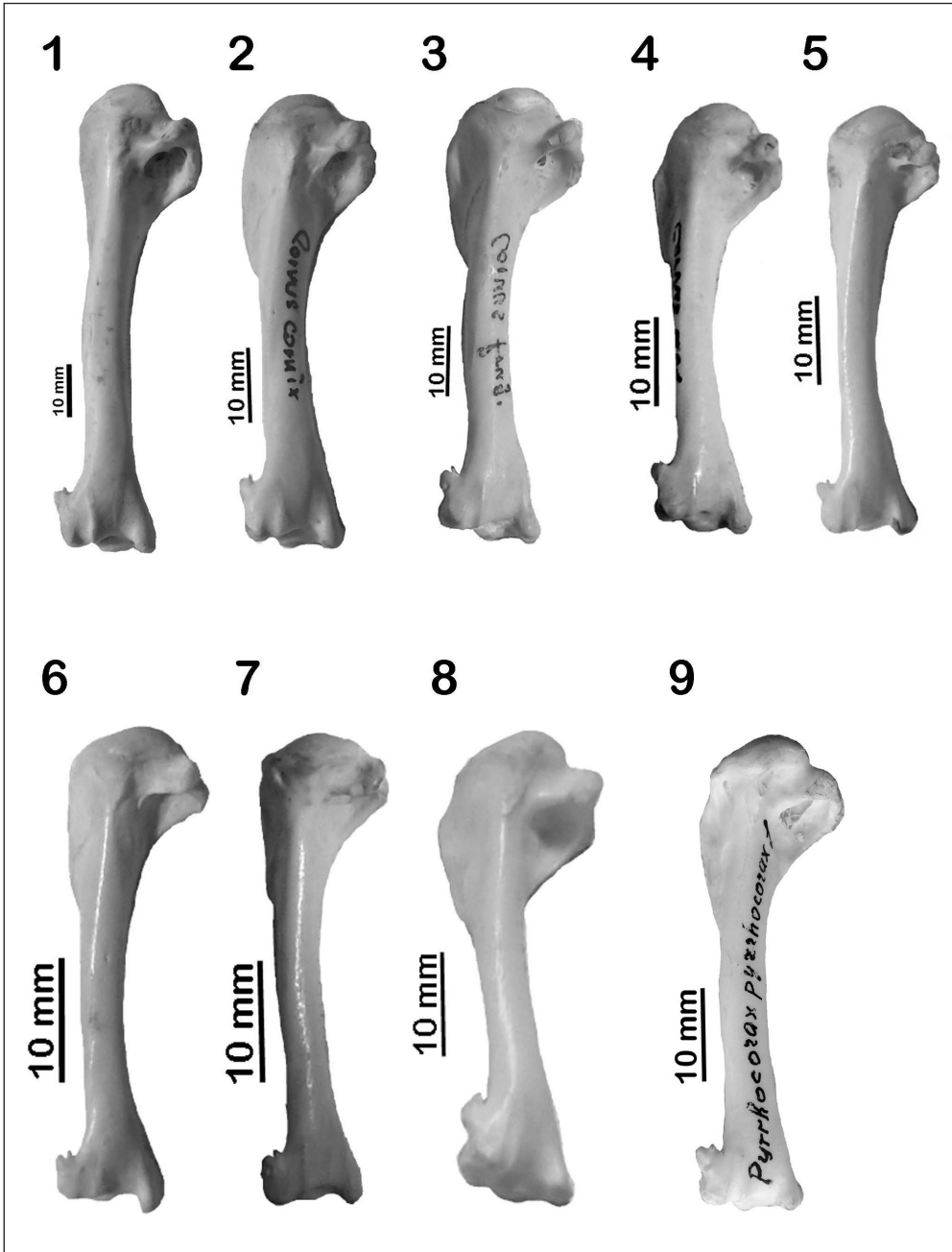


Figure 6. Left humerus (caudal surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

6. ábra Bal oldali felkarcsont (palmáris oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

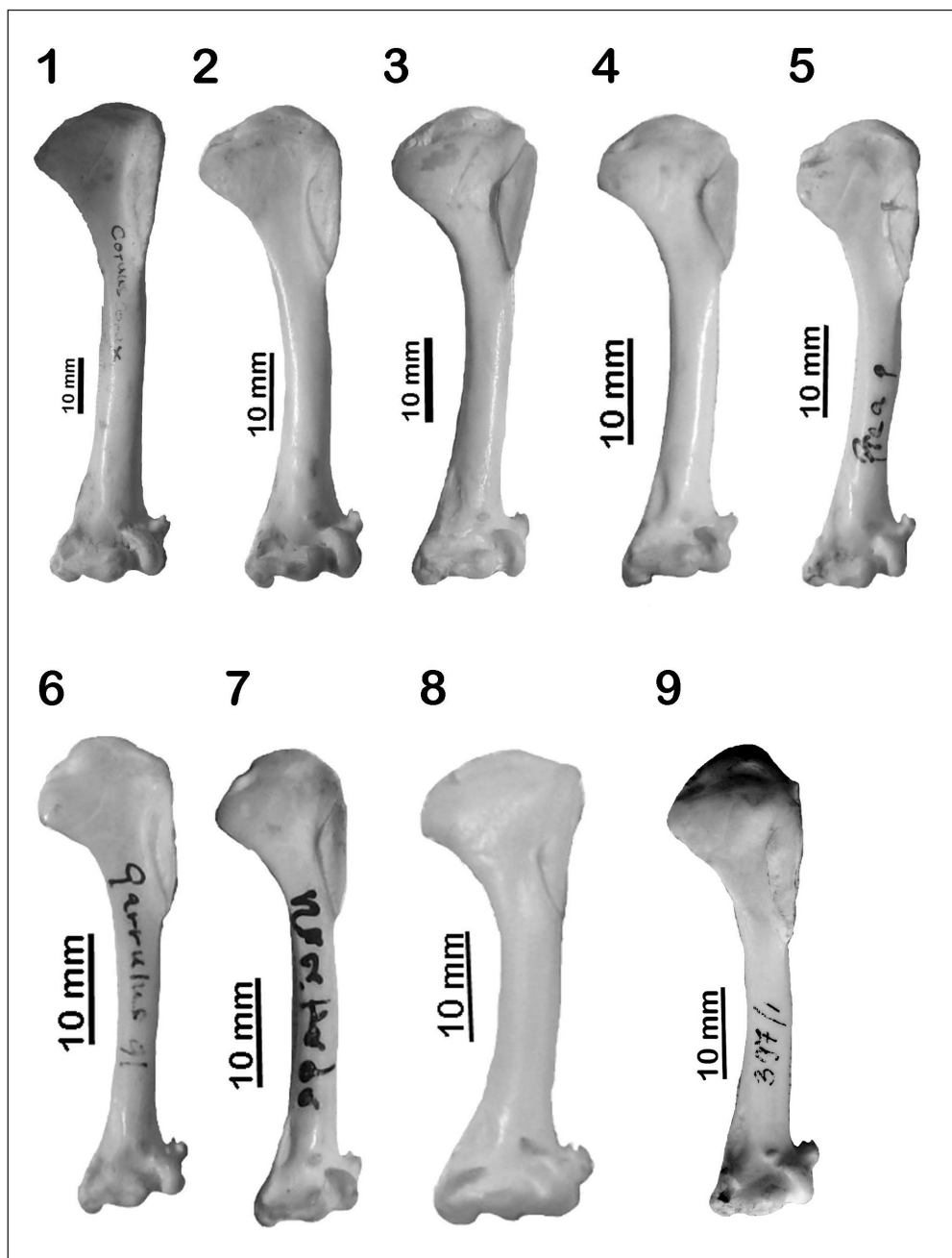


Figure 7. Left humerus (cranial surface): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

7. ábra Bal oldali felkarcsont (dorzális oldal): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

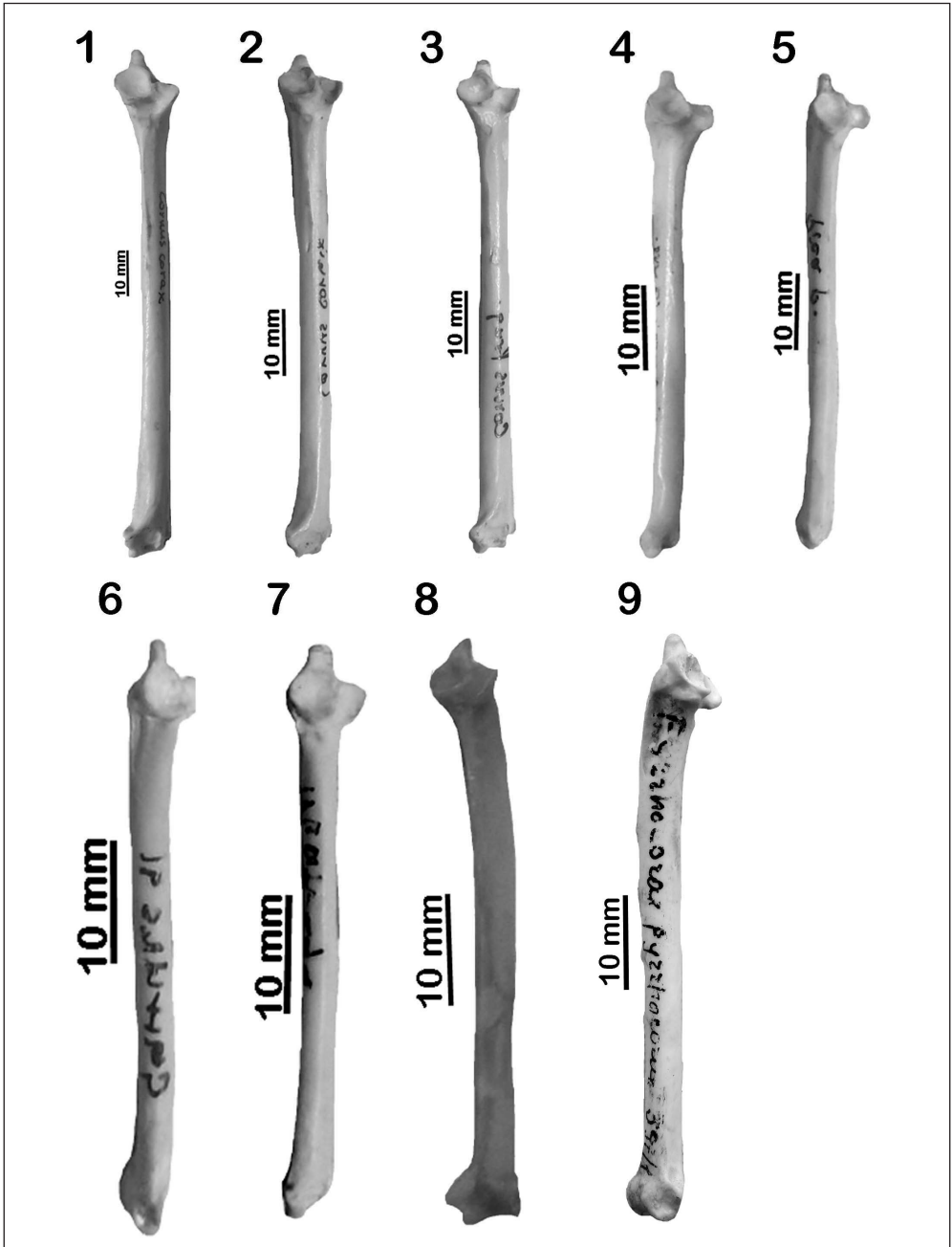


Figure 8. Left ulna (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

8. ábra Bal oldali singsont (hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

– not prominent: *Corvus corone*, *C. frugilegus*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;

5.b the *processus flexorius*:

– with rounded end: *Corvus frugilegus*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax graculus*;

– with truncated end: *Corvus corax*, *C. monedula*, *Pyrrhocorax pyrrhocorax*;

– with asymmetrical cone end: *Corvus corone*;

5.c the *condylus dorsalis*:

– rounded: *Corvus corax*, *C. corone*, *C. frugilegus*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;

5.d the *processus supracondylaris dorsalis*:

– two-pronged unequal: *Corvus corax*, *C. corone*, *C. frugilegus*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;

6. Ulna (proximal epiphysis) (Figure 8)

6.a the *olecranon*:

– short and blunt: *Corvus*;

– long and blunt: *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax pyrrhocorax*;

– asymmetrical and pointed: *Pyrrhocorax graculus*;

6.b the *cotyla dorsalis*:

– semicircular: *Garrulus*;

– conical asymmetrical: *Corvus corax*, *C. corone*, *C. frugilegus*;

– conical: *Nucifraga*;

– pointed conical: *Pyrrhocorax*;

– truncated: *Corvus monedula*;

– long and blunt: *Pica*;

6.c. the *tuberculum ligamentum collateralis ventralis*:

– developed: *Garrulus*;

– undeveloped: *Corvus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;

7. Ulna (distal epiphysis) (Figure 9)

7.a the shape of the *condylus dorsalis*:

– pointed cone: *Corvus corone*, *Nucifraga*;

– blunted cone: *Corvus corax*, *C. frugilegus*, *Pica*, *Pyrrhocorax*;

– rounded: *Corvus monedula*, *Garrulus*;

7.b the shape of the *sulcus intercondylaris*:

– curved: *Corvus corax*, *C. corone*, *Garrulus*;

– asymmetrically curved: *Corvus frugilegus*;

– pointed: *Corvus monedula*, *Nucifraga*, *Pica*, *Pyrrhocorax*;

7.d the shape of the *condylus ventralis*:

– conical: *Corvus corone*, *C. frugilegus*, *Nucifraga*, *Pyrrhocorax graculus*;

– blunt cone: *Corvus corax*, *Garrulus*;

– rounded: *Corvus monedula*, *Pica*;

– semicircle: *Pyrrhocorax pyrrhocorax*;

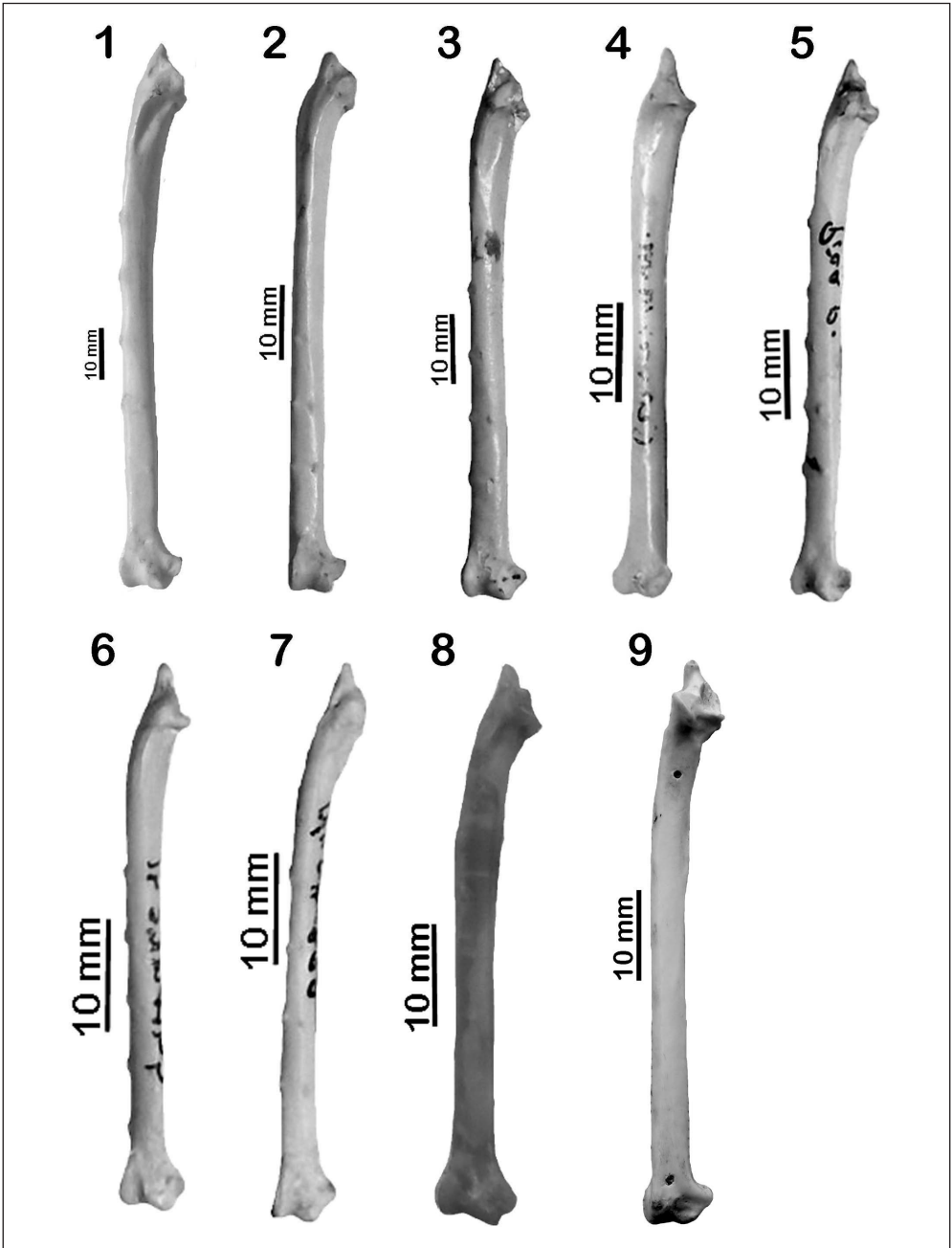


Figure 9. Left ulna (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

9. ábra Bal oldali singsont (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

7.e the shape of the *tuberculum carpale*:

- semicircular: *Corvus modeula*, *Garrulus*, *Pyrrhocorax*;
- conical: *Corvus frugilegus*, *Nucifraga*;
- asymmetrical: *Corvus corax*, *C. corone*;
- truncated: *Pica*;

8. *Radius* (Figure 10)**8.a the shape of the *tuberculum aponeurosis ventralis*:**

- conical: *Corvus corax*; *Garrulus glandarius*, *Nucifraga caryocatactes*;
- blunted cone: *Corvus corone*, *C. frugilegus*, *Pyrrhocorax pyrrhocorax*;
- rounded: *Pica*, *Pyrrhocorax graculus*;
- oblique rectangle: *Corvus monedula*;

8.b the shape of the *tuberculum aponeurosis dorsalis*:

- blunted cone: *Corvus corone*, *C. frugilegus*, *Garrulus*, *Pyrrhocorax pyrrhocorax*;
- symmetrical blunted cone: *Corvus corax*, *Nucifraga*;
- rounded: *Corvus monedula*, *Pyrrhocorax graculus*;
- semicircular: *Pica*;

8. *Carpometacarpus* (Figure 11)**8.a the shape of the *a trochlea carpalis*:**

- semicircle: *Corvus frugilegus*;
- asymmetrically semicircle: *Corvus corax*;
- symmetrically cone: *Corvus corone*, *C. monedula*;
- symmetrically blunt cone: *Pyrrhocorax*;
- asymmetrically blunt cone: *Garrulus*, *Nucifraga*, *Pica*;

8.b the form of the *processus extensorius*:

- pointed cone: *Pyrrhocorax graculus*;
- slanting pointy cone: *Corvus corone*, *C. frugilegus*;
- leaning blunt cone: *Corvus monedula*, *Garrulus*;
- extension with rounded end: *Corvus corax*, *Nucifraga*;
- asymmetrically: *Pica*, *Pyrrhocorax pyrrhocorax*;

8.c the shape of the *processus alularis*:

- rectangular: *Corvus corone*, *C. frugilegus*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;
- rounded: *Corvus corax*;

8.d the form of the *fovea subalaris*:

- conical groove: *Corvus corax*, *Pica*;
- irregular conical groove: *Corvus monedula*, *Nucifraga*;
- missed: *Corvus corone*, *C. frugilegus*; *Garrulus*, *Pyrrhocorax*;

8.e the shape of the *facies articularis digitale major*:

- rounded: *Corvus monedula*, *Garrulus*, *Pica*, *Pyrrhocorax*;
- straight: *Corvus frugilegus*, *Nucifraga*;
- oblique: *Corvus corax*, *C. corone*;

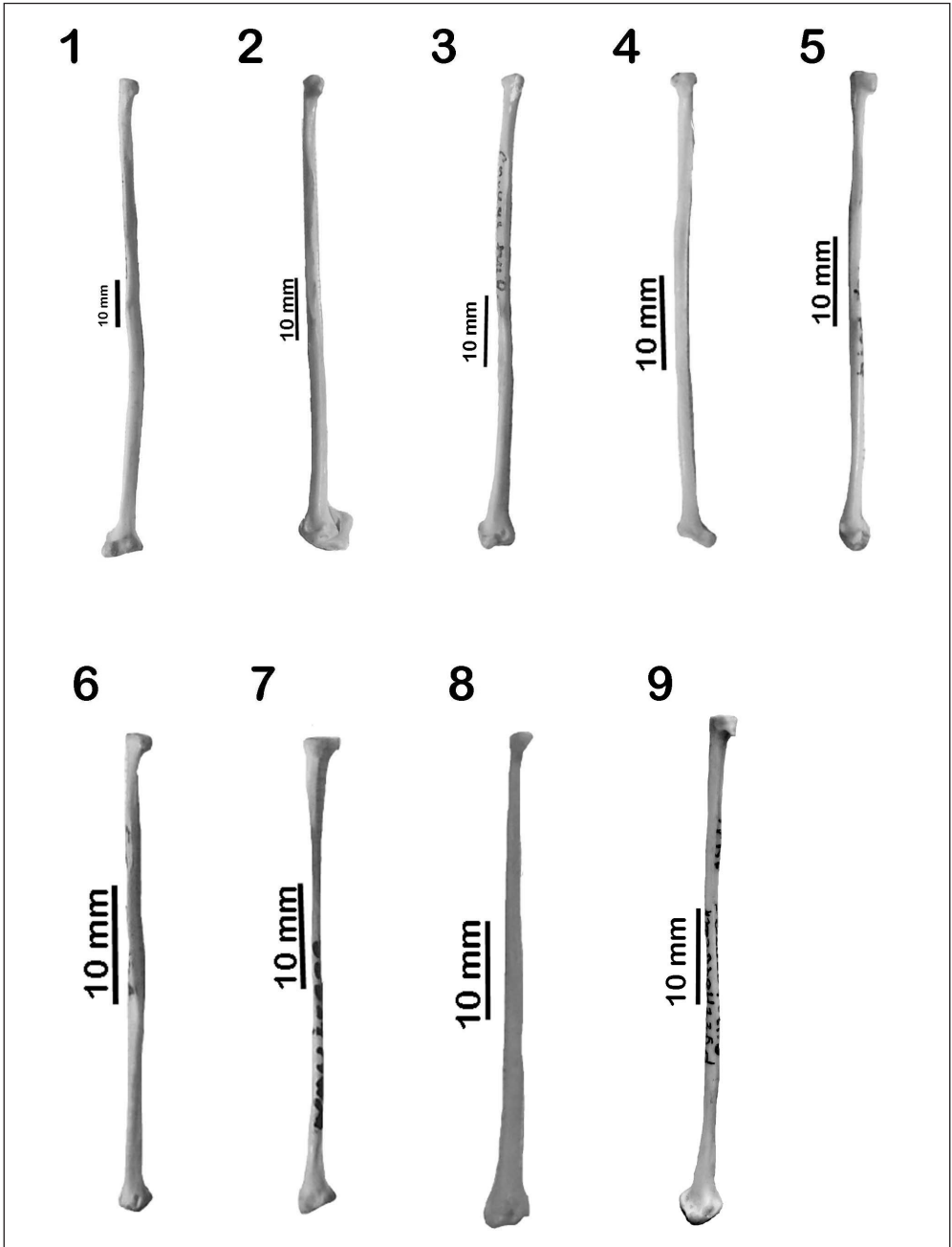


Figure 10. Left radius (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

10. ábra Bal oldali orsócsont (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

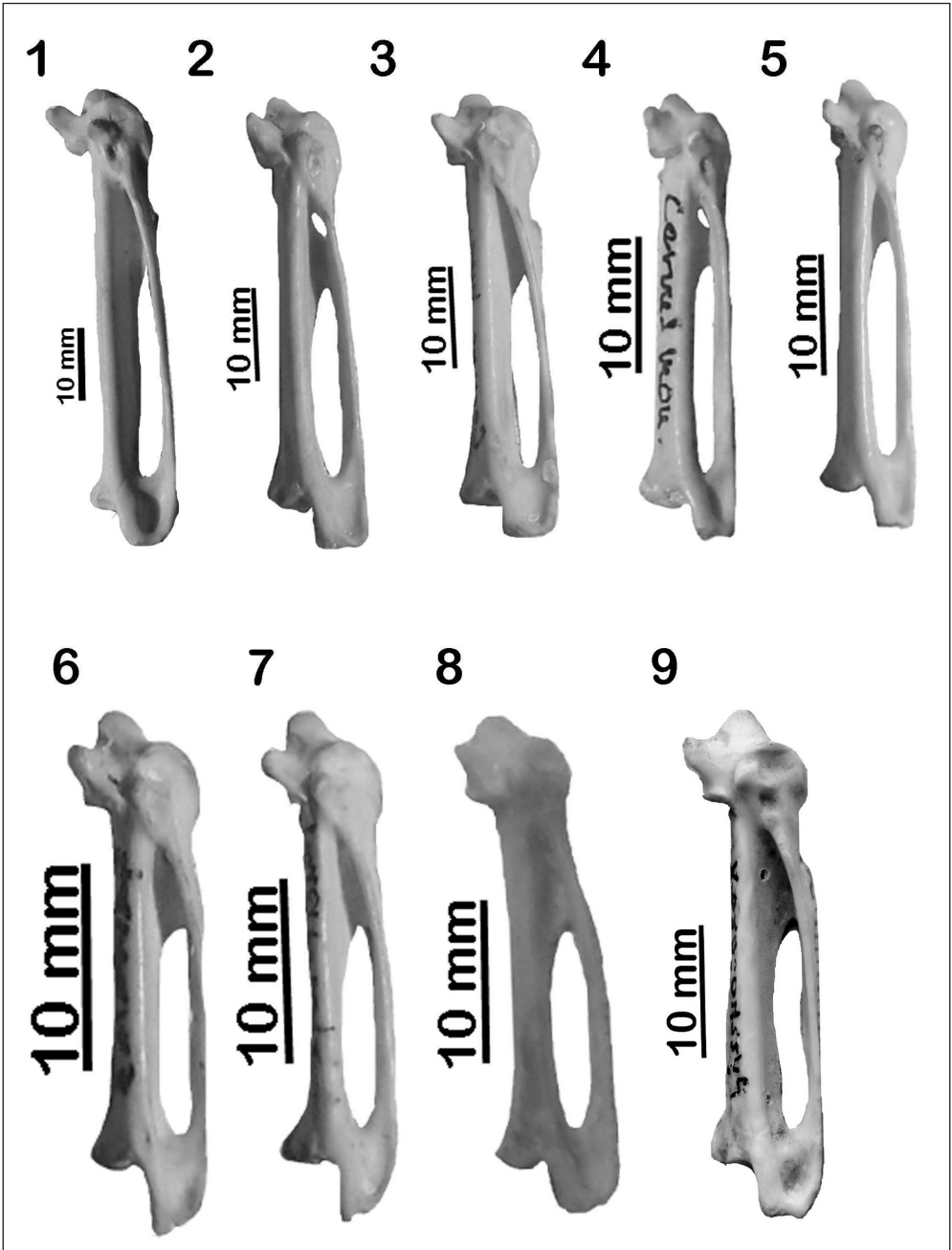


Figure 11. Left carpometacarpus (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

11. ábra Bal oldali kézközépcsont (hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

8.f the shape of the *facies articularis digitale minor*:

- rounded: *Corvus corax*, *Pyrrhocorax graculus*;
- with cut-off end: *Corvus corone*, *C. frugilegus*, *Pica*, *Pyrrhocorax pyrrhocorax*;
- asymmetrical cone: *Garrulus*, *Nucifraga*;
- concave: *Corvus monedula*;

9. *Phalanx proximalis digiti majoris* (Figure 12)**9.a the form of the *margo proximalis*:**

- strongly bulging: *Nucifraga*;
- weakly bulging: *Corvus corax*, *C. corone*, *Garrulus*;
- with a little protrusion: *Corvus frugilegus*, *Pyrrhocorax graculus*;
- flattened: *Corvus monedula*, *Pica*, *Pyrrhocorax pyrrhocorax*;

9.b the form of the *tuberculum ventralis*:

- rounded: *Corvus corax*, *C. corone*, *Pyrrhocorax graculus*;
- symmetrical blunt cone: *Corvus frugilegus*, *C. monedula*, *Pica*, *Pyrrhocorax pyrrhocorax*;
- asymmetrical blunt cone: *Nucifraga*;

9.c the form of the *tuberculum dorsalis*:

- pointed cone: *Pyrrhocorax*;
- symmetrical blunt cone: *Corvus corax*, *C. monedula*, *Nucifraga*, *Pica*;
- asymmetrical blunt cone: *Corvus corone*, *C. frugilegus*;
- semicircle: *Garrulus*;

9.d the character of the *margo dorsalis*:

- rounded: *Corvus corax*, *Pyrrhocorax pyrrhocorax*;
- straight: *Corvus corone*, *C. frugilegus*, *Pica*, *Garrulus*;
- wavy: *Corvus monedula*, *Nucifraga*, *Pyrrhocorax graculus*;

9.e the character of the *margo distalis*:

- rounded: *Garrulus*, *Pica*;
- wavy: *Corvus*, *Nucifraga*, *Pyrrhocorax*;

10. *Femur* (distal *epiphysis*) (Figure 13)**10.a the shape of the *condylus medialis*:**

- semicircle: *Corvus*;
- blunt cone: *Garrulus*, *Pica*, *Pyrrhocorax*;
- pointed cone: *Nucifraga*;

10.b the character of the *sulcus intercondylaris*:

- deeply concave: *Corvus moedula*, *C. frugilegus*, *Pica*, *Pyrrhocorax*;
- weakly concave: *Garrulus*, *Nucifraga*;
- cone shaped: *Corvus corax*, *C. corone*;

10.c the shape of the *condylus lateralis*:

- broadly rounded: *Nucifraga*;
- rounded: *Corvus*, *Pyrrhocorax*;
- conical: *Garrulus*, *Pica*;

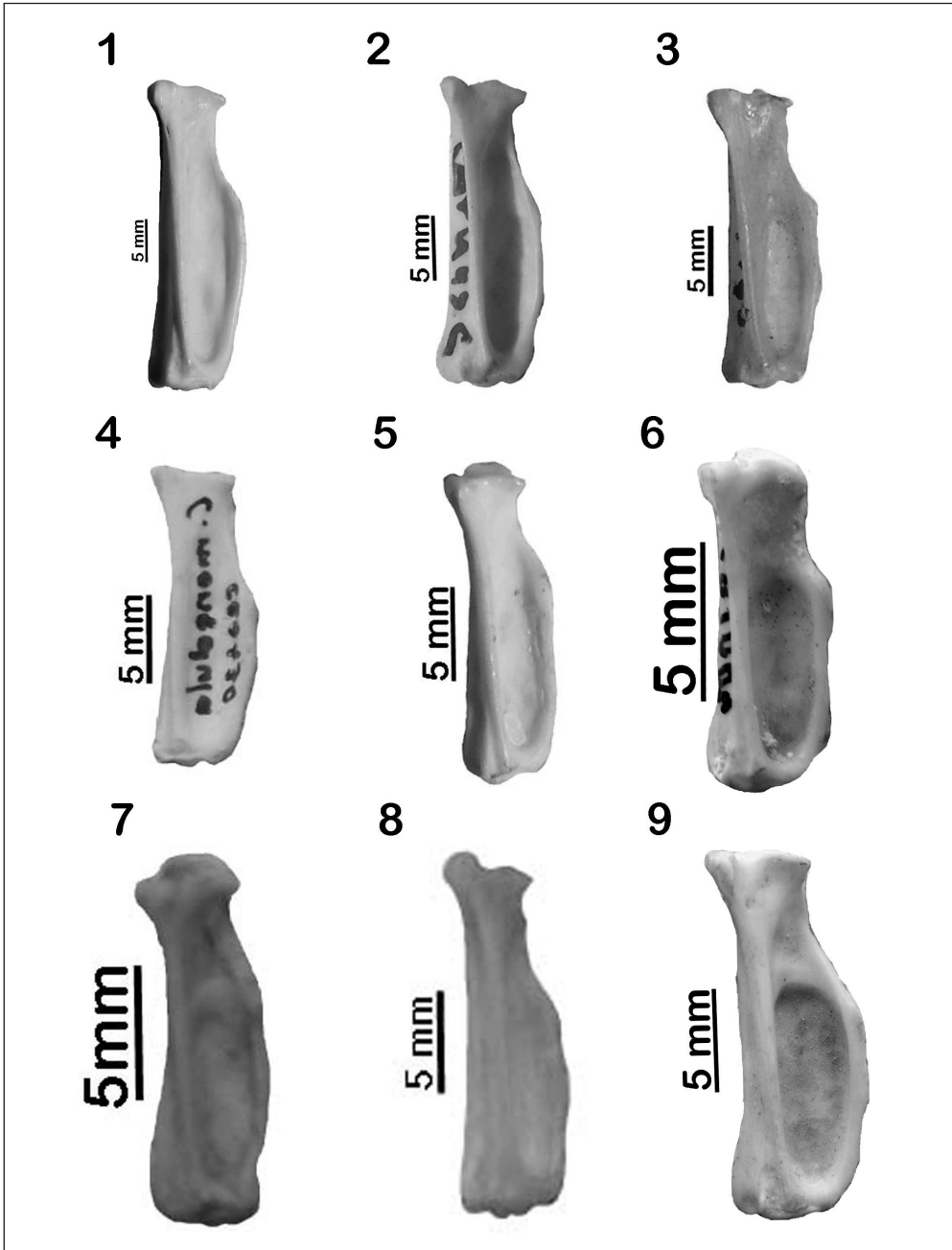


Figure 12. Left phalanx proximalis digiti majoris (ventral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

12. ábra Bal oldali kézujjperc (l. ujjperc, 2. ujj, hasi nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

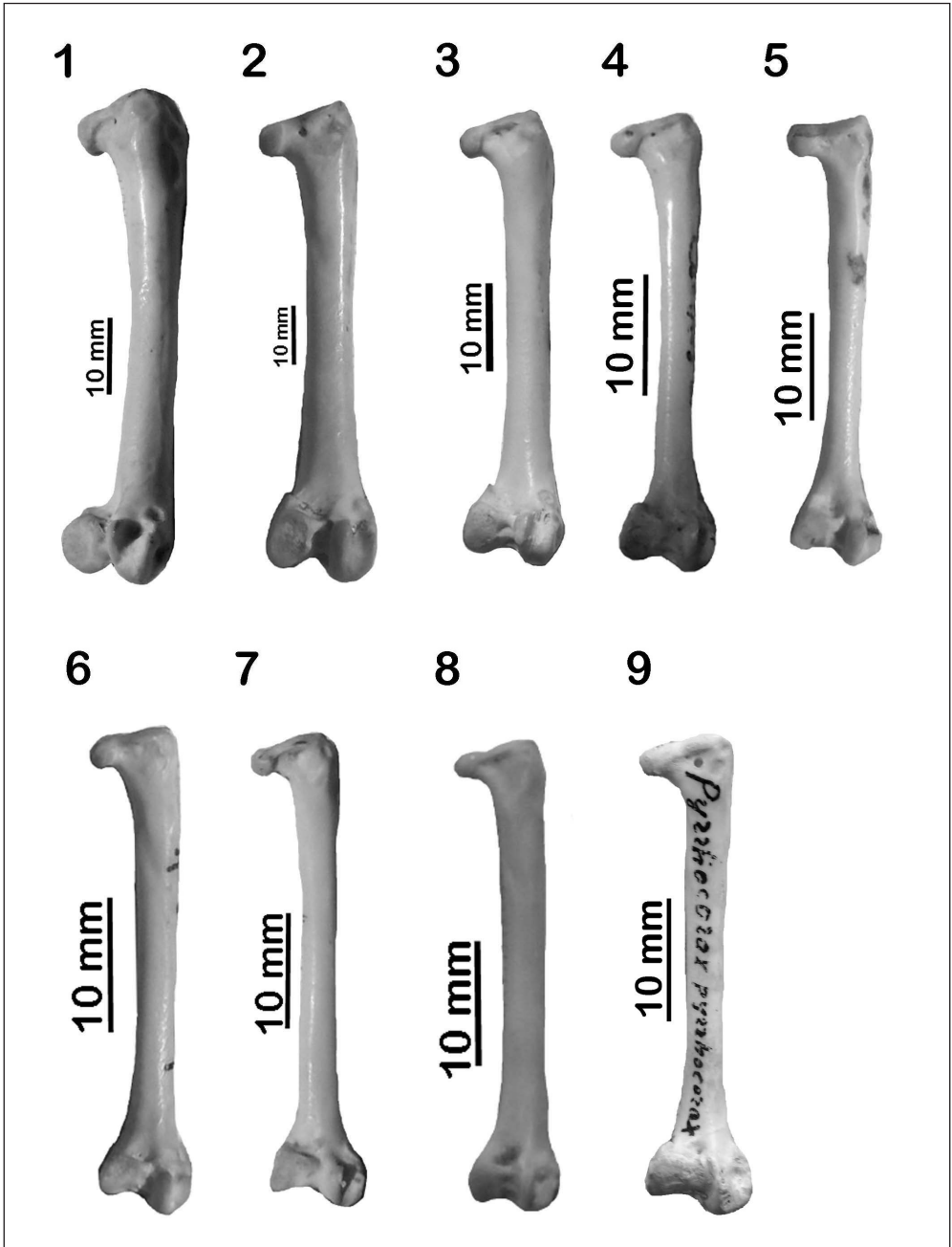


Figure 13. Right femur (caudal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

13. ábra Jobb oldali combcsont (palmáris nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

10.d the form of the *epicondylus medialis*:

- pointedly protruding: *Corvus*;
- rounded protruding: *Nucifraga*;
- not arching: *Garrulus*, *Pica*, *Pyrrhocorax*;

10.e the form of the *epicondylus lateralis*:

- rounded protruding: *Nucifraga*;
- bulging: *Corvus*, *Garrulus*, *Pyrrhocorax*;
- not arching: *Pica*;

11. *Tibiotarsus* (distal *epiphysis*) (Figure 14)**11.a the shape of the *epicondylus lateralis*:**

- rounded: *Corvus corone*, *G. frugilegus*, *Garrulus*, *Nucifraga*, *Pyrrhocorax*;
- semicircular: *Pica*;
- asymmetrical: *Corvus corax*, *C. monedula*;

11.b the form of the *incisura intercondylaris*:

- wavy: *Corvus corone*, *C. frugilegus*, *C. monedula*;
- asymmetrically arched: *Corvus corax*, *Pyrrhocorax*;
- asymmetrically wavy: *Garrulus*;
- flattened: *Nucifraga*, *Pica*;

11.c the character of the *tuberculum retinaculi musculi fibularis*:

- weakly protruding: *Corvus frugilegus*, *Pyrrhocorax*;
- strongly protruding: *Corvus corax*, *C. corone*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*;

12. *Tarsometatarsus* (distal *epiphysis*) (Figure 15)**12.a the character of the *margo medialis*:**

- straight: *Corvus corax*, *C. corone*, *C. monedula*, *Garrulus*, *Nucifraga*, *Pica*, *Pyrrhocorax*;
- concave: *Corvus frugilegus*;

12.b the shape of the *trochlea metatarsi II.*:

- with cut-off end: *Corvus frugilegus*, *Pica*;
- with rounded end: *Corvus corax*, *C. monedula*, *Garrulus*, *Nucifraga*;
- conical: *Corvus corone*, *Pyrrhocorax*;

12.c the shape of the *trochlea metatarsi III.*:

- symmetrical shaped: *Corvus*, *Garrulus*, *Pica*, *Pyrrhocorax*;
- asymmetrical shaped: *Nucifraga*;

12.d the shape of the *trochlea metatarsi IV.*:

- conical: *Corvus frugilegus*, *Nucifraga*;
- blunt cone: *Corvus corone*, *Corvus monedula*, *Garrulus*, *Pyrrhocorax pyrrhocorax*;
- asymmetrically: *Corvus corax*, *Pica*, *Pyrrhocorax graculus*;

13. *Phalanx unguularis* (Figure 16)

Knowing that there are four claws on one leg and they are different, I do not give a detailed description.

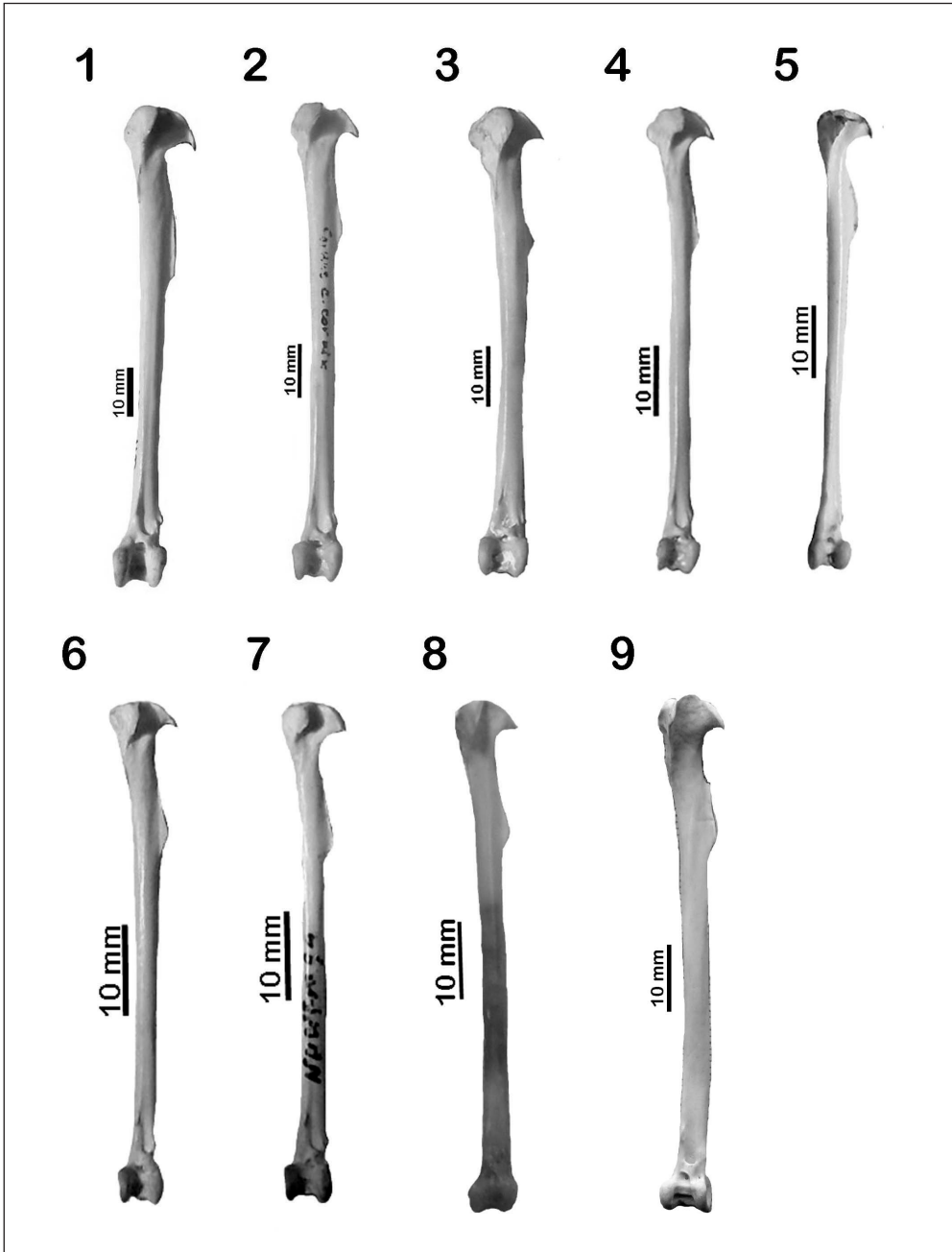


Figure 14. Left tibiotarsus (cranial aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

14. ábra Bal oldali lábszárcsont (dorzális nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

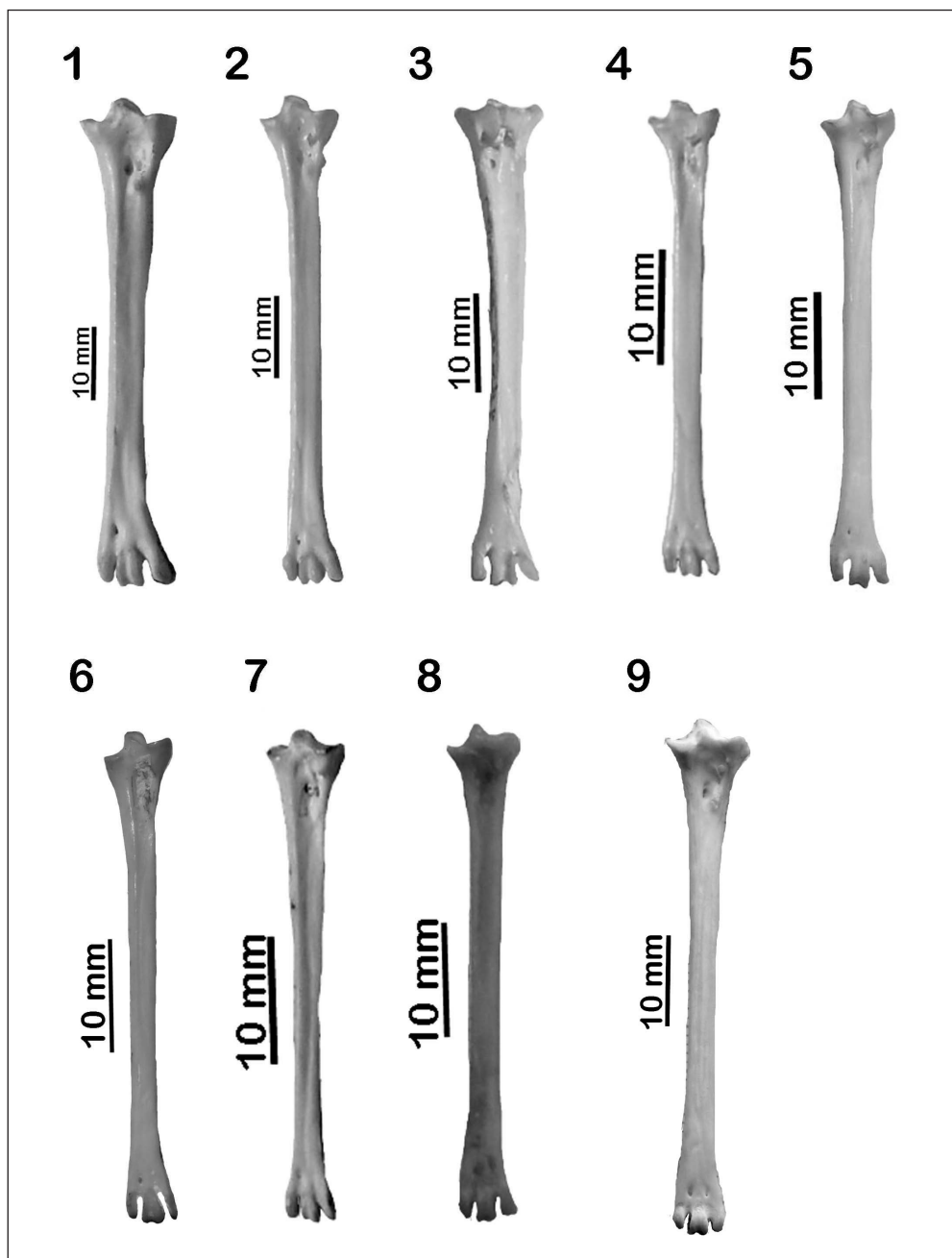


Figure 15. Right tarsometatarsus (dorsal aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

15. ábra Jobb oldali csüd (háti nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Garrulus glandarius*; 7. *Nucifraga caryocatactes*; 8. *Pyrrhocorax graculus*; 9. *Pyrrhocorax pyrrhocorax*

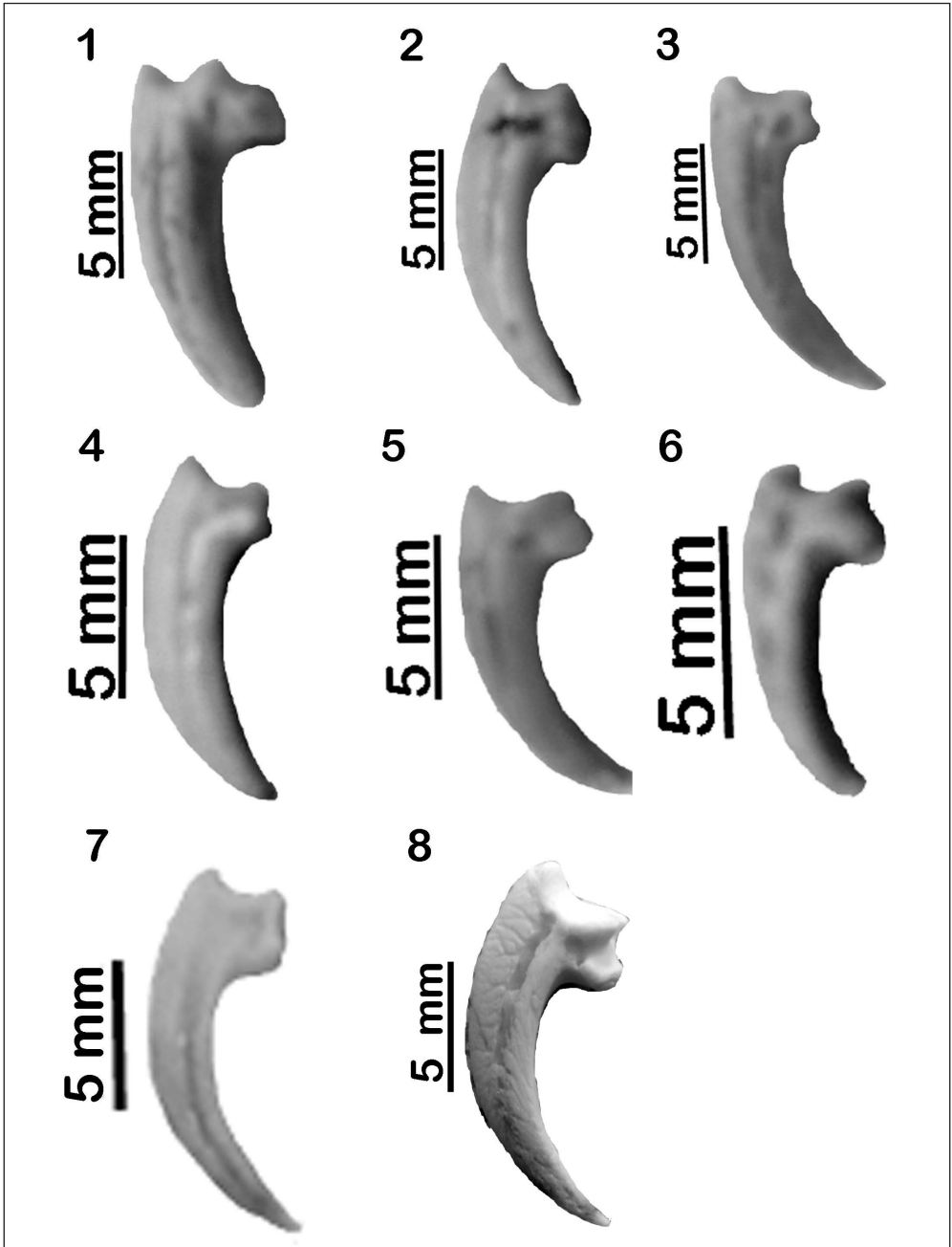


Figure 16. Phalanx unguis (lateral aspect): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Nucifraga caryocatactes*; 7. *Pyrrhocorax graculus*; 8. *Pyrrhocorax pyrrhocorax*

16. ábra Káromcsont (oldalsó nézet): 1. *Corvus corax*; 2. *C. corone cornix*; 3. *C. frugilegus*; 4. *C. monedula*; 5. *Pica pica*; 6. *Nucifraga caryocatactes*; 7. *Pyrrhocorax graculus*; 8. *Pyrrhocorax pyrrhocorax*

Systematics

Fam. Corvidae (Vigors, 1825) (Table 1–6)

Corvids are the largest songbirds in Europe, hence they are unmistakable with any other members of songbird families. They live from plains to snowy mountains. They have sedentary, as well as migratory, species. They nest in crevices of rocks or on trees. They are omnivores. Their species shift occurred mainly in the Pleistocene. They are well represented in fossilized materials both in species and in numbers. This is not only due to their large population, seasonal constancy and relatively slower flight, but mostly due to their remains that are large enough to be detected via traditional collection methods.

– *Corvus* Linnaeus, 1758

– *Corvus* † *pliocaenus* (Portis, 1889) / syn. *C.* † *betfianus* Kretzoi, 1962; (Table 1)

Site and era: Polgárdi, Upper Miocene (MN 13) (Hungary) (Kessler 2010); Beremend 26, Lower Pliocene (MN 15) (Kessler 2010); Beremend 15, 18, Upper Pliocene (MN 16) (Jánossy 1992, 1996); **Q1**: Beremend 16, 17 (Jánossy 1992, 1996) (all in Hungary); Betfia 9 (Gál 2002) (Romania); **Q2**: Betfia „Aven” (Kessler 1975, Jánossy 1979, Gál 2002), Betfia 5 (Kretzoi 1962, Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q3**: Tarkő 2 (Jánossy 1979) (Hungary). From sites in Europe outside the Carpathian Basin **Q1-2**: Czech Republic, France, Germany, Spain; **Q3**: France (Tyrberg 1998).

We described a similar species, *Corvus simionescui* (Kessler, 1979) (Mălușteni-Berești, Romania, Lower Pliocene, MN 15) next to the Carpathian Basin, Mlíkovský (2002) classified it to the recent *Corvus corone* species as well.

A common characteristic of taxa described with different names is that they range in size between crows and ravens. Mlíkovský (2002) classifies certain taxa (*C. antecorax*, *C. pliocaenus janossyi*) to ravens, while others (*Corvus pliocaenus*, *C. betfianus*) to the recent Hooded Crow (*C. corone*). In our opinion, it is a transitional species that had gone extinct in the Middle Pleistocene. Due to the age and dimensions of the finds, we deem the species *Corvus pliocaenus* as valid. This is the oldest corvid of this size in Europe.

– *Corvus* † *hungaricus* Lambrecht, 1916 /syn. *C. antecorax* Mourer-Chauviré, 1975; *C. pliocaenus janossyi* Mourer-Chauviré, 1975

Site and era: **Q1**: Beremend 17 (Kessler 2010), Nagyharsányhegy 2 (all in Hungary) (Lambrecht 1916, Kessler 2010).

Material: distal end of right *humerus*, right *tarsometatarsus* (as holotype) (Nagyharsányhegy); distal end of *humerus*, 2 proximal end of *carpometacarpus*, proximal end of *femur*, 3 fragments of *tarsometatarsus* (1 proximale, 2 distale), (Beremend 17).

Dimensions: *tarsometatarsus* A = 67 mm, C = 10 and 11.29 mm, E = 4.0 and 4.51, 4.27 mm, F = 8.67 and 7.94 mm, G = 5.26 and 4.56 mm; *humerus* C = 18.69 mm, D = 10.08 mm, F = 13.5 mm; *carpometacarpus* C = 12.68 and 12.36 mm, D = 6.91 and 6.94 mm.

It is a corvid with a lean skeleton and a size between crows and ravens. Mlíkovský (2002) suggests reevaluation of the taxon, which we conducted, and the results confirmed the original diagnosis. In addition, we found the proximal fragment of a *humerus* as well at the site

of Nagyharsány mountain. Its identification from Beremend also confirms the reality of the taxon, and since other raven-sized species known from the fossilized and recent avian fauna of Europe were described later, we suggest keeping the taxon based on the principal of priority as well.

From Late Pliocene – Early Pleistocene and Middle Pleistocene of France (Senéze, Saint-Estève-Janson, Lunel Viel, MN 17-18, Q2 and Q3) the *Corvus antecorax* (Mourer-Chauviré, 1975) and *Corvus pliocaenus janossyi* (Mourer-Chauviré, 1975) finds of similar sizes are known (Mourer-Chauviré 1975).

– *Corvus* † *harkanyensis* Kessler, 2010

Site and era: Csarnóta 2, Upper Pliocene (MN 15-16) (Hungary) (Kessler 2010).

Material: distal end of right *humerus* – as holotype; distal end of left *tibiotarsus* – as paratype.

Dimensions: *humerus*: E = 4.90 mm; F = 11.53 mm; G = 5.89 mm; H = 6.20 mm; *tibiotarsus* E = 3.10 mm; F = 5.60 mm; G = 5.71 mm;

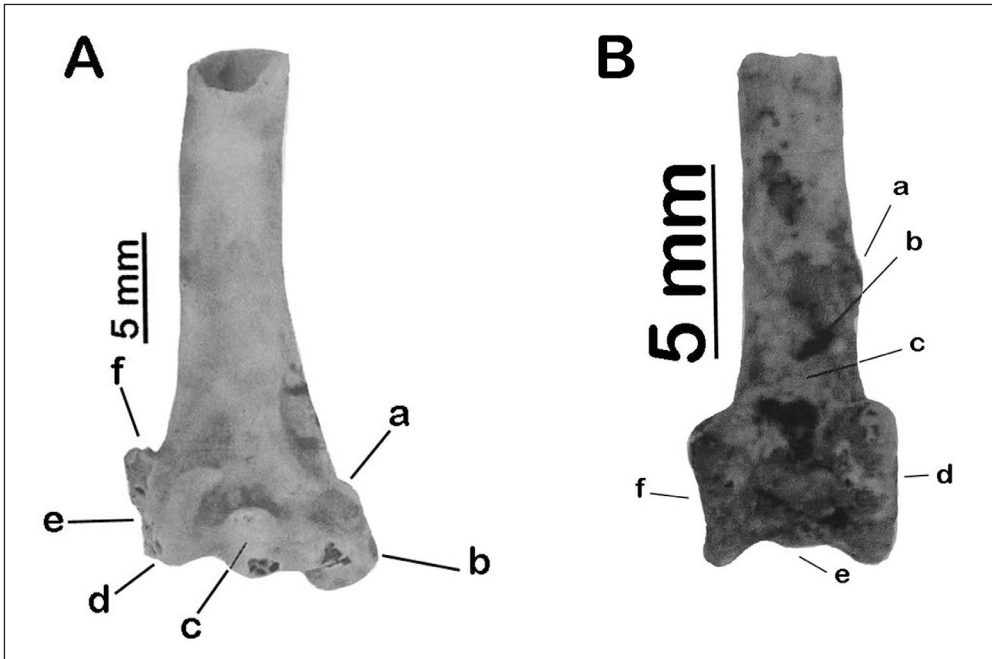


Figure 17. *Corvus harkanyensis* Kessler, 2010 – A. distal end of right humerus (holotype): a. *tuberculum supracondylare ventrale*; b. *processus flexorius*; c. *condylus dorsalis*; d. *condylus ventralis*; e. *epicondylus ventralis*; f. *processus supracondylaris dorsalis*; B. distal end of left tibiotarsus (paratype): a. *tuberculum retinaculum musculi fibularis*; b. *sulcus extensorius*; c. *pons tendineus*; d. *epicondylus lateralis*; e. *incisura intercondylaris*; f. *epicondylus medialis*

17. ábra *Corvus harkanyensis* Kessler, 2010 – A jobb oldali felkarcsont distális vége (holotípus): a. *tuberculum supracondylare ventrale*; b. *processus flexorius*; c. *condylus dorsalis*; d. *condylus ventralis*; e. *epicondylus ventralis*; f. *processus supracondylaris dorsalis*; B. bal oldali lábszárcsont distális vége (paratípus): a. *tuberculum retinaculum musculi fibularis*; b. *sulcus extensorius*; c. *pons tendineus*; d. *epicondylus lateralis*; e. *incisura intercondylaris*; f. *epicondylus medialis*

A corvid with the size of a Jackdaw, at the distal epiphysis of which in cranial view (*Figure 17A*) the tuberculum supracondylare ventrale (a) is more prominent than the present *Corvus* species, the *condylus ventralis* (c) is not ovoid but round in shape, the *epicondylus ventralis* (e), though damaged, is much wider and stouter, the *processus flexorius* (b) is curled up. On the distal end of the tibiotarsus (*Figure 17B*), in cranial view the end of the *sulcus extensorius* (c) above the *pons supratendineus* (b) is not rounded but has a pointed end (Kessler 2010).

Its name stems from the nearby town of Harkány. The fossilized species bearing characteristics and dimensions of the recent jackdaw was probably the ancestor of the form we see today in the Carpathian Basin.

Smaller *Corvus* species are only known from the Upper Pliocene (*C. cf. monedula*: Väršec Bulgária, MN 17; Boev 1995, 2000) among the avian fauna of Europe. From the Carpathian Basin and its immediate vicinity from the early Pleistocene of Stránská skála, Czech Republic, from where the *Corvus moravicus* (Mlíkovský 1995) extinct species was described, but the person describing it subsequently revoked it and reclassified the material as *C. monedula* (Mlíkovský 2002). The latter had been identified from several Middle and Upper Pleistocene sites (Jánossy 1979, Gál 2002).

– ***Corvus monedula* Linnaeus, 1758** / syn. *Corvus* cf. † *moravicus* Mlíkovský, 1996

Q1: Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002); **Q1-2:** Betfia „Aven” (Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q2:** Nagyharsányhegy 1-4 (Lambrecht 1916, 1933, Jánossy 1979) (Hungary); **Q3:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz – Drachenhöhle (Lambrecht 1933) (all in Austria); Velika Pecina (V. Malez 1984, 1986, 1988) (Croatia); Bajót-Baits Cave, Bajót-Hóman Cave (Jánossy 1979), Csákvár-Eszterházy Cave (Lambrecht 1933, Kretzoi 1954, Jánossy 1979), Felsőtárkány-Peskő Cave (Lambrecht 1912, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvár-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986), Tata-Kálváriahegy no. 4. Cave (Gál 2004, 2005b), Tokod-Nagyberek (Jánossy 1979) (all in Hungary); Homoródalmási-Orbán Balázs Cave (Vîrghiș-Peștera Mare) (Kessler 1977, Gál 2002), Körösmart (Rîpa), (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Nándor-Nándori Cave (Nandru-Peștera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábonor-Bordu Mare Cave (Ohaba Ponor-Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Bodajk-Rigólyuk (Kordos 1984), Budapest-Sas György Place, Csepel Vízművek (Gál 2015), Csákvár-Esterházy Cave (Kretzoi 1954), Felsőtárkány-Petényi Cave (Jánossy 1979), Legény-Cave (Lambrecht 1914), Szendrő-Felsővár (Gál 2015), Széchény (Gál 2015), Székesfehérvár-Sziget (Gál 2015) (all in Hungary); Bégakalodva (Cladova) (Gál 2004), Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Kisbács-Bácsitorok (Baciu, Gura Baciului) (Kessler 2013a), Körösbánlakai Cave (Peștera din Bálnaca) (Kessler 1982), Peterd-Tordai-Hasadék-Magyar Cave

(Petrești, Cheile Turzii-Peștera Ungurească) (Kessler & Gál 1998, Gál 2004), Remetelórév-Bólyikői Cave (Lorău-Peștera din Piatra Boiului) (Kessler 1982); Révi caves (Peșterile din Vadu Crișului) (Kessler 1982), Székelykeresztúr (Cristuru-Secuiesc) (Gál 2008, 2015), Szkerisoara-Sasok Cave (Scărișoara, Peștera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiș Cave, Vársonkolyos-Kis Magyar Cave (Șuncuiuș, Peștera Izbîndiș; Peștera Napiștileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Bulgaria, Czech Republic, France, Ukraine; **Q3:** Czech Republic, France, Germany, Spain, Ukraine; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Germany, Greece, Ireland, Italy, Montenegro, Moldova, Poland, Portugal, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

[Note: Gál (2002) identifies the species as *C. † moravicus* from the Betfia 9 site, but Mlikovský (2002) reclassifies the fossil taxon as *C. monedula* based on the Corvidae size database published by Kessler and Moldvai (1993). We find it necessary to distinguish between present jackdaws from the Upper Pliocene-Lower Pleistocene and Upper Pleistocene at least on a subspecies level, named *C. monedula † moravicus*.]

– *Corvus corax* Linnaeus, 1758

Q3/I: Hundsheim (Mlikovský 2009) (Austria); **Q3/II:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Velika Pecina (M. Malez & Rukavina 1975, V. Malez 1984, 1986, 1988) (Croatia); Bajót-Baits Cave, Bajót-Jankovich Cave (Jánossy 1979a, 1979b); Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő-Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Keszölc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933), Tatabánya-Szelim Cave (Jánossy 1979a, 1979b) (all in Hungary); Nándor-Nándori Cave (Nandru-Peștera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábonor-Bordu Mare Cave (Ohaba Ponor-Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Felsőnyék-Várhegy (Gál 2004, 2015), Felsőtárkány-Petényi Cave (Jánossy 1979), Mélyvölgy (Jánossy 1979), Pilisszentkereszt, Szendrő-Felsővár (Gál 2015) (all in Hungary), Kazánszoros-Climente Cave (Cazanele Mari-Peștera Climente I) (Kessler 1981, Gál 2002); Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Kazánszoros-Icoana Cave (Cazanele Mari, Peștera Icoana) (Kessler 1985, Jurcsák & Kessler 1986, 1988), Kovászna (Covasna) (Bindea 2008), Körösbánlaki Cave (Peștera din Bălnaca) (Kessler 1982) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Greece; **Q3:** Azerbaijan, Croatia, Czech Republic, France, Ukraine; **Q4:** Armenia, Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Montenegro, Moldova, Norway, Poland, Portugal, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Corvus corone* Linnaeus, 1758

Q3: Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Szilvásvárads-Istállóskői Cave (Lambrecht 1912, 1933, Jánossy 1952, 1955, 1979, 1986), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary); Körösmart (Rîpa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Rév-Pince Cave (Vadu Crișului, Peștera Pincelului) (Gál 2002) (all in Romania); **Q4/II:** Teufelslucke (Söergel 1966) (Austria); Bajcsa-Castle (Gál 2015), Balatonlelle-Kenderfölkék (Gál 2005b), Felsővadász-Várdomb, Hajdúnánás (Gál 2015), Nagysomlyói Fosse (Kessler 2010) (all in Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaki-Cave (Peștera din Bălnaca) (Kessler 1982), Peterd-Tordai-hasadék – Magyar Cave (Petrești, Cheile Turzii-Peștera Ungurească) (Kessler & Gál 1998, Gál 2005a), Remetelórév-Bólyikői Cave (Lorău-Peștera din Piatra Boiului) (Kessler 1982), Révi caves (Peșterile din Vadu Crișului) (Kessler 1982), Szkerisoara-Sasok Cave (Scărișoara, Peștera Vulturilor) (Kessler 1982, Jurcsák & Kessler 1986, 1988), Vársonkolyos-Kis Magyar Cave, Vársonkolyosi caves (Șuncuiuș-Peștera Napisteleu-Peșterile din Șuncuiuș) (Kessler 1977, Gál 2002) (all in Romania); Padina (Classon 1980, Gál 2004) (Serbia). From sites in Europe outside the Carpathian Basin **Q3:** Azerbaijan, Croatia, Czech Republic, France, Germany, Greece, Spain; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Italy, Malta, Portugal, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Corvus frugilegus* Linnaeus, 1758

Q4/I: Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); **Q4/II:** Bajcsa-Castle (Gál 2002, 2015), Balatonkeresztúr-Réti dűlő (Gál 2004), Bodajk-Rigólyuk (Kordos 1984), Endrőd 39 (Gál 2005a), Pilismarót-Malompaták (Jánossy 1985), Széchény (Gál 2015), Szendrő (Gál 2005b, Tassi 2006), Tác-Gorsium (Bökönyi 1984, Jánossy 1985), Visegrád-Palace (Gál 2015) (all in Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaki Cave (Peștera din Bălnaca) (Kessler 1982), Vársonkolyosi caves (Kessler 1977, Gál 2002) (Șuncuiuș-Peșterile din Șuncuiuș) (all in Romania); Padina (Classon 1980, Gál 2004) (Serbia). **Q3:** Azerbaijan, Germany, Greece; **Q4:** Belgium, Bosnia-Herzegovina, Croatia, France, Germany, Greece, Ireland, Italy, Netherlands, Ukraine, United Kingdom (Tyrberg 1998).

– *Corvus corone/frugilegus*

Q4/II: Kaposújlak-Várdomb, Paks-Gyapa, Dombóvár-Tesco (Gál 2017);

[Note: there are only very small morphological differences between the skeletal parts of the Hooded Crow (*Corvus corone cornix*) and the Rook (*C. frugilegus*), but the bones of the former species are slightly more robust. Incidentally, the subspecies – Carrion Crow, which is widespread in the western and southern parts of Europe, is also pure black, like the

juvenile crow. The latter is rarely reported from fossil finds, probably because of the great similarity. Presumably, it occurs in many materials because the two species could not be separated. All indications are that a separation of the two species may have occurred recently, probably in the Holocene.]

– *Corvus* sp. foss. indet.

Site and era: Litke 2 (MN 5) (Kessler & Hír 2011), Polgárdi 4 (MN 13) (Jánossy 1991, 1995), Beremend 26 (MN 15) (Kessler 2010), Villány 3 (MN 16) (Kessler 2010) (all in Hungary).

[Note: material from the Neogene mostly consists of claws. Claws of corvids have a typical shape, but since there is a size difference between the four claws, and those belonging to species of more or less similar sizes cannot be reliably distinguished, we can only classify them to the genus level.]

– *Corvus* sp. indet.

Q1: Villány 5 (Kessler 2010), Beremend 17 (Jánossy 1991, 1992) (all in Hungary); **Q4/I:** Szárazgerence (Jánossy 1979, 1986), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary), Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulas) (Lambrecht 1913, 1933) (Slovakia); **Q4/II:** Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Tatabánya-alsó – Törekvés Cave (Kessler 2010), Maroslele-Pana (Bökönyi 1964, Jánossy 1979, 1985, Gál 2005a, 2005b), Szolnok-Szanda (Jánossy 1985, Gál 2005a, 2005b) (all in Hungary).

Spread: From the Late Pliocene of Spain and Bulgaria (Puebla de Valverde, as well as Slivnica, MN 17-18) *Corvus* finds described to the genus level are known from the Neogene of Europe (Mlíkovský 2002).

– † *Miocorvus* Lambrecht 1933

– *Miocorvus* † *larteti* (Milne-Edwards, 1871)

Site and era: Tasádfő (Tășad, Romania), Middle Miocene (MN 7) (Gál & Kessler 2006, Kessler 2010); Mátraszőlős 3, Middle Miocene (MN 7/8); Rudabánya, Upper Miocene (MN 9) (Kessler 2010, Kessler & Hír 2012); Polgárdi 4, Upper Miocene (MN 13); Csarnóta 2, Beremend 26, Lower Pliocene (MN 15) (Kessler 2010) (all in Hungary).

Material: distal end of *humerus* (Mátraszőlős 3), distal end of *carpometacarpus*, *phalanx I. digiti II. alae* (Csarnóta 2), 4 distal fragments of *tibiotarsus* (Rudabánya 3, Polgárdi 4, Beremend 26), 4 *phal. pedis* (Tasádfő).

Dimensions: *humerus* F = 10.11 mm; *carpometacarpus* F = 5.6 mm, G = 3.3 mm; *phal. alae* C = 3.36 mm, E = 4.69 mm, F = 3.43 mm; *tibiotarsus* E=2.49, 2.80 and 2.92 mm, F=5.44, 5.51, 5.65 and 5.78 mm, G=5.72 and 6.89 mm; *tarsometatarsus* F = 5.6 mm, G = 3.3 mm.

The small (jay-sized) crow described by Milne-Edwards (*Corvus larteti* Milne-Edwards, 1871) was renamed by Lambrecht (1933). We classified the material described by Jánossy (1979, 1997) from the Csarnóta 2 site here as well, but this is highly questionable due to the age difference.

Outside of the typical site (the Middle Miocene of France) (Sansan, MN 6) (Milne-Edwards 1871), it was also reported in 2006 from the Middle Miocene of Tășad, Romania (MN 7) (Kessler & Venczel 2009) and the Middle Miocene of Dobrogea as well, also in Romania (Credința, MN 8) (Gál & Kessler 2006).

– *Garrulus Vieillot, 1816*

– *Garrulus glandarius* (Linnaeus, 1758)

Q1: Németóvár 4B (Deutsch-Altenburg, Austria) (Jánossy 1981), Beremend 17 (Q1) (Jánossy 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q1-2:** Betfia „Aven” (Kessler 1975, Jánossy 1979, Gál 2002), Kiskóh-Medvék Cave (Chișcău-Peștera Urșilor) (Kessler 1982) (all in Romania); **Q3/I:** Hundsheim (Mlíkovský 1998, 2002) (Austria); Vindija (M. Malez 1961, V. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria); Krapina, Velika Pecina, Veternica (V. Malez 1973, 1984, 1986, 1988, V. Malez-Bačić 1979) (all in Croatia); Bajót-Baits Cave, Bajót-Hóman Cave (Jánossy 1979), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvárads-Istállóskeői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Varbó-Lambrecht Kálmán-Cave (Jánossy 1964, 1979) (all in Hungary); Hidegszamos-Csont Cave (Someșul Rece) (Lambrecht 1915), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II:** Balatonkeresztúr-Réti dűlő (Gál 2004, 2015), Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Felsőtárkány-Petényi Cave (Jánossy 1979), Legény Cave (Kormos 1914), Miskolc-Felső-forrás, Anonym Cave (Kessler 2010), Rezi (Kessler 2009), Tatabánya-alsó – Törekvés Cave (Kessler 2010), Vác-Széchenyi street, Visegrád-Várkert (Gál 2015) (all in Hungary); Remetelórév-Bólyikői Cave (Lorău-Peștera din Piatra Boiului) (Kessler 1982), Révi caves (Peșterile din Vadu Crișului) (Kessler 1982), Szegyesztel-Drăcoiaia Cave (Sighiștel, Peștera Drăcoiaia) (Kessler 1982); Székelykeresztúr (Cristuru-Seceuișc) (Gál 2008, 2015), Vársonkolyos-Kis Magyar Cave (Șuncuiuș, Peștera Napiștileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** France, Germany; **Q3:** Czech Republic, France, Germany, Italy, Ukraine, United Kingdom; **Q4:** Austria, Belgium, Bosnia-Herzegovina, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Ireland, Italy, Luxemburg, Moldova, Poland, Portugal, Russia, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Nucifraga Vieillot, 1816*

– *Nucifraga caryocatactes* Linnaeus, 1758

Q1: Betfia 9 (Gál 2002) (Romania); **Q3:** Vindija (M. Malez 1961, M. Malez & Rukavina 1979, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria); Bajót-Öregkö (Kormos 1914), Balla-Cave, Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933,

Jánossy 1979, 1986), Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Galgóc (Lambrecht 1915, 1933), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986) (all in Hungary); Barcarozsnyó (Peștera Gura Cheii-Râșnov) (Gál 1998, 2002), Szegyestel-Măgura Cave (Sighiștel, Peștera Măgura) (Kessler 1982, 1985, Gál 2002) (all in Romania); Detrekőszentmiklós-Pálffy Cave (Dzeráva Skála-Plavecky Mikulás) (Lambrecht 1913, 1933) (Slovakia); **Q4/II**: Teufelslucke (Soergel 1966) (Austria); Felsőtárkány-Petényi Cave (Jánossy 1979) (Hungary); Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a Fischer & Stephan 1977), Révi caves (Peșterile din Vadu Crișului) (Kessler 1982), Szkerisoara-Coiba Mare Cave (Scărișoara, Peștera Coiba Mare) (Kessler 1982), Jurcsák & Kessler 1986, 1988), Vársonkolyos-Izbîndiș Cave, Vársonkolyos-Kis Magyar Cave (Șuncuiuș, Peștera Izbîndiș, Peștera Napiștileu) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2**: Spain; **Q3**: Czech Republic, France, Germany, Italy, Ukraine; **Q4**: Austria, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Italy, Poland, Portugal, Russia, Switzerland, Spain (Tyrberg 1998).

– *Pica* (Linnaeus, 1758)

– *Pica pica* † *major* Jánossy, 1979 (Table 2)

Site and era: **MN 15**: Beremend 26 (Kessler 2010), Csarnóta 2 (Jánossy 1979, Kessler 2010) (all in Hungary); **Q1**: Beremend 16, 17 (Jánossy 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (all in Romania); **Q2**: Betfia „Aven” (Kessler 1975, Jánossy 1977, 1979, Gál 2002) (Romania); **Q2**: Nagyharsányhegy 1-4 (Lambrecht 1916, 1933, Jánossy 1979) (Hungary); **Q3/I**: Hundsheim (Lambrecht 1933, Jánossy 1979) (Austria); Dorog-Hungáriahegy (Jánossy 1953, 1986, Jánossy & Vörös 1987), Vértesszőlős 2 (Jánossy 1979, 1990) (all in Hungary).

Mlikovský (2002) classifies the fossil magpie species to the recent Western Jackdaw (*Corvus monedula*) based on the material from Stránská Skála classified by Jánossy (1972). When examining the fossilized material, we determined that this does not apply to the material from the Carpathian Basin, as the dimensional and morphological characteristics both refute this. Based on examination of the Csarnóta 2, Beremend 26 and numerous Lower Pleistocene materials, the validity of the fossilized subspecies is evident. The magpie characteristics, as well as the larger sizes than that of the present species, can be clearly shown. The present species is only known from the Middle Pleistocene of Europe, and is probably the direct descendant of the fossil subspecies.

Mourer-Chauviré (1975) also describes the fossil subspecies (*Pica pica major*) from the Middle Pleistocene (Saint-Estève Janson, Lunel Viel, **Q3**), while the present species is only known from the Upper Pleistocene. Another magpie find described to the genus level (*Pica* sp.) is known from the late Pliocene of Bulgaria (Vărșec MN 17) (Mlikovský 2002).

– *Pica pica* (Linnaeus, 1758)

Q3/II: Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); **Q4/I**: Mixnitz-Drachenhöhle (Lambrecht 1933) (Austria);

Bajót-Öregkő (Lambrecht 1914), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Cserépfalu-Subalyuk Cave (Jánossy 1979); Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979a, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Kesztlőc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933), Szilvásvár-Ístállós-kői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Tatabánya-Kálváriahegy Cave no. 4. (Gál 2004, 2005b), Varbó-Lambrecht Kálmán Cave (Jánossy 1964, 1979) (all in Hungary); Körösmart (Rípa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál 2002), Oháaponor-Bordu Mare Cave (Ohaba Ponor-Peștera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003) (all in Romania); **Q4/II**: Teufelslucke (Soergel 1966) (Austria); Budapest-Sas György square – Teleki Palace (Gál 2015), Ecsegfalva (Pike-Tay *et al.* 2004, Gál 2007), Felsőtárkány-Petényi Cave (Jánossy 1979), Ludas-Budzsák (Bökönyi 1974, Gál 2005a), Pilismarót-Malompaták (Jánossy 1985) (all in Hungary); Bégakalodva (Cladova) (Gál 2005a), Kazánszoros-Töröklik Cave (Cazanele Mari, Peștera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977), Körösbánlaci Cave (Peștera din Bălnaca) (Kessler 1982), Remetelórév-Bólyikői Cave (Lorău-Peștera din Piatra Boiului) (Kessler 1982), Révi Cave (Peșterile din Vadu Crișului) (Kessler 1982), Vársonkolyosi caves (Peșterile din Șuncuiuș) (Kessler 1977, Gál 2002) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2**: Spain; **Q3**: Azerbaijan, Croatia, Czech Republic, France, Germany, Italy, Spain, Ukraine; **Q4**: Austria, Belgium, Bosnia-Herzegovina, Croatia, Czech Republic, France, Georgia, Germany, Ireland, Italy, Montenegro, Moldova, Poland, Portugal, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– *Pyrrhonorax Vieillot, 1816*

– *Pyrrhonorax graculus* † *vetus Kretzoi, 1962* (Table 3)

Site and era: **MN 15**: Beremend 26 (Kessler 2010), Csarnóta 2 (Jánossy 1972) (all in Hungary); **MN 16**: Villány 3 (Kessler 2010 as *Pyrrhonorax pyrrhonorax*) (Hungary); **Q1**: Beremend 17 (Jánossy 1991, 1992) (Hungary); Betfia 2, 9 (Kormos 1913, Čapek 1917, Lambrecht 1933, Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q1-2**: Betfia „Aven” (Kessler 1975, Jánossy 1979, Gál 2002) (Romania); **Q2**: Betfia 5 (Kretzoi 1962, Kessler 1975, Jánossy 1979, Gál 2002), Kiskóh-Medvék-Cave 2 (Chișcău-Peștera Urșilor) (Kessler 1982, Jurcsák & Kessler 1988, Gál 2002) (all in Romania); Méhész (Vcelare) (Jánossy 1979) (Slovakia); **Q3/I**: Hundsheim (Lambrecht 1933, Jánossy 1979, Mlikovský 1998, 2002) (Austria); Tarkó 3, 4 (Jánossy 1979) (Hungary); Gombaszög (Gombasek) (Kessler 2009) (Slovakia).

Mlikovský (2002) classified the subspecies with different sizes and especially ratios to those of the present alpine chough. This is countered by the facts that on the one hand, the differences indicated by the diagnosis are clearly visible, and on the other hand, its subsequent characteristics can be associated with much earlier materials (Csarnóta 2, Beremend 17, and numerous other Lower and Middle Pleistocene sites). All this supports our opinion that this is a fossil subspecies, as well as the direct ancestor, of the present species.

– *Pyrrhcorax graculus* (Linnaeus, 1766)

Q3/II: Vindija (M. Malez 1961, V. Malez 1973, 1986, 1988, M. Malez & Rukavina 1979, Musil 1980) (Croatia); **Q4/I:** Merkenstein (Wettstein & Mühlhofer 1938), Mixnitz-Drachenhöhle (Lambrecht 1933) (all in Austria); Velika Pecina (M. Malez & Rukavina 1975, V. Malez 1984, 1988) (Croatia); Bajót-Öregkő (Kormos 1914), Bajót-Hóman Cave (Jánossy 1979), Budapest-Remetehegyi Cave (Kormos 1914, Lambrecht 1933, Jánossy 1979, 1986), Cserépfalu-Subalyuk Cave (Jánossy 1979); Csobánka-Kiskevélyi Cave (Lambrecht 1912a, 1912b, 1915, 1933, Jánossy 1979), Kesztölc-Bivak Cave (Jánossy 1979), Pilisszántói I. Cave (Lambrecht 1915, 1933, Jánossy 1979, 1986), Szilvásvár-Ístállóskői Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1952, 1955, 1979, 1986), Vaskapu Cave (Mottl 1941) (all in Hungary); Barcarozsnyó (Gura Cheii-Cave, Râşnov) (Gál 1998, 2002), Hidegszamos-Csont Cave (Peştera cu Oase, Someşul Rece) (Lambrecht 1915), Măgura-Valea Coacazei Cave (Măgura-Peştera din Valea Coacăzei) (Gál 2002), Nándor-Nándori Cave (Nándru-Peştera Curata) (Jánossy 1965, Fischer & Stephan 1977, Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Ohábaponor-Bordu Mare Cave (Ohaba Ponor-Peştera Bordu Mare) (Kessler 1985, Jurcsák & Kessler 1988, Gál 2002, 2003), Peterd-Tordai-hasadék – Binder Cave (Cheile Turzii-Peştera Binder) (Kessler 1985, Gál 2002) (all in Romania); **Q4/II:** Knochenhöhle (Bocheński & Tomek 1994), Grosse Offenbergerhöhle (Bocheński & Tomek 1994), Hohlensteinhöhle (Bocheński & Tomek 1994), Tropfsteinhöhle, Tunnelhöhle (Fladerer 1993) (all in Austria); Felsőtárkány-Petényi Cave (Jánossy 1979), Hosszúhegyi Cave (Jánossy 1979b) (all in Hungary); Herkulesfürdő-Rablók Cave (Băile Herculane, Peştera Hoţilor) (Kessler 1981, Gál 2002), Kazánszoros-Climente Cave (Cazanele Mari, Peştera Climente I) (Kessler 1981, Gál 2002), Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977) (all in Romania). From sites in Europe outside the Carpathian Basin **Q1-2:** Bulgaria, Spain, Ukraine; **Q3:** Azerbaijan, Czech Republic, France, Georgia, Germany, Spain, Ukraine; **Q4:** Austria, Bulgaria, Croatia, Czech Republic, France, Georgia, Germany, Greece, Italy, Montenegro, Poland, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

The present species is also known from the Late Pliocene of Bulgaria and Spain (Väršec and Meda Gran, MN 17) – these, however, supposedly belong to the fossil subspecies above – as well as from numerous sites in France and a few in Greece from the Lower and Middle Pleistocene. It can nowadays be found in the Alps, Pyrenees and the Balkan Peninsula (as well as the Upper Pleistocene and Holocene sediments of the caves located there) (Mlikovský 2002).

– *Pyrrhcorax pyrrhcorax* (Linnaeus, 1758)

Q2: Nagyharsányhegy 1-4 (Kessler 2010) (Hungary); **Q3/I:** Hundsheim (Mlikovský 2009) (Austria); **Q3/II:** Vindija (M. Malez 1961, M. Malez & Rukavina 1975, V. Malez 1973, 1986, 1988, Musil 1980) (Croatia); Solymár-Ördöglyuk (Jánossy 1979) (Hungary); **Q4/I:** Luegloch (Mottl 1953) (Austria); Felsőtárkány-Peskő Cave (Lambrecht 1912a, 1912b, 1933, Jánossy 1979, 1986), Hámor-Puskaporos Cave (Lambrecht 1912a, 1912b, 1916, 1933, Jánossy 1979, 1986), Répáshuta-Balla Cave (Lambrecht 1912a, 1912b, 1933) (all in Hungary); Körösmart (Rípa) (Jánossy in Hamar & Csák 1969, Kessler 1974b, Gál

2002), Rév-Pince Cave (Vadu Crişului, Peştera Pincelului) (Gál 2002) (all in Romania); **Q4/II**: Grosse Offenbergerhöhle (Bocheński & Tomek 1994) (Austria); Kazánszoros-Töröklik Cave (Cazanele Mari, Peştera Cuina Turcului) (Kessler 1974a, Fischer & Stephan 1977) (Romania). From sites in Europe outside the Carpathian Basin **Q1-2**: Spain, Ukraine; **Q3**: Azerbaijan, Czech Republic, France, Georgia, Spain, Ukraine; **Q4**: Austria, Bosnia-Herzegovina, Bulgaria, Croatia, France, Georgia, Greece, Italy, Luxemburg, Portugalia, Romania, Russia, Switzerland, Spain, Ukraine, United Kingdom (Tyrberg 1998).

– ***Perisorius Bonaparte, 1831***

– ***Perisorius infaustus Bonaparte, 1831***

Q4/I: Répáshuta-Balla-Cave (Lambrecht 1912, 1933) (Hungary);

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

MN 15: Beremend 26 (Kessler 2010: as *Nucifraga caryocatactes*) (Hungary);

– ***Corvidae gen. et sp. indet.***

Q2: Ūrömhegy (Jánossy 1961, 1986); **Q4/I**: Tatabánya-Kálvária no. 4. Cave (Gál 2004, 2005b) (all in Hungary);

Conclusions

From the introduction of Corvids and by listing their finds from the Neogene and the Quaternary, it became evident that although their fossil and subfossil remains are frequent at several sites, the number of species is relatively low, both regarding extinct and present taxa.

Their classification is made harder – as it became evident when discussing osteology – by the fact that there is a large amount of morphological homogeneity, and identifying them is often only aided by size differences. It is no coincidence that on this basis, Mlíkovský (2002) classified numerous known extinct species to present taxa or synonymizes.

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Table 1. *Corvus t plicicaenus* (Portis), 1889

(Abbreviations: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotalaris*;

tmt=*tarsometatarsus*; ph.a=*phalanga 1. digiti II*; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x. xd=number of copies; A-G=see bone sizes)

1. táblázat *Corvus t plicicaenus* (Portis), 1889

(Rövidítések: cor=*coracoideum*; scap=*scapula*; hum=*humerus*; rad=*radius*; cmcp=*carpometacarpus*; fem=*femur*; tib=*tibiotalaris*; tmt=*tarsometatarsus*;
ph.a=*phalanga 1. digiti II*; ph. p.=*phalanga pedis*; ph.u.=*phalanga unguis*; x. xd=pédányszám; A-G=lásd: csontméretek)

Bones	Total length	Partial length	Breadth prox.end	Thickness prox.end	Breadth of corpus	Breadth distal end	Thickness dist.end	Other sizes	Localities	Source
<i>coracoideum</i>	44.00								Beremend 17	Jánossy 1992
"	50.00								"	"
<i>carpometacarpus</i>	61.00								"	"
<i>femur-exemplare</i>	54.60–655.00								"	"
<i>scapula</i>		12.06	6.33	6.65	5.37				Betfa 5	Gál 2002
<i>carpometacarpus</i>						10.08			Betfa "Aven"	"
"								E1=4.00	Betfa 5	"
"			6.30						"	"
<i>tarsometatarsus</i>					4.90				"	"
<i>coracoideum</i>					4.65		11.38		Polgárdi 5	Kessler 2010
<i>femur</i>			11.26		5.11				"	"
<i>coracoideum</i>					4.49				Beremend 17	"
<i>humerus</i>					8.20	18.69	10.08		"	"
<i>carpometacarpus</i>			12.36	6.94					"	"
"			12.68	6.91					"	"
<i>femur</i>			12.00	7.98					"	"
<i>ulna</i>						11.42	8.01		Beremend 26	"
<i>femur</i>					4.75	11.05	8.88		"	"

Table 2. *Pica pica* t major Jánosy, 1979

(Abbreviations: cor=coracoideum; scap=scapula; hum=humerus; rad=radius; cmcp=carpometacarpus; fem=femur; tib=tibiotarsus; tmt=tarsometatarsus; ph.a=phalanga 1. digiti II; ph. p.=phalanga pedis; ph.u.=phalanga unguis; x. xd=number of copies; A-G=see bone sizes)

2. táblázat *Pica pica* t major Jánosy, 1979
(Rövidítések: cor=coracoideum; scap=scapula; hum=humerus; rad=radius; cmcp=carpometacarpus; fem=femur; tib=tibiotarsus; tmt=tarsometatarsus; ph.a=phalanga 1. digiti II; ph. p.=phalanga pedis; ph.u.=phalanga unguis; x. xd=példányszám; A-G=lásd. csontméretek)

Bones	Total length	Partial length	Breadth prox.end	Thickness prox.end	Breadth of corpus	Breadth distal end	Thickness dist.end	Other sizes	Localities	Source
humerus			13.40						Hundshheim	Jánosy 1979
coracoideum				cca.7.50					Csarnóta 2	Kessler 2010
"					2.13				"	"
"					2.35				"	"
scapula		6.26	3.47	4.44	3.04				"	"
ulna			6.65		3.21				"	"
radius					1.81	4.48	2.51		"	"
phalanga 1. digiti II.	3.43		4.39						"	"
femur		7.54	4.03	3.51					"	"
tibiotarsus					3.50	5.52	5.76		"	"
phalanga pedis	6.70	2.55	1.24	1.71					"	"
"	9.00								"	"
coracoideum			5.80						Berevend 17	"
carpometacarpus	34.22	29.69	8.47	4.27		5.47	3.01		Barevend 26	"
"					cca.7.00			E1=3.10	"	"
phalanga pedis	12.50	3.78	1.85	3.10					"	"

Table 3. *Pyrrhocorax graculus tvetus* Kretzoi, 1962

(Abbreviations: cor=coracoideum; scap=scapula; hum=humerus; rad=radius; cmcp=carpometacarpus; fem=femur; tib=tibiotalarsus;

tmt=tarsometatarsus; ph.a=phalanga 1. digiti II; ph. p=phalanga pedis; ph.u.=phalanga unguis; x, xd=number of copies; A-G=see bone sizes)

3. táblázat *Pyrrhocorax graculus tvetus* Kretzoi, 1962

(Rövidítések: cor=coracoideum; scap=scapula; hum=humerus; rad=radius; cmcp=carpometacarpus; fem=femur; tib=tibiotalarsus; tmt=tarsometatarsus; ph.a=phalanga 1. digiti II; ph. p=phalanga pedis; ph.u.=phalanga unguis; x, xd=példányszám; A-G=lásd: csontméretek)

Bones	Total length	Partial length	Breadth prox.end	Thickness prox.end	Breadth of corpus	Breadth distal end	Thickness dist.end	Other sizes	Localities	Source
carpometacarpus	36.20	33.20			3.15	8.20	6.12	E1=3.00	Betfa "Aven"	Kretzoi 1862
tibiotalarsus					3.28	6.44	5.85		"	"
"					2.90				"	"
coracoideum	31.45	29.19	6.60	3.31	4.70				"	Gál 2002
humerus		20.64	12.82		4.16	7.73	5.57		"	"
ulna					3.65	7.60	4.82		"	"
"					3.32				"	"
radius			3.32	3.03	3.20	7.24	5.41		"	"
femur	37.81	35.95	7.15	4.08	3.40	7.89	5.74		"	"
"					3.30				"	"
tibiotalarsus	65.20		7.53	6.74	3.45	5.84	5.64		"	"
"					3.00				"	"
tarsometatarsus				6.76	2.53				"	"
coracoideum					2.75		8.50		Betfa 2	"
ulna					3.87	7.00	4.70		"	"
tibiotalarsus					3.00				"	"
"						6.22	5.05		"	"
tarsometatarsus					2.80				"	"
phalanga pedis	10.00	3.19	1.81	3.15					Betfa 9	"
"	9.50	3.65	2.00	3.29					"	"
humerus						10.84	5.78		Kiskőh 1	"
ulna	59.85	7.70	8.32	9.22	4.27	7.96	5.41		Gombaszög	Kessler 2010
femur			8.10	5.44	3.65				"	"
"						6.61	5.04		"	"
tibiotalarsus						6.19	5.70		"	"

Table 4. Corvidae – *mandibula*, *coracoideum*, *scapula*, *humerus* dimensions
4. táblázat Varjúfélék – also állkapocs, hollócsőrcsont, lapocka, felkarcsont méretek

Bone (Figure 3-6)	<i>Corvus corax</i>	<i>C. corone</i>	<i>C. frugilegus</i>	<i>C. monedula</i>	<i>Pica pica</i>	<i>Garrulus gland.</i>	<i>Nucifraga caryoc.</i>	<i>Pyrrhocorax gr.</i>	<i>P. pyrrhocorax</i>
<i>mandibula</i> – A	96.00	70.00	72.00	51.00	49.00	49.00	65.00	53.00	
– B	22.00	17.00	17.00	13.00	13.00	11.00	30.00	15.00	
– C	14.00	11.00	10.00	11.00	9.00	8.00	13.00	10.00	
<i>coracoideum</i> – A	58.80	41.40–44.40	39.20–43.00	32.00–33.10	29.60–35.90	29.00–30.70	32.90	31.50–32.72	33.00–35.87
– B	53.50	38.30–41.20	36.20–39.40	30.30–31.00	28.00–33.40	27.10–28.90	30.10	28.80–28.90	28.80–32.71
– C	12.10	9.00–9.20	8.10–8.90	5.90–7.00	5.80–7.10	5.20	5.30	7.50	7.50
– D	12.50	9.30–10.40	8.40–9.70	6.60–6.70	5.90–7.30	5.30–6.30	5.40	6.55–7.30	6.85–7.50
– E	5.00	2.70–3.40	3.00–3.20	2.30–2.40	2.00–2.40	1.90–2.00	2.10–3.00	2.50	3.00
– F	16.90	11.70–12.60	9.80–11.80	8.50–8.90	7.00–9.40	6.90–7.30	8.00	9.50–10.92	10.00–11.11
– G	14.50	12.00	10.00	8.70	8.00	6.50	7.00	9.52	9.62
<i>scapula</i> – A	64.80	47.20–50.00	43.40–48.40	34.90–35.50	35.80–40.60	34.00–36.00	36.00	38.00–40.36	42.00–42.17
– B	16.10	10.60–11.80	10.20–11.30	7.70–8.30	6.50–9.00	6.80–7.20	7.00	9.00–9.23	9.50–10.00
– C	8.20	5.20–5.30	4.40–5.40	3.70–4.00	3.40–4.30	3.20–3.30	3.90	3.70	3.70
– D	9.30	5.90–6.60	5.20–6.30	3.90–4.30	4.30–4.80	4.60–4.70	4.40	5.51	5.21
– E	6.10	4.00–4.50	3.70–4.00	2.70–2.90	2.60–3.60	2.50	2.40	3.50–4.00	3.63–4.00
<i>humerus</i> – A	93.00	60.20–67.00	60.50–64.60	41.40–48.80	40.60–49.20	39.00–42.10	40.20–42.40	41.60–45.60	53.44–54.30
– B	37.00	25.20–26.00	23.50–25.40	17.70–18.80	16.60–20.00	15.40–17.10	17.00	19.00–21.33	21.97–22.00
– C	26.40	18.00–18.40	16.20–19.00	12.80–15.40	12.20–14.00	11.3–13.2	12.20–12.80	12.50–14.07	14.74–16.00
– D	25.50	17.40–17.70	16.00–18.80	12.40–13.20	12.20–14.00	10.40–12.20	12.00	14.16	15.34
– E	8.50	6.00–6.30	5.30–6.00	4.10–4.60	3.80–4.90	3.40–4.10	3.50–3.80	4.60–5.18	5.205.50
– F	19.30	14.10–15.00	13.00–14.20	9.40–11.10	10.00–11.00	9.30–11.00	9.80–10.00	11.78–13.00	11.86–14.50
– G	11.30	7.80–8.60	7.80–8.20	5.4–6.10	5.40–6.80	4.40–5.00	4.80	6.17	6.22
– H	7.80	5.00	4.90	3.50	3.90	3.20	3.10	6.90	6.80

Table 5. Corvidae – *ulna*, *radius*, *carpometacarpus*, *phalanga 1. digiti II.* dimensions
5. táblázat Varjúfélék – singcsont, orsócsont, közézőpcson, szárny 1. ujjperc, II. ujj méretek

Bone (Figure 7–10)	<i>Corvus corax</i>	<i>C. corone</i>	<i>C. frugilegus</i>	<i>C. monedula</i>	<i>Pica pica</i>	<i>Garrulus gland.</i>	<i>Nucifraga caryoc.</i>	<i>Pyrrhocorax gr.</i>	<i>P. pyrrhocorax</i>
<i>ulna</i> – A	112.40	76.50–81.40	73.00–79.80	56.70–58.20	51.00–61.30	48.00–50.30	49.80	57.00–59.09	66.67–68.00
" – B	13.80	9.20–9.80	8.40–9.90	6.80–7.10	6.40–7.40	6.20–6.30	6.20	7.87–8.00	8.30–9.00
" – C	15.80	10.00	9.10–10.70	6.80–8.20	6.80–8.90	6.70–7.10	7.00	8.20–8.47	8.69–9.50
" – E	6.70	4.80–5.00	4.40–5.00	3.20–3.50	3.00–3.70	3.00–3.40	3.10	4.00	4.29–4.50
" – F	12.80	9.10–9.40	8.30–9.50	6.40–6.60	6.90–7.20	5.70–6.00	6.20	7.00–7.82	8.129.00
" – G	9.30	6.40–6.90	6.20–6.60	4.60–5.20	4.30–5.20	4.20–4.40	4.30	5.00–5.41	5.81
<i>radius</i> – A	102.00	69.40–73.80	67.30–73.00	51.00–54.00	45.40–55.00	42.80–44.40	44.70	51.00–53.70	60.26–62.00
" – C	5.80	3.90–4.70	3.40–4.10	3.00–3.10	2.80–3.70	2.80–3.10	3.00	3.50–4.08	3.89–5.00
" – D	4.40	3.20–3.70	3.00–3.40	2.30–2.40	2.20–2.80	2.20–2.30	2.60	2.81–2.90	2.81–3.50
" – E	3.40	2.00–2.40	1.80–2.00	1.40–1.50	1.30–1.60	1.30–1.50	1.50	1.60–1.90	1.58–2.00
" – F	8.50	5.70–6.00	5.50–6.00	4.00–4.10	3.50–4.00	2.90–3.50	3.70	4.80–5.48	5.02
<i>carpometacarpus</i> – A	70.00	46.60–49.80	44.60–48.10	34.80–35.20	30.10–37.70	25.60–28.00	29.20	35.00–36.49	38.00–39.75
" – B	60.50	40.00–42.50	38.50–42.30	30.40–31.00	25.00–34.20	21.30–22.80	24.30	29.00–31.22	33.15–34.00
" – C	15.00	10.30–11.00	9.70–10.60	7.30–7.70	7.00–8.70	7.00–7.20	7.20	7.60–9.10	8.30–9.39
" – D	7.40	5.30–5.80	4.90–5.30	3.60–3.90	3.20–4.40	3.00–3.50	3.40	4.57	4.31
" – E	11.20	7.80–8.20	7.80–8.40	5.40–6.20	5.40–6.20	5.00–5.20	5.00	6.00–6.98	6.00–6.68
" – E1	5.80	3.90–4.00	3.50–4.20	2.70–3.00	2.40–3.10	2.40–2.60	2.50	3.35–3.50	3.30–4.00
" – F	15.30	10.00–10.50	9.80–11.00	7.10–7.70	6.40–8.00	6.00–6.30	6.30	8.50–8.81	9.22–9.50
" – G	7.00	4.50–4.60	4.00–5.00	3.10–3.20	2.80–3.70	2.50–2.80	3.10	3.65	3.90
<i>phalanga 1. digiti II.</i> – A	35.00	21.00	22.00	17.00	18.00	11.00	13.00	15.00	18.00
" – C	8.50	6.00	6.50	5.00	4.00	3.50	3.50	5.00	5.50
" – E	9.50	7.00	7.00	5.50	4.50	4.00	4.00	6.00	6.50
" – F	8.00	6.00	6.00	4.50	4.00	3.00	3.00	4.50	5.00

Table 6. Corvidae – femur, tibiotarsus, tarsometatarsus dimensions
6. táblázat Varjúfélék – combcsont, lábszárcsont, csüd méretek

Bone (Figure 11-13)	<i>Corvus corax</i>	<i>C. corone</i>	<i>C. frugilegus</i>	<i>C. monedula</i>	<i>Pica pica</i>	<i>Garrulus gland.</i>	<i>Nucifraga caryoc.</i>	<i>Pyrrhocorax gr.</i>	<i>P. pyrrhocorax</i>
femur – A	67.70	45.80–53.50	45.50–47.90	36.40–38.60	36.20–42.20	36.60–37.90	38.70	40.00–41.10	40.90–42.50
– B	64.00	42.50–50.00	42.80–45.00	34.20–36.20	34.00–40.00	34.40–35.70	36.70	38.50–39.1	38.50–40.50
– C	15.30	9.60–10.30	9.00–10.00	6.90–7.70	7.00–8.00	6.90–7.20	7.00	7.30–8.00	8.30–9.00
– D	9.10	6.20–6.50	5.80–6.80	4.00–4.40	4.20–5.30	4.30–4.70	4.20	4.64–50	5.20–5.60
– E	6.50	4.30–4.80	4.00–4.30	3.00–3.10	3.20–3.60	3.00–3.20	3.00	3.49–3.60	4.03
– F	14.70	10.00–10.60	9.20–10.00	6.90–7.80	7.00–7.90	6.80–7.00	7.70	7.60–8.25	9.23–9.60
– G	11.60	8.00–8.80	7.50–8.20	5.80–6.20	5.40–6.20	5.20–5.80	5.80	6.71–6.90	7.67–8.00
tibiotarsus – A	112.00	81.30–89.20	79.00–84.00	63.10–64.80	58.40–70.60	58.30–61.40	59.30	71.95–77.50	69.00–75.38
– B	18.20	12.40–13.80	13.00	8.90–9.60	8.70–10.20	8.70–9.20	8.10	10.69–12.30	10.00–12.19
– C	12.80	8.90–9.20	7.50–8.80	5.80–6.90	6.00–7.40	6.30–7.00	6.10	7.25–10.00	8.22–8.80
– D	6.00	4.10–4.80	3.80–4.60	2.80–3.10	2.80–3.50	2.70–2.90	3.00	3.20	4.45–5.00
– E	5.00	3.60	3.70	2.40	2.70	2.50	2.40	4.00	3.20
– F	12.00	8.10–8.80	7.50–8.60	5.70–6.00	5.40–6.70	5.40–6.20	5.90	7.32–7.50	6.50–7.08
– G	10.70	8.00–8.20	7.1–8.00	5.80–6.20	5.30–6.30	5.30–5.50	5.40	6.57–7.00	6.10–6.92
tarsometatarsus – A	66.00–69.00	51.40–60.00	51.20–55.00	41.20–44.10	40.80–50.20	40.50–43.50	40.70	44.80–47.65	51.00–56.50
– C	12.00–13.20	8.80–10.00	8.30–9.30	6.10–6.90	6.50–7.10	5.90–6.20	6.20	7.04–7.50	8.48–9.50
– D	12.20–14.00	8.60–9.30	8.60–9.60	6.20–7.50	6.90–7.50	6.60–7.20	6.00	6.70–7.88	8.00–8.45
– E	4.80–5.00	3.40–3.80	3.00–3.40	2.30–2.70	2.30–2.70	2.10–2.40	2.30	2.80	3.02
– F	9.20–9.50	6.80	6.00–7.00	5.10–5.20	4.20–4.70	4.20–4.70	4.60	5.51–5.66	5.90–6.00
– G	5.50–6.00	4.00–4.40	3.50–4.20	2.80–3.10	2.80–2.90	2.80–2.90	3.00	2.89–3.00	3.35–3.50

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