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The wing phalanges *(Phalanx proximalis digiti majoris)* of European Accipitriformes and Falconiformes

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Abstract The authors compared the first phalanx of the second wing finger of 33 European diurnal raptors. The importance of studying this bone lies in the fact that, although it has diagnosable characteristics, it was practically neglected by osteologists and paleontologists. Thus, fossil materials can be identified through them, as well as those from owl pellets. The comparison was made possible by the comparative avian skeleton collection of the Hungarian Natural History Museum. In a preliminary investigation we examined the morphological diversity of the first phalanx of the second wing finger among the different species. We used principal component (PC) analyses on measurements. The PC described the curvature of the anterior surface of the bone and the relative size of the distal and proximal epiphyses. The principal component analysis showed slightly overlapping in shape between the taxons but the accipitriform and falconiform birds diverged in the morphospace. The attributes and geometry of the first phalanx of the second wing finger reflects more on taxonomic background than flying behaviour. The avian wing is a complex and highly modulable structure, therefore, probably body mass and size affect flying performance than the other morphological features of this bone. The text is supplemented by 6 figures and one size table.

Keywords: Europe, diurnal raptors, *phalanx proximalis digiti majoris*, osteology

Összefoglalás A szerzők 33 európai nappali ragadozómadár faj szárnyának második ujja első ujjpercét hasonlították össze. A vázrész tanulmányozásának jelentősége abban áll, hogy bár jól meghatározható jellegekkel rendelkezik, gyakorlatilag el lett hanyagolva a csonttannal és őslénytannal foglalkozók részéről. Általuk mind a fosszilis anyagok, mind a bagolyköpetek anyagai jól meghatározhatóak. A vizsgálatot a MTM összehasonlító madárcsont gyűjteménye tette lehetővé. Egy előzetes vizsgálatban tanulmányoztuk a szárny második ujjának első ujjpercének morfológiai diverzitását. A vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a csont anterior irányú görbületét, valamint a proximális és a disztális epifízisek egymáshoz viszonyított nagyságát magyarázzák. Az analízis eredményei szerint némi átfedés látható a fajok között, de a vágómadár-alakúak és a sólyomalakúak elkülönülnek egymástól a morfotérben. Az eredmények azt sugallják, hogy az ujjperc alakja és tulajdonságai sokkal inkább tükrözik a fajok rendszertani hovatartozását, semmint a repülés módját. A madarak szárnya egy komplex modulálható struktúra, így feltehetőleg a testtömegnek és a méretnek nagyobb szerepe van a repülést illetően, mint az ujjperc alaktani sajátságainak. A szöveget 6 ábra és egy mérettáblázat egészíti ki.

Kulcsszavak: Európa, nappali ragadozómadarak, *phalanx proximalis digiti majoris*, csonttan

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Introduction

In this study, the authors discuss a lesser-known part of the avian skeleton used for description. The relatively simple first *phalanx* of the second wing finger is rather small, even in the largest avian species – only 6–7 centimetres long, and even though it bears excellent diagnostic characteristics, it has never been the focus of experts studying avian bones. There are virtually no study results, or most of the time not even a mention.

Of the four wing *phalanges* only one bears such morphological characteristics, namely the first *phalanx* of the second wing finger. Its morphometrical analysis results can be used for comparative anatomical, paleontological, archaeological, taxonomical or ornithological examinations of owl pellets.

The morphological terminology and measurement method of the skeletal part was used based on the works of Baumel *et al.* 1979 and Kessler 2013. The wing phalanx can primarily

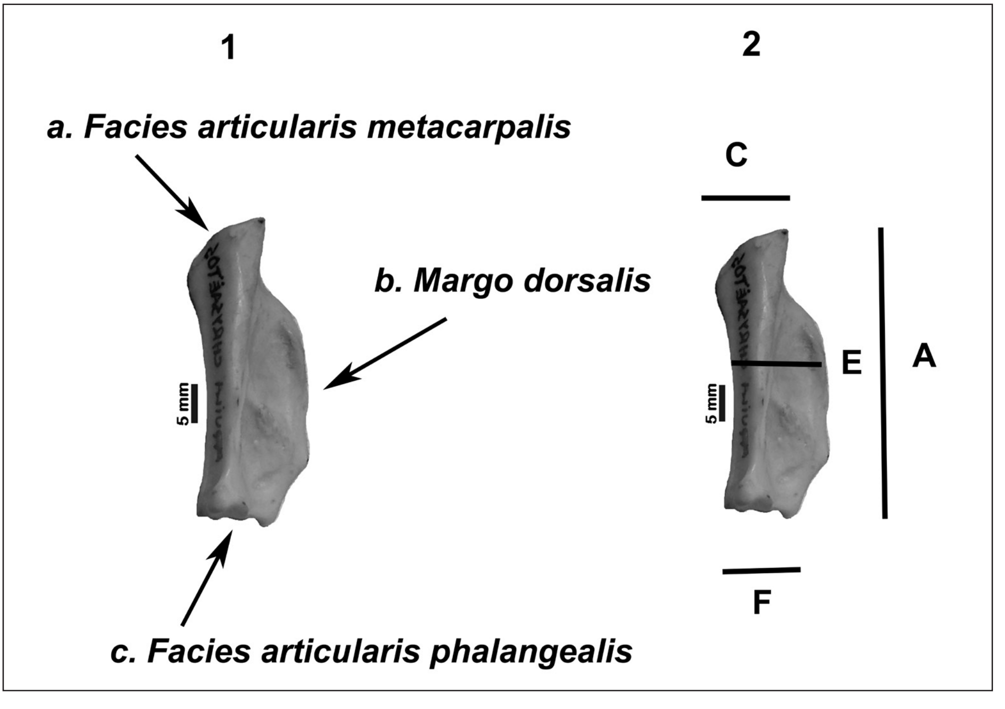

Figure 1. Aquila chrysaetos (Linnaeus, 1758)
1. *Phalanx proximalis digiti majoris* osteology characteristics:
a. proximal end – *Facies articularis metacarpalis*; b. the dorsal side – *margo dorsalis*; c. distal end – *Facies articularis phalangealis*
2. Measurements methods of bone:
A. total length; C. breadth of the proximal end; E. breadth of the *corpus*; F. breadth of the distal end
1. ábra Aquila chrysaetos (Linnaeus, 1758)
1. A nagy (középső) kézujj első ujjperce csonttani jellegei: a. proximális vég – *facies articularis metacarpalis*; b. dorsalis oldal – m*argo dorsalis*; c. disztális vég – *facies articularis phalangealis*;
2. A csont mérési mintái:
A. teljes hossz; C. proximális vég szélessége; E. a test szélessége; F. a disztális vég szélessége

be found within the literature in the works of Milne-Edwards 1867–1868, Solti 1980, 1981a, 1981b, 1996, Gilbert *et al*. 1981, Cohen & Serjeantson 1996, Kessler 2015, 2016a, 2016b, 2019, 2020 discussed or illustrated, but usually only in the case of a few species.

The measured sizes given in *Table 1* are for information purposes only, since in the case of species of this order, a size difference in favour of females is quite frequent, and we do not have the corresponding skeletal parts from both sexes in all species.

In this study, we also made an attempt to investigate the morphological diversity of this bone among the different species. Our objective was to increase our knowledge on the possible relationship between shape and flying behaviour of diurnal raptors. The differences in force acting on this skeletal part during flying and gliding may be related to shape and geometry of wing finger. To investigate the morphological diversity, we used landmark-based morphometric methods.

Abbreviations

MTM/NHMUS: Natural History Museum of Hungary Budapest, Department of Paleontology and Geology
A – total length
C – the width of the proximal end
E – the largest width of the middle phalanx
F – the width of the distal end
wingspan – the distance between the two wing tips
wing – half the wingspan
wing/phalanx – wing length to phalanx ratio
New genus, sp. name – Gill *et al*. 2020

We used the following anatomical terminology *(Figure 1)*:
Facies articularis metacarpalis – this is the proximal end
Margo dorsalis – this is the largest width of the middle phalanx
Facies articularis phalangealis – this is the distal end

Osteological description

In the case of vultures *(Figure 2a–d)*:

a) Shape of *facies articularis metacarpalis*:
- strongly protuberant, with a protruding ventral tip: *Gypaetus barbatus*;
- slightly convex, with a rounded ventral end: *Aegypius monachus*;
- obliquely cut, lifting from the ventral end towards the dorsal: *Gyps fulvus, Neophron percnopterus*;

b) The arc of the *margo dorsalis*:
- forms a regular arc: *Gypaetus barbatus*;
- the arch is protuberant: *Aegypius monachus*;

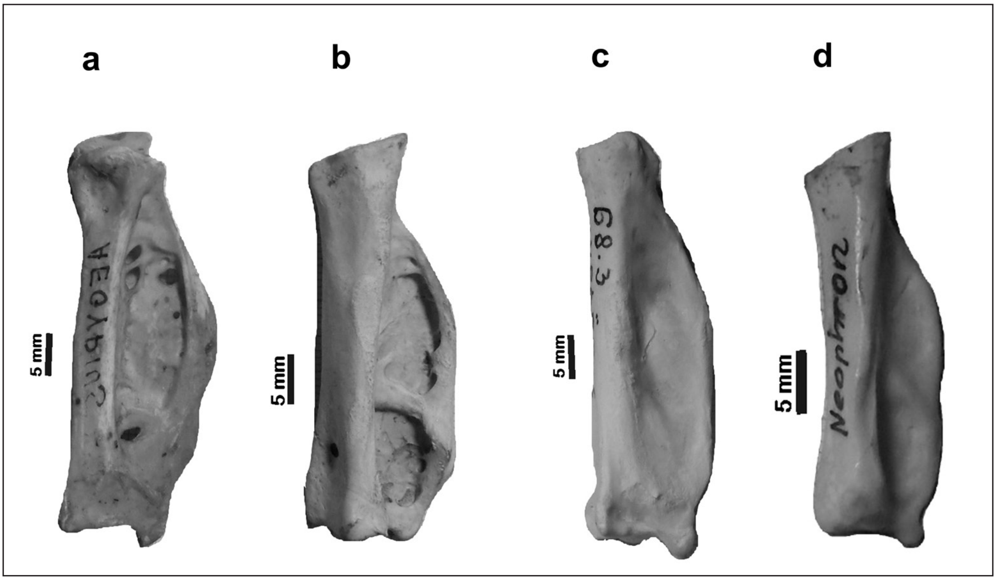

Figure 2. Left *phalanx proximalis digiti majoris* (ventral aspect)
2. ábra Bal oldali kézujjperc (1. ujjperc, II. ujj, alulnézet)
a. *Aegypius monachus* (Linnaeus, 1766); b. *Gypaetus barbatus* (Linnaeus, 1758); c. *Gyps fulvus* (Hablizl, 1783); d. *Neophron percnopterus* (Linnaeus, 1758)

– the middle of the arc is cut straight: *Gyps fulvus*;
– the slightly protuberant arc is wavy: *Neophron percnopterus*;
c) Shape of *facies articularis phalangealis*:
– oblique, with a strongly protruding dorsal projection: *Aegypius monachus*;
– wavy, with a strongly protruding dorsal projection: *Gypaetos barbatus*;
– wavy, with a slightly protruding dorsal projection: *Gyps fulvus*;
– concave, with a strongly protruding dorsal projection: *Neophron percnopterus*;

In the case of eagles *(Figure 3a–i)*:
a) Shape of *facies articularis metacarpalis*:
– obliquely convex, with a rounded ventral end: *Pandion haliaetus*;
– slightly convex: *Haliaeetus albicilla*;
– oblique straight rise from the ventral end: *Aquila chrysaetos, A. heliaca, A. fasciata, Clanga clanga, C. pomarina*;
– the dorsal projection is like a pointy cone: *Aquila chrysaetos, Clanga clanga, C. pomarina*;
– the dorsal projection is like a blunt cone: *Aquila heliaca*;
– straight waves: *Aquila rapax*;
– convex, with a dorsally protruding cone-like projection: *Hieraaetus pennatus*;
b) The arc of the *margo dorsalis*:
– convex, with a cut arch: *Aquila chrysaetos, A. fasciata, Clanga clanga, Haliaetos* spp.;
– slightly convex, with a symmetrical arch: *Clanga pomarina*;

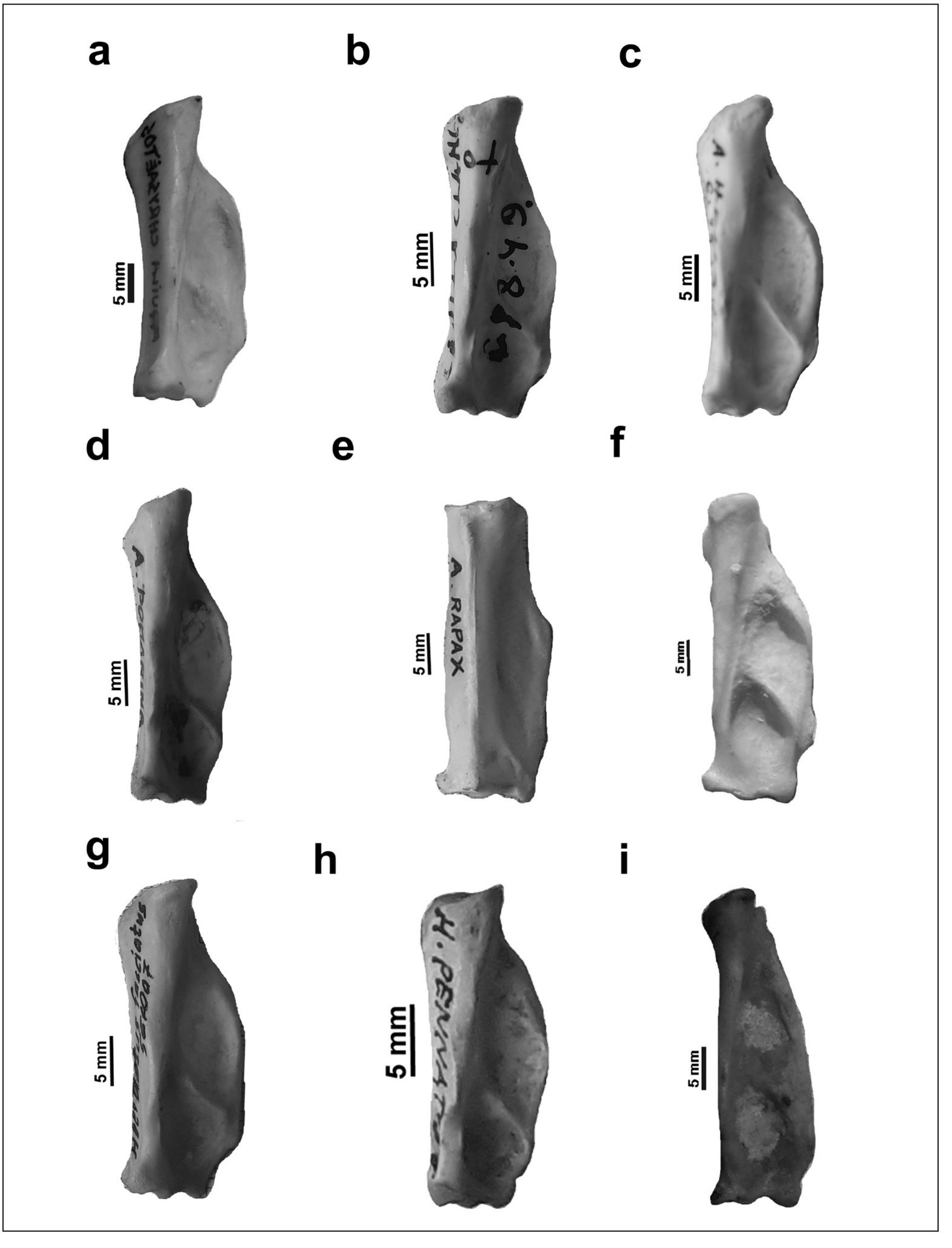

Figure 3. Left *phalanx proximalis digiti majoris* (ventral aspect)
3. ábra Bal oldali kézujjperc (1. ujjperc, II. ujj, alulnézet)
a. *Aquila chrysaetos* (Linnaeus, 1758); b. *Clanga clanga (*Pallas, 1811); c. *Aquila heliaca* (Savigny, 1809); d. *Clanga pomarina* (Brehm, 1831); e. *Aquila rapax* (Cabanis, 1854); f. *Haliaeetus albicilla* (Linnaeus, 1758); g. *Aquila fasciata* (Vieillot, 1822); h. *Hieraaetus pennatus* (Gmelin, 1788); i. *Pandion haliaetus* (Linnaeus, 1758)

– symmetrically and strongly arched: *Aquila heliaca, Hieraaetus pennatus*;
– asymmetrically and slightly arched: *Pandion haliaetus*;
– asymmetrical and cut: *Aquila rapax*;
c) Shape of *facies articularis phalangealis*:
– wavy, with a strongly protruding, blunt cone-like projection: *Aquila chrysaetos, Pandion haliaetus*;
– wavy, with a strongly protruding, pointy cone-like projection: *Clanga clanga, Aquila rapax*;
– wavy, with a slightly protruding projection: *Aquila heliaca, A. fasciata, Clanga pomarina, Haliaetos haliaetus, Hieraaetus pennatus*;

In the case of buzzards and kites *(Figure 4a–g)*:
a) Shape of *facies articularis metacarpalis*:
– slightly convex: *Buteo lagopus*;
– slightly obliquely cut, with a straight ventral end and a small dorsal point: *Buteo rufinus, Circaetus gallicus, Milvus migrans*;
– obliquely convex, with a pointed dorsal projection: *Milvus milvus*;
– obliquely rising, with a dorsal pointed projection: *Pernis apivorus*;
– oblique and slightly raised, with a dorsal pointed projection: *Buteo buteo*;
b) The arc of the *margo dorsalis*:
– the bulge is cut: *Buteo rufinus*, *Circaetus gallicus, Milvus migrans*;
– strongly protuberant, with a symmetrical arch: *Buteo buteo, Pernis apivorus*;
– slightly protuberant, with a symmetrical arch: *Buteo lagopus*;
– slightly protuberant, with an asymmetrical arch: *Milvus milvus*;
c) Shape of *facies articularis phalangealis*:
– wavy, with a slightly protruding projection: *Circaetus gallicus, Milvus milvus, Pernis apivorus*;
– convex, with a pointy dorsal projection: *Buteo buteo, B. lagopus*;
– convex, with a blunt dorsal projection: *Buteo rufinus, Milvus migrans*;

In the case of goshawks and harriers *(Figure 4h–l)*:
a) Shape of *facies articularis metacarpalis*:
– convex: *Accipiter gentilis, Circus pygargus*;
– obliquely cut, with a pointy dorsal point: *Circus aeruginosus, C. cyaneus, C. macrourus*;
b) The arc of the *margo dorsalis*:
– the arch is cut: *Accipiter gentilis, Circus aeruginosus, C. cyaneus, C. macrourus, C. pygargus*;
c) Shape of *facies articularis phalangealis*:
– straight and wavy: *Circus cyaneus*;
– oblique and wavy: *Accipiter gentilis, Circus pygargus*;
– concave: *Circus aeroginosus, C. macrourus*;

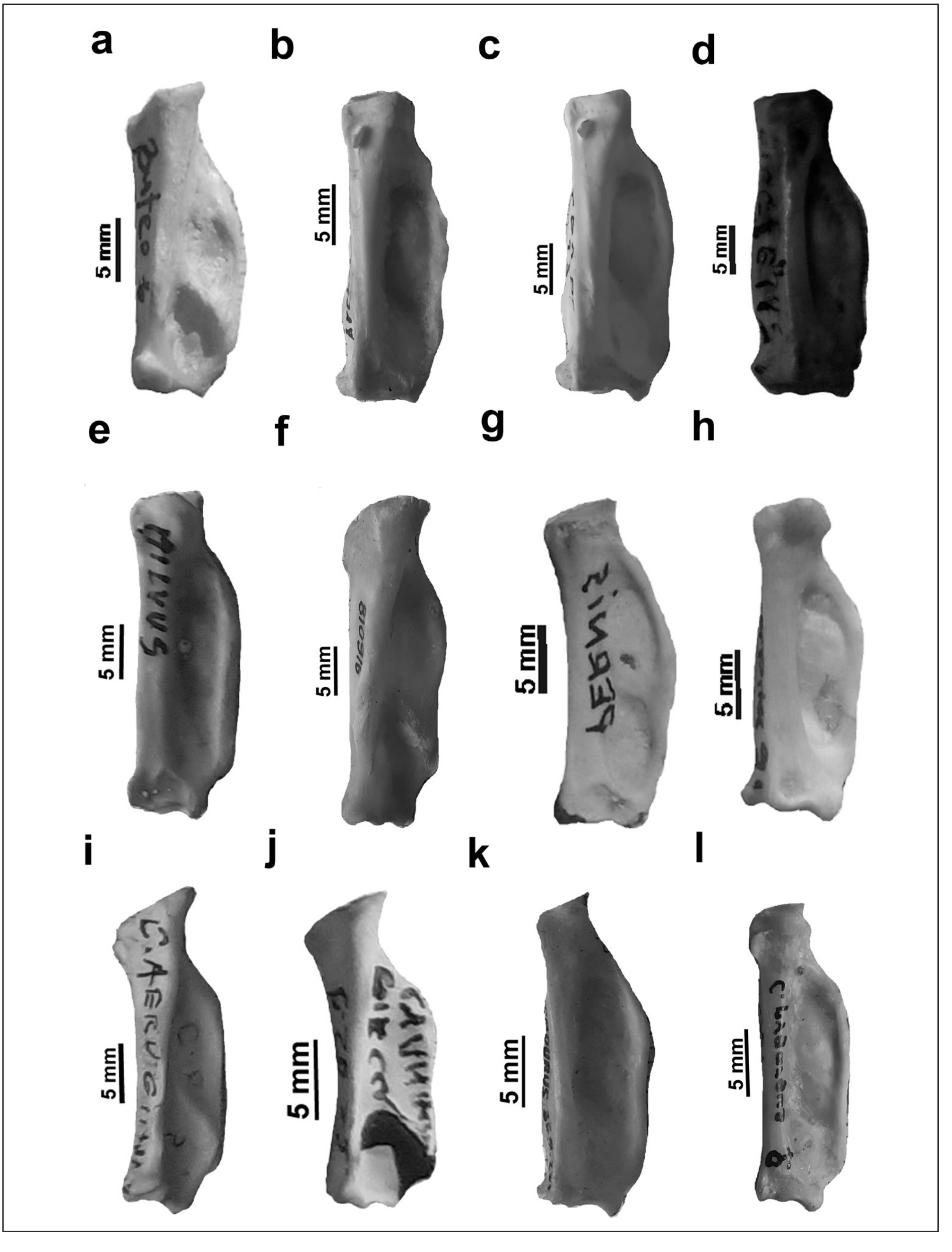

Figure 4. Left *phalanx proximalis digiti majoris* (ventral aspect)
4. ábra Bal oldali kézujjperc (1. ujjperc, II. ujj, alulnézet)
a. *Buteo buteo* (Linnaeus, 1758); b. *Buteo lagopus* (Pontoppidan, 1763); c. *Buteo rufinus* (Cretzschmar, 1827); d. *Circaetus gallicus* (Gmelin, 1788); e. *Milvus migrans* (Boddaeert, 1783); f. *Milvus milvus* (Linnaeus, 1758); g. *Pernis apivorus* (Linnaeus, 1758); h. *Accipiter gentilis* (Linnaeus, 1758); i. *Circus aeruginosus* (Linnaeus, 1758); j. *Circus cyaneus* (Linnaeus, 1758); k. *Circus macrourus* (Gmelin, 1771); l. *Circus pygargus* (Linnaeus, 1758)

In the case of falcons and kestrels *(Figure 5a–g)*:

a) Shape of *facies articularis metacarpalis*:
- protuberant: *Falco columbarius*;
- protuberant, with a well-developed blunt conelike dorsal projection; *Falco cherrug*;
- protuberant, with a well-developed pointed conelike projection: *Falco peregrinus*;
- protuberant, with a small pointed projection: *Falco subbuteo*;
- obliquely cut: *Falco rusticolus, F. vespertinus*;
- obliquely cut, with a long pointed conelike projection: *Falco tinnunculus*;

b) The arc of the *margo dorsalis*:
strongly and symmetrically arched: *Falco cherrug, F. peregrinus, F. columbarius, F. subbuteo, F. tinnunculus*;
slightly arched: *Falco rusticolus*;
the arch is cut: *Falco vespertinus*;

c) Shape of *facies articularis phalangealis*:
obliquely wavy, without a protruding dorsal projection: *Falco rusticolus, F. tinnunculus*;
obliquely wavy, with a protruding dorsal projection: *Falco cherrug, F. peregrinus, F. columbarius, F. subbuteo, F. vespertinus*

Examination of the first phalanx of the second wing finger

For the morphometric comparison, we examined the morphological variability of the first phalanx of the second wing finger. For each specimen, we used 300 sliding landmarks to examine the shape of the whole bone in ventral view.

These landmarks were allowed to slide along their corresponding curve. It is necessary in the minimalisation of the bending energy. The coordinates of the 2D landmarks were digitised using the software TpsDig 2.16 (Rohlf 2010). The resulted coordinates were transformed using the Procrustes superimposition method. The consensus configurations and relative warps were conducted. Variability in shape was assessed using the scores obtained for each individual on the first two relative warps. We conducted principal component analyses (PCA) on these morphological variables. The relative warps are corresponding to the principal components (PCs) and define the shape space in which individuals are replaced. We used PAST v.1.7 software (Hammer *et al*. 2001) for principal component analysis and to extract deformation grids. We only considered those PCs explaining individually >10% of the variance.

The first two PCs explained 53% and 21% of the variance in bone shape. The first PC axis described the curvature of the anterior surface of the proximal phalanx of the major digit (PC1). The second PC axis described the relative size of the distal and proximal epiphyses (PC2). The Osprey *(Pandion haliaetus)* and the Eastern Imperial Eagle *(Aquila heliaca)* showed the most convex shape and the Peregrine Falcon *(Falco peregrinus)* showed the most concave shape on the anterior curvature. The Red-footed Falcon *(F. vespertinus)* and the Eurasian Hobby *(F. subbuteo)* showed very narrow proximal epiphyses compared to the Red Kite *(Milvus milvus)* which showed prominent proximal epiphysis but the distal epiphysis was very narrow *(Figure 6)*.

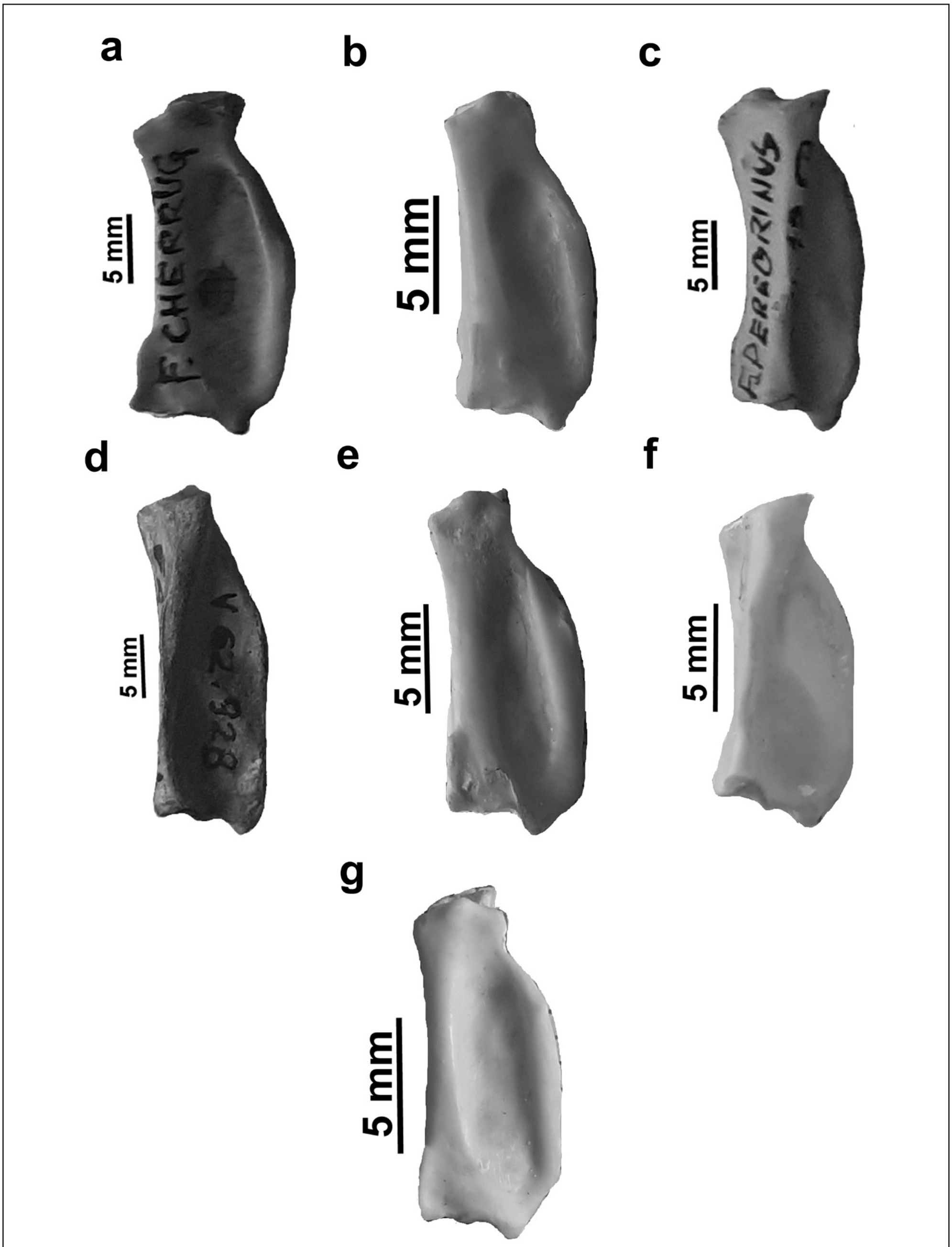

Figure 5. Left *phalanx proximalis digiti majoris* (ventral aspect)
5. ábra Bal oldali kézujjperc (1. ujjperc, II. ujj, alulnézet)
a. *Falco cherrug* (Gray, 1844); b. *Falco columbarius* (Linnaeus, 1758); c. *Falco peregrinus* (Tunstall, 1771); d. *Falco rusticolus* (Linnaeus, 1758); e. *Falco subbuteo* (Linnaeus, 1758); f. *Falco tinunculus* (Linnaeus, 1758); g. *Falco vespertinus* (Linnaeus, 1766)

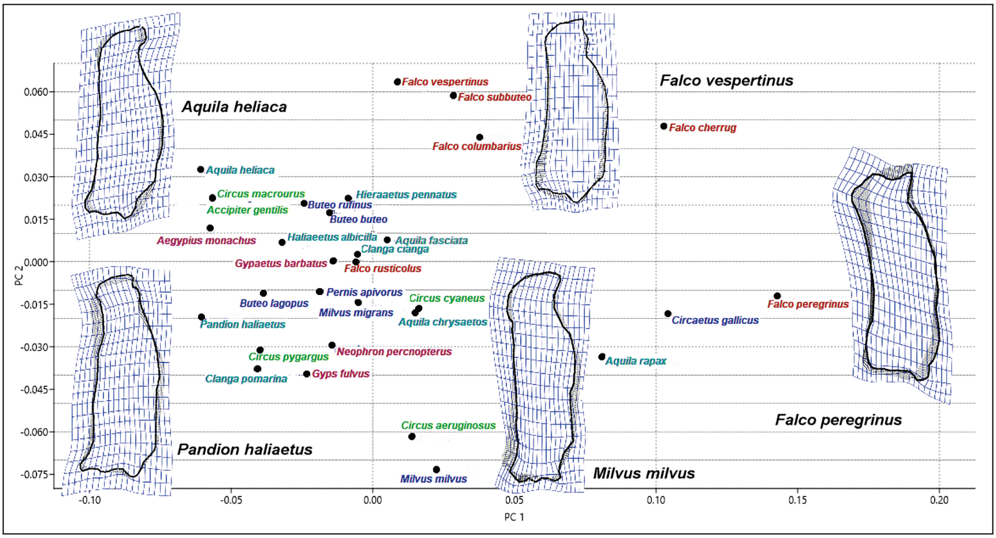

Figure 6. Graphical output of PCA performed on the two-dimensional landmark data (ventral view). PC1–PC2 biplot. The first PC axis described the curvature of the anterior surface of the proximal phalanx of the major digit (PC1). The second PC axis described the relative size of the distal and proximal epiphyses (PC2). Thick black areas show the differences compared to the computer generated mean shape

Purple: vultures; Cyan: eagles; Blue: buzzards and kites; Green: goshawk and harriers; Red: falcons and kestrels

6. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (alulnézet). A főkomponensek a csont anterior irányú görbületét (PC1) valamint a proximális és a disztális epifízisek egymáshoz viszonyított nagyságát magyarázzák (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

Lila: keselyűk; Világoskék: sasok; Kék: ölyvek és kányák; Zöld: héja és rétihéják; Piros: sólymok és vércsék

Conclusions

In the case of examined diurnal raptor species living in wet habitats, the shape and size of the phalanx is quite diverse. What is more, we see sexual dimorphism in the case of most species. This can be quite substantial in buzzards, goshawks and falcons in favour of females.

The changes in form of the studied characteristics are worth comparing in terms of size differences, since the difference between vultures and kestrels is quite significant even if the similarities in form do exist. Representatives of other families and genera are between these two extremes in terms of size.

The first *phalanx* of the second wing finger of Accipitriformes is typically long and medium wide. The length to width ratio varies between 1/2 and 1/4. More specifically, it is around 1/2 at the Egyptian Vulture *(Neophron percnopterus)*, Golden Eagle *(Aquila chrysaetos)*, Booted Eagle *(Hieraaetus pennatus)*, Bonelli's Eagle *(Aquila fasciata)*, European Honney-buzzard *(Pernis apivorus)*, Common Kestrel *(Falco tinnunculus)*, Eurasian Hobby *(F.*

subbuteo) and Red-footed Falcon *(F. vespertinus)*. This ratio is around 1/4 at the Bearded Vulture *(Gypaetus barbatus)*, Western Marsh Harrier *(Circus aeruginosus)*, while in the other species it is about 1/3.

Studying the ratio between wingspan / length phalanx x/2, from the size tables *(Table 1)* we found the followings:

In the case of the vulture – eagle group, we did not find an extraordinary relationship between the wingspan and the length of the phalanx, except of Egyptian Vulture, Bonelli's Eagle and Osprey. In the Egyptian Vulture and Bonelli's Eagle the ratio of wing length to phalanx length is much higher (39.47–47.37) than in the other species in the group (17.50–29.05). In the case of the Osprey, however, the situation is reversed (13.80–19.57).

In the case of the buzzard, kites, goshawks and harriers group, we did not find an extraordinary relationship between the wingspan and the length of the phalanx, except of European Honney-buzzard, where the ratio of wing length to phalanx length is much higher (35.53–39.47) than in the other species in the group (17.92–29.79).

In the case of the falcon and kestrel group, we found a difference between falcons (14.23–23.08) and kestrels in the wingspan and the length of the phalanx ratio, where the value is higher (22.58–27.88).

We can assume that the flight speed of these species is clearly consistent with these data but previous studies showed that the mechanism of flights in raptors is more complex (Hart *et al*. 2018, Krishnan *et al*. 2020). The effects of different attributes like body size and wing morphology on flight speed also very important, but the phylogenetic relationships accounted for an important part of the remaining variation in flight speed among species. Differences in flight apparatus and behaviour among species of different evolutionary origin, and with different ecology, behaviour and flight styles are likely to influence cruising flight in performance (Alerstam *et al*. 2007, Usherwood *et al*. 2020). Many raptors shared similar size and attributes, but the modularity of wing shape during locomotion and action has a key role because avian wings are not rigid parts of the body (Klaasen *et al*. 2016, Cheney *et al*. 2021). Previously, it was also observed that typical flight strategies of some migrating raptors that climbing rate in thermal circling did not differ between species, indicating that chiefly the strength of thermal updrafts determined the climbing rate and that morphological features were less relevant. Heavier species glided faster and had smaller gliding angles therefore body mass and size have more effect on flying performance. Eagles and buzzards are using mostly soaring and gliding flight, furthermore soaring in a straight line whilst gliding was extensively used by the Lesser Spotted Eagle *(Clanga pomarina)* and Booted Eagle and even more frequently by the species like the Griffon Vulture *(Gyps fulvus)* and Short-toed Snake Eagle *(Circaetus gallicus)* (Spaar 1997).

The tissues which are related to the metacarpophalangeal joint and the craniodorsal surface are mostly ligaments and muscles and affecting on the physical characteristics of the proximal phalanx of the major digit. On the anterior surface *tendo m. extensor longus digiti majoris* and *retinaculum dorsalis digiti majoris*, on the proximal epiphysis *tendo m. interosseus dorsalis* and *m. interosseus ventralis*, while on the distal epiphysis *m. interosseus ventralis* have key roles in the appearance of the bone (Hyeronymus 2016). The principal component analysis showed slightly overlapping in shape between the taxa but the accipitriform and

Table 1. Size table of *phalanx proximalis digiti majoris*
A – total length of bone (mm); C – breadth of proximal end; E – breadth of corpus; F – breadth of distal end. New name (Gill *et al.* 2020)

1. táblázat A *phalanx proximalis digiti majoris* mérettáblázata
A – teljes hossz (mm); C – proximális vég szélessége; E – a test szélessége; F – disztális vég szélessége. Új név – New name (Gill *et al.* 2020)

Species	New genus, sp. name	A	C	E	F	wing	wing/ phalanx
Aegypius monachus		60.00	11.50	22.00	12.00	1250-1500	20.83-25.00
Gypaetus barbatus		66.00	12.00	15.00	15.00	1155-1415	17.50-21.44
Gyps fulvus		58.00	14.50	20.00	13.50	1200-1400	20.69-24.14
Neophron percnopterus		18.00	8.00	12.00	10.00	775-850	**43.06-47.22**
Aquila chrysaetos		39.00	11.00	16.50	9.50	950-1100	24.36-28.21
Aquila clanga	*Clanga*	32.00	7.00	11.00	9.00	800-900	25.00-28.16
Aquila heliaca		39.00	6.50	11.50	7.00	900-1075	23.08-27.56
Aquila pomarina	*Clanga*	33.00	7.00	10.50	7.50	675-800	20.45-24.24
Aquila rapax		41.00	11.00	14.50	13.00	795-930	19.39-22.31
Haliaeetus albicilla		42.00	8.00	15.50	14.50	965-1240	22.98-29.05
Hieraaetus fasciatus	*Aquila fasciata*	19.00	8.50	11.00	9.50	750-900	**39.47-47.37**
Hieraaetus pennatus		22.00	7.00	9.50	5.50	500-605	22.73-27.50
Pandion haliaetus		46.00	8.00	14.00	12.00	635-900	**13.80-19.57**
Buteo buteo		23.50	5.50	7.50	6.50	545-700	23.19-29.79
Buteo lagopus		27.50	6.50	10.00	7.50	600-750	21.80-27.27
Buteo rufinus		31.50	7.00	11.00	8.50	625-740	19.84-23.49
Circaetus gallicus		34.00	9.00	13.00	12.00	810-975	23.82-28.68
Milvus migrans		30.50	9.00	10.00	7.00	800-900	26.63-29.51
Milvus milvus		34.00	8.50	10.00	8.50	875-895	25.74-26.32
Pernis apivorus		19.00	5.00	8.00	5.00	675-750	**35.53-39.47**
Accipiter gentilis		26.50	5.00	7.50	5.00	475-625	17.92-23.58
Accipiter nisus		15.50	3.00	5.50	4.00	295-400	19.03-25.81
Circus aeruginosus		28.00	7.50	7.50	5.00	575-650	20.54-23.21
Circus cyaneus		21.00	5.50	7.00	5.00	500-600	23.81-28.57
Circus macrourus		23.00	4.00	7.50	5.50	475-600	20.65-26.09
Circus pygargus		25.00	5.00	7.50	5.00	525-600	21.00-24.00
Falco cherrug		28.00	8.00	11.00	9.00	510-600	18.21-21.43
Falco columbarius		14.50	4.00	5.50	4.50	250-310	17.24-21.38
Falco peregrinus		26.00	8.50	9.00	8.00	370-600	14.23-23.08
Falco rusticolus		30.00	7.00	9.50	7.50	525-675	17.50-22.50
Falco subbuteo		16.50	4.50	6.50	4.00	410-460	**24.85-27.88**
Falco tinnunculus		15.50	5.50	6.00	4.50	350-400	**22.58-25.81**
Falco vespertinus		13.50	3.50	5.50	3.50	350-375	**25.93-27.78**

falconiform birds diverged in the morphospace. These results suggested that the attributes and geometry of the proximal phalanx of the major digit are affected rather by phylogenetic factors than physical or mechanical demands of different flight modes. Moreover, these characteristics can be used for identify the remains of raptor species.

In further studies, the phylogenetic control would be necessary. We should also increase our knowledge about the effect of growth factors and age on these parts of the avian skeletal system.

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