Analysis of skull morphometric characters in diurnal raptors (Accipitriformes and Falconiformes)

Tibor Pecsics[1*], Miklós Laczi[1,3], Gergely Nagy[1], Tamás Kondor[1] & Tibor Csörgő[2]

Abstract Diurnal birds of prey (Accipitriformes and Falconiformes) has traditionally been known as comprising a single order. Recently, this classification has been used in the non-taxonomic sense as referring to a convergent group of birds that are largely classified as predatory birds. Although these birds are similar in their morphology, the species differ in their foraging methods and prey preference. The cranial shape and the physical attributes determine the efficiency of the resource use. The aim of this study is to increase our knowledge of the relationship between skull shape, prey preference, and foraging habits. A geometric morphometric approach was used to analyse two-dimensional cranial landmarks. We used principal component (PC) analyses on measurements that may be related to prey preference and foraging habits. The PCs are resulted described the relative height of the skull and beak, the variation in the relative size, the orientation and robustness of the lacrimal bone, the variation in the relative size of the *neurocranium* compared to the *viscerocranium*, and the orientation of the palatine bone. The dietary categories significantly overlap. The skull morphology reflects more on foraging habits than diet or prey preference.

Keywords: cranial morphology, morphometric, anatomy, jaw, skull, shape, convergent evolution, diurnal predator, prey preference

Összefoglalás A nappali ragadozó madarakat (Accipitriformes és Falconiformes) ma is szokás egy csoportként kezelni, bár nem rendszertani értelemben. Külső jegyeiket és megjelenésüket tekintve nagyon hasonlóak, ám a fajok eltérnek a táplálkozás-mechanizmust és a prédaállatokat illetően. Mindezek a koponyán is megfigyelhető adaptációt mutatnak. Tanulmányunkban e madarak cranialis jegyeinek elemzésével a táplálékpreferencia, a táplálkozásmód és a morfológiai jellemzők közötti lehetséges összefüggéseket kerestük. A vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a koponya és a csőr relatív magasságát, a könnycsont nagyságát, helyzetét és robuszticitását, az agy- és arckoponya egymáshoz viszonyított nagyságát, valamint a *palatinum* relatív nagyságát és helyzetét magyarázzák. Az egyes táplálkozási csoportok nagymértékben átfednek egymással. A koponyamorfológia sokkal inkább tükrözi a táplálékszerzés módját, mint a táplálékpreferenciát.

Kulcsszavak: koponya-sajátosságok, morfometria, anatómia, állkapocs, koponya, alak, konvergens evolúció, nappali ragadozó, táplálékpreferencia

[1] *Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C, Hungary*
[2] *Department of Anatomy, Cell- and Developmental Biology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/C, Hungary*
[3] *The Barn Owl Foundation, 8744 Orosztony, Temesvári út 8., Hungary*
* *corresponding author: nobilis.equus@gmail.com*

Introduction

Birds of prey are small to large raptors which hunt and feed on other animals. Many species of these birds are apex predators in the food chain. There are insectivores, piscivores, avivores, mammalivores, scavengers, and we can find both generalist and highly specialized species (Bijleveld 1974, Cramp 1980).

Traditionally, this group includes the diurnal and the nocturnal predators. The diurnal birds of prey are formally classified into five families of three orders: Accipitridae (hawks, eagles, buzzards, harriers, kites and Old World vultures), Pandionidae (Osprey – *Pandion haliaetus*), Sagittariidae (Secretary Bird – *Sagittarius serpentarius*), Falconidae (falcons, caracaras and forest falcons) and Cathartidae (New World vultures) (Yuri *et al.* 2013, Jarvis *et al.* 2014).

Diurnal birds of prey have traditionally been treated as comprising a single order. However, as relationships between different higher taxa are uncertain and the whole assemblage is polyphyletic, that is why the phrase "diurnal bird of prey" should be used in non-taxonomic sense as referring to a convergent group of predatory birds (Helbig *et al.* 1994). Recent analyses show that the traditional raptor families Accipitridae (hawks, eagles, kites, Old World vultures) and Falconidae (falcons, caracaras) are not sister taxa (Barker *et al.* 2004, Cracraft *et al.* 2004, Hackett *et al.* 2008, McCormack *et al.* 2013, Jarvis *et al.* 2014, Prum *et al.* 2015). Currently, Accipitriformes is the order including hawks, eagles, and kites (Nagy & Tökölyi 2014), and Falconiformes are reserved for the falcons, falconets, forest falcons, and caracaras (Mindell *et al.* 2018).

Although the number of morphological similarities is great, ultimately the groups differ in their foraging methods. The foraging performance and the cranial morphology are functionally linked in a number of vertebrate taxa (Anderson *et al.* 2008). The cranial shape and the physical attributes determine the efficiency of the resource use (Dumont 2003). The feeding methods provide an example of the link between morphological modification and performance (Benkman 2003). Numerous vertebrate taxa show that cranial dimensions are related to the amount of bite force (Csermely *et al.* 1998, Ward *et al.* 2002, McBrayer 2004, Van der Meij & Bout 2004, Anderson *et al.* 2008, Sustaita & Hertel 2010). The feeding system of most vertebrates produces bite force by the musculoskeletal system of the head (Herrel *et al.* 2005).

The feeding strategies are highly diverse and the morphological adaptations for feeding are a notable feature of avian evolution (Zweers *et al.* 1994). The oral apparatus is comprised of musculoskeletal and neural systems. The avian skull shows a great variety of morphological variation (Zusi 1993). Larger animals generally have access to larger prey due to their greater muscular power and size. These factors are further related to allometry. Allometry has a key role in craniofacial form across a range of bird clades (Marugán-Lobón & Buscalioni 2006, Kulemeyer *et al.* 2009, Fabbri *et al.* 2017).

There are numerous physical similarities in the prey preference of some groups (e.g. hawks and falcons) but there are notable differences in hunting strategies (Cade & Digby 1982). For example, accipiters are known for using their legs and talons. The grip force has a clear implication and connectedness to the ability to subdue and kill prey (Csermely

et al. 1998, Csermely & Gaibani 1998). Different characteristics of the talons are also seen to have important roles. The morphology and talon size are related to grasp and killing the prey (Csermely & Rossi 2006, Fowler *et al.* 2009). Compared to the accipiters, falcons subdue their prey with their feet, but ultimately kill the prey with their beaks. Their jaws deliver powerful bites to the prey's neck and kill the prey by breaking the cervical bones, producing damage to the nerves and spinal cord (Hertel 1995, Csermely *et al.* 1998, Sustaita & Hertel 2010).

The bird-eaters have wide skulls and beaks, while the scavenger birds have narrow beaks with greater curvature (Hertel 1995, Ladyguin 2000, Jones *et al.* 2007, Sustaita & Hertel 2010).

In most avian lineages, male to male competition for females has led to an increase in male size due to sexual selection; therefore the males are larger than females (Andersson 1994, Colwell 2000). However, in some groups like raptors and owls reversed size dimorphism exists and females are the larger sex (Mueller 1990, Owens & Hartley 1998) with the exception of the New World vultures (Graves 2017). Reversed sexual dimorphism (RSD) increases with prey size, consistent with the small-male hypothesis (Andersson & Norberg 1981, Møller & Garamszegi 2012). The intrasexual dimorphism is visible in the case of numerous vertebrate taxa. In kestrels, the directional selection on a particular size may be under contrasting pressures by the environment, and in breeding females, the advantages of large size can be counterbalanced during harsh environmental conditions (Massemin *et al.* 2000). However, morphological differences in shape between males and females are undetectable (Verwaijen *et al.* 2002).

The morphology of the skull, the maxillary and mandibular characteristics and the important details of the skull structure are determinants of the different foraging groups. These two dimensional methods allow size and shape to be considered independently, preserve geometric information, and offer techniques for studying in form (Adams *et al.* 2004). A previous study in a 2-D geometric morphometric work explored the relationship among skull shape and ecology in scavenging raptors, which reflected the size and structure of the jaw muscles but did not provide further information on other trophic guilds (Si *et al.* 2015).

In this study, we investigated the cranial and morphological diversity among the different groups. Our objective was to increase our knowledge on the relationship between skull shape and foraging habits of diurnal raptors, to find those characters that are related to diet and prey preference, and to find the possible convergent attributes. The differences in force acting on the beak during feeding may be related to skull geometry and jaw musculature. If there is a significant overlap in skull geometry between the species, it would suggest that skull geometry has evolved along similar pathways and has the same mechanical demands. The differences between the species may reflect selection pressures related to the different foraging habits. To investigate the morphological diversity of the skulls between the species, we used landmark-based morphometric methods.

Materials and methods

Specimens

This study is based on 142 skulls of 81 species. All skulls are from adult specimens of raptors and belong to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural History Museum (Budapest, Hungary), and the digital archives of Wageningen University (Wageningen, Netherlands) and Canterbury Museum (Christchurch, New Zealand). No bird has been killed to get its skull; all birds died either of natural causes, accidental death or died in captivity.

Groups and diet

Before the analyses, we created seven groups, which represent the following diet categories (Hertel 1995, Guangdi *et al.* 2015). This study seeks to test that the different prey preference may have an effect on skull morphology.
− A: Avivores (Newton 1978, Lindberg & Odsjö 1983, Hinsley *et al.* 1995, Dixon *et al.* 2018)
− B: Mammalivores (Korpimäki 1985, Puzović 2008, Pomichal *et al.* 2014, Kotymán *et al.* 2015)
− C: Generalists (Bielefeldt *et al.* 1992, Graham *et al.* 1995, Tóth 2014)
− D: Herpetivores (Bakaloudis *et al.* 1998)
− E: Piscivores (Gende *et al.* 1997, Sulkava *et. al* 1997)
− F: Scavengers (Brown & Plug 1990, Moreno-Opo *et al.* 2010)
− G: Insectivores (Itämies & Mikkola 1972, Palatitz *et al.* 2015, Szövényi 2015).

Landmarks and procedures

The variation of cranial morphology is analysed using landmark-based geometric morphometry. In our former study, we used conventional morphometric variables which were selected *a priori* (Pecsics *et al.* 2017), however in this case the meaningful variables are discovered by the analysis presented in a more recent study (Pecsics *et al.* 2018). We should not choose them before the analysis. We tried to find landmarks for this analysis to cover the geometric form of the skull. The landmarks provide a comprehensive sampling of morphology and the features of biological significance can be explored. The ideal landmarks are discrete and noticeable anatomical features, do not alter their topological positions relative to other landmarks, and provide adequate coverage of the morphology (Zelditch *et al.* 2004). The landmarks were taken from high resolution (1200×1600 pixels) photos. We took 3 photographs from each specimen (lateral, ventral, and dorsal) with closed jaws and without lower jaw. Images were standardised for the *foramen magnum occipitale* and the tip of the beak. We investigated the repeatability of the measurements by Spearman's correlation. The test was between two separate digital measures performed on skull photos ($n = 20$). For each specimen, 12 fixed landmarks *(Table 1)* were recorded in ventral view

Table 1. Number and description of land-marks. Terminology according to (Baumel 1993, Sun *et al.* 2018)

1. táblázat Az egyes landmarkok száma és le-írása. Terminológia Baumel (1993) és Sun *et al.* (2018) alapján

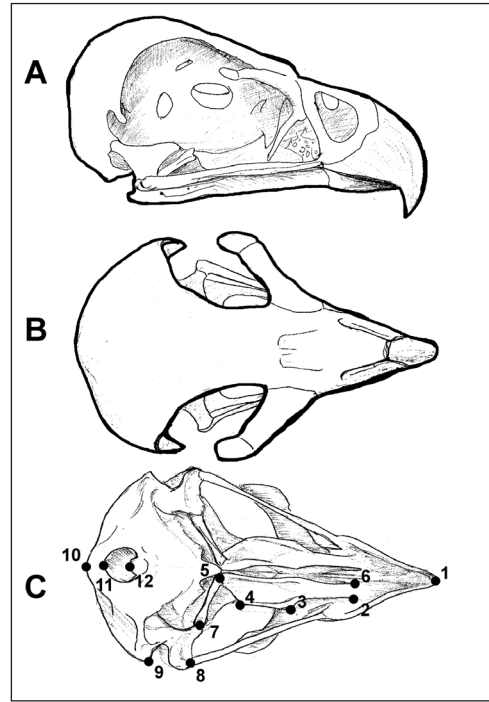| Number of landmark	Description of landmark
1	tip of the maxilla
2	the lateral associating point of palatine and maxilla
3	the most anterior-lateral point of pars lateralis
4	the most posterior-lateral point of pars lateralis
5	processus pterygoideus of palatine
6	articulation point of palatine and maxilla
7	articulation point pf pterygoid and quadrate
8	articulation of quadrate and jugal
9	most lateral point of opisthotic
10	prominentia cerebellaris
11	most caudal point of foramen magnum
12	most caudal point of condylus occipitalis

Figure 1. Position and number of landmarks. A: whole skull shape in lateral view, B: whole skull shape in dorsal view, C: the shape fixed landmarks in ventral view (numbers correspond to *Table 1*)

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: a teljes koponya oldalnézetből, B: a teljes koponya felül-nézetből, C: fix landmarkok alulnézet-ből (a számok megnevezését lásd az *1. táblázat*ban)

(Guangdi *et al.* 2015, Sun *et al.* 2018). We used 800 sliding landmarks to examine the shape of the whole skull in dorsal and lateral view *(Figure 1)*. These landmarks were al-lowed to slide along their corresponding curve due to the minimalization of the bending en-ergy. The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010) and were transformed using the Procrustes superimposition method. Consensus con-figurations 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 princi-pal component analyses (PCA) on these morphological variables. The relative warps cor-respond to the principal components (PCs) and define the shape space in which individu-als are replaced. We used PAST v.1.7 software (Hammer *et al.* 2001) to perform principal component analysis and extract deformation grids. We only considered those PCs which explain >10% of the variance.
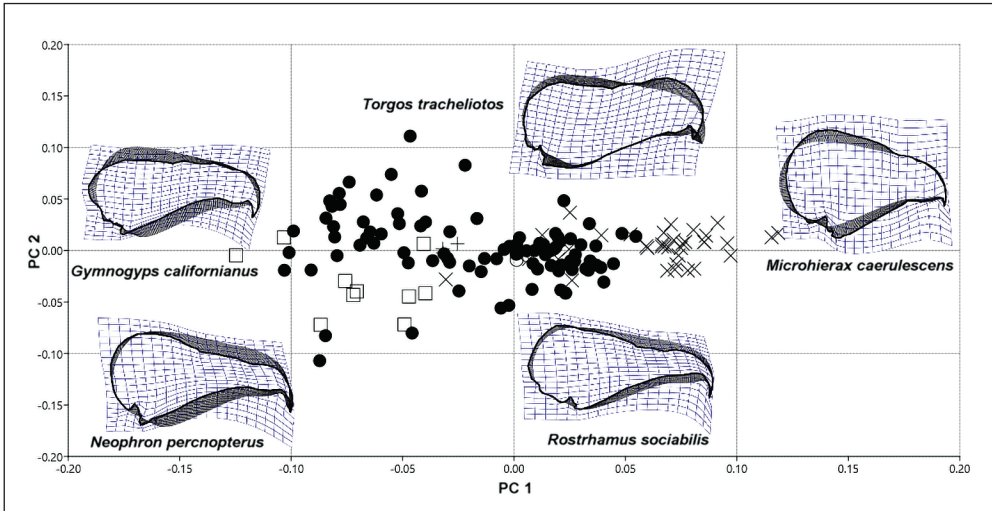
Figure 2. Graphical output of PCA performed on the two-dimensional landmark data (lateral view). PC1-PC2 biplot. The first PC axis described the relative height of the skull (PC1). The second PC axis described the relative highness of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae

2. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (oldalnézet). Az első főtengely a koponya relatív magasságát magyarázza (PC1). A második főtengely a csőr relatív magasságával hozható kapcsolatba (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae
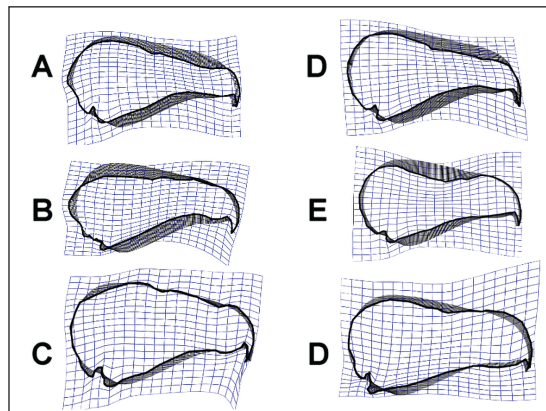

Figure 3. Various vulture species sharing very similar convergent attributes. A: Black Vulture *(Coagyps atratus)*, B: Californian Condor *(Gymnogyps caliornianus)*, C: King Vulture *(Sarcoramphus papa)*, D: Hooded Vulture *(Necrosyrtes monachus)*, E: White-backed Vulture *(Gyps africanus)*, F: Rüppell's Griffon Vulture *(Gyps rueppelli)*

3. ábra Az egyes keselyűfajok hasonló konvergens bélyegeket hordoznak. A: Hollókeselyű *(Coagyps atratus)*, B: Kaliforniai kondor *(Gymnogyps caliornianus)*, C: Királykeselyű *(Sarcoramphus papa)*, D: Csuklyás keselyű *(Necrosyrtes monachus)*, E: Fehérhátú keselyű *(Gyps africanus)*, F: Karvalykeselyű *(Gyps rueppelli)*

Results

Our measures were significant, irrespective of measuring mode (all $r > 0.97$, all $P < 0.0001$).

The first analysis focused on the whole skull from lateral view *(Figure 2)*. We used sliding landmarks (800) to describe the cranial shape of the raptors. The first two PCs explained 59% and 17% of the variance in skull shape. The first PC axis described the relative height of the cranium (PC1). The Old World and New World vultures have long narrow head with relatively long beaks, while falcons and falconets have broad and round *neurocraniums* with short beaks. The second PC axis described the relative highness of the beak (PC2). Species like Lappet-faced Vulture *(Torgos tracheliotos)*, Cinereous Vulture *(Aegypius monachus)*, Philippine Eagle *(Pithecophaga jefferyi)* and Steller's Sea Eagle *(Haliaeetus pelagicus)* have high beaks and longer culmens. The Snail Kite *(Rosthramus sociablis)*, Black Vulture *(Coragyps atratus)*, Hooded Vulture *(Necrosyrtes monachus)* and Egyptian Vulture *(Neophron percnopterus)* have a very narrow and slender beak. Old World vulture and New World vulture species share similar morphology *(Figure 3)*.

During the second analysis we used sliding landmarks (800) to describe the skull in dorsal view. The first two PCs explained 63% and 21% of the variance in shape *(Figure 4)*. The first PC axis described variation in the relative size of the lacrimal bone and the beak (PC1). The

Figure 4. Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1-PC2 biplot. The first PC axis described variation in the relative size of the lacrimal bone and the beak (PC1). The second PC axis described differences in the orientation and robusticity of the lacrimal bone (PC2). Thick black areas show the differences compared to the computer generated mean shape
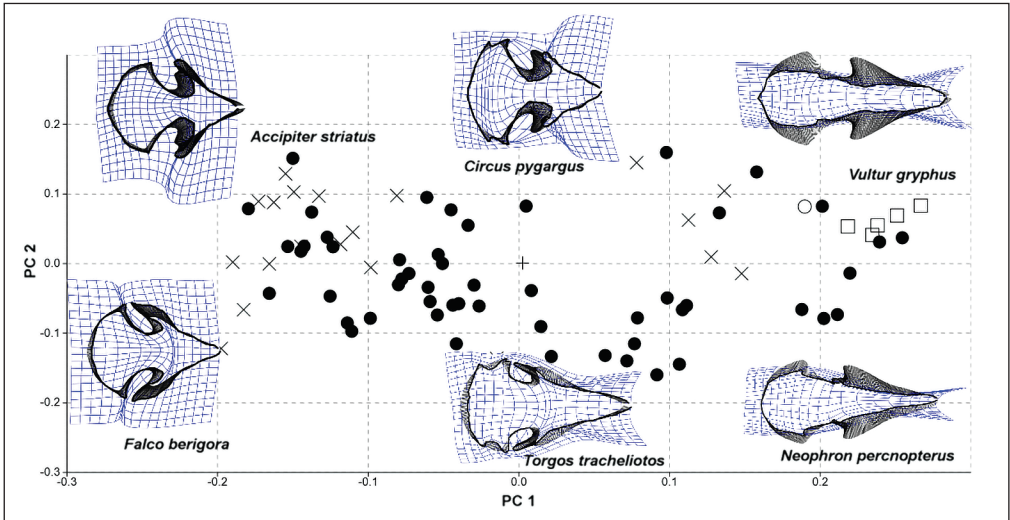
● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae

4. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). Az első főtengely (PC1) a könnycsont és a csőr relatív nagyságát, a második főtengely a könnycsont relatív helyzetét és robuszticitását magyarázza. A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

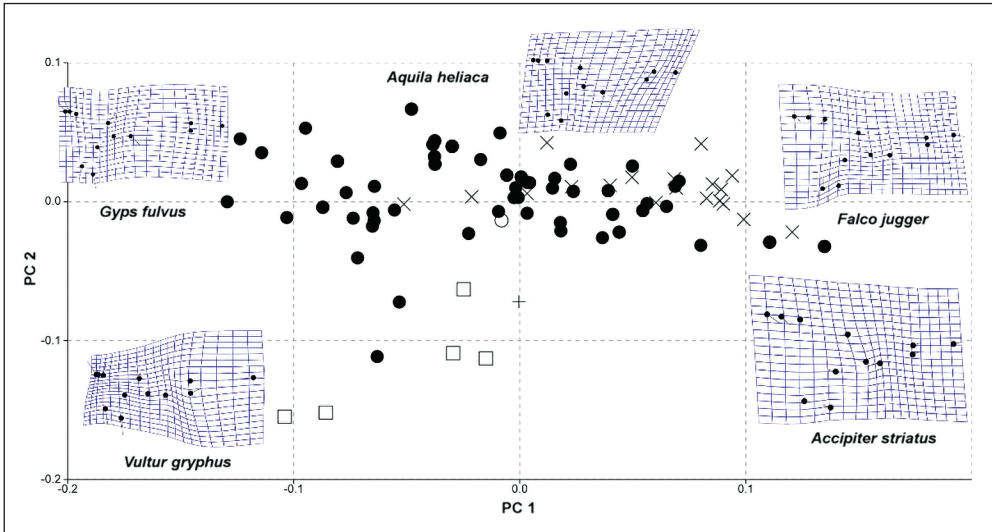● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae

Figure 5. Graphical output of PCA performed on the two-dimensional landmark data (ventral view). PC1-PC2 biplot. The first PC axis described variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC1). The second reflects the relative size of the palatine bone and its distance from the tip of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae

5. ábra A PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet). A PC tengelyek a *neurocranium* és a *viscceroscranium* relatív nagyságát (PC1), valamint a *palatinum* relatív nagyságát és távolságát mutatják a csőrhegytől (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

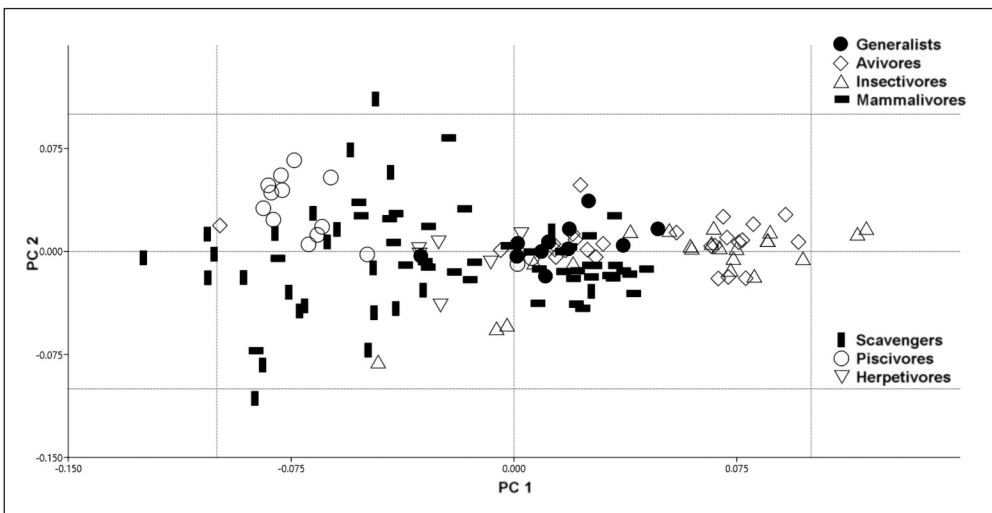● Accipitridae, × Falconidae, □ Cathartidae, ○ Pandionidae, + Sagittaridae

Figure 6. The species of different diet categories combined with the cranial shape in ventral view
6. ábra Kombinált ábra az egyes fajok oldalnézeti koponyaalakja és táplálékbázisa megjelenítésével

falcons and *Accipiter* species have long lacrimal bones and shorter beaks compared with vultures with very tiny lacrimal bones and long beaks. The second PC axis (PC2) described differences in the orientation and robustness of the lacrimal bone *(Figure 4)*.

The third analysis tried to describe the shape of the *cranium* fixed landmarks (12) in dorsal view. The first two PCs explained 52% and 21% of the variance in shape. The first PC axis described variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC1) and the second reflected to the relative size of the palatine bone and its distance from the tip of the beak (PC2). The analysis showed that New World vulture species differ considerably from other raptors *(Figure 5)*.

In every case, the generalist species are in the middle of the morphospace.

We tried to identify the differences between the diet categories *(Figure 6)*. There are no clear differences between the categories, as different groups are overlapping.

Discussion

We found that in the lateral view there are differences in the shape of the relative height of the cranium and the beak. Larger species have longer beaks compared to the *neurocranium*. The allometric head growth reflected variation in head length. It can explain some of the differences between species because the smaller species usually have bigger *neurocranium* and smaller *viscerocranium*. Allometric patterns within populations do not necessarily parallel interspecific allometry (Grant *et al.* 1985). The shape of the skull of vulture species (e.g. Andean Condor) strongly differs from the skull of small raptors like falconets (e.g *Microhierax caerulescens*) and small accipitrids *(Accipiter nisus)*. But at the similar size, for example Egyptian Vulture *(Neophron percnopterus)* and bigger falcons *(Falco cherrug, Falco rusticolus)*, species also strongly differ due to the variant foraging habits and mechanical demands. Smaller and slender beaks allow the bird to deftly collect small food items from difficult to reach places. The Snail Kite *(Rosthramus sociablis)*, Black Vulture *(Coragyps atratus)*, Hooded Vulture *(Necrosyrtes monachus)* and Egyptian Vulture *(Neophron percnopterus)* have very narrow and slender beak. Molluscivore Snail Kite extracts the food with a highly specialized bill from the snail shell (Bergmann *et al.* 2013). Smaller vulture species have similar bills due to the same conditions. These species are scavengers that feed primarily on carrions, collecting the small meat pieces from between the ribs, bones, and holes. This action demands a very similar beak shape. Larger vulture species have even larger and more hooked bills. Only the largest species (Lappet-faced Vulture and Cinereous Vulture) can tear open a big carcass, later allowing smaller vulture species to access the innards (Kruuk 1967, Schüz & König 1983, Hille *et al.* 2016, Ballejo *et al.* 2018). Steller's Sea Eagle, Philippine Eagle and Harpy Eagle *(Harpia harpyja)* have also high beaks and long culmens similar to the larger vulture species. The diets of these predators' consist primarily of live prey. While tearing the prey, the bigger and stronger beak is necessary due to the larger size of their prey. Sometimes raptors swallow the prey animal whole but larger prey size demands that the raptor possess stronger beaks and requires them to use their feet and claws to tear apart their prey, enabling them to swallow the pieces bit by bit.

Without big claws, larger scavengers need stronger adductor and neck muscles (Kulemey-er *et al.* 2009). In our analyses, the extinct Haast's Eagle *(Harpagornis moorei)* was mor-phologically closer related to vultures and sea eagles. The fossil data and remains suggest that the giant eagle was an active avivore hunter (Brathwaite 1992). Accipitrid raptor's feet and claws have a key role in immobilizing, killing and treating the prey (Csermely & Gai-bani 1998, Fowler *et al.* 2009). The skull morphology is reflecting more on foraging hab-its than diet or prey preference. The falcons have shorter and stronger beaks because these species are killing their prey with their bite (Hull 1991, Sustaita & Hertel 2010). Like other bird taxa, the strong and tapered beak is in positive correlation with bite performance (Van der Meij & Bout 2004, Herrel *et al.* 2005). As a result of convergent evolution, different scavengers share very similar morphology. These species have slender and lower skulls, longer bills, small sideward orbits, and caudally positioned quadrates. New World vultures can be distinguished by their large nostrils, narrow crania, and small orbits, and the nostrils are not divided by a septum.

The second analysis showed obvious differences between the Sharp-shinned Hawk *(Ac-cipiter striatus)* and Andean Condor *(Vultur gryphus)*. The orbit size is associated with the mobility and the size of prey. Scavengers have small orbits with very tiny lacrimal bones, due to dead and immobile prey. Orbits of other groups of raptors are even larger. The pur-suit-hunter insectivores and avivores have very large orbits with long lacrimal bones which correspond with acute vision and broad visual field (Martin 2007). More evolved binocular vision enables them to examine environments without moving the neck (Jones *et al.* 2007). The orbits of these species are larger and more anterior in position (Heesy 2004). While fly-ing, pursuit-hunters always catch prey by initiating quick, stooping attacks above prey ani-mals (O'Rourke *et al.* 2010). The larger species also have large, round cranium which sug-gests that these species should have excellent flying and maneuvering skills.

Mammalivore species bear a reduced attachment area for the adductor muscles, a rela-tively large palatine, long maxilla, and caudally positioned quadrate (Sun *et al*. 2018). The caudally positioned quadrate can increase the bite force (Van der Meij & Bout 2004). The herpetivore species have very similar attributes as mammalivore raptors due to the same mechanical demands. The mammalian and reptilian prey animals may have tougher skin (Hertel 1995).

The third analysis showed differences in the relative length of the cranium. Larger species have longer bills and more caudally positioned quadrate bone and *foramen magnum occipi-tale*. *Aquila* and *Haliaeetus* species have large palatine with wide quadrate bone. The other big raptors (Harpy and Philippine Eagle) share similar attributes. Convergent evolution and similar ecological demands allow that hawk and eagle-like species evolved in different sub-families (Haring *et al.* 2007). We also found in our analyses that Caracara species are very close to buzzards and closer to the smaller vulture species in morphospace. These scaven-gers largely differ from the other falcon species. The New World vultures showed extremi-ties with relative long and narrow craniums but relatively short and divided palatine bones with long maxilla. This could be due to the highly developed nasal region of these species; it is a well-known fact that these birds have excellent sense of smell whereas the Old World vultures find carcasses only by sight (Houston 1986).

The study showed that the generalist species are in the middle of the morphospace, which corresponding with the relatively high degree of overlap in skull shape and diet. These non-specialised raptors are very successful and have a wide range in prey spectrum and distribution.

In future studies, it would be interesting to perform combined analyses with cranial shape and attributes of the leg and talons. Similarities in the skull shape can reflect also the phylogenetic relation. In this study, we did not investigate the effect of phylogeny. The phylogenetic control would be necessary in a further analysis.

Acknowledgements

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