Skull morphometric characters in parrots (Psittaciformes)

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Abstract Parrots (Psittaciformes) are a unique and diverse avian group and vary tremendously in size, shape, and colour. Mainly distributed throughout the tropics and subtropics, most species of parrots are largely or exclusively arboreal with several exceptions. The species also differ in diet and habitat, which led to different musculoskeletal adaptations of the skull. However, parrots have conspicuous generalized external features; in this recent study, we tried to increase our knowledge of the cranial shape 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 diet. The PCs described the relative height of the *cranium*, the relative length and curvature of the beak, differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits, variation in the size and position of the palatine bone and the relative width of the *cranium,* and variation in the relative size of the *neurocranium* compared to the *viscerocranium*. The dietary categories overlap in the morphospace but the analysis in lateral and ventral view resulted in significant differences.

Keywords: cranial morphology, morphometrics, anatomy, jaw, skull, shape, convergent evolution, parrot, diet preference, bill shape

Összefoglalás A papagájalakúak rendje (Psittaciformes) egyedi és jól elkülöníthető madárcsoport, amelybe méretükben és színezetükben rendkívül változatos fajok tartoznak. Néhány kivételtől eltekintve a fajok többsége trópusi, illetve szubtrópusi erdőkben és ligetekben található. Az egyes fajok különböznek méretükben és táplálékpreferenciájuk tekintetében, ennek megfelelő eltéréseket mutatnak koponyájuk csontozatában és izomzatában. Habár a papagájok jól megfigyelhető egyetemes tulajdonságokat mutatnak, jelen vizsgálatunkban a cranialis jegyek és a táplálékpreferencia közötti lehetséges kapcsolatokat kerestük. A geometriai morfometriai vizsgálat során kétdimenziós landmarkok használatával főkomponens-analíziseket végeztünk. A főkomponensek a koponya relatív magasságát, a csőr relatív hosszúságát és görbületét, a könnycsont relatív helyzetét és a szemüreg felső részének ívét, a szájpadcsont viszonylagos helyzetét és nagyságát, valamint az agykoponya és az arckoponya egymáshoz viszonyított nagyságát mutatják. Az egyes táplálkozási csoportok átfednek egymással, azonban a vizsgálatok oldal- és alulnézetben észrevehető különbségeket mutattak.

Kulcsszavak: koponyasajátosságok, morfometria, anatómia, állkapocs, koponya, alak, konvergens evolúció, papagáj, táplálékpreferencia, csőrforma

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Introduction

Parrots (Psittaciformes) are a unique and diverse group of birds. The species vary tremendously in size, shape, and colour. Although there is an extraordinary degree of variation in their external appearance, parrots are one of the most easily recognisable birds due to their conspicuous external features. Prominent and obvious characteristics include the strong curved bill, fleshy cere, proportionately large, broad head, and zygodactyl feet (Forshaw 2010). The parrots are mainly distributed throughout the tropics and subtropics and most species are largely or exclusively arboreal, but there are exceptions. Some species are exclusively terrestrial, inhabit grasslands, or prefer alpine vegetation (Bryant 1994).

This large and diverse order is traditionally classified into four families: Nestoridae (New Zealand parrots), Cacatuidae (cockatoos), Psittacidae (African and NewWorld parrots) and Psittaculidae (Old World parrots) (Christidis & Boles 2008, Hackett *et al.* 2008, Mayr 2010, Jarvis *et al.* 2014, Prum *et al.* 2015, Provost *et al.* 2017). The order contains over 390 species in 74 genera and most of the species are concentrated in the tropical and subtropical regions of the Southern Hemisphere (Barker *et al.* 2004, Homberger 2006, McCormack *et al.* 2013). Diversity in South America and Australasia suggests that the order may have evolved in Gondwana during the Cretaceous period (Cracraft 1973, Barker *et al.* 2004, Cracraft *et al.* 2004, Forshaw 2010). The few early fossils that have been discovered do not have modern parrot-like cranial morphology (Mayr *et al.* 2013). However, parrots possibly evolved in Gondwana; early psittaciform remains have mainly been found in the northern hemisphere and fossil evidence of a stem group in Europe concludes that there was diversification following the Mesozoic era (Dyke & Mayr 1999, Waterhouse 2006).

Parrots are the focus of an increasing number of studies in such areas as vocal communication (Bradbury 2003), brain evolution (Iwaniuk *et al.* 2005, Carril *et al.* 2016) and craniofacial morphology (Tokita 2006, Tokita & Nakayama 2014).

These birds developed novel cranial morphology and show considerable morphological diversity in the cranial musculoskeletal system. This includes two novel structures: the suborbital arch and the *musculus pseudomasseter* (Tokita 2003, Tokita *et al.* 2007). A previous study in geometric morphometric work explored the relationship among skull shape and ecology, which reflected the size and structure of the jaw muscles. Parrots are characterised by their large beaks and are renowned for their ability to produce high bite forces. Factors that influenced the evolution of psittaciform birds' distinctive cranial morphologies were tested (Bright *et al.* 2019).

Although the fundamental pattern of the skull development of birds is conserved in parrots, some differences were observed between parrots and other avian orders. In parrots, the vacuity in the interorbital septum did not emerge throughout ontogeny. This feature is referring to the attachment of the unique jaw muscle at interorbital septum, *musculus ethmomandibularis*. In parrots, the cranio-facial hinge was brought about by secondary transformation of dermal bones. In other groups of birds with a standard prokinetic skull, the nasal-frontal suture directly becomes a hinge of bending. The parrot-specific structures like suborbital arch and cranio-facial hinge are not seen until the juvenile birds leave the nest and can feed alone. These structures are necessary for eating tough food material (Tokita 2003).

Parrots occupy varied dietary niches that require an agile, mobilized, but sturdy feeding apparatus. Cranial kinesis, or the flexibility of intracranial joints, has a central role in the unique feeding apparatus (Cost *et al.* 2017).

Neotropical parrots are ecologically important because of their role as seed eaters and the impact on the structure of tropical forests (Janzen 1969, Terborgh *et al.* 1990, Galetti & Rodrigues 1992). Neotropical species usually forage for nectar, flowers, leaves, fruit pulp, and seeds. Due to the mosaics of the vegetation, these birds use the abundantly available resources. Smaller and larger species foraged on fruits; parakeets largely consumed the pulp, while larger parrot species used pulp and seeds (Ragusa-Netto & Fecchio 2006).

The diversity in morphology, body size, and foraging behaviour are in relation to diet and geographical range. Parrots are granivores rather than seed dispersers and in many cases where they are seen consuming fruit, they are only eating the fruit to get at the seed. The seeds often have poisons or toxins; therefore, the parrots carefully remove coats of the seed. Geographical range and body size explain diet composition rather than phylogeny (Benavidez *et al.* 2018).

The foraging performance and the cranial morphology are functionally linked to numerous vertebrate taxa (Dumont 2003, Anderson *et al.* 2008). The feeding system of most vertebrates produces bite force by the musculoskeletal system of the head (Herrel *et al.* 2005). The feeding methods provide an example of the link between morphological modification and performance (Benkman 2003). Numerous vertebrate taxa show that cranial attributes are related to 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 strategies are highly diverse and the morphological adaptations for feeding are a notable feature of avian evolution (Zweers *et al.* 1994). The avian skull shows a great variety of morphological variation (Zusi 1993). Allometry possibly has a key role in craniofacial form across a range of avian orders (Colwell 2006, Marugán-Lobón & Buscalioni 2006, Kulemeyer *et al.* 2009, Fabbri *et al.* 2017).

Most of the parrot species are omnivorous (Lill 2009) and opportunistic when presented with new feeding opportunities, but sometimes also feed on plants and insects (Clarke 1971, Brejaart 1988).

Lories, lorikeets, hanging parrots, and swift parrots are primarily nectar and pollen consumers. Specialization to nectarivory is associated with radiations within different bird groups. Their shift to nectarivory may have created an ecological opportunity that promotes species proliferation and radiation. Morphological specializations of the feeding apparatus to nectarivory have been described for parrots (Schweizer *et al.* 2014).

Some other examples are more extraordinary than nectarivore species. Pigmy parrots (*Micropsitta* spp.) are suspected to rely heavily on fungi and lichens for food (Rand 1942, Elliott *et al.* 2019). Kea have been reported feeding on chicks and eggs (Temple 1996), mice (Beggs & Mankelow 2002), and domesticated sheep (Marriner 1908) and carrion (Edgar 1974).

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. The

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).

In this preliminary 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 the foraging habits of parrots and possibly find those characteristics that are related to diet and foraging habits. We also tried to find the convergent attributes. The differences in force acting on the beak during feeding may be related to skull geometry and jaw muscles. The significant overlap in skull geometry between the species would suggest that skull geometry has evolved along similar pathways. Differences may reflect selection pressures related to the different foraging habits and mechanical demands. To investigate the morphological diversity of the skulls, we used landmark-based morphometric methods.

Materials and methods

Specimens

This study is based on 150 skulls of 108 species. All skulls are from adult specimens of parrots 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). No bird has been killed to obtain its skull; all birds died either of natural causes, whether accidental death or whether it died in captivity.

Groups and diet

This study seeks to test that the different diet and foraging method may have an effect on skull morphology. Before the analyses, we created five groups which represent the following diet categories (Pizo *et al.* 1995, Perrin 2009, Lee *et al.* 2014).
– A: Nectarine, soft food item eaters (Schweizer *et al.* 2014)
– B: Predominantly seed eaters (Boyes & Perrin 2009)
– C: Big and rough food item eaters (Wood 1988, Vaughan *et al.* 2006)
– D: Generalists (McInnes & Carne 1978, Brejaart 1988, Galetti 1993, Wirminghaus *et al.* 2002, Boyes & Perrin 2010)
– E: Other (Diamond & Bond 1991, Schwing 2010).

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). In this case, the meaningful variables are discovered by the analysis that was performed in previous studies (Pecsics *et al.* 2018, 2019).

Table 1.   Number and description of landmarks (terminology according to Baumel 1993, Sun *et al*. 2018)
1. táblázat Az egyes landmarkok száma és leírása (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	most caudal point of the maxilla
9	articulation of quadrate and jugal
10	most lateral point of opisthotic
11	most caudal point of *condylus occipitalis*
12	most caudal point of *foramen magnum*
13	*prominentia cerebellaris*

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. Ideal landmarks are discrete and noticeable anatomical features that do not alter their topological positions, providing 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 the lower jaw. Images were standardised for the *foramen magnum occipitale* and the tip of the mandible. 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, 13 fixed landmarks *(Table 1)* were recorded in ventral view (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 allowed to slide along their corresponding curve due to the minimization of the bending energy. The coordinates of the landmarks were digitised using TpsDig 2.16 software (Rohlf 2010) and were transformed using the Procrustes superimposition method. 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 correspond 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) to perform the principal component analysis and extract deformation grids. We only considered those PCs which explain >10% of the variance.
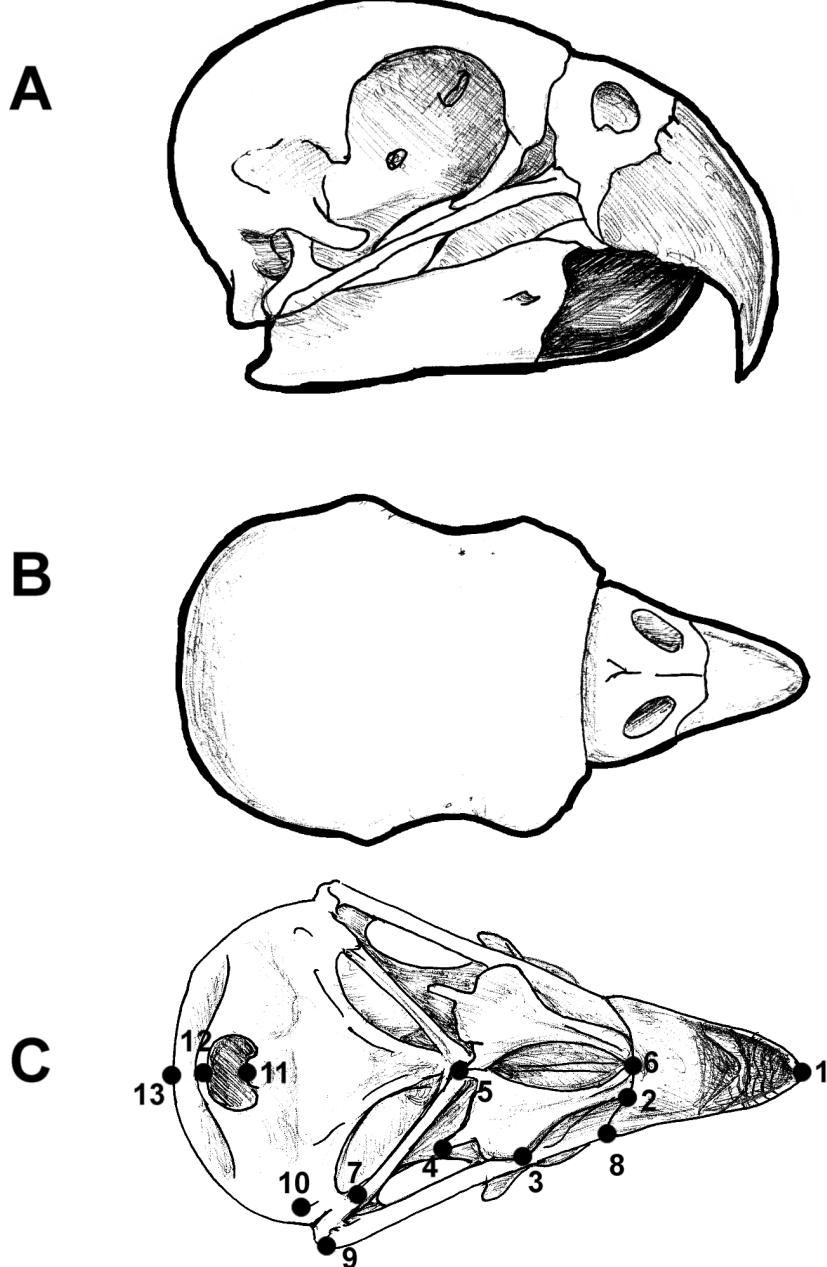
Figure 1. Position and number of landmarks. A: whole skull shape in lateral view, B: whole skull shape in dorsal view, C: the shape fixed landmarks in ventral view (numbers correspond to *Table 1*)

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: a teljes koponya oldalnézetből, B: a teljes koponya felülnézetből, C: fix landmarkok alulnézetből (a számok megnevezését lásd a *1. táblázatban*)

Results

Our measures were repeatable, irrespective of measuring mode (all $r > 0.98$, all $P < 0.001$).

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 parrots. The first three PCs explained 38%, 23% and 14% of the variance in skull shape. The first PC axis described the relative height of the *cranium* (PC1). The macaw species have robust heads with relatively high and massive beaks, while lories and lorikeets have relatively longer and slender skulls with short and delicate beaks. The second and third PC axes described the relative length and curvature of the beak (PC2 and PC3). Species like Barred Parakeet *(Bolborhynchus lineola)*, Turquoise Parrot *(Neophema pulchella)* and Red-headed Lovebird *(Agapornis pullarius)* have very short and curved beaks. The Kea *(Nestor notabilis)* and Slender-billed Parakeet *(Enicognathus leptorhynchus)* are bearing a long, narrow, and slender beak. True parrots and cockatoos 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 51% and 17% of the variance in shape *(Figure 4)*. The first PC axis described variation in the relative length of the beak (PC1). The Red-shouldered Macaw *(Diopsittaca nobilis)* and Australian King-parrot *(Alisterus scapularis)* have relatively big *neurocranium* and shorter beaks compared with Kea *(Nestor notabilis)* and Slender-billed Parakeet *(Enicognathus leptorhynchus)*. The second PC axis (PC2) described differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits *(Figure 4)*.

For the third analysis, we used fixed landmarks (13) to describe the shape of the *cranium* in dorsal view. The first two PCs explained 48% and 16% of the variance in shape. The first PC axis described the size and position of the palatine bone (PC1). The second PC axis reflected the relative width of the cranium and variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC2) *(Figure 5)*.

In every case, the generalists are in the middle of the morphospace. We tried to fix the skulls in a standard position to minimize the impact of cranial kinesis *(Figure 6)*.

Except Kea – which is bearing very unique skull attributes – there are no clear differences between taxonomic groups and the species are overlapping in the morphospace.

Discussion

The first analysis resulted differences in the relative height of the *cranium* and the beak in lateral view. Larger species usually have larger beaks compared to the *neurocranium*. The macaw species have robust heads with high and massive beaks. The Hyacinth Macaw *(Anodorhynchus hyacinthinus)* and the Palm Cockatoo *(Probosciger aterrimus)* have strong beaks; these species are able to crack hard food items, like nuts of pods and coconuts. The Alexandrine Parakeet *(Psittacula eupatria)* shares similar morphological attributes to the Scarlet Macaw *(Ara macao)*. The shape of the skull of the macaw species strongly differs from the skull of small lorikeets (e.g. *Charmosyna pulchella*) and small hanging parrots (e.g. *Loriculus vernalis*).
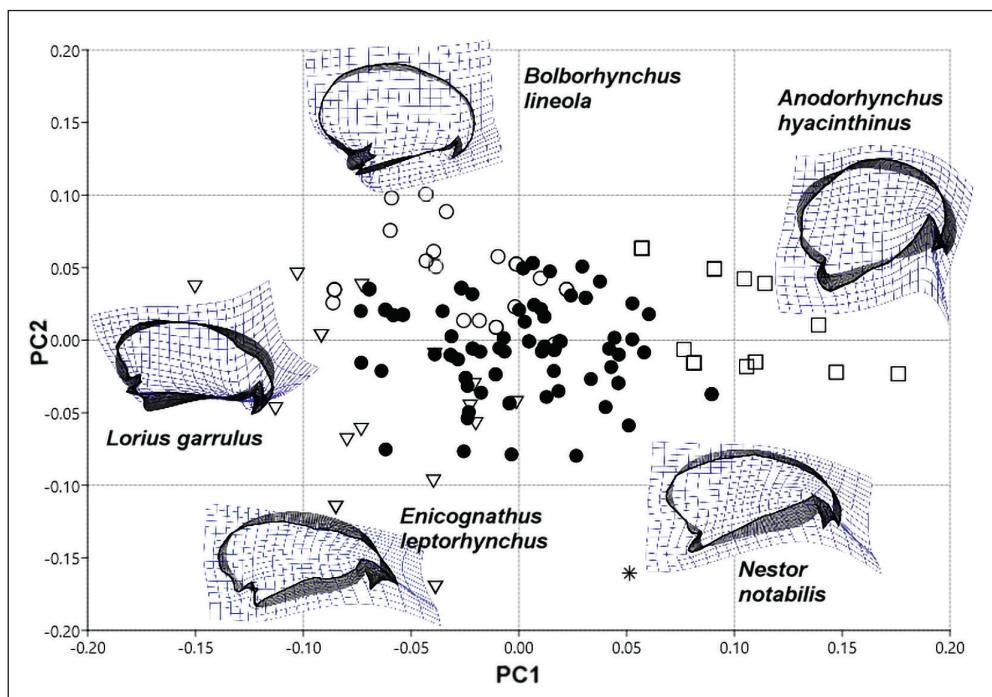
Figure 2. Graphical output of PCA performed on the two-dimensional landmark data (lateral view). PC1–PC2 biplot. The first PC axis described the relative height of the *cranium* (PC1). The second PC axis described the relative length and curvature of the beak (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▽ Nectarine, soft food item eaters, □ Big and rough food item eaters, ○ Predominantly seed eaters, * Other

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 hosszúságával és görbületével hozható kapcsolatba (PC2). A fekete, vastagított terület a komputergenerált átlagformától való eltérést mutatja

● Generalisták, ▽ Nektár és lágy táplálékot fogyasztók, □ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, * Egyéb

Allometry can explain some of the differences between species because the smaller species usually have bigger *neurocranium* and smaller *viscerocranium* (Grant *et al.* 1985). Although Pesquet's Parrot *(Psittrichas fulgidus)* has a large body size, it has a similar skull shape to lories, possibly caused by its highly specialized diet (Pryor *et al.* 2001). Species like Barred Parakeet *(Bolborhynchus lineola)*, Turquoise Parrot *(Neophema pulchella)* and Red-headed Lovebird *(Agapornis pullarius)* have very short and curved beaks for extracting the edible part of the seeds. The strong and tapered beak is in positive correlation with bite performance (Van der Meij & Bout 2004, Herrel *et al.* 2005). With its long, narrow, and slender beak, the Kea *(Nestor notabilis)* digs grubs from rotten logs and roots from the ground (O'Hara *et al.* 2012). This shape has a significant role in the development of extractive foraging techniques. This species has extremely broad diet and there
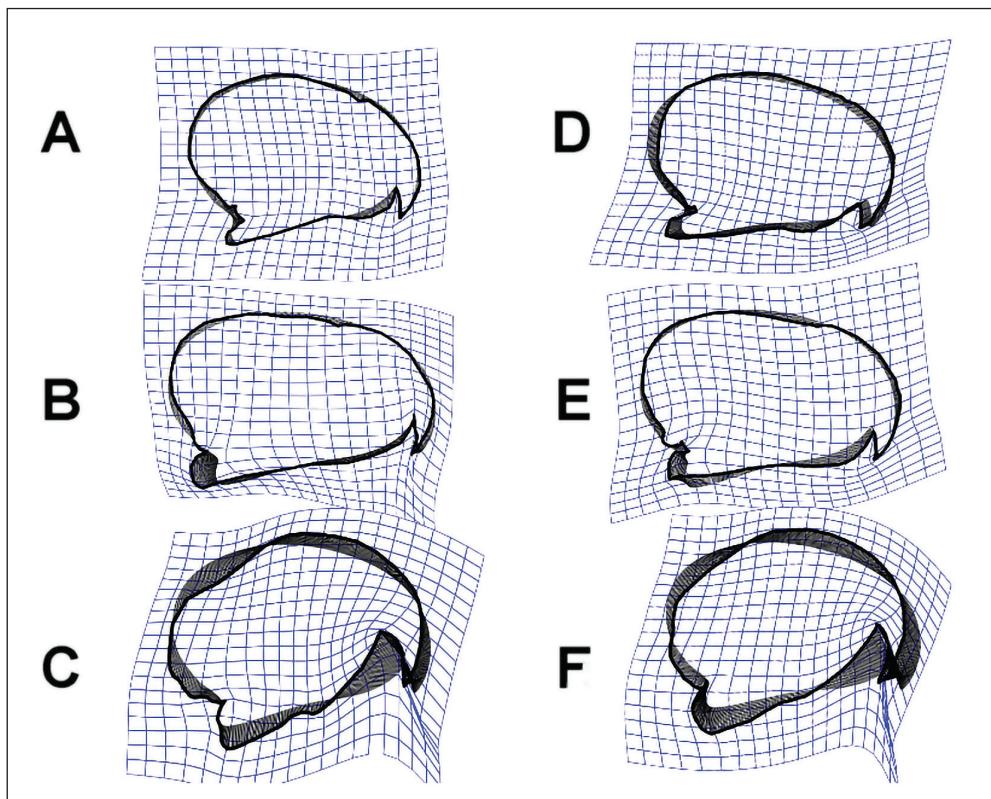
Figure 3. Various cockatoo and parrot species sharing convergent attributes. A: Cockatiel *(Nymphicus hollandicus)*, B: Pale-headed Rosella *(Platycercus adscitus)*, C: Yellow-crested Cockatoo *(Cacatua sulphurea)*, D: Cuban Amazon *(Amazona leucocephala)*, E: Palm Cockatoo *(Probosciger aterrimus)*, F: Hyacinth Macaw *(Anodorhynchus hyacinthinus)*

3. ábra   Az egyes kakaduk és papagájok hasonló konvergens bélyegeket hordoznak. A: Nimfapapagáj *(Nymphicus hollandicus)*, B: Sápadtfejű rozella *(Platycercus adscitus)*, C: Aranyosarcú kakadu *(Cacatua sulphurea)*, D: Kubai amazon *(Amazona leucocephala)*, E: Pálmakakadu *(Probosciger aterrimus)*, F: Jácintkék ara *(Anodorhynchus hyacinthinus)*

are relatively subtle morphological differences between individuals and the noticeable intraspecific variation in the foraging ecology. It is clear that bill and head morphology is related to diet in this species (Greer 2015). Slender-billed Parakeet *(Enicognathus leptorhynchus)* – like other parrots – is an intelligent species, which likely promotes its persistence in dynamic landscapes. These characteristics may facilitate the adaptation of foraging behaviour to include most available resources within a given area (Carneiro *et al*. 2012). An overall increased bill length may improve the power or efficiency with which these species can rip off mud and flowers, extract grubs from live wood, or demolish decaying wood. Slender beaks allow the bird to deftly collect small food items from difficult to reach places.

The second analysis showed variety in the relative size of the *neurocranium* and *viscerocranium* like in the first analysis. Seed eaters and the species foraging on rough food
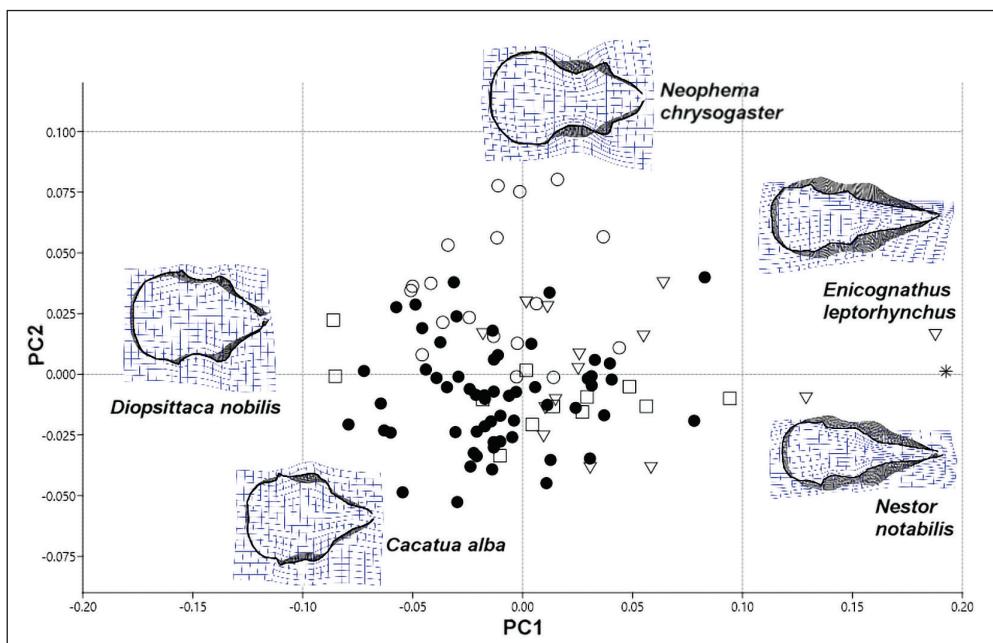
Figure 4. Graphical output of PCA performed on the two-dimensional landmark data (dorsal view). PC1–PC2 biplot. The first PC axis described variation in the relative length of the beak (PC1). The second PC axis (PC2) described differences in the orientation and curvature of the lacrimal bone and the upper margin of orbits. Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▽ Nectarine, soft food item eaters, □ Big and rough food item eaters, ○ Predominantly seed eaters, ∗ Other

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

● Generalisták, ▽ Nektár és lágy táplálékot fogyasztók, □ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, ∗ Egyéb

material usually have shorter tapered beak. In this analysis, the Kea and the Slender-billed Parakeet showed extreme differences with their elongated beak. The feeding categories are highly overlapping in the morphospace, but in dorsal view the curvature and the height of the beak is non-qualifiable. This analysis also showed differences in the curvature of the upper margin of the orbits. Cockatoo (*Cacatua* sp.) species have broad skulls and the increased distance between the orbits at the line of frontal bone. Australasian cockatoos have pronounced ossified periorbital structures. These birds have a well-developed suborbital arch and *musculus pseudomasseter* (Homberger 2017). At the postorbital region, the *neurocranium* showed a concave surface to the *musculus adductor mandibulae externus*. The amazon parrots (*Amazona* sp.) share similar attributes like cockatoos. Red-rumped Parrot *(Psephotus haematonotus)* and grass parrots (*Neophema* sp.) showed differences in the morphospace. These seed eaters have different skull structures. The frontal region
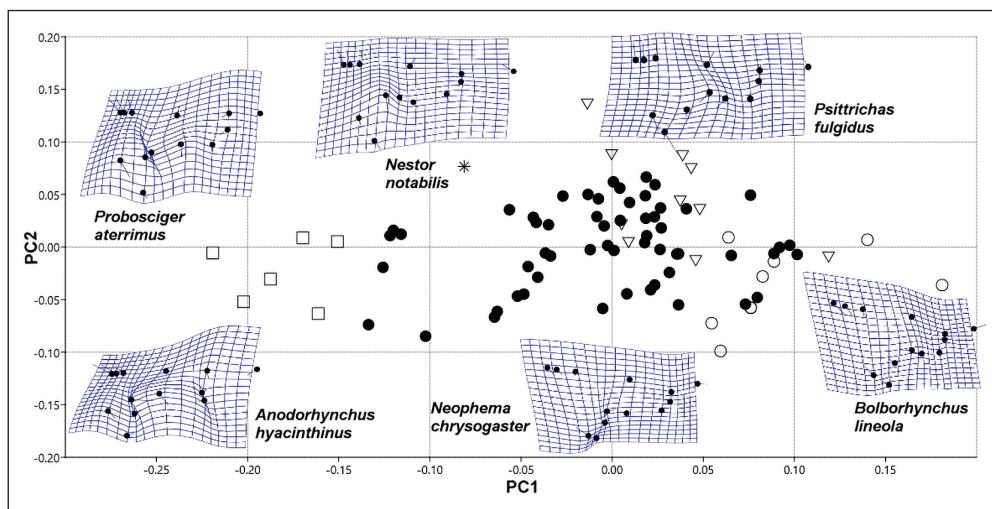
Figure 5. Graphical output of PCA performed on the two-dimensional landmark data (ventral view). PC1–PC2 biplot. The first PC axis described variation the size and position of the palatine bone (PC1). The second PC axis reflected to the relative width of the *cranium* and variation in the relative size of the *neurocranium* compare to the *viscerocranium* (PC2). Thick black areas show the differences compared to the computer generated mean shape

● Generalists, ▽ Nectarine, soft food item eaters, □ Big and rough food item eaters, ○ Predominantly seed eaters, ∗ Other

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

● Generalisták, ▽ Nektár és lágy táplálékot fogyasztók, □ Nagy és kemény táplálékot fogyasztók, ○ Elsődlegesen magevők, ∗ Egyéb

is narrower at the line of the orbits. The arboreal species have a wider, broad frontal region compared to those species which are mostly foraging on the ground. Arboreal species might use their beak more often as well as their feet to grip branches and haul themselves through the treetops.

The third analysis showed differences in the relative length of the *cranium*. Those species which are foraging on mechanically resistant food (e.g. macaw species and Palm Cockatoo) have a wider and more caudally positioned quadrate bone and *foramen magnum occipitale*. The palatine bone is extremely large with robust pterygoids. These structures support the surface in order to maximize the bite performance and the effectiveness of jaw closure muscles to crash nuts and hard-shelled seeds. These species have high skulls, which also correspond with the size of *musculus ethmomandibularis*. Several features enable parrots to exert strong bite forces during feeding and locomotion, including the strong adductor muscles that are evolutionary novelties in this group. The presence (or absence) and degree of development of these musculoskeletal structures are highly variable among different species (Burton 1974, Tokita 2003). Nectarivore parrots and the Pesquet Parrot generally have narrow skulls with slender quadrate bones and relatively
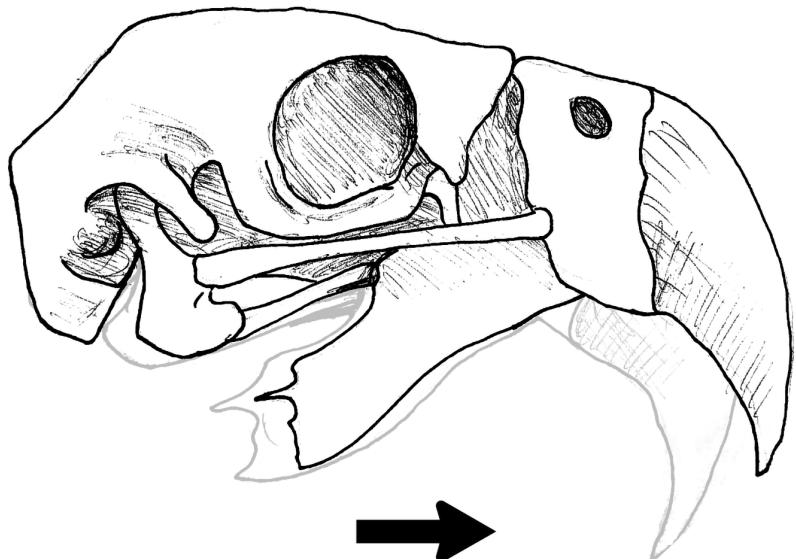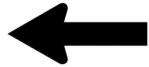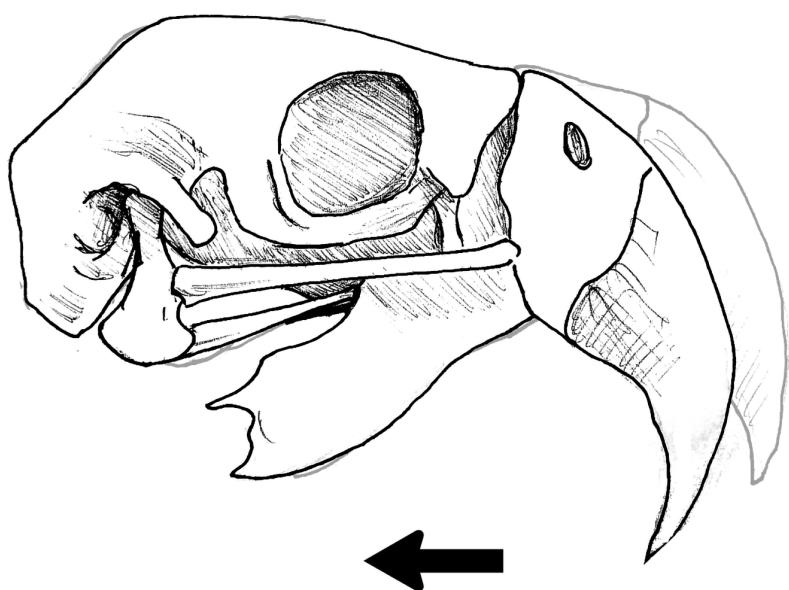
Figure 6. Kinesis of the cranium of a macaw with upper mandible raised (A), with upper mandible lowered (B)

6. ábra Kraniális kinezis egy ara példáján, a felső állkapocscsont felső (A) és alsó pozíciójában (B)

gracile palatine and pterygoid bones. This indicates that these species have smaller and weaker pterygoid and adductor muscles. Lories and lorikeets have thinner and structurally weaker beaks than granivorous parrots of a similar size (Holyoak 1973). These lories constitute a highly nectarivorous parrot clade and their diet, associated with morphological innovation, allows them to explore underutilized niches and promote diversification (Schweizer *et al.* 2014). Seed eaters have relatively large *neurocranium*; the maxilla is short and wide. The quadrate bone is wide and positioned anteriorly and pterygoids are longer with broad and divided palatine bones. Bite force and speed of jaw closure perhaps play an important role. Cracking the seeds requires many fast, small, and precise movements in the oral cavity (Homberger 2017). Seed characteristics, size, and shape affected handling time with reference to bill structure (Hrabar & Perrin 2002). Parrots occupy varied dietary niches that require an agile, mobilized feeding apparatus. Cranial kinesis – flexibility among intracranial joints – has a central role in the unique feeding apparatus of this avian order. These birds possess a highly mobile, streptostylic quadrate by moving the rod-like pterygoids. The palatomaxillary system of articulation rotates the rostrum about the synovial craniofacial hinge, providing prokinetic movement between the frontal and nasal bones (Cost *et al.* 2017).

Our results show relationships between cranial attributes and diet preference, but also highlight the morphological complexity and dietary diversity of the feeding apparatus. Future studies reflecting on avian feeding apparatus may increase our knowledge and might be useful to understand the preferences of those species, which are threatened due to habitat loss. It would be interesting to perform combined analyses with cranial shape and attributes of the feet and hypotarsal structures to measure the differences between the arboreal species and those parrots which are conservatively feeding on grasslands. However numerous of species are sexually monomorphic (Miyaki *et al.* 1998), it is possible that there are species – e.g. the Great-billed Parrot *(Tanygnathus megalorynchos)* – where the sexual dimorphism might have role in the cranial shape, as it was observed previously in the case of the Kea (Bond *et al.* 1991). 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.

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