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Diversity of cranial shape in European Woodpecker species (Picidae)

Tibor Pecsics[1,2*], Martin Segesdi[3,4], Sándor Faragó[1], Gerard Gorman[5] & Tibor Csörgő[6]

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Abstract The woodpecker family (Picidae) includes numerous species that vary in size and plumage colouration, but which share many easily recognisable external features. These birds possess pronounced anatomical adaptions that enable them to exploit arboreal habitats and live in niches that are inaccessible to most other birds. The aim of this study was to increase our knowledge on the relationships between skull shape, habitat preference, pecking abilities and foraging habits of 10 European woodpecker species. A geometric morphometric approach was used to analyse two-dimensional cranial landmarks. We used principal component (PC) analyses on those measurements that may be related to habitat preference and foraging habits. The PCs resulted in descriptions of the relative length and width of the bill, variation in its relative size, orientation of the nostrils variation in the elongation of the *neurocranium,* the relative size and position of the palatine bone, length of the *rostrum*, and the thickness of the mandible bone. The analysis showed and confirmed the presence of some cranial elements that are strongly associated with habitat preference, pecking behaviour and excavation abilities.

Keywords: woodpecker, skull shape, cranial morphology, morphometrics, anatomy, mandibles, kinetics, habitat preference

Összefoglalás A harkályok családja (Picidae) számos fajt tartalmaz, melyek többek között különböznek méretükben és tollazatuk mintázatában, azonban mindannyian rendelkeznek könnyen felismerhető közös külső jegyekkel. Ezek a madarak olyan szembeötlő tulajdonságokkal bírnak, amelyek lehetővé tették számukra olyan erdei élőhelyek és ökológiai fülkék meghódítását, amelyek más madarak számára elérhetetlenek. Tanulmányunkban az európai fajok *cranialis* jegyeinek elemzésével az élőhely-preferencia, a kopácsolási képességek és a morfológiai jellemzők közötti lehetséges összefüggéseket kerestük. A vizsgálat során kétdimenziós landmarkok használatával főkomponens analíziseket végeztünk. A főkomponensek a csőr relatív hosszát és szélességét, az orrnyílások relatív nagyságát és helyzetét, az agykoponya relatív nyújtottságát és annak görbületét, az arc- és agykoponya egymáshoz viszonyított méretét, a *palatinum* relatív nagyságát és helyzetét, valamint a *rostrum* relatív hosszát és a *mandibula* vastagságát, robuszticitását magyarázzák. A vizsgálat kimutatta, illetve megerősítette egyes koponyasajátosságok meglétét, amelyek az élőhely preferenciával, a táplálék megszerzésének módjával és a kopácsolási képességekkel szorosan összefüggnek.

Kulcsszavak: harkály, koponyasajátosságok, morfometria, anatómia, állkapocs, kinetika, élőhely-preferencia

[1] *University of Sopron, Institute of Wildlife Management and Wildlife Biology, 9400 Sopron, Bajcsy-Zsilinszky utca 4., Hungary*
[2] *Behavioural Ecology Group, Department of Systematic Zoology and Ecology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary*
[3] *Department of Paleontology, Institute of Geography and Earth Sciences, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary*
[4] *Department of Paleontology and Geology, Hungarian Natural History Museum, 1431 Budapest, Pf. 137, Hungary*
[5] *Independent Researcher, Hungarian Woodpecker Working Group, c/o MME BirdLife Hungary, Budapest, Hungary*
[6] *Department of Anatomy, Cell- and Developmental Biology, Eötvös Loránd University, 1117 Budapest, Pázmány Péter sétány 1/c, Hungary*
** corresponding author, e-mail: nobilis.equus@gmail.com*

Introduction

Woodpeckers are the members of the avian family Picidae. They vary in size and plumage colouration, but generally share many easily recognisable external features. Woodpeckers have a global distribution, occurring from sea-level to high mountains on every continent except Madagascar, Australia-Oceania and Antarctica (Gorman 2014). These birds possess prominent anatomical adaptions that enable them to exploit arboreal habitats and live in niches that are inaccessible to most other birds (Cramp 1985). With the exception of a few species that live in treeless habitats, the Picidae are essentially arboreal, many being habitat specialists (Kerpez & Smith 1990). Some woodpecker species are closely associated with certain forest types and some with particular tree species (Moorea & Migliab 2009). Dead wood is also an important habitat requirement for many woodpecker species (Smith 2007, Nappi *et al.* 2015).

The family contains 230–250 species in 37 genera (Fuchs & Pons 2015, Shakya *et al.* 2017) but their taxonomy is complex and the exact relationships the axact relationships between species are still not calrified (Benz *et al.* 2006). In addition, the phylogenetic tree of the family is rather complicated due to hybridization between some species (Cracraft *et al.* 2004, Fuchs *et al.* 2013, Seneviratne *et al.* 2016).

Some recent studies suggest that woodpeckers have undergone convergent evolution and developed similar attributes independently (Moore *et al.* 2006, Dufort 2016).

The earliest picid ancestors probably evolved around 50 million years ago (Prum *et al.* 2015), although the fossil record is poor (James 2005, Kessler 2016) However, remains are known from the Late Oligocene (Mayr 2001) and Miocene epochs (De Pietri *et al.* 2011).

Numerous skull adaptations have evolved which facilitate excavation (reinforced *rhamphotheca*, frontal overhang, and *processus dorsalis pterygoidei*) and drumming and tapping (enlarged *condylus lateralis* of the quadrate and fused lower mandible) (Manegold & Töpfer 2013). These anatomical features function as shock-absorbers, preventing brain injuries and damage to the brain cavity. A curved maxilla and the presence of spongy tissue between the upper mandible and skull reduce pressure on the brain (Yoon & Park 2011, Liu *et al.* 2015). Micro-CT investigations have shown the presence of plate-like spongy bones and tissues in the skull, which are highly accumulated in the frontal and occipital regions (Wang *et al.* 2011).

A specially adapted hyoid bone allows these birds to retract and extend their tongue to extreme degrees (Yaraghi *et al.* 2016). When under tension, this structure also helps stabilize the skull and neck, and thus acts as a "seat belt" which also helps to prevent damage due to impacts occurring (Jung *et al.* 2019). The skull is thick and situated above the line of the bill, therefore the forces that occur while excavating, pecking and drumming are transmitted below the brain and the braincase through the mandibles. Furthermore, the quadrate bone and joints play important roles in extending impact time, which decreases impact load to the brain tissue (Xu *et al.* 2021).

The cranial bone has a high mineral density with plate-like structures and a high number of trabeculae packed together, which results in a lower deformation while pecking (Wang *et al.* 2013). The hearing apparatus has shock-proof adaptations and a thick membrane in the inner ear which further help in resisting damage (Kohllöffel 1984).

Another adaptation that mitigates damage is the relatively small size of the brain (Gibson 2006). However, although it is widely accepted that woodpecker skulls have special adaptations, some studies dispute the function of the cranial structures and suggest that these birds benefit from their overall small size and key skull features in order to safely hammer on and into wood to find invertebrates and to excavate nesting cavities (Biewener 2022).

Most woodpecker species are insectivorous but some are omnivorous and opportunistic. Their diet includes numerous species of arthropods, but also the eggs of other birds, nestlings, small vertebrates, fruits, nuts, seeds and other plant matter, tree sap and even carrion (Gregory *et al.* 2007, Gorman 2014).

Drumming is a form of non-vocal communication used by most (but not all) woodpecker species which has possibly played a key role in the development of cranial morphology and musculoskeletal attributes (Miles *et al.* 2018).

In this preliminary study, we investigated the cranial and morphological diversity among 10 European woodpecker species: Eurasian Wryneck *(Jynx torquilla)*, Lesser Spotted Woodpecker *(Dryobates minor)*, Middle Spotted Woodpecker *(Dendrocoptes medius)*, White-backed Woodpecker *(Dendrocopos leucotos)*, Great Spotted Woodpecker *(Dendrocopos major)*, Syrian Woodpecker *(Dendrocopos syriacus)*, Black Woodpecker *(Dryocopus martius)*, Eurasian Three-toed Woodpecker *(Picoides tridactylus)*, Eurasian Green Woodpecker *(Picus viridis)* and Grey-headed Woodpecker *(Picus canus)*. Our objective was to expand our knowledge on the relationship between skull shape and foraging habits and to identify any characteristics that are related to habitat preference and pecking and excavation abilities. The differences in the forces that act on the bill during pecking and excavation work may be related to skull geometry and jaw musculature. The differences between the various species may also reflect selection pressures related to their different foraging habits and habitat preferences (particularly concerning the hardness of wood). Furthermore, we aimed to re-examine the previous morphological observations that had involved both the most specialised and the least specialised species in terms of how they obtain food by pecking into trees (Bock 1999, Tarbill *et al.* 2015). To investigate the morphological diversity of the skulls of the ten species, we used landmark-based morphometric methods.

Materials and Methods

Specimens

This study is based on 70 skulls from 10 European species. All skulls are from adult specimens of woodpeckers in the collection of the Eötvös Loránd University (Budapest, Hungary, n=21), the collection of the Hungarian Natural History Museum (Budapest, Hungary, n=31), the digital archives of Wageningen University (Wageningen, Netherlands, n=5), the Museum of Natural Sciences of Barcelona (Barcelona, Spain, n=2) and the Natural History Museum of Krakow (Krakow, Poland, n=11). No birds were deliberately killed in order to obtain their skull; all either died of natural causes, accidentally or whilst in captivity.

Table 1. List of woodpecker species examined in this study
1. táblázat A vizsgálatban szereplő harkályfajok

Common name	**Scientific name**	**n**
Eurasian Wryneck	*Jynx torquilla*	7
Lesser Spotted Woodpecker	*Dryobates minor*	2
Middle Spotted Woodpecker	*Dendrocoptes medius*	5
White-backed Woodpecker	*Dendrocopos leucotos*	8
Great Spotted Woodpecker	*Dendrocopos major*	17
Syrian Woodpecker	*Dendrocopos syriacus*	8
Black Woodpecker	*Dryocopus martius*	4
Eurasian Three-toed Woodpecker	*Picoides tridactylus*	5
Eurasian Green Woodpecker	*Picus viridis*	10
Grey-headed Woodpecker	*Picus canus*	4

Landmarks and procedures

The variation of cranial morphology was analysed using landmark-based geometric morphometry. In this study, the meaningful variables were revealed by the analysis. We sought to find landmarks for this analysis to cover the geometric form of the skull. The landmarks enabled a comprehensive sampling of morphology and thus features of biological significance could be explored. The ideal landmarks were discrete but noticeable anatomical features, which did not alter their topological positions relative to other landmarks and provided adequate coverage of the morphology (Zelditch *et al.* 2004). The landmarks were obtained

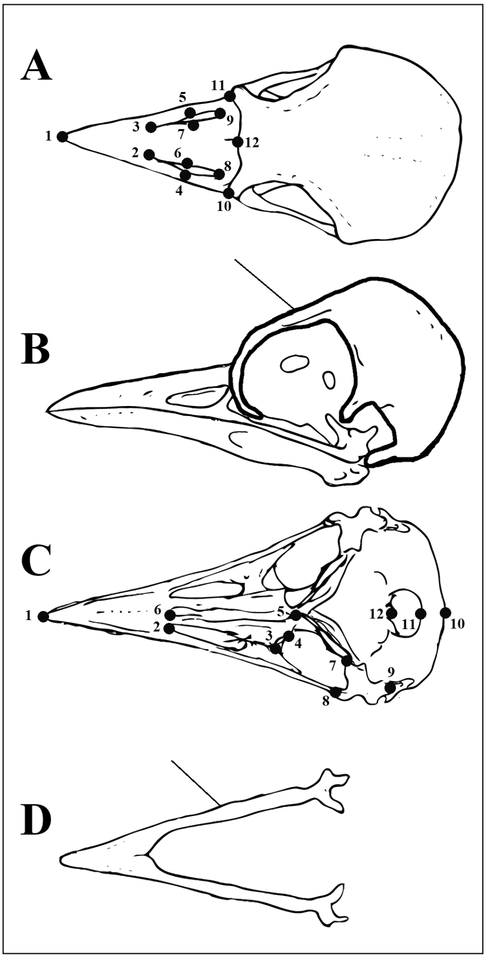

Figure 1. Position and number of landmarks. A: the bill in dorsal view (numbers correspond to *Table 2*), B: the *neurocranium* in lateral view, C: fixed landmarks in ventral view (numbers correspond to *Table 3*), D: the mandible in ventral view

1. ábra A vizsgálatban használt landmarkok száma és pozíciója. A: a csőr felülnézetből (a számok megnevezését lásd a *2. táblázatban*), B: az agykoponya oldalnézetből, C: fix landmarkok alulnézetből (a számok megnevezését lásd a *3. táblázatban*), D: az alsó állkapocs alulnézetből

Table 2. Number and description of landmarks. Terminology according to (Baumel 1993)
2. táblázat Az egyes landmarkok száma és leírása. Terminológia Baumel (1993) alapján

Number of landmark	Description of landmark
1	tip of the *maxilla*
2	the most anterior point of the left nostril
3	the most anterior point of the right nostril
4	the most lateral point of the left nostril
5	the most lateral point of the right nostril
6	the most medial point of the left nostril
7	the most medial point of the right nostril
8	the most posterior point of the left nostril
9	the most posterior point of the right nostril
10	the most posterior point of the left *maxilla*
11	the most posterior point of the right *maxilla*
12	the middle of the nasofrontal hinge

Table 3. Number and description of landmarks. Terminology according to (Baumel 1993, Sun *et al.* 2018)
3. 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 of 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*

via high resolution (1200 × 1600 pixels) photographs. We took four photographs of each specimen (lateral, ventral, and dorsal) with closed jaws and without the mandibles. Images were standardised for the *foramen magnum occipitale* and the tip of the bill. Those specimens which lacked the *ramphotheca* but on which the tip of the bill was identifiable, were measured. An investigation was performed regarding the repeatability of the measurements by using Spearman's correlation. The test was between two separate digital measurements performed on skull photos (n=20). We used 12 fixed landmarks in dorsal and ventral views to examine the shape of the bill and 500 sliding landmarks to examine the shape of the *neurocranium* in lateral view and a further 200 sliding landmarks to examine the shape of the mandible *(Figure 1)*. These landmarks were allowed to slide along their corresponding curves due to the minimisation of the pliable 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 principal component analysis and extract deformation grids. We only considered those PCs which showed >10% of variance.

Results

Our measurements were meaningful, irrespective of the measuring mode (all r > 0.98, all P < 0.001).

The first analysis tried to describe the shape of the bill with fixed landmarks (12) in dorsal view. The first two PCs showed 64% and 14% of variance in shape. The first PC axis

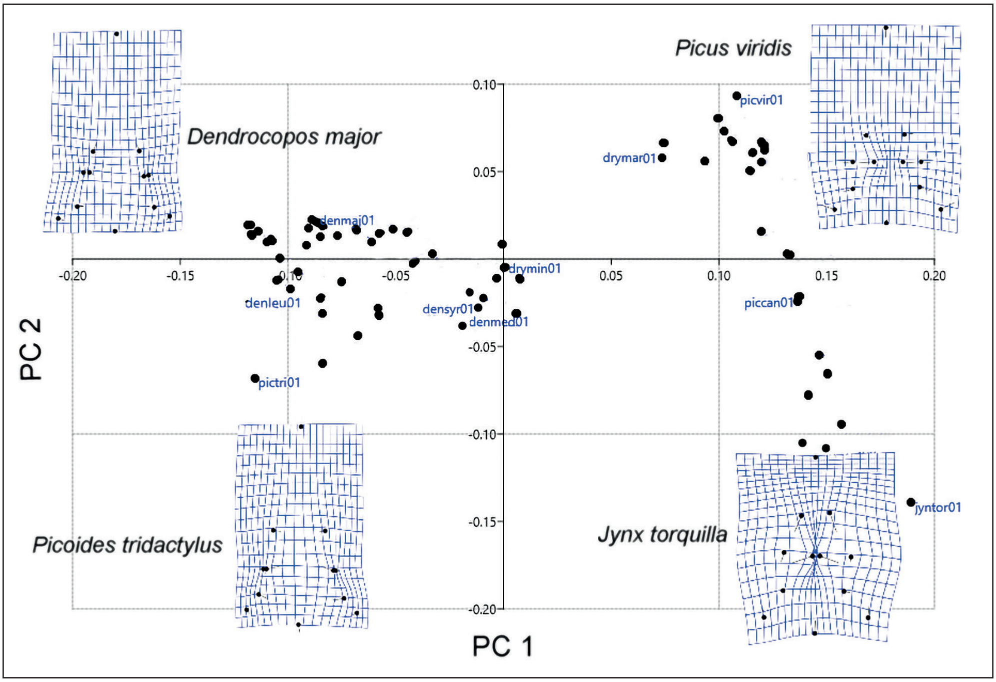

Figure 2. Graphical output of first PCA performed on the two-dimensional landmark data (dorsal view). PC1–PC2 biplot

2. ábra Az első PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (felülnézet)

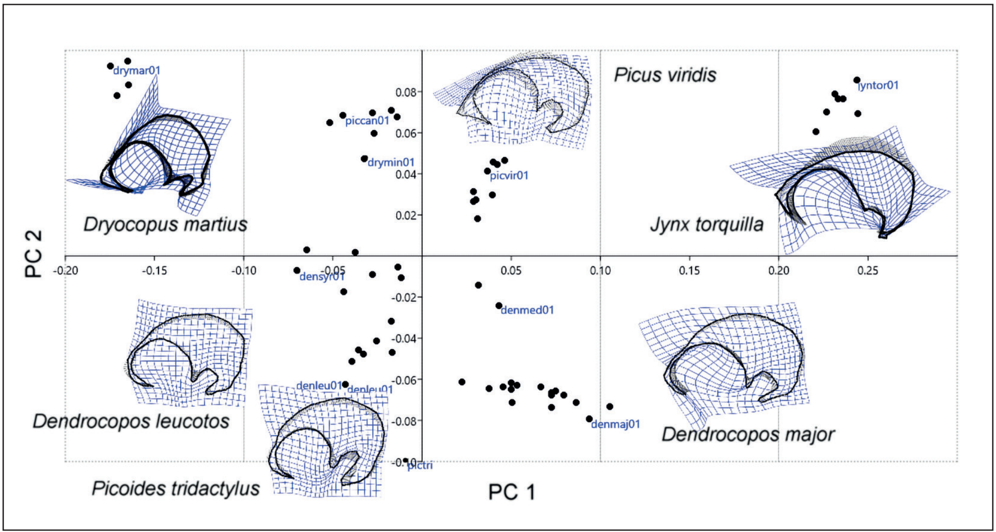

Figure 3. Graphical output of second PCA performed on the two-dimensional landmark data (lateral view). PC1–PC2 biplot

3. ábra A második PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (oldalnézet)

described variation in the relative length and width of the bill (PC1) and the second reflected to the relative size of the nostril and its distance from the tip of the bill (PC2). The analysis showed that the Eurasian Wryneck differs considerably from its relatives *(Figure 2)*.

The second analysis focused on the *neurocranium* and the orbits from the lateral view *(Figure 1)*. We used sliding landmarks (500) to describe the cranial shape of each

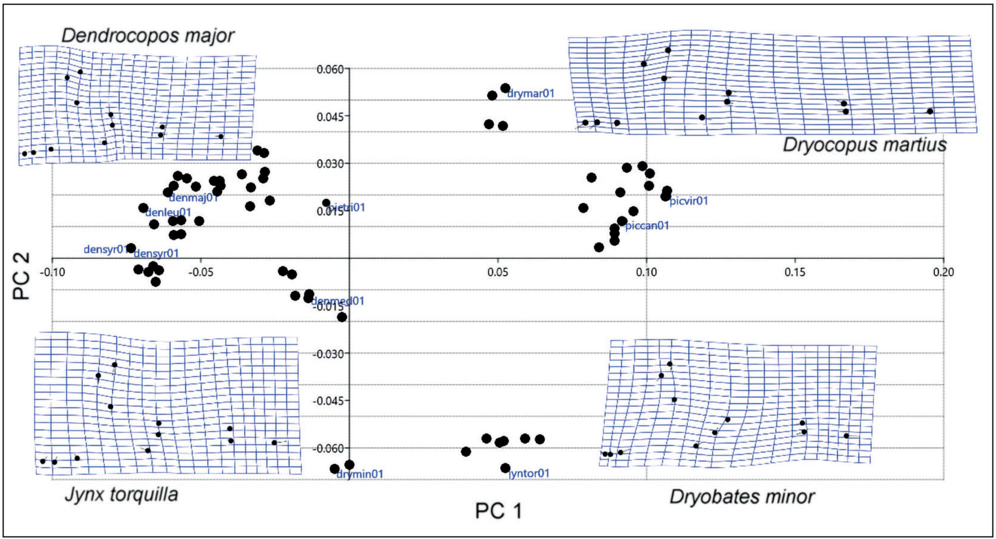

Figure 4. Graphical output of third PCA performed on the two-dimensional landmark data (ventral view). PC1–PC2 biplot

4. ábra A harmadik PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (alulnézet)

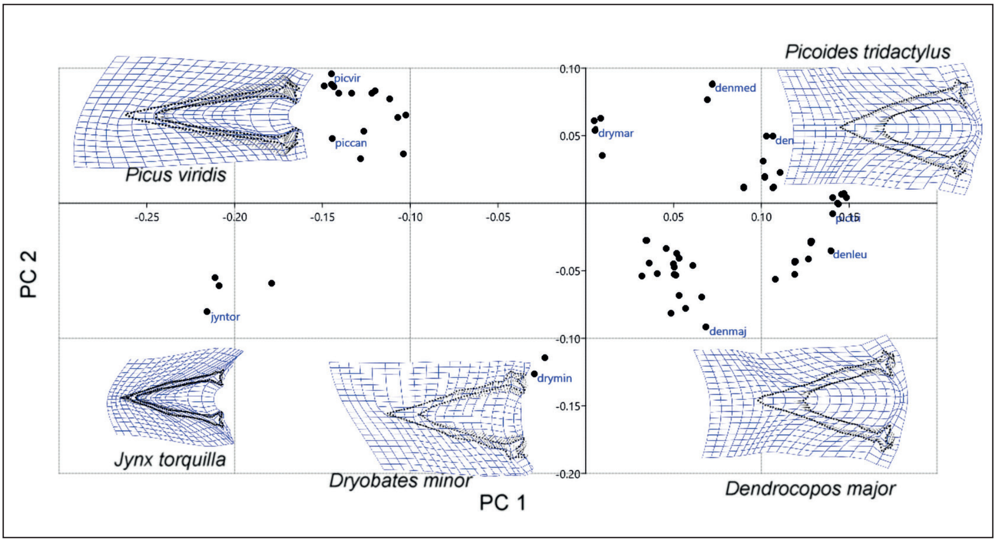

Figure 5. Graphical output of fourth PCA performed on the two-dimensional landmark data (ventral view). PC1–PC2 biplot

5. ábra A negyedik PCA grafikus megjelenítése kétdimenziós landmark adatok alapján (alulnézet)

woodpecker. The first three PCs showed 52%, 22% and 12% of variance in skull shape. The first PC axis described the relative length and elongation of the *neurocranium* (PC1). The Eurasian Wryneck, European Green Woodpecker and Grey-headed Woodpecker also showed differences, with relatively low and narrow *neurocranium* compared to other species with short skulls. The second PC axis described the relative height and curvature of the *neurocranium* (PC2). Species like Eurasian Three-toed Woodpecker and White-backed Woodpecker share similar morphology *(Figure 3)*. The third PC axis (PC3) showed the position and thickness of *processus postorbitalis* and *processus paroccipitalis*. The species that are more adapted for excavating into and pecking on wood showed more scores and bearing wider and stronger bony processes *(Figure 3)*.

During the third analysis we used fixed landmarks (12) in dorsal view *(Figure 1)*. The first two PCs showed 48% and 14% of the variance in shape. The first PC axis described variation in the relative size of the *neurocranium* compared to the *viscerocranium* (PC1) and the second reflected to the relative size of the palatine bone and its distance from the tip of the bill (PC2). The analysis showed that more primitive forms are different from those species that have more evolved attributes for pecking and excavating *(Figure 4)*.

The fourth analysis focused on the mandible bone in ventral view *(Figure 1)*. We used 200 sliding landmarks to find the main differences between the species. The first two PCs showed 65% and 24% of variance in shape. The first PC axis related to the variation of the relative thickness and length of the *rostrum* (PC1). The second PC axis described the relative thickness of mandible bone (PC2) *(Figure 5)*.

In every case, the generalist species are situated the middle of the morphospace. The less evolved species with more ancient attributes differ prominently from those woodpeckers that share more adaptations for working on harder wood surfaces *(Figure 7)*.

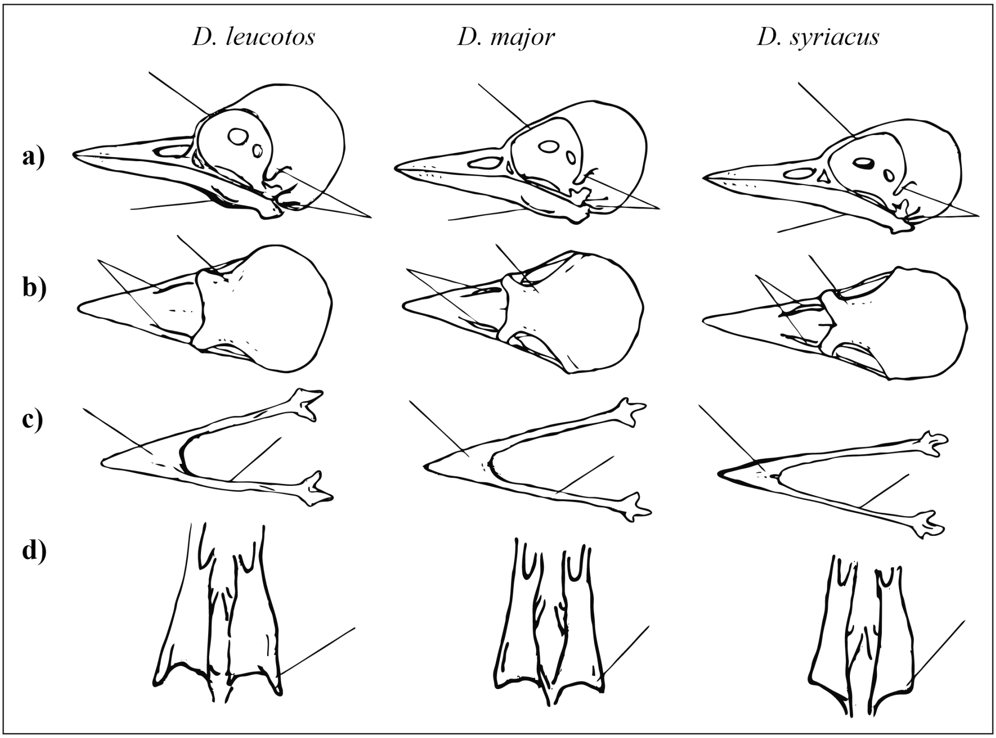

Figure 6. Various *Dendrocopos* species differ in some skull attributes that are related to the preferred wood materials and the mass of jaw closure muscles: a) skull in lateral view, b) skull in dorsal view, c) mandible in ventral view, d) palatine bone in ventral view

6. ábra Egyes *Dendrocopos* fajok különböznek azokban a koponyatulajdonságaikban, amelyek a preferált faanyaggal és az állkapcsot záró izomzat tömegével vannak összefüggésben: a) koponya oldalnézetben, b) koponya felülnézetben, c) a *mandibula* alulnézetben, d) a *palatinum* alulnézetben

Discussion

We found that in dorsal view there are differences in the shape of the relative length and width of the bill and the relative size and position of the nostrils. Larger species like Black Woodpecker and European Green Woodpecker, have longer bills compared to the *neurocranium*. The allometric head growth could reflect variation in head length. It might also explain some of the differences between species because birds with a smaller body size usually have a bigger *neurocranium* and a smaller *viscerocranium* as in the case of the Lesser Spotted Woodpecker. Allometric patterns within populations do not necessarily parallel interspecific allometry (Grant *et al.* 1985). Despite the comparable size of Great Spotted Woodpecker and Middle Spotted Woodpecker, the ratio between *neurocranium* and *viscerocranoum* are different. The Middle Spotted Woodpecker has a shorter bill and relatively elongated skull which corresponds to its behaviour as a mostly foraging species that works on surfaces and does not bore deeply into wood (Pettersson 1983, Török 1990,

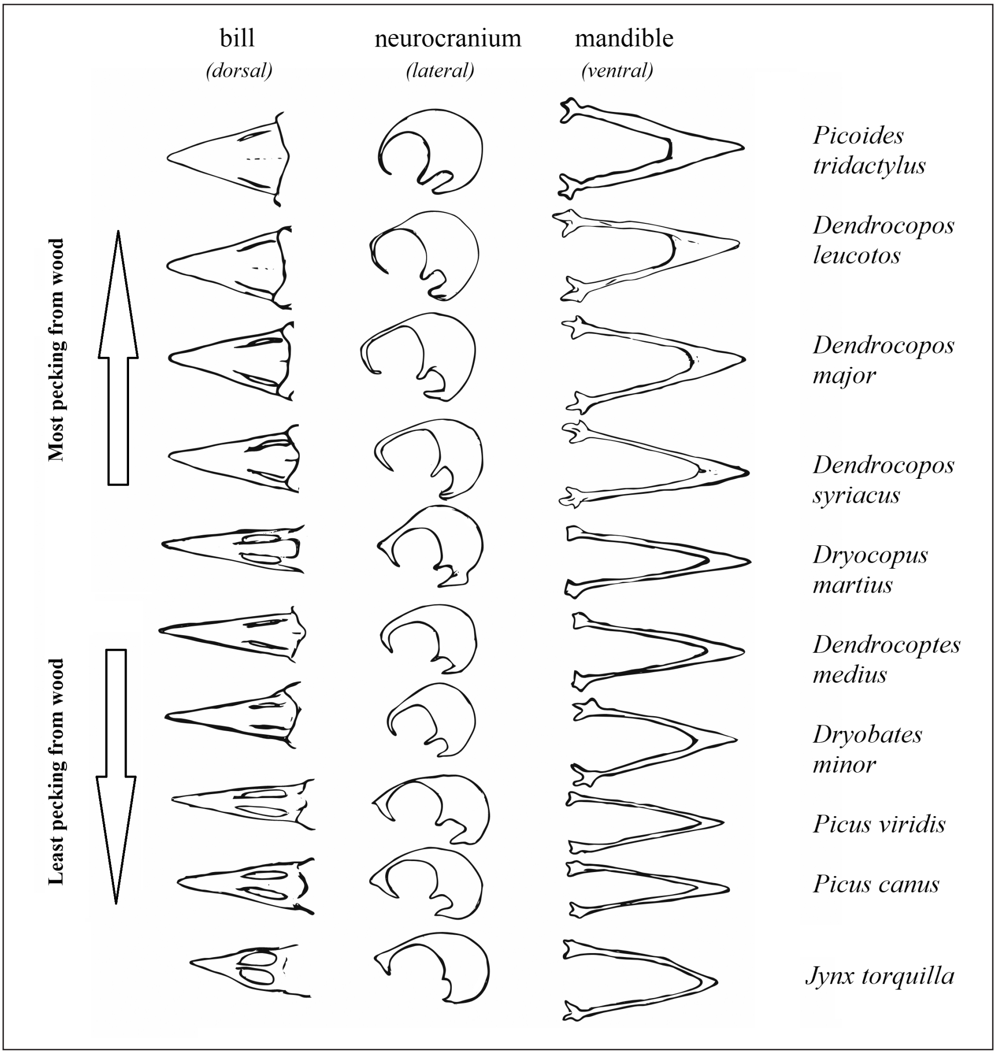

Figure 7. Differences in cranial morphology between species in case of pecking and excavation abilities

7. ábra A koponyamorfológiában megmutatkozó különbségek az egyes fajok között a táplálék megszerzését és a fakopácsolási képességeket illetően

Gorman 2014, 2020). The most primitive form of European woodpeckers is the Eurasian Wryneck in that it does not possess progressive adaptations for extracting food items from under the surface of trees. However, despite the lack of specialisation of skull attributes, Wrynecks still perform some basic drumming (Turner & Gorman 2021). It is possible that these nest-related activities could have led the ancestors of modern picids to those complex movements and behaviours that enable them to obtain their food from difficult to reach places within wood (Short 1971, Bock 1999). Species that forage on the surface or collect their food from dead wood, have mostly elongated bills and their nostrils are closer to each other. Their skulls cannot resist the mechanical stresses and demands that those of the more evolved and advanced species can, such as the European Three-toed Woodpecker (Lee *et al.* 2016, Moody *et al.* 2022). The more adapted species that mostly peck into wood have a wider base on their upper mandible and a larger space between the nostrils. The width and shape of the flexible region between the *nasale* and the *frontale* determines the mechanical stability of the structure, and the nostrils follow passively the edge of the flexible region, therefore the nostrils are getting into an increasingly "marginal" position (Jung *et al.* 2019).

The second analysis showed clear differences between those species that peck least and those that peck most. Wryneck, Green Woodpecker and Grey-headed Woodpecker have elongated *neurocranium* with a lower forehead. The species that peck more, have a higher forehead, the curvature of their frontal bone is more pronounced and prominent and the shape of the *neurocranium* is also rounder. These attributes are undisputed adaptations for obtaining food from within hard wood and to help resist the shocks sustained during pecking and excavating (Young *et al.* 2019). Between the closely related *Dendrocopos* species we can observe a gradient regarding these cranial attributes which corresponds their tree and habitat preferences (Ónodi & Csörgő 2012, 2013, 2014) *(Figure 6)*. With the exception of the Wryneck, those species that possess an elongated skull mostly have a longer bill as well. The Black Woodpecker is also an exception to this rule because of its size and habitat preferences (Rolstad & Rolstad 1995, Rolstad *et al.* 1998, Bocca *et al.* 2007). Black Woodpecker is highly insectivorous, its diet mainly includes ants (especially carpenter ants) and wood-boring beetles. The densities of these prey species are higher in forests rich in mature and dead wood. Their long bill enables them to reach prey, especially larvae, which are found deep within trees (Mikusinski 1995, Garmendia *et al.* 2006). The orbits of advanced pecking species are located more frontally and the lacrimal bones are completely covered at the front to help resist shocks from impacts and protect the sensitive eyes from forces of inertia. The position and thickness of cranial processes, like *processus postorbitalis* and *processus paroccipitalis,* are positively loaded with the mass and strength of mandible closing muscles (Donatelli 2012).

The third analysis showed differences in the relative length of the *viscerocranium* but also the mandible closing muscles. Those species with a larger surface of palatine bones also possess more mandible closing muscles in order to maximize their forces. These factors were relatively underestimated in previous studies on this subject, however, mandible closing muscles play an essential role when these birds are drumming, pecking and excavating. The palatine bones with pterygoids play a key role during cranial kinesis as they increase the shock-absorbing ability of the bony structures of the cranium (Spring 1965, Jung *et al.* 2019).

The fourth analysis described variation of the relative length of the *rostrum* and the relative thickness of the mandible bone. A clear gradient was evident from those species that peck and excavate less, to those that do so more. The mandible bone has a key role during excavating and pecking (Spring 1965, Wang *et al.* 2013). The relative length of the *rostrum* and the relative thickness of the mandible bone both increase in the more evolved species as an adaptive response to mechanical demands. The characteristics of the mandible bone are suitable as a means to identify the different species (Kessler 2016). The habitat preferences of each woodpecker species corresponds with their cranial attributes, because these species are mostly non-migratory (Pasinelli 2006) and their home ranges are linked to certain trees and forests (Michalczuk *et al.* 2018, Vadász *et al.* 2022). Climatic changes and changes in flora elements through glacial and interglacial periods most likely had major effects on closely related species (like the *Dendrocopos*) and worked as a significant factor during speciation (Varga 2009, Horsák *et al.* 2015, Szatmári 2015, Shakya *et al.* 2017). It is also possible that some unique attributes may have evolved in isolated populations.

Our results show relationships between cranial attributes and habitat preferences, and furthermore, they highlight the complexity and diversity of foraging behaviours. Future studies reflecting on avian cranial apparatus may well increase our knowledge and may be useful in understanding the preferences of different woodpecker species. With a larger sample size, a future investigation could possibly highlight differences between the sexes and elucidate a more complex picture of the behaviour of these birds. The diversity in appearance of those cranial elements that are essential in special movements and adaptations of shock absorbing, may help our understanding of how modern picids evolved from primitive ones. Collecting skull samples of species from different regions of the continent might reveal differences in subspecies and provide a detailed view of the possible polarisation of morphological patterns and niche segregation. More specified future studies might reveal more morphological characteristics that possess informative attributes (e.g. the musculoskeletal structures of the neck) (Péczely 1963). In this study, we did not investigate the effect of phylogeny, but a phylogenetic control would be advisable in any subsequent analysis.

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