

The cranial morphometrics of the wildfowl (Anatidae)

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Abstract Wildfowl (Anatidae) are a diverse group of birds and globally distributed. These birds feed by widely varying methods, there are generalist and specialist species. In a number of vertebrate taxa trophic specializations have led to distinct differences in the morphology of the skull, like in birds. Our knowledge and understanding of the relationship between cranial morphology and feeding mechanism of wildfowl are limited. The aim of this article is to increase our knowledge of the relationship between skull shape and foraging habits and find the identifiable attributes of the differently adapted groups. We used morphometric methods with 7 linear measurements of the skull. We used principal component (PC) analysis to identify the groups with different foraging habits. The PCs were related to measurements which represent the demanded muscle mass for feeding and the amount of capable food items. The grazers have a narrower bill and bigger bone surface which requires more muscle tissue than the broad billed filter-feeders. We observed the structural and functional differences between grazers and filter-feeders. There are no important differences in the bill measurements between omnivore dabbling and diving ducks. Only the bill is not enough to deduce the foraging habits.

Keywords: cranial morphology, morphometrics, anatomy, prey composition, prey preference, foraging methods

Összefoglalás A récefélék (Anatidae) családja nagy fajsámú, rendkívül diverz csoport. Táplálkozási típusuk szerint lehetnek generalisták és specialisták is. A koponya tulajdonságait és a különböző tápláléktípusokhoz való adaptációt számos gerinces esetében vizsgálták, azonban a récefélék esetében még kevésbé ismert a különböző morfológiai és fenotípusos jellemzők környezettel való interakciója. Jelen cikkben a récefélék cranialis jegyeinek morfometriai elemzésével a táplálékpreferencia és a morfológiai jellemzők közötti összefüggést kerestük, és a különböző tápláléktípusokhoz adaptálódott formák közötti különbségeket próbáltuk megtalálni. A craniomorfometriai vizsgálat során – a koponyákon felvett hét méret felhasználásával – főkomponens-analízist végeztünk. A főkomponensek a táplálék felvételéhez szükséges izomzat nagyságával, valamint a felvehető táplálék mennyiségével hozhatók kapcsolatba. A szárazföldi növényekkel táplálkozó formák keskenyebb csőrrel, és az erőteljesebb állkapcsi és nyakizmok miatt nagyobb tapadási felszínnel rendelkeznek, mint a széles csőrű, filtráló specialisták. Felépítésbeli és funkcionális különbség a legelő és a filtráló specialisták között mutatható ki. Az omnivor úszó- és bukórécék között a csőr tulajdonságaiban a vizsgálat nem mutatott nagy eltérést, tehát a csőr önmagában nem informatív a táplálkozást illetően.

Kulcsszavak: koponyasajátosságok, morfometria, anatómia, táplálékösszetétel, táplálékpreferencia, táplálékszerzés

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Introduction

Foraging performance and cranial morphology are functionally linked. In a number of vertebrate taxa, trophic specializations have led to distinct differences in the morphology of the skull (Courant *et al.* 1997, Pérez-Barbería & Gordon 1999, Van Cakenberghe *et al.* 2002) including wildfowl (Anatidae) too (Kurk 2008).

The family contains around 55–60 genera with 150 species (Kear 2005), but other studies mentioned different numbers (Johnsgard 1978, Livezey 1986). While the status of the family is clear the subfamilies and the relationship of the different tribes and species are disputed and poorly understood (Livezey 1997, Donne-Goussé *et al.* 2002). Probably a bigger sample size would increase the power of the new phylogenetic studies (Stidham & Hilton 2015, Wang *et al.* 2016). The fact that some of the species have the ability to produce fertile hybrids made the taxonomic studies more difficult (McGuire *et al.* 2007).

Anatid species show a wide variety of diet types ranging from specialization on terrestrial or aquatic vegetation, tubers, invertebrates and fish to extreme generalization (Johnsgard 1978, 2010). Ecomorphological studies provide insight in the adaptive significance of interspecific differences in morphology (Nudds & Bowbly 1984, Nudds & Kaminski 1984). Feeding in different environments on different types of food is associated with differences in feeding mechanism and linked to differences in morphology. Hence, the interspecific differences in skull and bill morphology reflect interspecific differences in feeding ecology (Kehoe & Thomas 1987). Species of Anatidae differ in the functional anatomy of their feeding apparatus due to the different food and environment requirements (Nudds & Bowbly 1984, Werner 1984, Moermond 1986, Wainwright 1996). Aquatic and terrestrial feeding demand different bill structure but not only the bill morphology may be related to resource use. The jaw muscle size is also associated with resource use (Kooloos *et al.* 1989, Kurk 2008). The anatids exhibit a great variation in bill morphology so they are often considered an example of adaptive radiation (Owen & Black 1990). The bill is moderately long, mostly flattened, blunt-tipped, and covered by a thin layer of skin. It bears a nail at the tip of the maxilla and fine lamellae along the margins of the maxilla and mandible. The bill can be highly specialized (e.g. mergansers and shovelers) or lesser specialized (e.g. scoters) (Cramp 1978, Johnsgard 2010). The wildfowl species mostly differ in body size and bill morphology (Pöysä *et al.* 1994). The different attributes of the bill can show more of the ecology, evolutionary history, functional anatomy and the jaw mechanism of these birds. Unfortunately, despite numerous studies and the enormous data with regards to the feeding ecology of anatids, our knowledge about the potential relationships between cranial morphology and feeding mechanism is very limited.

Our objective in this study was to determine the differences in skull morphology and to find the potential relationships between skull morphology and feeding habit.

Materials and methods

This study is based on 269 skulls of 103 species. The specimens belong to the collection of Eötvös Loránd University (Budapest, Hungary), the collection of the Hungarian Natural

History Museum and the digital archive of Wageningen University (Wageningen, Netherlands).

Eight skull measurements were taken from the skulls. The distance of the *maxilla* and *premaxilla* (PRMM), the distance of the *maxilla* and the *quadratum* (MQD), the maximum height of the *maxilla* (MMAX), the maximum width of the *premaxilla* (PRMW), the maximum height of the occipital region (the distance of the ventral edge of the *foramen magnum occipitale* and the ventral point of the sagittal crest) (CONSAG), on the mandible the highest point of the coronoid process (CORPR), the distance of the highest point of the coronoid process and central point of the joint of the jaws (glenoid) (CGD), and the distance of the left and right paroccipital processes (PAROCD) (Figure 1). The measurements are from adult and subadult specimens. We had specimens of both sexes from three species. Skull morphology did not differ between sexes, therefore we did not analyse the effect of sex.

We separated the species into six groups according to diet composition. Each group was created following other studies (Cramp 1978, Kear 2005, Johnsgard 2010, Baldassare *et al.* 2014): terrestrial plant eaters, omnivore dabbling ducks, omnivore diving ducks, fish eaters, aquatic plant eaters, filter-feeders.

We collected body mass data of the species from Dunning (1992). If the sex of a given specimen was known, we used the corresponding mass data. In other cases we used male mass data. For the analyses we couldn't use the domestic forms of ducks and geese, because

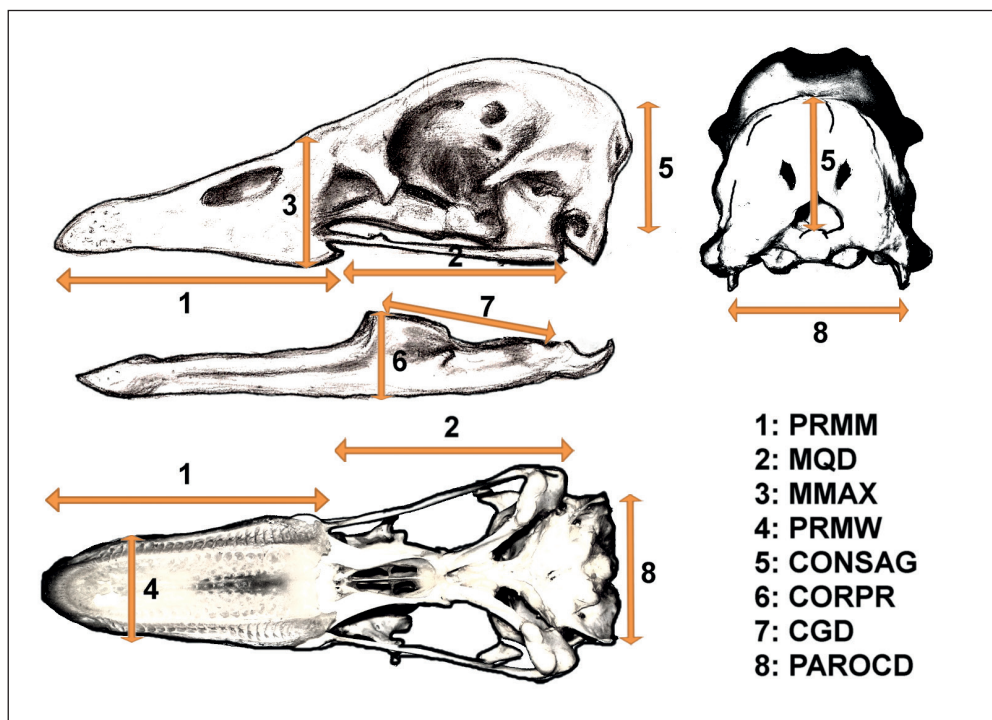


Figure 1. Linear measurements used in this study. A goose skull in left lateral, caudal and ventral views
1. ábra A vizsgálatban használt lineáris paraméterek. Egy lúdkoponya bal oldali, hátsó és alsó nézetben

the reason of the huge differences between the breeds is not the natural but the human selection. Accordingly to this, many osteological and craniological changes resulted only from the domestication (Guay & Iwaniuk 2008).

We tested the normality of the frequency distributions of the variables and the model residuals using Kolmogorov–Smirnov tests. Body mass and morphological variables differed significantly from normal distribution. We $(-1 \times 1/\text{square root}(x+100))$ transformed body mass data to fit normal distribution. In different subsets of the specimens we investigated the repeatabilities of the measurements by Spearman's correlation: we tested repeatability of digital measures performed on skull photos ($n=20$), manual measures on skulls ($n=20$). Additionally we tested repeatability between digital and manual measures ($n=20$) (all $P < 0.0001$, all $r > 0.989$). For subsequent analyses we used data of the first measurements. In the next step, we divided each morphological parameter of every skull by the given PAROCD to standardize the variables for skull size. We conducted principal component analyses (PCA) on these morphological variables. We took PCA for two reasons: we wanted dimension reduction of variables, and we wanted to create composite but independent variables from each other because the original morphological variables highly correlated to each other (results not shown here). We rotated the principal component (PC) axes using the varimax algorithm in order to strengthen the interpretability of the patterns of PC loadings. This method preserves the orthogonality of the PC axes. Based on the Kaiser criterion, for the subsequent analyses we used only PCs with eigenvalues greater than one. We took into consideration a loading, if its value was larger than 0.52 according to the formula described in Norman and Steiner (2008). We used general linear mixed models in PROC MIXED of SAS version 9.1 (SAS Institute Inc., Cary, North Carolina, USA) to reveal if morphological PCs associated to different feeding groups. In this model one PC was the dependent variable, feeding group was the categorical predictor and body mass was the continuous co-variable. Furthermore species was used as random factor. We used the latter two variables controlling for species relatedness and body size. We applied backward stepwise model selection (Hegyí & Laczi 2015). Degrees of freedom in the mixed models were estimated using the Satterthwaite option, furthermore to make pairwise comparisons of different groups we used CONTRAST statement. All other analyses were performed in Statistica 8.0 (StatSoft Inc., Thulsa, Oklahoma, USA).

Results

Our measures were highly significant irrespective of measuring mode (all $r > 0.98$, all $P < 0.00001$). The PCA resulted three PCs which explained 75.98% of inter-individual total variance (Table 1). The first skull PC (PC1) loaded positively with MMAX, CONSAG and CORPR, PC2 related positively to PRMM and PRMW, while PC3 loaded positively with MQD and CGD. This means that a specimen with higher PC score had higher values of the respective skull variable. Species, feeding type and feeding had significant effects on all PCs, while body mass related to PC1 and PC3 only (Table 2). *Post-hoc* tests showed that in the case of PC1 group 4 differed from all of the other groups, and group 1 and group 3 differed from each other (Figure 2). With respect to PC2, each group showed differences from each other except group

	PC1	PC2	PC3
PRMM	0.01	0.85	0.4
MQD	0.25	0.19	0.66
MMAX	0.85	0.24	-0.05
PRMW	0.16	0.94	-0.08
CONSAG	0.77	0.21	0.1
CORPR	0.86	-0.1	0.26
CGD	0.08	0.09	0.86
eigenvalue	2.14	1.75	1.43
% variance	30.53	24.99	20.46

Table 1. Summary of the loadings of the principal component analysis performed on morphological skull variables. Morphological variables were corrected for skull size. Loading values exceeding the 0.52 threshold are shown in bold

1. táblázat A koponyamorfológiai változókon végrehajtott főkomponens analízis összesítése. A morfológiai változók a koponyaméret alapján lettek korrigálva. A 0,52-es határt meghaladó értékeket félkövérrel jelentettük meg

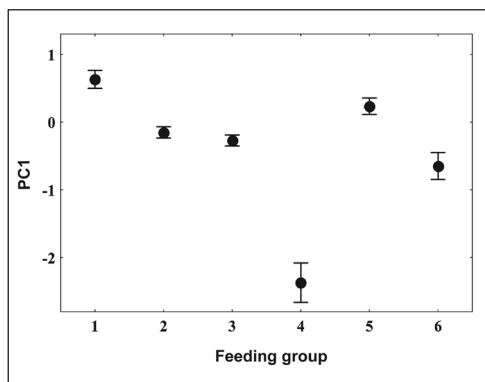


Figure 2. The differences of PC1 (mean±SE) between the feeding groups

1: terrestrial plant eaters, 2: omnivore dabbling ducks, 3: omnivore diving ducks, 4: fish eaters, 5: aquatic plant eaters, 6: filter-feeders

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Note: on the plot the points are the means of the values and the SE values are presented as whiskers

2. ábra

A PC1 eltérése (átlag±SE) a különböző táplálkozásmódú csoportok között

1: szárazföldi növényeket fogyasztók, 2: vegyes táplálkozású úszórécék, 3: vegyes táplálkozású bukórécék, 4: hallal táplálkozó, 5: vízínövényeket fogyasztók, 6: filteráló specialisták

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Megjegyzés: A pont az értékek átlagát mutatja, a vonallal jelzett tartomány az SE értéket jelöli

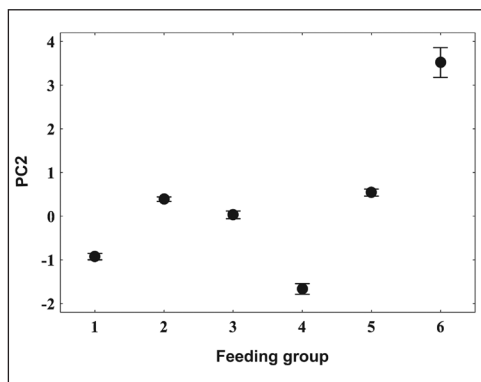


Figure 3. The differences of PC2 (mean±SE) between the feeding groups

1: terrestrial plant eaters, 2: omnivore dabbling ducks, 3: omnivore diving ducks, 4: fish eaters, 5: aquatic plant eaters, 6: filter-feeders

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Note: on the plot the points are the means of the values and the SE values are presented as whiskers

3. ábra

A PC2 eltérése (átlag±SE) a különböző táplálkozásmódú csoportok között

1: szárazföldi növényeket fogyasztók, 2: vegyes táplálkozású úszórécék, 3: vegyes táplálkozású bukórécék, 4: hallal táplálkozó, 5: vízínövényeket fogyasztók, 6: filteráló specialisták

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Megjegyzés: A pont az értékek átlagát mutatja, a vonallal jelzett tartomány az SE értéket jelöli

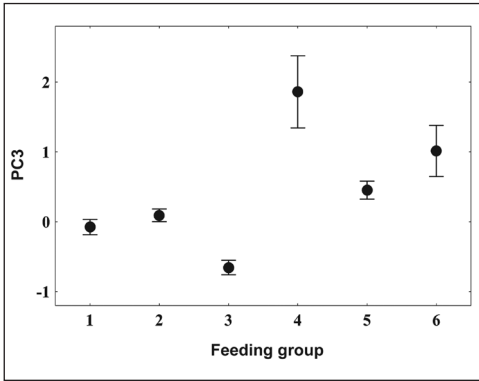


Figure 4. The differences of PC3 (mean±SE) between the feeding groups

1: terrestrial plant eaters, 2: omnivore dabbling ducks, 3: omnivore diving ducks, 4: fish eaters, 5: aquatic plant eaters, 6: filter-feeders

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Note: on the plot the points are the means of the values and the SE values are presented as whiskers

4. ábra A PC3 eltérése (átlag±SE) a különböző táplálkozásmódú csoportok között

1: szárazföldi növényeket fogyasztók, 2: vegyes táplálkozású úszóréccék, 3: vegyes táplálkozású bukóréccék, 4: hallal táplálkozó, 5: vízinnövényeket fogyasztók, 6: filtráló specialisták

$n_1: 69; n_2: 83; n_3: 63; n_4: 8; n_5: 40; n_6: 6$

Megjegyzés: A pont az értékek átlagát mutatja, a vonallal jelzett tartomány az SE értéket jelöli

Table 2. Effects of species, body mass and feeding group on skull morphology PCs

2. táblázat A fajok, a testtömeg és a kijelölt táplálkozási csoportok hatásai a koponyamorfológia főkomponenseire

		df	F	P
PC1	Species	0.1376,0.06718	2.05	0.02
	Body mass	1,48	9.12	0.004
	Feeding group	5,44.5	9.94	<0.0001
PC2	Species	0.2051,0.04828	4.25	<0.0001
	Body mass	1,67.3	3.30	0.07
	Feeding group	5,64.5	50.23	<0.0001
PC3	Species	0.4561,0.1193	3.82	<0.0001
	Body mass	1,64.7	8.04	0.006
	Feeding group	5,58.2	8.40	<0.0001

2 vs. group 5, and the difference between group 1 and group 4 was only marginal (Figure 3). In the case of PC3 group 3 differed from all other groups, and group 4 also differed from all the others except group 6 (Figure 4). For detailed results see Table 3.

Discussion

The cranial kinesis is the significant movement of neurocranium and viscerocranium to each other in addition to movement at the joint between upper and lower jaw. Most of the vertebrates have a kinetic skull. Cranial kinesis is usually linked to feeding and foraging. Animals with high bite force have usually akinetic skulls like crocodylians (Crocodylia) and turtles (Testudines) (Iordansky 1989). The mammals have akinetic skulls too (except the hares (Leporidae)) compared with some lizards (Lacertilia) and snakes (Serpentes) which have highly kinetic skulls (Kardong 1995). Bock (1964) has analysed the kinetics of the

Table 3. Pairwise post-hoc comparisons of different feeding groups

3. táblázat Páronkénti post-hoc teszt összehasonlítása a különböző táplálkozási csoportoknál

	Groups	df	F	P
PC1	1 vs 2	1, 56.7	2.26	0.14
	1 vs 3	1, 48.4	5.86	0.019
	1 vs 4	1, 97.3	46.43	<0.0001
	1 vs 5	1, 43.9	0.19	0.66
	1 vs 6	1, 3	2.65	0.11
	2 vs 3	1, 41.3	0.98	0.33
	2 vs 4	1, 92.3	36.21	<0.0001
	2 vs 5	1, 37.9	0.55	0.46
	2 vs 6	1, 29.3	1.14	0.29
	3 vs 4	1, 87.9	28.62	<0.0001
	3 vs 5	1, 38.9	2.40	0.13
	3 vs 6	1, 29.5	0.42	0.52
	4 vs 5	1, 78.6	36.80	<0.0001
	4 vs 6	1, 41.9	8.15	0.01
	5 vs 6	1, 29.8	1.87	0.18
PC2	1 vs 2	1, 118	125.94	<0.0001
	1 vs 3	1, 64	42.65	<0.0001
	1 vs 4	1, 76.6	3.94	0.05
	1 vs 5	1, 63.4	74.04	<0.0001
	1 vs 6	1, 47.5	94.50	<0.0001
	2 vs 3	1, 65	5.18	0.03
	2 vs 4	1, 76.9	52.27	<0.0001
	2 vs 5	1, 64.2	0.71	0.40
	2 vs 6	1, 47.7	42.88	<0.0001
	3 vs 4	1, 71.5	31.32	<0.0001
	3 vs 5	1, 57.8	6.79	0.01
	3 vs 6	1, 47.2	52.67	<0.0001
	4 vs 5	1, 70.5	50.87	<0.0001
	4 vs 6	1, 52.1	93.91	<0.0001
	5 vs 6	1, 47.6	35.87	<0.0001
PC3	1 vs 2	1, 95.2	2.74	0.10
	1 vs 3	1, 59.3	4.56	0.04
	1 vs 4	1, 74.8	22.26	<0.0001
	1 vs 5	1, 57.1	3.21	0.08
	1 vs 6	1, 42.1	3.91	0.05
	2 vs 3	1, 58.6	11.84	0.001
	2 vs 4	1, 75.1	14.63	0.0003
	2 vs 5	1, 56.8	0.23	0.63
	2 vs 6	1, 42	2.12	0.15
	3 vs 4	1, 69.4	32.81	<0.0001
	3 vs 5	1, 52.6	10.61	0.002
	3 vs 6	1, 41.7	7.35	0.01
	4 vs 5	1, 66.9	9.88	0.003
	4 vs 6	1, 47.3	0.65	0.43
	5 vs 6	1, 42.3	1.39	0.25

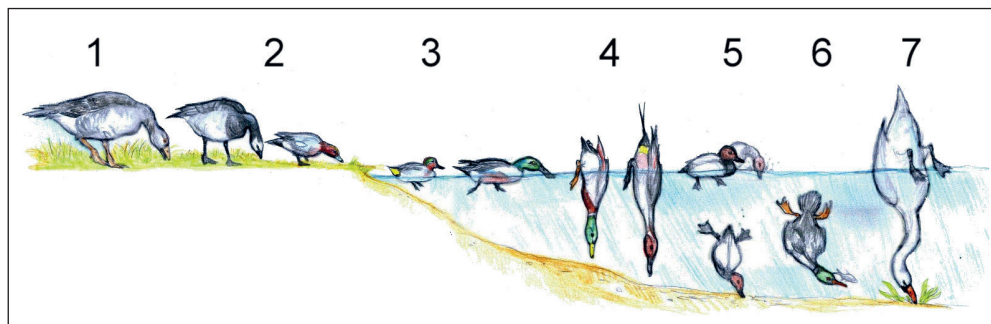


Figure 5. Feeding methods of the anatids: 1. grubbing (Greylag Goose), 2. grazing (Barnacle Goose, and Eurasian Wigeon), 3. dabbling (Eurasian Teal and Shoveler), 4. upending (Mallard and Pintail), 5. diving (Common Pochard), 6. pursuit diver (Red-breasted Merganser), 7. upending (Mute Swan). Own drawing modified from Kear (2005)

5. ábra A récefélékre jellemző táplálkozási módok: 1. keményebb növényi részeket legelők és gyökereket, magokat fogyasztók (nyári lúd), 2. lágyabb növényi részeket legelők (apácálúd, fűtyülőréce), 3. filtrálók, felszínről táplálkozók (csörgő réce, kanalas réce), 4. testük elülső részével alábukók (tőkés réce, nyílfarkú réce), 5. víz alá bukók, merülők (barátréce), 6. víz alatt úzve, halakkal táplálkozók (örvös bukó), 7. testük elülső részével alábukók (bütykös hattyú) (saját ábra, Kear (2005) nyomán)

avian skull and proposed a model for a prokinetic skull in connection to mandibular kinetics. The birds show a great variety of cranial kinetic hinges (Zusi 1984, Zweers 1999). The simplest form of kinetic movement is prokinesis, where the upper beak moves at the point where it's hinged with the neurocranium. Several different types of cranial kinesis are present within modern birds (Neognathae). The amphikinesis provides an unusual movement for the bill with protraction and retraction (e.g.: rails and shorebirds (Rallidae). The rynchokinesis is a more complex form than prokinesis and subdivided into other different types. Rynchokinesis was observed in cranes (Gruidae), shorebirds (e.g. Scolopacidae), swifts (Apodidae), hummingbirds (Trochillidae) and some primitive birds (Paleognathae) like the Emu (*Dromaius novaehollandiae*) and the Ostrich (*Struthio camelus*). There are birds with akinetic skulls (e.g. toucans (Ramphastidae) (Zusi 1984). The cooperative tissues like the elements of the cranial musculoskeletal system (muscles, joints and ligaments) are the indicators of different kinesis forms (Metzger 2002).

Darwin's finches (*Geospizinae*) of the Galápagos Islands, Ecuador, are one of the most studied birds because these birds have evolved an impressive array of specializations in beak form and function (Bowman 1961). In anatids as well the cranial and bill characters are related to bite force and the reaction forces in the joints with the upper bill (Herrel *et al.* 1995). It is uncertain if the ligaments and the quadrate bone are responsible for the mobility. The movement of the quadrate bone is too fast and complex and really difficult to measure and determine the movement of the bone (Dawson *et al.* 2011). Anatids grebes (Podicipedidae) and flamingos (Phoenicopteridae) differ in foraging methods but their tongues play a very important role during feeding in water (Zweers *et al.* 1995). The different foraging methods and kinesis types are well known but it is still a mystery how these cranial movements evolved (Hanken & Hall 1993).

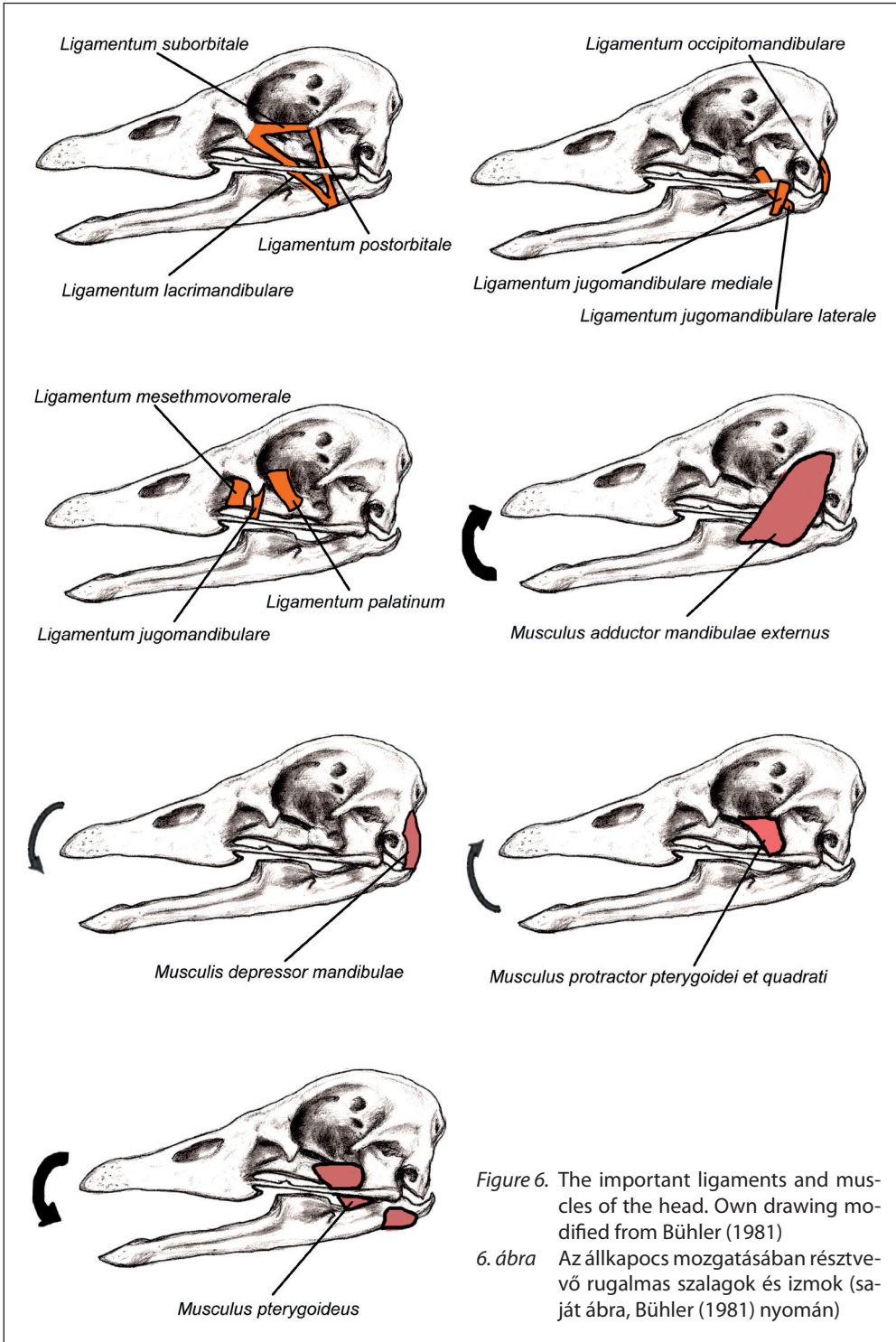


Figure 6. The important ligaments and muscles of the head. Own drawing modified from Bühler (1981)

6. ábra Az állkapocs mozgásában résztvevő rugalmas szalagok és izmok (saját ábra, Bühler (1981) nyomán)

Kooloos *et al.* (1989) and Kooloos and Zweers (1991) analysed performance gradients of filter feeding in several anatid species, such as the Mallard (*Anas platyrhynchos*), the Shoveler (*Anas clypeata*) and the Tufted Duck (*Aythya fuligula*). They found that the gapes and amplitudes of bill rotations are positively correlated with the size of the seeds during filter feeding (Zweers 1999). The interspecific differences of the bill, such as the density of the lamellae, reflect the difference in diet composition and the different size of the food items (Mott 1994). There may be a positive correlation between the lamella density and the size of the food items (Guillemain *et al.* 2002) but other studies disagree (Nummi & Väänänen 2001) or show that the size and the morphology of the bill are more important (Lagerquist & Ankney 1989, Pöysä 1983a). It might be that these differences are connected with the different requirements of the environment or other resource using habits and methods (Werner 1984, Moermond 1986, Wainwright 1996). More specified studies demand more morphological characters which are more informative and reflect to the foraging habits (e.g. the neck length) (Pöysä 1983b).

In our analysis the PC1 showed strong relationships with variables which are in connection with muscles involved in food intake and bite performance. Based on the PC1 axis we found differences between the following feeding groups: terrestrial plant eaters or grazers and the aquatic plant eaters, fish eaters, and filter feeders. The terrestrial plant eaters and the aquatic plant eaters had the highest PC1 values but the fish eaters and the filter feeders had the lowest PC1 values. This means that the fish eater filter feeder species have smaller and weaker pterygoid and adductor muscles. The herbivore species have massive skull with large quadrato-mandibular surface in order to maximize the effectiveness of jaw closure muscles, which is necessary for grazing. The relative length of the occipital region is in positive correlation with bite performance (Herrel *et al.* 2001, Van Cakenberghe *et al.* 2002, Stayton 2005). The filter feeders do not need strong neck and jaw muscles (Zusi 1963).

The PC2 values positively loaded with those morphological characters which are in connection with the amount of capable food. Species with narrower beak are feeding on terrestrial plants and grass and the fish eaters with low PC2 values. The geese are picking, the mergansers are catching their prey, but the shovelers are filtering millions of planktonic organisms with their highly specialized bill. The other groups took intermediate position. Through the example of the grazers the observation is true which means that the strong and narrow, tapered beak is in positive correlation with bite performance (Van der Meij & Bout 2004, Herrel *et al.* 2005).

The PC3 showed strong relationship with those morphological characters which are related to the elongation of the skull. The grazers and the omnivore dabbling ducks have a relative short and high skull compared to the fish eaters and filter feeders which have long and very gracile skull. Compare with the PC1 values, the groups with higher PC3 values have generally weaker jaw and jaw muscles. In the case of mergansers, not only the food but the hydrodynamic demands and the drag forces affect the cranial morphology (Harrison 1957). In species that have to detach shellfish or hold a twisting and squirming fish one might expect relatively large adductor muscles (Kear 2005). The analysis suggested that the species with higher PC3 values (fish eaters, aquatic plant eaters and filter feeders) are feeding underwater. Due to the large resisting forces these species should have stronger jaw opener

muscles. But this speculation should be irrelevant because many grazer species (e.g. Greylag Goose) tend to have large jaw opener muscles because these birds are not only feeding on the aerial parts of the plants but also on the underground parts. During grabbing the bill pushes against the mud, which needs larger force (Gauthier *et al.* 1984).

The structural and functional differences are only demonstrable between grazers and filter feeders (Kurk 2008). The *condylus occipitalis* is caudally directed in grazers and ventrally directed in filter feeders. The grazer's pterygoid bone is longer and the palatine bone is shorter compare to the filter feeders (Marugán-Lobón & Buscalioni 2006). The birds with a ventrally directed beak have bigger and stronger jaw closure muscles compared to birds with an orthogonally directed beak (Van der Meij & Bout 2004).

Grazing has evolved several times within the anatids. The species with similar morphology and diet but different phylogenetic background represent an example for convergent evolution (Kear 2005, Wang *et al.* 2016). In some cases the similarities in the skull shape reflect the phylogenetic connection. In this study we did not investigate the effect of phylogeny and the similarities due to phylogeny. In further analyses the phylogenetic control would be necessary.

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References

- Baldassarre, G. A. 2014. Ducks, geese, and swans of North America. Vol. 1. – JHU Press
- Bock, W. J. 1964. Kinetics of the avian skull. – *Journal of Morphology* 144: 1–42.
- Bowman, R. I. 1961. Morphological differentiation and adaptation in the Galápagos Finches. – University of California Press
- Bühler, P. 1981. Functional anatomy of the avian jaw apparatus. Form and function in birds. Vol. 2. – Academic Press, London, pp. 439–468.
- Courant, F., David, B., Laurin, B. & Chaline, J. 1997. Quantification of cranial convergences in arviculids (Rodentia). – *Biological Journal of the Linnean Society* 62(4): 505–517. DOI: 10.1006/bijl.1997.0172
- Cramp, S. 1978. The Birds of the Western Palearctic. Vol. 1. Ostrich to Ducks. – Oxford University Press, Oxford
- Dawson, M. M., Metzger, K. A., Baier, D. B. & Brainerd, E. L. 2011. Kinematics of the quadrate bone during feeding in Mallard Ducks. – *Journal of Experimental Biology* 214(12): 2036–2046. DOI: 10.1242/jeb.047159
- Donne-Goussé, C., Laudet, V. & Hänni, C. 2002. A molecular phylogeny of Anseriformes based on mitochondrial DNA analysis. – *Molecular Phylogenetics and Evolution* 23(3): 339–356. DOI: 10.1016/S1055-7903(02)00019-2
- Dunning J. B. Jr. (ed.) 1992. CRC Handbook of Avian Body Masses. – CRC Press
- Gauthier, G., Bédard, J. & Bédard, Y. 1984. Comparison of daily energy expenditure of Greater Snow Geese between two habitats. – *Canadian Journal of Zoology* 62(7): 1304–1307. DOI: 10.1139/z84-187
- Guay, P. J. & Iwaniuk, A. N. 2008. Captive breeding reduces brain volume in waterfowl (Anseriformes). – *The Condor* 110(2): 276–284. DOI: 10.1525/cond.2008.8424
- Guillemain, M., Martin, G. R. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). – *Functional Ecology* 16(4): 522–529. DOI: 10.1046/j.1365-2435.2002.00652.x

- Hanken, J. & Hall, B. K. 1993. Mechanism of skull diversity and evolution. Vol. 3. The Skull. – University of Chicago Press, Chicago, pp. 1–36.
- Harrison, J. G. 1957. A review of skull pneumatization in birds. – *Bulletin of the British Ornithologists* 77: 70–77.
- Hegyí, G. & Laczi, M. 2015. Using full models, stepwise regression and model selection in ecological data sets: Monte Carlo simulations. – *Annales Zoologici Fennici* 52: 257–279. DOI: 10.5735/086.052.0502
- Herrel, H., Cleuren, J. & De Vree, F. 1995. Prey capture in the lizard *Agama stellio*. – *Journal of Morphology* 224: 313–329. DOI: 10.1002/jmor.1052240306
- Herrel, A., Damme, R. V., Vanhooydonck, B. & Vree, F. D. 2001. The implications of bite performance for diet in two species of lacertid lizards. – *Canadian Journal of Zoology* 79(4): 662–670. DOI: 10.1139/z01-031
- Herrel, A., Podos, J., Huber, S. K. & Hendry, A. P. 2005. Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak. – *Functional Ecology* 19: 43–48. DOI: 10.1111/j.0269-8463.2005.00923.x
- Iordansky, N. 1989. Evolution of cranial kinesis in lower tetrapods. – *Netherlands Journal of Zoology* 40: 32–54. DOI: 10.1163/156854289X00174
- Johnsgard, P. A. 1978. Ducks, geese, and swans of the world. – University of Nebraska Press, 1st edition, Lincoln, Nebraska
- Johnsgard, P. A. 2010. The world's Waterfowl in the 21st century: A 2010 supplement to ducks, geese, and swans of the world. – University of Nebraska Press, Lincoln
- Kardong, K. V. 1995. Vertebrates: Comparative anatomy, function and evolution. – Brown, W. C., Dubuque, Iowa
- Kear, J. 2005. Bird Families of the World: Ducks, Geese and Swans. – Oxford University Press, New York
- Kehoe, F. P. & Thomas, V. G. 1987. A comparison of interspecific differences in the morphology of external and internal feeding apparatus among North American Anatidae. – *Canadian Journal of Zoology* 65(7): 1818–1822. DOI: 10.1139/z87-275
- Kooloos, J. G. M., Kraaijeveld, A. R., Langenbach, G. E. J. & Zweers, G. A. 1989. Comparative mechanics of filter feeding in *Anas platyrhynchos*, *Anas clypeata* and *Aythya fuligula* (Aves, Anseriformes). – *Zoomorphology* 108(5): 269–290. DOI: 10.1007/BF00312160
- Kooloos, J. G. M. & Zweers, G. A. 1991. Integration of pecking, filter feeding and drinking mechanisms in waterfowl. – *Acta Biotheoretica* 39(2): 107–140. DOI: 10.1007/BF00046595
- Kurk, C. D. 2008. The bill of evolution. Trophic adaptations in anseriform birds. – PhD Thesis, Leiden University, The Netherlands
- Lagerquist, B. A. & Ankney, C. D. 1989. Interspecific differences in bill and tongue morphology among diving ducks (*Aythya* spp., *Oxyura jamaicensis*). – *Canadian Journal of Zoology* 67(11): 2694–2699. DOI: 10.1139/z89-381
- Livezey, B. C. 1986. Phylogeny and historical biogeography of steamer-ducks (Anatidae: Tachyeres). – *Systematic Biology* 35(4): 458–469. DOI: 10.2307/2413109
- Livezey, B. C. 1997. A phylogenetic analysis of basal Anseriformes, the fossil *Presbyornis*, and the interordinal relationships of waterfowl. – *Zoological Journal of the Linnean Society* 121(4): 361–428.
- Marugán-Lobón, J. & Buscalioni, Á. D. 2006. Avian skull morphological evolution: exploring exo- and endocranial covariation with two-block partial least squares. – *Zoology* 109(3): 217–230. DOI: 10.1016/j.zool.2006.03.005
- McGuire, J. A., Linkem, C. W., Koo, M. S., Hutchison, D. W., Lappin, K. A., Orange, D. L. & Lemos-Espinal, J. 2007. Mitochondrial introgression and incomplete lineage sorting through space and time: Phylogenetics of crotaphytid lizards. – *Evolution* 61: 2879–97. DOI: 10.1111/j.1558-5646.2007.00239.x
- Metzger, K. 2002. Cranial kinesis in lepidosaurs: skulls in motion. Topics in functional and ecological vertebrate morphology. – Shaker Publishing, Maastricht, pp. 15–46.
- Moermond, T. C. 1986. Mechanistic approach to the structure of animal communities: anolis lizards and birds. – *American Zoologist* 26(1): 23–37.
- Mott, K. N. 1994. A functional morphological approach to the study of filter-feeding in dabbling ducks (*Anas* spp.). – MSc Thesis, University of Guelph, Guelph, Ontario
- Norman, G. R. & Streiner, D. L. 2008. Biostatistics: The Bare Essentials. – Bc Decker, Hamilton
- Nudds, T. D. & Bowlby, J. N. 1984. Predator-prey size relationships in North American dabbling ducks. – *Canadian Journal of Zoology* 62: 2002–2008. DOI: 10.1139/cjz-2016-0063
- Nudds, T. D. & Kaminski, R. M. 1984. Sexual size dimorphism in relation to resource partitioning in North American dabbling ducks. – *The Canadian Journal of Zoology* 62: 2009–2012. DOI: 10.1139/cjz-2016-0063
- Nummi, P. & Väänänen, V. M. 2001. High overlap in diets of sympatric dabbling ducks—an effect of food abundance? – *Annales Zoologici Fennici* 38(2): 123–130.

- Owen, M. & Black, J. M. 1990. Waterfowl ecology. – Blackie and Son, Ltd., Chapman and Hall, New York, pp. 11–12.
- Pérez-Barbería, F. J. & Gordon, I. J. 1999. The functional relationship between feeding type and jaw and cranial morphology in ungulates. – *Oecologia* 118: 157–165. DOI: 10.1007/s004420050714
- Pöysä, H. 1983a Morphology-mediated niche organization in a guild of dabbling ducks. – *Ornis Scandinavica* 14(2): 317–326. DOI: 10.2307/3676325
- Pöysä, H. 1983b Resource utilization pattern and guild structure in a waterfowl community. – *Oikos* 40(2): 295–307. DOI: 10.2307/3544594
- Pöysä, H., Elmberg, J., Nummi, P. & Sjöberg, K. 1994. Species composition of dabbling duck assemblages: ecomorphological patterns compared with null models. – *Oecologia* 98: 193–200. DOI: 10.1007/BF00341472
- Stayton, C. T. 2005. Morphological evolution of the lizard skull: a geometric morphometrics survey. – *Journal of Morphology* 263(1): 47–59. DOI: 10.1002/jmor.10288
- Stidham, T. A. & Hilton, R. P. 2015. New data on stiff-tailed duck evolution and dispersal from a new species of diving duck (Anseriformes: Anatidae: cf. Oxyurinae) from the Miocene High Rock Caldera in north-west Nevada, USA. Vol. 2., Part 1. – *Papers in Palaeontology*, pp. 41–58. DOI: 10.1002/spp2.1029
- Van Cakenberghe, V., Herrel, A. & Aguirre, L. F. 2002. Evolutionary relationships between cranial shape and diet in bats (Mammalia: Chiroptera). – In: Aerts, P., D’Aout, K., Herrel, A. & Van Damme, R. (eds.) *Topics in Functional and Ecological Vertebrate Morphology*. – Shaker Publishing, Maastricht, pp. 205–236.
- Van der Meij, M. A. A. & Bout, R. G. 2004. Scaling of jaw muscle size and maximal bite force in finches. – *Journal of Experimental Biology* 207(16): 2745–2753. DOI: 10.1242/jeb.01091
- Wang, J., Liu, G., Zhou, L., Qing, H., Li, L., Li, B. & Zhang, L. 2016. Complete mitochondrial genome of Tundra Swan *Cygnus columbianus jankowskii* (Anseriformes: Anatidae). – *Mitochondrial DNA Part A* 27(1): 90–91. DOI: 10.3109/19401736.2013.873917
- Wainwright, P. C. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. – *Ecology* 77(5): 1336–1343. DOI: 10.2307/2265531
- Werner, E. E. 1984. The mechanisms of species interactions and community organization in fish. – In: Strong, D. R. Jr., Simberloff, D., Abele, L. G. & Thistle, A. B. (eds.) *Ecological communities: conceptual issues and evidence*. – Princeton University Press, Princeton, NJ.
- Zusi, R. L. 1963. Functional anatomy of the feeding apparatus in waterfowl. – *The Auk* 80(4): 562–564. DOI: 10.1111/j.1096-3642.1997.tb01285.x
- Zusi, R. L. 1984. A functional and evolutionary analysis of rynchokinesis in birds. – *Smithsonian Contributions to Zoology*, Smithsonian Institution Press, Washington
- Zweers, G., De Jong, F., Berkhoudt, H. & Berge, J. V. 1995. Filter feeding in Flamingos (*Phoenicopterus ruber*). – *Condor* 97(2): 297–324. DOI: 10.2307/1369017
- Zweers, G. A. 1999. Cranial kinesis in birds: Consequences for the evolution of the jaw apparatus. – In: Adams, N. J. & Slotow, R. H. (eds.) *Proc. 22. International Ornithologist Congress, Durban*, pp. 82–93.

Supplement 1. The species of the different feeding groups

1: terrestrial plant eaters, 2: omnivore dabbling ducks, 3: omnivore diving ducks, 4: fish eaters, 5: aquatic plant eaters, 6: filter-feeders

Melléklet 1. A különböző táplálkozási csoportokba tartozó fajok

1: szárazföldi növényeket fogyasztók, 2: vegyes táplálkozású úszórécék, 3: vegyes táplálkozású bukórécék, 4: hallal táplálkozók, 5: vízinövényeket fogyasztók, 6: filtráló specialisták

1: *Aix galericulata*, *Aix sponsa*, *Alopochen aegyptiacus*, *Anas americana*, *Anas penelope*, *Anas sibilatrix*, *Anser albifrons*, *Anser anser*, *Anser brachyrhynchus*, *Anser erythropus*, *Anser fabalis*, *Anser indicus*, *Anser serrirostris*, *Branta bernicla*, *Branta bernicla hrota*, *Branta bernicla nigricans*, *Branta canadensis*, *Branta hutchinsii*, *Branta leucopsis*, *Branta ruficollis*, *Cereopsis novahollandiae*, *Chen caerulescens*, *Chen canagica*, *Chen rossii*, *Chenonetta jubata*, *Chloephaga picta*, *Chloephaga poliocephala*, *Neochen jubata*, *Nettapus auritus*, *Nettapus pulchellus*

2: *Amazonetta brasiliensis*, *Anas acuta*, *Anas bahamensis*, *Anas bernieri*, *Anas capensis*, *Anas carolinensis*, *Anas castanea*, *Anas crecca*, *Anas cyanoptera*, *Anas discors*, *Anas flavirostris*, *Anas formosa*, *Anas georgica*, *Anas hottentotta*, *Anas luzonica*, *Anas platyrhynchos*, *Anas querguedula*, *Anas rubripes*, *Anas undulata*, *Anas versicolor*; *Cairina moschata*, *Callonetta leucophrys*, *Marmaronetta angustirostris*, *Rhodonessa caryophyllacea*, *Sarkidiornis melanotos*, *Speculanas specularis*, *Tadorna ferruginea*, *Tadorna radjah*, *Tadorna tadorna*

3: *Aythya americana*, *Aythya collaris*, *Aythya ferina*, *Aythya fuligula*, *Aythya marila*, *Aythya nyroca*, *Aythya valisineria*, *Bucephala albeola*, *Bucephala clangula*, *Bucephala islandica*, *Clangula hyemalis*, *Heteronetta atricapilla*, *Histrionicus histrionicus*, *Melanitta americana*, *Melanitta deglandi*, *Melanitta fusca*, *Melanitta nigra*, *Melanitta perspicillata*, *Netta peposaca*, *Netta rufina*, *Oxyura jamaicensis*, *Oxyura leucocephala*, *Somateria molissima*, *Somateria spectabilis*, *Tachyeres brachypterus*

4: *Merganetta armata*, *Mergellus albellus*, *Mergus merganser*, *Mergus serrator*

5: *Anas strepera*, *Coscoroba coscoroba*, *Cygnus atratus*, *Cygnus bewickii*, *Cygnus buccinator*, *Cygnus columbianus*, *Cygnus cygnus*, *Cygnus melancoryphus*, *Cygnus olor*, *Dendrocygna autumnalis*, *Dendrocygna bicolor*, *Dendrocygna eytoni*, *Dendrocygna javanica*, *Dendrocygna viduata*

6: *Anas clypeata*, *Anas rhynchotis*