Zoodiversity, **57**(3): 251–266, 2023
DOI 10.15407/zoo2023.03.251

UDC 595.42(477)

COVARIATION IN SHAPES BETWEEN THE STERNUM AND PELVIS IN AQUATIC BIRDS WITH DIFFERENT LOCOMOTOR MODES

O. V. Shatkovska[1*] & M. Ghazali[2]

Schmalhausen Institute of Zoology NAS of Ukraine,
vul. B. Khmelnytskogo, 15, Kyiv, 01054 Ukraine
[1]E-mail: shatkovskayaoksana@gmail.com
[2]E-mail: ghazali.maria@gmail.com
**Corresponding author*

O. V. Shatkovska (http://orcid.org/0000-0002-5758-4364)
M. Ghazali (http://orcid.org/0000-0001-9195-0914)

urn:lsid:zoobank.org:pub:E5C90ED2-CF01-42E9-BFD6-9AC6174ED8DC

Covariation in Shapes between the Sternum and Pelvis in Aquatic Birds with Different Locomotor Modes. Shatkovska, O. V. & Ghazali, M. — Birds associated with aquatic environments have diverse locomotor and foraging strategies. We hypothesise that aquatic birds have different covariation patterns in the shapes of the sternum and pelvis depending on the locomotor mode and the predominant use of wings or hind limbs when moving through the water. The study was conducted on 26 bird species, among which we identified three ecological categories: surface swimmers, wing- and foot-propelled divers. The last two categories included only species that dive from the water surface. Geometric morphometric methods were applied to analyze shapes, and covariance was investigated with two-block PLS analysis. We show that wing- and foot-propelled divers have different patterns of covariation between sternum and pelvis shapes. A narrower, elongated and flattened sternum correlates with a shortened postacetabular region of a pelvis in wing-propelled divers. A widened and shortened sternum with a deep keel correlates with an elongated post-acetabular region of a pelvis in foot-propelled divers. Surface swimmers have a wide variety of combinations of sternum and pelvis shapes, which is apparently explained by their lower specialisation for specific aquatic locomotion, and by the influence of different ecological factors.

Key words: surface swimmers, wing-propelled divers, foot-propelled divers, geometric morphometrics, morphological integration.

Introduction

Ecomorphology is a key aspect in understanding the evolution of different taxonomic groups of animals. Habitat specialisations often are well seen in skeletal traits on different taxonomic levels (Ghazali et al., 2017; Dzeverin, 2020). Shifts to different adaptive zones often lead to rebuilding of covariation patterns of different parts of the organism (Shatkovska et al., 2018; Shatkovska & Ghazali, 2020). In the case of aquatic locomotion, the level of specialisation for movement in water correlates with the scale of morphological transformations of an animal's body, which was shown in an example of fossil cetaceans (Gol'din et al., 2013; Gol'din, 2014; Davydenko et al., 2021).

Aquatic birds are of particular interest in this respect, since they demonstrate a wide range of gradations in relation to the aquatic environment during feeding. The specific lifestyle imposes specific restrictions on the body shape of aquatic birds: they have a streamlined body, short hindlimbs and an elongated pelvis, which contribute to their hydrodynamic characteristics related to propulsion through water (Dabelow, 1925; Kurochkin, 1971; Zeffer et al., 2003; Stoessel et al., 2013). At the same time, waterbirds have diverse locomotor and foraging strategies. It is possible to distinguish species that swim and graze on aquatic surface or filter the prey by dipping the head or front part of the body into water like many ducks (Hinić-Frlog & Motani, 2010). The second type includes birds that search for prey by diving. Among underwater foraging birds, there are species that move with wings (wing-propelled divers) such as most alcids and penguins (Kaftanovskii, 1951; Watanuki et al., 1997) or use hindlimbs (foot-propelled divers) such as loons, cormorants, grebes and some ducks (Townsend, 1909; Heath et al., 2006; Ibáñez & Tambussi, 2012) or species that use both wings and feet such as some eiders and scoters (Heath et al., 2006). Here, we consider only underwater foraging birds, which dive from the water surface. Many other birds such as gannets, some pelicans, kingfishers, petrels, gulls and terns also dive for prey, but these birds are not true divers as they plunge-dive into water using the momentum gained in the air and gravity (Kurochkin, 1971, Shealer, 2002, Chang et al., 2016, Shoop & Tilson, 2022).

Divers are more highly specialised than surface swimmers, as they moved to dive from swimming (Kurochkin, 1971). They have a number of morphological features that distinguish them from those swimming on the water surface. Diving birds have narrow pelvic girdles (Kurochkin, 1971; Rainkow, 1985; Bogdanovich, 2003), posteriorly positioned feet (Storer, 1960; Johnsgard, 1987; Ibáñez & Tambussi, 2012), reduced bone pneumaticity (Kurochkin, 1967; Johnsgard, 1987; Llimona & del Hoyo, 1992), high wing loading (Kurochkin, 1971; Livezey & Humphrey, 1986), a number of features in shapes of wing and leg bones (Kurochkin, 1971; Raikow, 1985; Livezey & Humphrey, 1986), pygostyle form (Felice & O'Connor, 2014). Hinić-Frlog & Motani (2010) revealed that measurements of appendicular skeletons successfully separated diving birds from surface swimmers and flyers.

Wing-proplled divers obviously differ from foot-propelled divers in the functional load on muscles of different locomotor modules that implies morphological variation in these groups of aquatic birds. Diametrically opposed ways of specialisation to underwater locomotion in wing- and foot-propelled divers are of particular interest in terms of the presence of covariation between the sternum and pelvis as skeletal regions that belong to different locomotor modules. As flying animals, birds have a number of limitations that are associated with both an increase in overall body mass and an increase in individual parts of a body, which is associated with the position of the center of gravity of a body (Gladkov, 1949; Gatesy, 1990; Stegmann, 1949). Building up muscles of one of the locomotor modules in divers cannot but cause changes in other parts of the body. It is assumed that muscle development of differently specialised locomotor modules in birds, like wing and hindlimb, is inversely related: strengthening of one is associated with weakening of the other (Hartman, 1961; Sych, 1992; Bogdanovich, 2014). For example, grebes that use foot-propelled underwater locomotion, have short wings with poorly developed muscles (Johnsgard, 1987). We can expect that an increase in one of the locomotor modules in divers is correlated with a decrease in the other, which is also accompanied by a change in shape, since the shape of skeletal elements depends on muscles that attach to them (Shmalgauzen, 1982; Bogdanovich, 2014). An example of the relationship between the shape and size of the sternum and pelvis in wing- and foot-propelled divers is shown in fig. 1. An additional argument in favor of the presence of covariation between shape and size of the sternum and pelvis in birds is that these neighboring regions should be spatially combined with each other within the body. Diving birds, with their particularly streamlining and elongation bodies (Kurochkin, 1971), have additional restrictions on reshaping of these skeletal regions. A recent study of the integration of skeletal regions in a wide sample of bird species showed that the integration of element shapes has a strong relationship to ecology (Orkney et al., 2021).

With this in mind, we assume that divers as a highly specialised group of birds have a greater degree of sternum and pelvis integration than surface swimmers. We also expect that wing-propelled and foot-propelled divers have opposite directions of change in both shape and size of the sternum and pelvis. So, we tested several hypotheses in this paper. The first is the presence of integration between shapes of the sternum and pelvis in

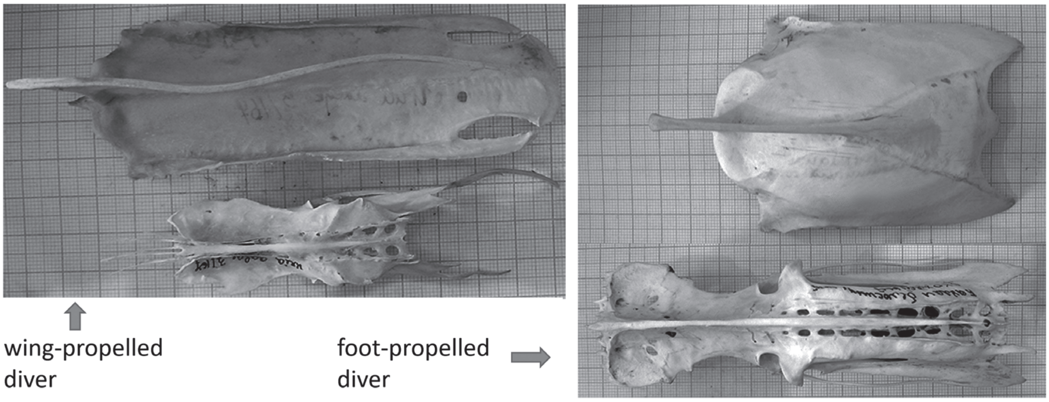

Fig. 1. The sternum and pelvis in Common guillemot (*Uria aalge*) (wing-propelled diver) and Imperial cormorant (*Phalacrocorax atriceps*) (foot-propelled diver).

aquatic birds. The second is the effect of aquatic locomotion style on covariate changes in shape of the sternum and pelvis among aquatic birds in general and among divers in particular. We also hypothesise that the covariation between shapes of the sternum and pelvis may be related to the size ratio of these skeletal regions, since the strengthening of one of the locomotor modules may be accompanied by a weakening of the other. To test this hypothesis, we examined the correlation between the covariate changes in the shape of the sternum and pelvis and the ratio of their sizes.

In this study, we tried, first of all, to evaluate the integration between different locomotor modules, which has not previously been the subject of a special study in water birds. Studies of locomotion mechanisms in aquatic birds revealed a significant variation in hindlimb movement patterns even among foot-propelled divers (Johansson & Norberg, 2003; Clifton & Biewener, 2018), which affects some structural features of both the pelvis and hind limbs (Kurochkin, 1971; Bogdanovich, 2014). These data extend the understanding of pathways of narrow adaptations in water birds. However, the question of the presence of correlated systems within a whole organism and their ability to respond in a consolidated manner to environmental influences remains open.

Material and Methods

Our sample consists of sternum and pelvis of 26 bird's species representing 7 orders (fig. 2). The studied skeletal regions belonged to one individual per species. Taxonomy is given according to Jetz et al. (2012). Data on the studied species is presented in Appendix 1. Materials were gathered from the collection of the National Natural Science Museum of NAS of Ukraine (Kyiv).

Bird species were divided into ecological categories according to predominant aquatic locomotor modes. We use simplified classification of Hinić-Frlog & Motani (2010) and recognised foot-propelled underwater swimmers (FP) (divers that use feet for propulsion and chasing prey), wing-propelled underwater swimmers (WP) (divers that use wings for propulsion and pursuit of prey) and surface swimmers (SSW) that grazing or seizing and filtering the prey mainly during surface swimming. Species that occupy semi-aquatic habitats and search for food among thickets of coastal aquatic vegetation, as members of Rallidae family, or in fields like many geese, but also swim and find food on water surface (Spangenberg, 1951; Flint et al., 1968; Flint, 1991), were classified as surface swimmers. Among the Rallidae family, Coot (*Fulica atra*) also uses diving for foraging, but since the leading method of taking food is pecking (Spangenberg, 1951), we referred this species to surface swimmers. We analysed two sets of species: the first was a total sample with all species representing three locomotor categories (FP, WP and SSW), the second one included only underwater swimmers (FP and WP: 11 species).

Skeletal regions were photographed in ventral view for sternum and dorsal view for pelvis and lateral projections for both. When photographing the pelvis from the dorsal view, the pelvis was oriented so that a preacetabular region was parallel to a supporting surface. Sternum in ventral view oriented so that a dorsal surface of the corpus sterni rests on the supporting base. Thus, the corpus sterni and the preacetabular region of the pelvis had approximately parallel planes, which correspond to a common anatomical plan of the bird's body structure. Also, the lateral and dorsoventral planes were common for the sternum and pelvis, which makes it possible to correctly analyze covariant changes in shapes of these skeletal regions across two projections. The length of the sternum and synsacrum were obtained by measuring skeletal specimens using a caliper with an accuracy of

0.1 mm (fig. 3, Appendix 1). To test whether centroid sizes adequately displayed sternum and pelvic dimensions, we tested the Pearson correlation (as coefficient of determination of linear regression, R^2) between the lengths obtained by measuring the skeletal regions with a caliper and their centroid sizes; MORPHOJ (Klingenberg, 2011) and PAST (Hammer et al., 2001) were applied. We revealed a high degree of correlation between the centroid size of sternum or pelvis and their length ($R^2 \geq 0.92$, permutation $p = 0.0001$ for all traits). So, we believed that the chosen projections adequately reflect not only shapes of the sternum and pelvis but also their sizes.

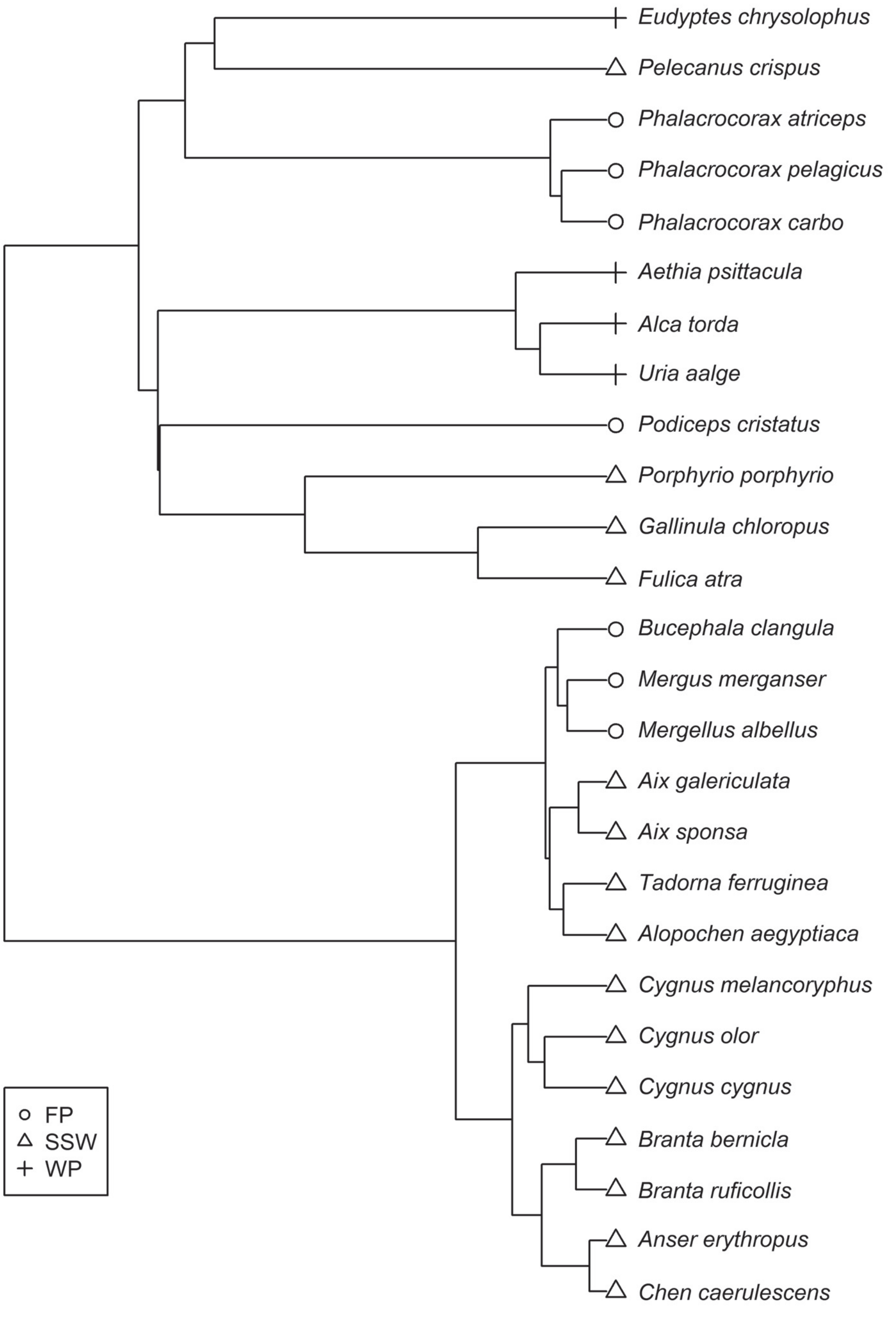

Fig. 2. Phylogenetic relationships among the studied birds based on Jetz et al. (2012), with their locomotor modes marked as: FP for foot-propelled divers, WP for wing-propelled divers, and SSW for surface swimmers.

Table 1. Definitions of the landmarks and semilandmarks used on the sternum

Number	Description
Lateral view landmarks	
1	The *rostrum sterni*
2	The maximum concavity in the base of the *processus craniolateralis*
3	The most distal point of the *processus craniolateralis*
4	The most distal point of the *processus caudolateralis*
5	The most cranial point of the *incisura medialis*
6	The most caudo-lateral point of the *corpus sterni*
7	The mid-point at the caudal margin of the *sternum*
8	The *apex carinae*
Semilandmarks	
	Semilandmarks under the ventral margin of the *carina sterni*, located between landmarks 1 and 7
	Semilandmarks over the lateral margin of the *sternum*, between landmarks 3 and 4
Ventral view landmarks	
1	The *rostrum sterni*
2	The maximum concavity in the base of the *processus craniolateralis*
3	The most distal point of the *processus craniolateralis*
4	The most distal point of the *processus caudolateralis*
5	The most cranial point of the *incisura medialis*
6	The most caudo-lateral point of the *corpus sterni*
7	The mid-point at the caudal margin of the *sternum*
Semilandmarks	
	Semilandmarks over the lateral margin of the *sternum*, between landmarks 3 and 4

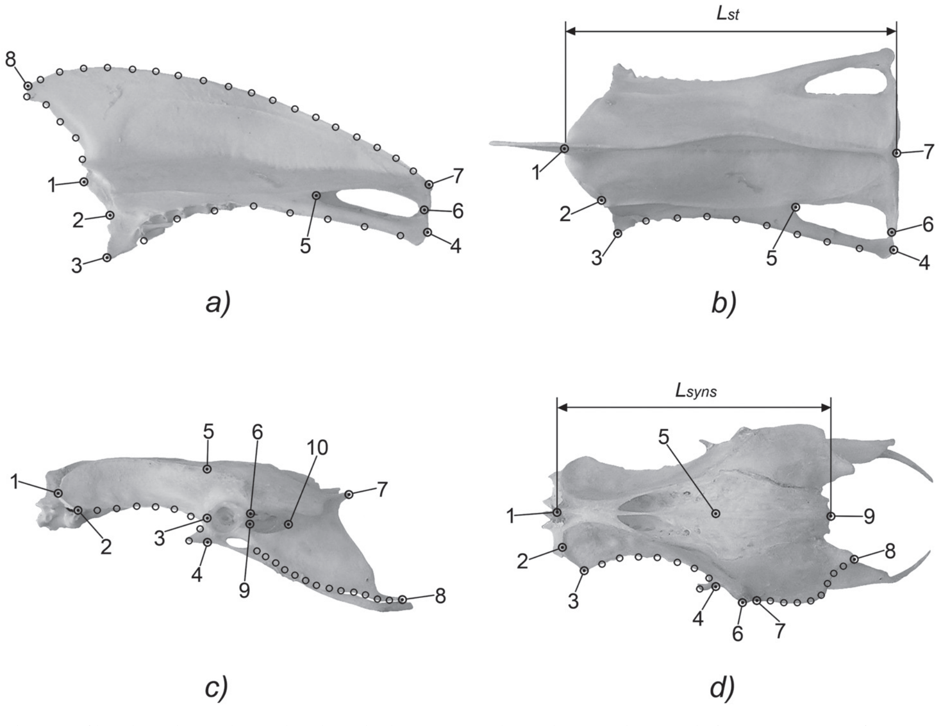

Fig. 3. Scheme of landmarks and semilandmarks location on lateral (*a*) and ventral (*b*) projections of sternum and lateral (*c*) and dorsal (*d*) projections of pelvis in *Aix galericulata*. Descriptions of the landmarks and semilandmarks are given in tables 1, 2. Measurements: *Lst* — length of sternum, *Lsyns* — length of synsacrum.

Table 2. Definitions of the landmarks and semilandmarks used on the pelvis

Number	Description
Lateral view landmarks	
1	The most cranial point of the *crista iliaca dorsalis*
2	The most ventral point of the *ala preacetabularis ilii*
3	The most cranial point of the *foramen acetabuli*
4	The most cranial point of the *foramen acetabuli* projected to ventral rim of the iliac bone
5	A point located on the dorsal margin, vertically landmark 3
6	The most caudal point of the *processus antitrochantericus*
7	The most caudal point of the *processus terminalis ilii*
8	The most caudal point of the *processus terminalis ischii*
9	The most cranial point of the *foramen ilioischiadicum*
10	The most caudal point of the *foramen ilioischiadicum*
Semilandmarks	
	Semilandmarks located between landmarks 2 and 4
	Semilandmarks located on the ventral margin of the ischial bone
Dorsal view landmarks	
1	The most cranial point of the *synsacrum*
2	The most cranial point of the *crista iliaca dorsalis*
3	The most lateral point of the *ala preacetabularis ilii* edge
4	The most cranial point of the *foramen acetabuli*
5	A point located in the midline of pelvis, medially to landmark 4
6	The most caudal point of the *processus antitrochantericus*
7	The most lateral point of the *crista supratrochanterica* (or analog structure)
8	The most caudal point of the *processus terminalis ilii*
9	The most caudal point of the *synsacrum*
Semilandmarks	
1	Semilandmarks located between landmarks 3 and 4
2	Semilandmarks located between landmarks 7 and 8

Methods of geometric morphometrics were applied to the analysis of covariation of sternum and pelvis shapes. We digitised two-dimensional coordinates of homologous landmarks and equally spaced semilandmarks on curves in lateral and dorsal (ventral for sternum) projections of the sternum and pelvis using tpsDig2 v. 2.31 (Rohlf, 2017) (fig. 3). We tried to take into account as much as possible both the overall shape of the sternum and pelvis, and proportions of individual components, like height of keel in the sternum and a ratio of pre- and postacetabular regions in the pelvis. Anatomical description of landmarks and semilandmarks is presented in tables 1, 2. The semilandmark curves were slid by minimizing Procrustes distances with function gpagen in geomorph v. 3.2.1 R package.

Statistical analyses of shapes covariation were conducted in MORPHOJ (Klingenberg, 2011). Procrustes superimpositions were made for sternum and pelvis projections to remove effects of size, position, or orientation of skeletal regions. Procrustes shape coordinates were used in further analyses. We performed pairwise PLS analyses between sternum and pelvis separately for the lateral and dorsal projections. RV coefficients were used as a measure of covariance between blocks. Null hypothesis of complete independence of two blocks was tested with the permutation test. Number of randomization rounds was 10 000.

To test the influence of aquatic locomotor strategy on covariation of blocks, we ran pooled within-group PLS analyses. Also, we repeated PLS analysis for sample of WP-FP in order to determine impact of different underwater locomotion on blocks covariation. Confidence intervals of the RV coefficients were estimated with the function RVrarefied in GeometricMorphometricsMix v. 0.0.7.9000 (Fruciano, 2019) R package for each PLS analysis. To assess differences in the covariation of sternum and pelvis shapes between ecological groups, we performed a pairwise comparison of PLS axis 1 scores (PLS1) with One-way NPMANOVA in PAST (Hammer et al., 2001). PLS1 scores are presented in Appendix 1.

Evolutionary shape covariation of blocks was explored with phylogenetic independent contrasts. Phylogenetic hypothesis (fig. 2) was reconstructed as the maximum clade credibility tree of 5000 trees imported from the database http://birdtree.org (Jetz et al., 2012). Ericson All Species subset was chosen. Best tree (fig. 2) was chosen with the function maxCladeCred in R package phangorn v. 2.4.0 (Schliep, 2011; R Core Team, 2020). We estimated angles between vectors of standard and evolutionary PLS analyses in MORPHOJ.

To test hypothesis that covariations of shapes of the sternum and pelvis are related to their size ratio, we examined the correlation between PLS1 scores and the ratio of centroid sizes of the sternum and pelvis using RMA regression analysis in PAST (Hammer et al., 2001). Determination coefficient R^2 was used as an indicator of correlation strength.

Phylogenetic ANOVA and pairwise post-hoc comparisons (R package phytools v. 0.6-99 (Revell, 2012), function phylANOVA, 2000 simulations) were applied to test differences between locomotor categories in the ratio of centroid sizes of the sternum and pelvis. We applied false discovery rate (FDR) correction for multiple tests when interpreting pairwise comparisons. Centroid sizes for lateral and dorsal projections were averaged for each species before analysis.

Visualizations were performed with R packages geomorph v. 3.2.1 (Adams et al., 2019) and phytools.

Results

Covariation between shapes of the sternum and pelvis

Standard PLS analysis in the total sample revealed weak covariation between shapes of the sternum and pelvis: correlation between first PLS axes r = 0.579, p = 0.039 for dorsal projection, and r = 0.605, p = 0.023 for lateral projection; covariation between shapes estimated with RV coefficients was weak but significant (table 3). Corrected for locomotor categories PLS analysis showed that the RV coefficient slightly increased for lateral view and decreased for dorsal one (table 3). Rarefied RV coefficients were similar for both standard and pooled within-group PLS analyses, which indicated that locomotor strategy did not significantly affect blocks covariation in the total sample. PLS analysis of phylogenetic independent contrasts showed that the RV coefficient decreased and became insignificant for both projections (table 3). Accordingly, the results of phylogenetic PLS did not confirm evolutionary integration between the studied blocks in the total sample of species.

Standard PLS analysis in the divers' sample showed that RV coefficients strongly increased compared to those in the total sample (table 3), which suggested that different functional loads during diving affected the covariation of studied regions. Angles between standard PLS and phylogenetic PLS analyses in the divers' sample were about 30–40 degrees (except an angle for sternum in dorsal view) (table 4), which indicated that the direction of integration of studied blocks coincided with evolutionary integration in this sample

Table 3. Results from the PLS analysis showing covariation between shapes of the sternum and pelvis

Projections	n	Standard PLS		Corrected for locomotory categories PLS		Phylogenetic PLS	
		RV	p	RV	p	RV	p
Lateral (total sample)	26	0.2795	0.0103	0.2967	0.0099	0.1366	0.6004
Dorsal/ventral (total sample)	26	0.2631	0.0145	0.2249	0.0339	0.1842	0.1773
Lateral (WP-FP)	11	0.6185	0.0084	0.5723	0.0238	0.2559	0.5972
Dorsal/ventral (WP-FP)	11	0.6044	0.0047	0.5925	0.0059	0.5309	0.0185

Note. n — number of the studied species; RV— coefficient of association between blocks; p — significance of the permutation test for the null hypothesis RV = 0; FP — foot-propelled divers; WP— wing-propelled divers.

Table 4. Angular comparison of vector directions of PLS analyses in wing- and foot-propelled divers

Pair of PLS axes	Angles (in degrees)	P-values
Lateral view		
PLS Bl 1–PLS ind contr Bl 1	32.3	< .00001
PLS Bl 2–PLS ind contr Bl 2	38.9	< .00001
Dorsal view		
PLS Bl 1–PLS ind contr Bl 1	70.5	0.06733
PLS Bl 2–PLS ind contr Bl 2	34.6	< .00001

Note. PLS — standard PLS; PLS ind contr — phylogenetic PLS; Bl 1 — sternum; Bl 2 — pelvis.

of species. The covariation of sternum and pelvis shapes occurred due to the opposite ways of sternum and pelvis changes in wing- and foot-propelled divers and the presence of different patterns of blocks covariation in them. Within locomotor groups, the covariation was not significant.

Morphospace of PLS analysis

The PLS1 accounted for most part of the covariation (77.9 % for lateral view and 84.6 % for dorsal view). So, we studied the covariance of skeletal regions across the PLS1 axis in detail. According to the PLS1, covariant changes in shapes are mainly associated

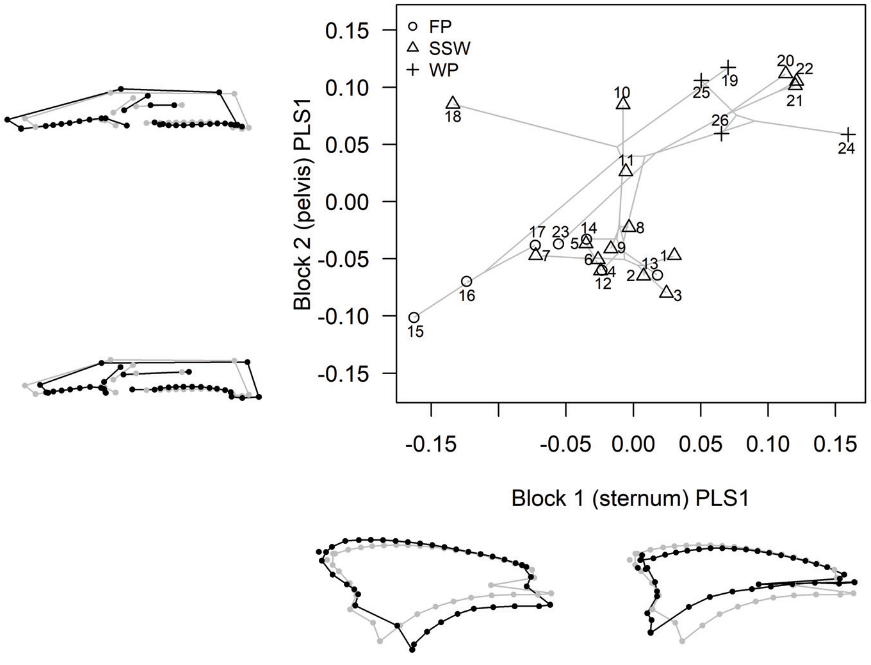

Fig. 4. Covariation between lateral projections of the sternum and pelvis estimated with the standard PLS analysis. Phylogenetic relationships are projected onto the PLS1 morphospace. Grey wireframe represents mean shape. Species points are marked by locomotor categories (FP — foot-propelled divers, WP — wing-propelled divers, SSW — surface swimmers) and numbers: 1 — *Cygnus cygnus*, 2 — *Cygnus olor*, 3 — *Cygnus melancoryphus*, 4 — *Chen caerulescens*, 5 — *Anser erythropus*, 6 — *Branta ruficollis*, 7 — *Branta bernicla*, 8 — *Alopochen aegyptiaca*, 9 — *Tadorna ferruginea*, 10 — *Aix sponsa*, 11 — *Aix galericulata*, 12 — *Mergellus albellus*, 13 — *Mergus merganser*, 14 — *Bucephala clangula*, 15 — *Phalacrocorax carbo*, 16 — *Phalacrocorax pelagicus*, 17 — *Phalacrocorax atriceps*, 18 — *Pelecanus crispus*, 19 — *Eudyptes chrysolophus*, 20 — *Porphyrio porphyrio*, 21 — *Fulica atra*, 22 — *Gallinula chloropus*, 23 — *Podiceps cristatus*, 24 — *Aethia psittacula*, 25 — *Uria aalge*, 26 — *Alca torda*.

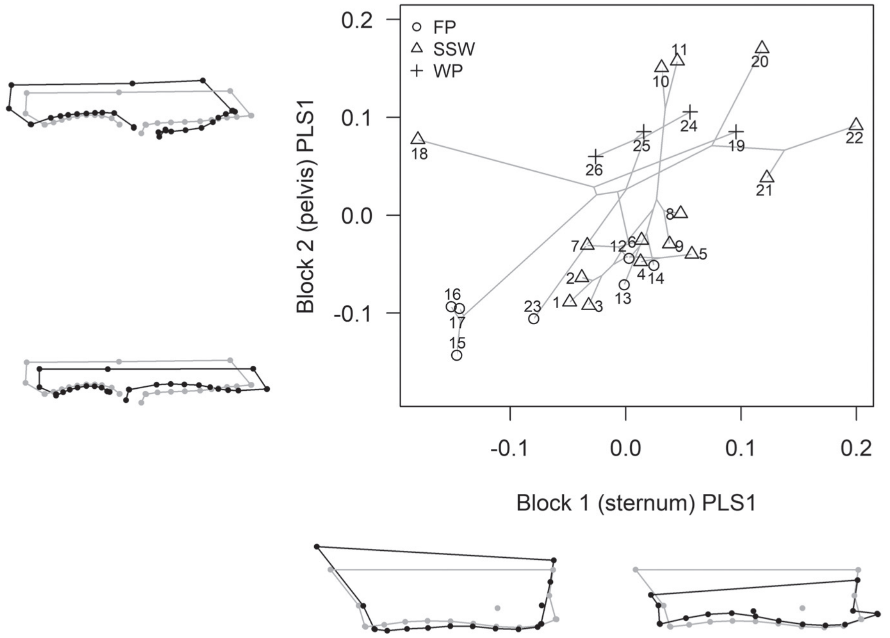

Fig. 5. Covariation between dorsal projections of the sternum and pelvis estimated with the standard PLS analysis. Phylogenetic relationships are projected onto the PLS1 morphospace. Grey wireframe represents mean shape. Species designation as in fig. 4.

with width of the sternum, size of carina sterni, orientation of processus craniolateralis, curvature of incisura medialis and unequal development of the pre- and postacetabular regions of pelvis, narrowness of ala postacetabularis ilii (figs 4 and 5).

In the PLS1 morphospace, ecological groups, although overlapping, still occupy separate regions (figs 4 and 5). One end of a range is presented by foot-propelled underwater swimmers, which had the widened sternum in ventral view with high carina sterni and less pronounced incisura medialis in lateral view that correlated with the pelvis, which had elongated postacetabular region in comparison with preacetabular one in both projections and narrowed ala postacetabularis ilii in dorsal view. The opposite extreme is mainly occupied by the wing-propelled divers, which had narrowed in ventral view and flattened in lateral view sternum with lower height of carina sterni that correlated with the wider pelvis in dorsal view, which had a caudally shifted acetabulum in both aspects.

Surface swimmers generally fell between foot- and wing-propelled divers (figs 4 and 5). Although some of the surface swimmers overlapped with the wing-propelled divers. These were members of family Rallidae and genus *Aix*.

Pelican (*Pelecanus crispus*) is an outlier in our species sample, it had an unusual combination of sternum and pelvis features: expanded sternum with high *carina sterni* that is matched with elongated preacetabular region of pelvis.

Differences between ecological groups

One-way NP MANOVA analysis of PLS1 scores revealed differences mainly between wing- and foot-propelled divers (table 5). The RMA analysis revealed a low to moderate positive correlation between PLS1 scores and the ratio of sternum and pelvis centroid sizes (table 6). This correlation was mainly due to the contrast between diving birds with differ-

Table 5. Results of One-way NP MANOVA analyses of PLS1 scores between ecological groups in lateral (upper triangle) and dorsal (bottom triangle) projections. Values that remained significant after Bonferroni correction are marked in bold

Groups	Foot-propelled divers	Surface swimmers	Wing-propelled divers
Foot-propelled divers	–	0.1558	**0.0025**
Surface swimmers	**0.0042**	–	0.8788
Wing-propelled divers	**0.0019**	0.021	–

Table 6. Correlation between PLS1 scores and the ratio of sternum and pelvis centroid sizes

Groups	n	PLS1 scores of sternum		PLS1 scores of pelvis	
		R^2	permutation p	R^2	permutation p
Total sample (lateral view)	26	0.39	0.0004	0.30	0.0023
Total sample (dorsal view)	26	0.20	0.0192	0.38	0.0005
Underwater swimmers (lateral view)	11	0.83	0.0002	0.69	0.0027
Underwater swimmers (dorsal view)	11	0.51	0.0128	0.89	0.0001
Surface swimmers (lateral view)	15	0.09	0.2766	0.11	0.2297
Surface swimmers (dorsal view)	15	0.35	0.019	0.36	0.02

Note. n — number of the studied species; R^2 — coefficient of determination.

ent underwater locomotion. When underwater swimmers and surface swimmers were analyzed separately, the correlation between PLS1 scores and the ratio of sternum and pelvis centroid sizes was higher among divers than surface swimmers (table 6).

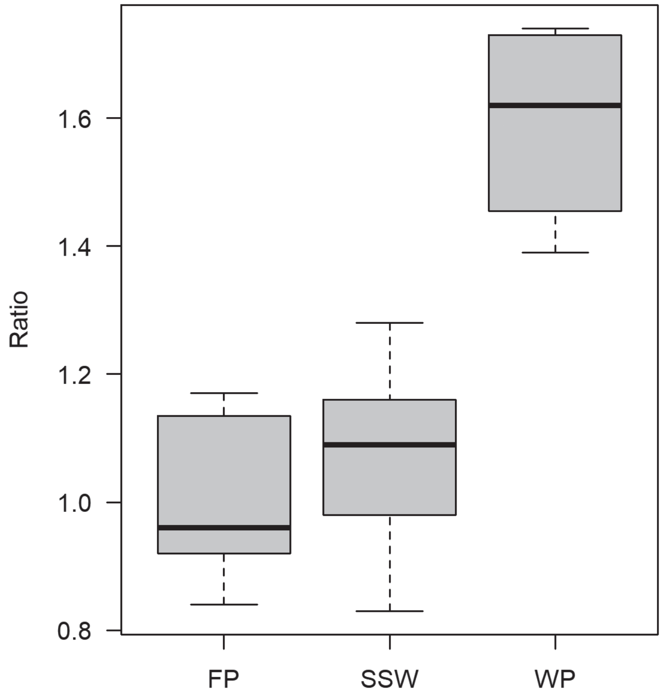

Fig. 6. Boxplot of the ratio of sternum and pelvis centroid sizes. Box represents interquartile range with solid line inside as median, whiskers are minimal and maximal values. Locomotor categories: FP — foot-propelled divers, WP — wing-propelled divers, SSW — surface swimmers.

Pairwise comparison revealed that wing-propelled divers differed from others in the ratio of sternum and pelvis centroid sizes ($p = 0.009$ in both cases), they had the highest value of this index (fig. 6). Foot-propelled divers did not differ from surface swimmers in this parameter ($p = 0.627$). Since the high degree of correlation exists between the centroid size of sternum or pelvis and their length ($R^2 \geq 0.92$, permutation $p = 0.0001$ for all traits), the highest value of the ratio of sternum and pelvis centroid sizes meant that wing-propelled divers had an elongated sternum and shortened pelvis compared to other ecological groups.

Discussion

Aquatic birds exhibit a wide range of diversity in covariations of sternum and pelvis shapes, despite strong selective limitations on elongated and streamlined body. The variety of integrative relationships between shapes of the sternum and pelvis is mainly related to the level of specialisation of birds for aquatic movement. This is most clearly seen in the case of wing- and foot-propelled underwater swimmers. Although both ecological groups share a number of distinctive features, such as posterior position of legs on a long axis of a body (Kurochkin, 1971; Johnsgard, 1987; Ibáñez & Tambussi, 2012), narrow elongated pelvis (Raikow, 1970, 1985; Kurochkin, 1971; Bogdanovich, 2003), a great height of the acetabular zone (Ibáñez & Tambussi, 2012; Anten-Houston et al., 2017), low pelvic angles (Anten-Houston et al., 2017) that facilitate their movement under water (Kurochkin, 1971; Ibáñez & Tambussi, 2012), the result of our study showed that covariant changes of the sternum and pelvis in these groups have opposite directions.

A need for the predominant development of one of the locomotor modules, used in underwater locomotion, combined with a particular orientation of pelvic limbs probably determine the specificity of sternum and pelvis shapes covariation in divers. The results of the regression analysis of the PLS1 axis on the ratio of sternum and pelvis centroid sizes show that the correlation between sternum and pelvis shapes and their relative sizes is particularly pronounced among divers. Wing-propelled divers require predominant development of muscles, which lower and raise a wing (the pectoralis and supracoracoideus), as they flap their wings to propel themselves underwater while their pelvic limbs remain motionless (Watanuki et al., 1997). Foot-propelled divers, in contrast, need the predominant development of pelvic limb muscles. The lengthening of their hip is associated with an increase in the area of attachment of muscles for holding the thigh stationary, and together with strengthening of the knee joint contributes to increasing propulsive forces transmitted by the tarsometatarsus (Hinić-Frlog & Motani, 2010). The muscle power is proportional to the muscle area and the larger mass of the muscles associated with the increase in size of the skeletal regions to which they are attached. In wing-propelled divers, sternum is larger than pelvis while foot-propelled divers have significantly lower ratio of sternum and pelvis centroid sizes.

Sternum size alteration in birds may be limited by the orientation of pelvic limbs. Due to a subhorizontal orientation of a femur in a standing position, the knee joint is pointed cranially. It is important that the knee joints avoid contact with the abdominal cavity and thorax. During underwater locomotion, the thigh is oriented horizontally and is a fixed part of the pelvic limb; locomotion is carried out due to the distal elements of the limb (Hinić-Frlog & Motani, 2010). It would seem that the possibility of contact with the thorax is reduced. However, divers' thigh is short (Kurochkin, 1971; Raikow, 1985) and the pelvis is very narrow (Kurochkin, 1971; Raikow, 1985; Bogdanovich, 2003; Ibáñez & Tambussi, 2012; Frank et al., 2022). In addition, foot-propelled divers have elongated cnemial process on tibiotarsus (Raikow, 1985; Livezey & Humphrey, 1986; Hinić-Frlog & Motani, 2010), which is oriented cranially. Given the combination of such characteristics, the ability to reduce thigh-to-thorax contact is also relevant during underwater locomotion. Accordingly, elongation of the sternum and thorax in the caudal direction becomes difficult. Nevertheless, divers, with the exception of penguins, are flying birds and require developed pectoral muscles. In this case, a compromise between the need for wing muscles development, the narrowness of the pelvis and the limiting position of the femur can be achieved in several ways. The first is the shortening and widening of a sternum in order to reduce contact with thigh bones, and the second is the narrowing and lengthening of a sternum along with more caudal displacement of pelvic limbs.

Both of these variants are observed in diving birds. Despite the generally posterior arrangement of pelvic limbs in divers, the location of the acetabulum in wing-propelled and foot-propelled divers is significantly different. The relationship between the position of the acetabulum and locomotion of birds has been repeatedly noted earlier (Hertel & Campbell, 2007; Ibáñez & Tambussi, 2012; Anten-Houston et al., 2017). Wing-propelled divers have a caudally shifted acetabulum, and foot-propelled divers have a cranial displacement. The cranially displaced acetabulum in foot-propelled divers apparently limits the possibility of caudal lengthening of the sternum, and the sternum is shortened and widened in these birds. The shortening and relative widening of a sternum was previously noted in grebes, cormorants, and diving ducks (Kurochkin, 1971). A teardrop body shape in foot-propelled divers contributes to the generation of downward force when diving (Johansson, 2002). Narrowing and lengthening of the sternum in wing-propelled divers is probably due to the more caudal position of the acetabulum. These shape transformations allow neighboring regions, like the sternum and pelvis, to align spatially within a body. Previously, it was suggested that the lengthening and narrowing of the sternum in auks is associated with the need to protect internal organs from hydrostatic pressure when diving to great depths (Kurochkin, 1971). Thus, sternum shape is associated with its size alterations in diving birds: lengthening and narrowing of the sternum are accompanied by its increase in wing-propelled divers while widening and shortening of the sternum in foot-propelled divers are associated with its decrease.

Surface swimmers have the wide variety of sternum and pelvis shapes according to PLS 1. Although most of them (members of Anseriformes) fall between the extremes are represented by the diving species, surface swimmers also partially overlap with them. The greater variability in the pelvis shape in surface swimmers compared to divers was noted previously (Kurochkin, 1971). This is probably because Anseriformes is a generalized group among birds that have adapted to aquatic locomotion. Most of them are not highly specialised. Many geese graze on crops or meadows (Ptushenko, 1952; Flint et al., 1968), staying on water mainly to rest or at night. Members of Anseriformes do not have strict restrictions on shapes of sternum and pelvis, like divers, although their body is elongated and streamlined, which is generally associated with movement in the water. These results are consistent with earlier findings by Hinić-Frlog & Motani (2010), who noted that skeletal elements are not a good predictor of habitats among birds which use multiple environments.

Nevertheless, not all covariate combinations of sternum and pelvis shapes in studied birds can be explained in terms of specialisation to aquatic locomotion. Members of the *Aix* (*Aix galericulata, Aix sponsa*) and rails have a shortened postacetabular region of pelvis, which is similar in this trait to that of wing-propelled divers. These birds also have a somewhat narrowed and elongated sternum. However, the covariance of forms of the sternum and pelvis in members of the genus *Aix* is not associated with diving, since they dive very rarely (Flint et al., 1968), they often forage on land, a significant part of diet consists of plant seeds or invertebrates (Isakov, 1952). Among the rails, diving to find food is mainly used only Coot (*Fulica atra*) (Spangenberg, 1951). A reason for the morphological peculiarities of sternum and pelvis shapes in these ducks and rails lies in some other specialisations that require further research on more extensive material.

An unusual combination of covariate changes in shapes of sternum and pelvis is observed in the Dalmatian pelican (*Pelecanus crispus*). Widened and short sternum is accompanied with elongated pelvis with shortened post-acetabular region. Reasons for these characteristics are not entirely clear. Given that pelicans have a large body mass of up to 10.5 kg and are migratory birds (Kurochkin, 1991), it can assume that they have well-developed pectoral muscles. The caudal displacement of the acetabulum does not seem to prevent elongation of the sternum in a caudal direction. However, this does not happen. An explanation of this phenomenon may lie in a position of the center of body's gravity, which is located on the line connecting the centers of wings (Gladkov, 1949). Pelicans are known to have a very massive beak. Probably to reduce the impact of the massive skull, pelicans lay heads on backs when flying or resting on the water (Sudilovskaya, 1951; Flint et al., 1968). We assume that in order to balance the massive skull and avoid shifting the center of body's gravity, pectoral muscles should be located compactly, closer to the center of body's gravity that prevents the possibility of caudal lengthening of the sternum.

Our sample is represented by a small number of species. Nevertheless, the listed facts show that the group of surface swimmers includes species with a wide variety of sternum and pelvis shapes, which may be morphologically similar to those of divers. In our sample of species, surface swimmers do not differ significantly from foot-propelled divers in the ratio of centroid sizes. This seems to us, to be because movement through the water in the members of both groups is carried out by the pelvic limbs. On the other hand, multifunctionality of pelvic limbs can also obscure a clear association between pelvic morphology and aquatic locomotion traits, as previously noted by Ibáñez and Tambussi (2012). Nevertheless, results of the study show that highly specialised birds, such as wing- and foot-propelled divers, have covariations between sternum and pelvis shapes, which are clearly related to underwater locomotion patterns. Our sample does not include species that use both wings and pelvic limbs in underwater locomotion, such as eiders and scoters (Heath et al., 2006). It is likely that such species would be closer to foot-propelled divers in the shape and size ratio of the sternum and pelvis since these birds use their feet in a similar fashion to FP divers in the water (Hinić-Frlog & Motani, 2010), while the use of wings alone is not as efficient for diving in this group of birds (Heath et al., 2006). However, the inclusion of such species in the study may further expand understanding of mechanisms of trade-offs between the parity use of the two locomotor modules.

Acknowledgments

The authors thank M. S. Komar and L. Gorobets for facilitatating work with the osteological collection of birds. The study was partially funded by National Research Foundation of Ukraine, grant 2020.02/0247

References

Adams, D. C., Collyer, M. L. & Kaliontzopoulou, A. 2019. *Geomorph: Software for geometric morphometric analyses. R package version 3.1.0.* https://cran.r-project.org/package=geomorph

Anten-Houston, M. V., Ruta, M. & Deeming, D. C. 2017. Effects of phylogeny and locomotor style on the allometry of body mass and pelvic dimensions in birds. *J. Anat.,* **231** (3), 342–358. https://doi.org/10.1111/joa.12647

Bogdanovich, I. A. 2003. Morphological aspects of phylogeny of Hesperornithidae (Ornithurae, Aves). *Vestnik. Zoologii,* **37** (6), 65–71 [In Ukrainian with English summary].

Bogdanovich, I. A. 2014. Origin and evolutionary morphological characteristics of terrestrial locomotion apparatus of birds. *Vestnik Zoologii,* **31**, 1–80 [In Russian with English summary].

Chang, B., Croson, M., Straker, L., Gart, S., Dove, C., Gerwin, J. & Jung, S. 2016. How seabirds plunge-dive without injuries. *Proceedings of the National Academy of Sciences*, **113** (43), 12006–12011.

Clifton, G. T. & Biewener, A. A. 2018. Foot-propelled swimming kinematics and turning strategies in common loons. *Journal of Experimental Biology,* **221**, jeb168831. doi:10.1242/jeb.168831

Dabelow, A. 1925. Die Schwimmanpassung der Vögel. Ein Beitrag zur biologischen Anatomie der Fortbewegung. *Morphologisches Jahrbuch,* **54**, 288–321.

Davydenko, S., Mörs, T. & Gol'din, P. 2021. A small whale reveals diversity of the Eocene cetacean fauna of Antarctica. *Antarctic Science*, **33** (1), 81–88. doi:10.1017/S0954102020000516

Dzeverin, I. 2020. The skull integration pattern and internal constraints in *Myotis myotis–Myotis blythii* species group (Vespertilionidae, Chiroptera) might be shaped by natural selection during evolution along the genetic line of least resistance. *Evol Biol,* **47**, 18–42. https://doi.org/10.1007/s11692-019-09488-4

Felice, R.N. & O'Connor, P.M. 2014. Ecology and Caudal Skeletal Morphology in Birds: The Convergent Evolution of Pygostyle Shape in Underwater Foraging Taxa. *PLoS One*, **9** (2): e89737. doi:10.1371/journal.pone.0089737

Flint, V. E., Boeme, R. L., Kostin, Y. V. & Kuznetsov, A. A. 1968. *Birds of the USSR*. Mysl. Moscow, 1–637 [In Russian].

Flint, V. E. 1991. Ordo Anseriformes. *In*: Ilichev, V. D., ed. *Fauna of the world: Birds: Handbook*. Agropromizdat, Moscow, 60–68 [In Russian].

Frank, T. M., Dodson, P. & Hedrick, B. P. 2022. Form and function in the avian pelvis. *J Morphol*, **283** (6), 875–893. Doi: 10.1002/jmor.21479

Fruciano, C. 2019. GeometricMorphometricsMix: Miscellaneous functions useful for geometric morphometrics. R package version 0.0.7.9000.

Gatesy, S. M. 1990. Caudofemoral musculature and the evolution of theropod locomotion. *Paleobiology,* **16**, 170–186. DOI: https://doi.org/10.1017/S0094837300009866

Ghazali, M., Moratelli, R. & Dzeverin, I. 2017. Ecomorph evolution in *Myotis* (Vespertilionidae, Chiroptera). *J Mammal Evol,* 2**,** 475–484. https://doi.org/10.1007/s10914-016-9351-z

Gladkov, N. A. 1949. Biological principles of bird flight. Izdatelstvo MOIP, Moscow, 1–247 [In Russian].

Gol'din, P., Startsev, D. & Krakhmalnaya, T. 2013. The anatomy of the Late Miocene baleen whale *Cetotherium riabinini* from Ukraine. *Acta Palaeontologica Polonica* **59** (4), 795–814. https://doi.org/10.4202/app.2012.0107

Gol'din, P. 2014. Naming an innominate: pelvis and hindlimbs of Miocene whales give an insight into evolution and homology of cetacean pelvic girdle. *Evol Biol*, **41**, 473–479. https://doi.org/10.1007/s11692-014-9281-8

Hammer, O., Harper, D. A. T. & Ryan, P. D. 2001. PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron,* **4**, 1–9. http://palaeo-electronica.org/2001_1/past/issue1_01.htm

Hartman, F. A. 1961. Locomotor mechanisms of birds. *Smithson. misc. collect.*, **143** (1), 1–91.

Heath, J. P., Gilchrist, H. G. & Ydenberg, R. C. 2006. Regulation of stroke pattern and swim speed across a range of current velocities: diving by common eiders wintering in polynyas in the Canadian Arctic. *J. Exp. Biol.,* **209**, 3974–3983. doi:10.1242/jeb.02482

Hertel, F. & Campbell, K. E. 2007. The antitrochanter of birds: form and function in balance. *Auk,* **124** (3), 789–805. DOI: 10.1093/auk/124.3.789

Hinić-Frlog, S. & Motani, R. 2010. Relationship between osteology and aquatic locomotion in birds: determining modes of locomotion in extinct Ornithurae. *J. Evol. Biol.,* **23**, 372–385. doi:10.1111/j.1420-9101.2009.01909.x.

Ibáñez, B. & Tambussi, C. P. 2012. Foot-propelled aquatic birds: pelvic morphology and locomotor performance. *Ital. J. Zool.,* **79** (3), 356–362. http://dx.doi.org/10.1080/11250003.2011.650713

Isakov, Y. A. 1952. Subfamily Anatinae. *In*: Dement'ev, G. P. & Gladkov, N. A., eds. *The birds of the Soviet Union*, vol. 4. Sovietskaya Nauka, Moscow, 344–635 [In Russian].

Jetz, W. W., Thomas, G. H. G., Joy, J. B. J., Hartmann, K. K. & Mooers, A. O. A. 2012. The global diversity of birds in space and time. *Nature*, **491**, 444–448. https://doi.org/10.1038/nature11631

Johansson, L. C. 2002. *Swimming in Birds: Propulsive Mechanisms and Functional Morphology*. PhD Thesis, Goteborg University, Goteborg.

Johansson, L. C. & Norberg, R. A. 2003. Delta-wing function of webbed feet gives hydrodynamic lift for swimming propulsion in birds. *Nature*, **424**, 65–68.

Johnsgard, P. A. 1987. *Diving Birds of North America*. NE: University of Nebraska Press, Lincoln. https://digitalcommons.unl.edu/bioscidivingbirds

Kaftanovskii, Y. M. 1951. *Alcidine birds of the East Atlantic*. MOIP, Moscow, 1–170 [In Russian].

Klingenberg, C. P. 2011. MorphoJ: an integrated software package for geometric morphometrics. *Mol Ecol Resour,* **11**, 353–357. DOI: 10.1111/j.1755-0998.2010.02924.x

Kurochkin, E. N. 1971. Adaptive structural features and locomotion of waterfowl. *In*: Nichiporovich, A. A., ed. *Itogi nauki. Zoologiya pozvonochnyh* 1969. VINITI, Moscow, 94–135 [In Russian].

Kurochkin, E. N. 1991. Familia Pelecanidae. *In*: Ilichev, V. D., ed. *Fauna of the world: Birds: Handbook*. Agropromizdat, Moscow, 44–45 [In Russian].

Livezey, B. C. & Humphrey, P. S. 1986. Flightlessness in Steamerducks (Anatidae: Tachyeres): its morphological bases and probable evolution. *Evolution*, **40**, 540–558. https://doi.org/10.1111/j.1558-5646.1986.tb00506.x

Llimona, F. & del Hoyo, J. 1992. Order Podicipediformes. *In*: del Hoyo, J., Elliott, A. & Sargatal, J., eds. *Handbook of the birds of the world*. Links edicions, Barcelona, 174–197.

Orkney, A., Bjarnason, A., Tronrud, B. C., & Benson, R. B. 2021. Patterns of skeletal integration in birds reveal that adaptation of element shapes enables coordinated evolution between anatomical modules. *Nature Ecology & Evolution*, **5** (9), 1250–1258. DOI: 10.1038/s41559-021-01509-w

Ptushenko, E. S. 1952. The Order Anseriformes. *In*: Dement'ev, G. P. & Gladkov, N. A., eds. *The birds of the Soviet Union*, vol. 4. Sovietskaya Nauka, Moscow, 247–636 [In Russian].

Raikow, R. J. 1970. Evolution of diving adaptations in the stiff-tailed ducks. *Univ. Calif. publ. zool.* **94**, 1–52 .

Raikow, R. 1985. Locomotor system. *In*: King, A. S. & McLelland, J., eds. *Form and Function in birds*, vol. 3. Academic Press, London, 57–147.

R Core Team. 2020. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna. URL http://www.R-project.org/

Revell, L. J. 2012. phytools: An R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol.*, **3**, 217–223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Rohlf, F. J. 2017. *tpsDig, digitize landmarks and outlines, version 2.31*. Department of Ecology and Evolution, State University of New York at Stony Brook.

Schliep, K. P. 2011. phangorn: phylogenetic analysis in R. *Bioinformatics*, **27** (4), 592–593. DOI: 10.1093/bioinformatics/btq706

Shatkovska, O. V., Ghazali, M., Mytiai, I. S. & Druz, N. 2018. Size and shape correlation of birds' pelvis and egg: Impact of developmental mode, habitat, and phylogeny. *Journal of Morphology,* **279**, 1590–1602. https://doi.org/10.1002/jmor.20888

Shatkovska, O. V. & Ghazali, M. 2020. Integration of skeletal traits in some passerines: impact (or the lack thereof) of body mass, phylogeny, diet and habitat. *J Anat*, **236**, 274–287. https://doi.org/10.1111/joa.13095

Shealer, D. A. 2002. Foraging behavior and food of seabirds. *In*: Schreiber, E. A. & Burge. J., eds. *Biology of marine birds*, **14**, 137–177.

Shoop, W. & Tilson, E. 2022. Plunge diving by Brown Pelicans resembles a Split-S Turn. *Journal of Field Ornithology*, **93** (1), 2. https://doi.org/10.5751/JFO-00064-930102

Shmalgauzen, I. I. 1982. *Organizm kak celoe v individual'nom i istoricheskom razvitii [The organism as a whole in individual and historical development]*. Nauka, Moscow, 1–383 [In Russian].

Spangenberg, E. P. 1951. The Order Ralliformes. *In*: Dement'ev, G. P. & Gladkov, N. A., eds. *The birds of the Soviet Union*, vol. 3. Sovietskaya Nauka, Moscow, 604–677 [In Russian].

Stegmann, B. K. 1949. The center of gravity of birds and its significance for the position of wings during flight. *Izvestiya akademii nauk*. Seriya biologicheskaya, **2**, 208–217.

Stoessel, A., Kilbourne, B. M. & Fischer, M. S. 2013. Morphological integration vs. ecological plasticity in the avian pelvic limb skeleton. *J. Morphol.,* **274**, 483–495. https://doi.org/10.1002/jmor.20109

Storer, R. W. 1960. Evolution in the diving birds. *In*: Bergman, G., Donner & K. O., Haartman, L. V., eds. *Proceedings of the Twelth International Ornithological Congress*. University of Helsinki, Zoological Institute, Finland, 694–707.

Sudilovskaya, A. M. 1951. The Order Pelecaniformes. *In*: Dement'ev, G. P. & Gladkov, N. A., eds. *The birds of the Soviet Union*, vol. 1. Sovietskaya Nauka, Moscow, 13–68 [In Russian].

Sych, V. F. 1992. On the role of morpho-functional correlations in aberrant locomotory system appearance in Galliform birds. *Vestnik Zoologii*, **4**, 64–68.

Townsend, C. W. 1909. The use of wings and feet by diving birds. *Auk*, **26**, 234–248. https://doi.org/10.2307/4070795

Watanuki, Y., Kato, A., Naito, Y., Robertson, G. & Robinson, S. 1997. Diving and foraging behaviour of Adélie penguins in areas with and without fast sea-ice. *Polar Biol.* **17**, 296–304. https://doi.org/10.1007/PL00013371

Zeffer, A., Johansson, L. C. & Marmebro, A. 2003. Functional correlation between habitat use and leg morphology in birds (Aves). *Biol. J. Linn. Soc. Lond.*, **79**, 461–484. https://doi.org/10.1046/j.1095-8312.2003.00200.x

Received 16 March 2023
Accepted 26 April 2023

Appendix 1. Data on sternum and pelvis variables in studied birds

Catalogue number	Species	Ecological categories	*Lst*	*Lsyns*	Sternum centroid size		Pelvis centroid size		PLS1 scores (lateral view)		PLS1 scores (dorsal view)		Ratio of averaged centroid sizes of sternum and pelvis
					lateral view	dorsal view	lateral view	dorsal view	sternum	pelvis	sternum	pelvis	
9-175	*Aethia psittacula*	WP	73.3	34.9	18.262	11.382	8.922	8.295	0.1594	0.0585	0.0558	0.1055	1.72
40-11-1	*Aix galericulata*	SSW	66.6	47.8	19.268	10.016	12.340	10.717	-0.0057	0.0262	0.0448	0.1575	1.27
40-10-1	*Aix sponsa*	SSW	66.1	60.9	18.508	9.795	12.337	9.803	-0.0077	0.0847	0.0311	0.1508	1.28
7-165	*Alca torda*	WP	102.1	49.6	27.540	14.147	13.070	10.893	0.0655	0.0594	-0.0260	0.0599	1.74
39-8-1	*Alopochen aegyptiaca*	SSW	97.9	104.6	29.953	15.510	24.849	18.475	-0.0033	-0.0226	0.0476	0.0016	1.05
38-12-5	*Anser erythropus*	SSW	92.2	98.4	29.074	15.452	24.893	20.270	-0.0352	-0.0368	0.0574	-0.0398	0.99
38-21-1	*Branta bernicla*	SSW	86.5	99.8	29.731	13.953	24.564	19.012	-0.0725	-0.0472	-0.0333	-0.0308	1
38-22-2	*Branta ruficollis*	SSW	87.2	91.2	30.382	14.491	22.295	16.850	-0.0262	-0.0507	0.0138	-0.0255	1.15
41-11-1	*Bucephala clangula*	FP	71.3	78.6	23.454	11.073	15.811	13.740	-0.0348	-0.0328	0.0243	-0.0512	1.17
205-2	*Chen caerulescens*	SSW	106.1	107.8	32.603	17.775	24.147	19.505	-0.0243	-0.0606	0.0129	-0.0476	1.15
38-5-4	*Cygnus cygnus*	SSW	224.0	220.0	52.627	29.777	48.783	42.105	0.0304	-0.0472	-0.0485	-0.0888	0.91
38-3-1	*Cygnus melancoryphus*	SSW	161.0	178.0	46.127	21.315	42.915	35.252	0.0245	-0.0801	-0.0321	-0.0922	0.86
204	*Cygnus olor*	SSW	199.0	208.0	55.437	29.173	46.978	40.185	0.0075	-0.0651	-0.0381	-0.0637	0.97
11-M	*Eudyptes chrysolophus*	WP	136.1	105.4	38.206	20.850	24.058	18.495	0.0703	0.1173	0.0956	0.0852	1.39
60-1-1	*Fulica atra*	SSW	61.0	66.4	16.532	11.121	13.032	12.101	0.1201	0.1015	0.1224	0.0381	1.1
59-119-1	*Gallinula chloropus*	SSW	37.1	51.3	12.206	7.208	9.342	8.406	0.1211	0.1053	0.1996	0.0916	1.09
NA	*Mergellus albellus*	FP	59.8	62.6	19.161	9.995	13.862	11.185	-0.0234	-0.0600	0.0028	-0.0440	1.16
21-19-1	*Mergus merganser*	FP	109.3	101.4	31.813	15.424	23.757	18.886	0.0179	-0.0644	-0.0013	-0.0712	1.11
19-7-1	*Pelecanus crispus*	SSW	161.0	280.0	49.545	23.446	50.913	37.005	-0.1340	0.0853	-0.1800	0.0772	0.83
32	*Phalacrocorax atriceps*	FP	89.1	122.6	30.112	15.306	25.945	23.036	-0.0728	-0.0382	-0.1440	-0.0953	0.93
16-1-1	*Phalacrocorax carbo*	FP	81.3	118.2	28.761	12.419	27.211	21.528	-0.1629	-0.1013	-0.1464	-0.1428	0.84
16-17-2	*Phalacrocorax pelagicus*	FP	71.6	101.9	25.690	11.512	21.922	18.818	-0.1238	-0.0699	-0.1512	-0.0933	0.91
3-186	*Podiceps cristatus*	FP	48.0	68.1	20.004	8.676	16.381	13.600	-0.0556	-0.0371	-0.0797	-0.1059	0.96
45-1	*Porphyrio porphyrio*	SSW	70.9	63.5	20.777	12.364	14.286	13.406	0.1130	0.1118	0.1182	0.1702	1.2
39-9-2	*Tadorna ferruginea*	SSW	87.9	80.5	27.494	13.824	18.913	16.514	-0.0167	-0.0413	0.0379	-0.0294	1.17
2-167	*Uria aalge*	WP	124.0	67.9	29.853	17.568	17.239	13.901	0.0504	0.1059	0.0158	0.0853	1.52

Note. *Lst* — length of sternum, *Lsyns* — length of synsacrum, FP — foot-propelled divers, SSW — surface swimmers, WP — wing-propelled divers.