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MORPHOECOLOGICAL PECULIARITIES OF PELVIS IN SEVERAL GENERA OF RAILS WITH SOME NOTES ON SYSTEMATIC POSITION OF THE COOT, *FULICA ATRA* (RALLIDAE, GRUIFORMES)

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Morphoecological Peculiarities of Pelvis in Several Genera of Rails with Some Notes on Systematic Position of the Coot, *Fulica atra* (Rallidae, Gruiformes). Bogdanovich, I. A. — Some features of pelvic and hindlimb morphology of several ecologically different species of rallids are studied. Adaptive significances of these features are revealed. A special attention is paid to the hindlimb skeleton of the Coot (*Fulica atra,* Linnaeus, 1758), which retained the locomotor universalism despite adaptations to swimming and diving.

K e y w o r d s: Rallidae, skeleton, hind limbs, adaptations.

Морфоэкологические особенности таза у нескольких родов пастушков, с некоторыми замечаниями о систематическом положении лысухи, *Fulica atra* (Rallidae, Gruiformes). Богданович И. А. — Рассмотрены особенности строения таза и некоторых других признаков скелета тазовой конечности разно специализированных представителей семейства пастушковые. Отмечены морфологические решения для достижения той или иной адаптации. Отдельное внимание уделено комплексу скелетных черт лысухи (*Fulica atra,* Linnaeus, 1758), которые обеспечивают достаточно глубокую специализацию к освоению водной среды наряду с сохранением своеобразного локомоторного универсализма.

К л ю ч е в ы е с л о в а: Rallidae, задние конечности, скелет, адаптации.

Introduction

The causes, mechanisms, and directionality of morphogenesis determining the specifics of individual organs and systems undoubtedly are key points of evolutionary morphology and evolution (as the origin of new forms) as a whole. The jaw apparatus and terrestrial locomotion apparatus of birds are the best models for such studies. Transformations of these systems correlate with the change of feeding objects and manners of its obtaining. Possible ways and mechanisms of the origin and early evolution of bipedal locomotion apparatus of birds accompanying the origin of birds as a class have been well studied in general. Survey of the literature on the problem is adequately represented (Kurochkin, Bogdanovich, 2008; Hutchinson, Allen, 2009, etc.).

The main ways of the pelvic limb morphogenetic rearrangements of birds that resulted in adaptation to the different living conditions (mainly terrestrial or arboreal, swimming, diving, etc.) are also well known. At the level of orders and families they are well distinguished morphologically (Kurochkin, 1971; Bogdanovich, 1997; Zinoviev, 2006, 2007, etc.).

The main goal of this work is to determine some mechanisms for achieving adaptive (morphological) solutions in rather closely related members of a certain family.

The rails (Rallidae, Gruiformes) were chosen as a model group due to their well-known and diverse ecology. Corncrake (*Crex crex,* Linnaeus, 1758) is a terrestrial cursorial species inhabiting wetland without open water; Water rail (*Rallus aquaticus,* Linnaeus, 1758) is well-running and swimming inhabitant of marshy habitats and shallow waters, in nesting confined only to the land; Moorhen (*Gallinula chloropus,* Linnaeus, 1758) lives in similar habitat as the Water rail, but spends more of the time on the water, being a good swimmer, which can dive; Coot (*Fulica atra,* Linnaeus, 1758) is the most closely associated with water species among the rallids; it

can dive up to 4 m (Borodulina, 1964). Cormorant (*Phalacrocorax carbo*, Linnaeus, 1758) (Phalacrocoracidae, Pelecaniformes) as a good diver, two species of ducks (Anatidae, Anseriformes): Garganey (*Anas querquedula,* Linnaeus, 1758), Pochard (*Aythya ferina,* Linnaeus, 1758) and Pheasant (*Phasianus colchicus*, Linnaeus, 1758) (Phasianidae, Galliformes) as the representative of terrestrial cursorial birds were chosen for morphoecological comparison (table 1).

Material and methods

The following number of individuals: *Crex crex* (n = 3), *Rallus aquaticus* (n = 2), *Gallinula chloropus* (n = = 3), *Fulica atra* (n = 4), *Anas querquedula* (n = 2), *Aythya ferina* (n = 2), *Phasianus colchicus* (n = 3), *Phalacrocorax carbo* (n = 1) was used.

Morphoecological method , which combines comparative anatomy, functional analysis and comparative ecology, was used. The mentioned method was developed by Yudin (1957) and is successfully used to date (Zinoviev, 2006, 2007, 2010, etc.).

The anatomical terminology follows Nomina Anatomica Avium (Baumel et al., 1993).

Results and discussion

Pelvis can be considered as one of the most interesting structures of avian apparatus of bipedal locomotion. On the one hand, pelvis is a place of origin of the most powerful locomotor muscles of the pelvic limb. On the other hand, the shape of the pelvis (along with the shape of the sternum) determines the shape of the entire body. The length of pelvis in relation to length of the body is slightly different in investigated species (table 1). This is true due to the fact that the pelvis is an essential part of the body. Moreover, the comparison of the proportions of different parts of the pelvis appears to be very interesting from the functional point of view (table 1). The length of postacetabular part of pelvis exceeds that of preacetabular part among rails only in *Fulica*, resembling the situation in ducks (table 1). In *Crex* and *Rallus* postacetabular part of pelvis is shorter than preacetabular like in a good running terrestrial bird species (Bogdanovich, 1997), such as *Phasianus* (table 1). Relative length of postacetabular part of the pelvis in *Gallinula* is intermediate between those of *Fulica* from the one side and *Crex* and *Rallus*, from the other. It is interesting, that the extension of postacetabular part of the pelvis in *Fulica* is achieved due to the significant caudal expansion of processus dorsolateralis.

Table 1. Amplitude and average size of morphometric indexes of pelvis

Таблица 1. Размах и средняя величина морфометрических индексов таза

Species	L_p	L_{post}	B_d	B_v
Crex crex (n = 3)	49.2–52.0 50.7	0.75–0.79 0.77	0.44–0.49 0.46	0.34–0.39 0.37
Rallus aquaticus (n = 2)	53.0–54.9 54.0	0.72–0.75 0.74	0.48–0.53 0.51	0.40–0.41 0.41
Gallinula chloropus (n = 3)	52.8–56.0 53.9	0.89–0.93 0.91	0.43–0.47 0.45	0.36–0.39 0.38
Fulica atra (n = 4)	51.5–55.1 53.4	1.08–1.12 1.10	0.32–0.35 0.34	0.34–0.38 0.36
Anas querquedula (n = 2)	56.8–58.3 57.6	1.27–1.29 1.28	0.50–0.53 0.52	0.58–0.61 0.60
Aythya ferina (n = 2)	58.8–60.2 59.5	1.32–1.33 1.33	0.46–0.48 0.47	0.51–0.55 0.53
Phasianus colchicus (n = 3)	56.8–57.6 57.2	0.85–0.90 0.89	0.57–0.58 0.58	0.52–0.53 0.52
Phalacrocorax carbo (n = 1)	–	1.75	29.6	30.3

N o t e. L_p — total length of the pelvis (% from the length of the body); L_{post} — length of pelvis postacetabular part (without ossa pubes) in relation to the length of preacetabular part; B_d — dorsal width of the pelvis (between pr. antitrochanterici) in relation to its length; B_v — ventral width of the pelvis (the maximum distance between the pubic bones) in relation to its length.

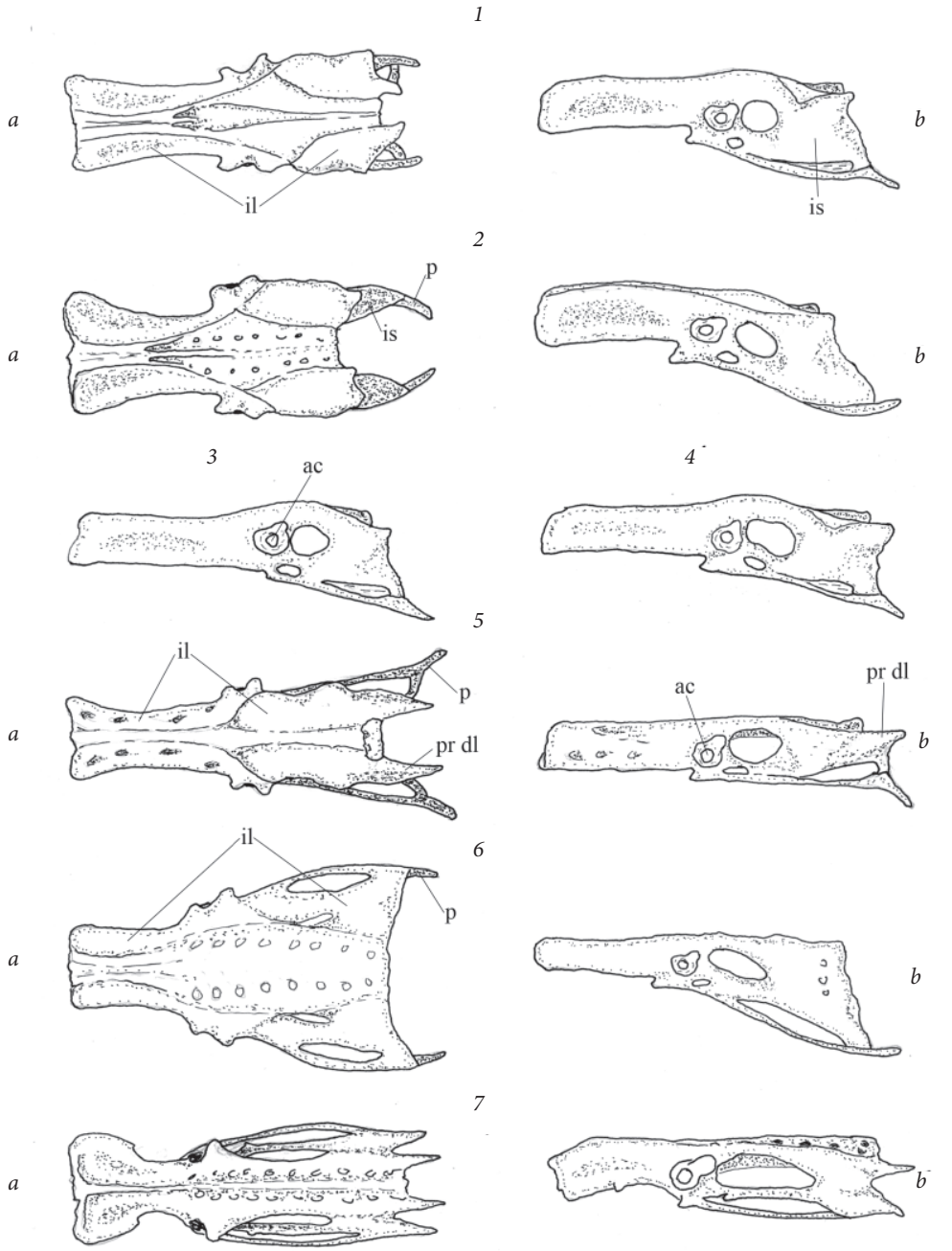

Fig. 1. Pelves of studied birds (not to the scale): *1 — Crex crex*; *2 — Phasianus colchicus*; *3 — Rallus aquaticus* (in lateral view); *4 — Gallinula chloropus* (in lateral view); *5 — Fulica atra*; *6 — Anas querquedula*; *7 — Phalacrocorax carbo*.
N o t e. *a* — in dorsal view; *b* — in lateral view; is — ischium, il — ilium, p — pubis, ac — acetabulum, pr dl — processus dorsolateralis.

Рис. 1. Таз исследованных птиц (для удобства сравнения пропорций рисунки приведены к одной длине): *1 — Crex crex*; 2 — *Phasianus colchicus*; 3 — *Rallus aquaticus* (сбоку); *4 — Gallinula chloropus* (сбоку); *5 — Fulica atra*; *6 — Anas querquedula*; 7 — *Phalacrocorax carbo*.
П р и м е ч а н и е. Для позиций *1*, *2*, *5–7*: *a* — вид сверху; *b* — вид сбоку.

Dorsal and ventral pelvic widths in *Crex*, *Rallus* and *Gallinula* somewhat differ, but remain smaller than those in *Phasianus* (table 1). The narrowest pelvis of *Fulica* brings it closer to *Phalacrocorax* (table 1). Another feature, which unites *Phalacrocorax* and *Fulica* with Anatidae (along with a significant lengthening of postacetabular part of pelvis) is widening of pelvis caudoventrally; *Crex*, *Rallus*, *Gallinula* and *Phasianus* show the opposite trend (table 1). Ischiac bones (ossa ischii) in *Fulica*, like in the other rails and *Phasianus*, are brought under the iliac bones (unlike in ducks and *Phalacrocorax*). Widening of caudoventral part in this case is due to the lateral divergence of the pubic bones (ossa pubes) in the more caudal region (fig. 1).

Selected features have the morphoecological explanations. It is known, for example, that expanded postacetabular part of the pelvis is typical for waterfowl (Raikow, 1970 and others). Most of their pelvic organs are moved caudally behind the center of gravity which is essential for the effective functioning of hind limbs during the swimming. Thus the greater postacetabular part of the pelvis in the Coot among the rails is due to its stronger association with the water. The filming showed that the center of gravity in *Fulica* is more caudally located than in *Rallus* and *Gallinula* (Leo, 1959).

Relatively narrow pelves of *Crex*, *Rallus* and *Gallinula* are traditionally linked to the advantage of moving in the dense vegetation. The narrowed pelvis of *Fulica* is clearly the other case, since it approaches the pelvis of *Phalacrocorax* (table 1), which does not move in the terrestrial vegetation. Dorsal narrowing of the pelvis is in fact necessary to bring the femoral heads closer to the axis of the body. This increases the efficiency of swimming due to the reduction of the cross sectional area of the body (Kurochkin, 1971). The narrowing of the pelvis is obviously the most advantageous in diving birds. It has been explicitly shown on ducks with different degrees of diving adaptations (Bogdanovich, 2003). It is of interest that the narrowing of pelvesin *Fulica* and *Phalacrocorax* is achieved in different ways. Iliac bones of postacetabular part of pelvis in *Phalacrocorax* are oriented nearly vertical, almost in the same plane with the ischia; iliac bones in *Fulica* are oriented typical for other rallids and, for example, *Phasianus* (fig. 1). The caudal expansion of pelvis provides an increasing stability in water (Stolpe, 1932). This brings *Fulica* closer to Anatidae, than to *Phalacrocorax*, whose pelvis in the most caudal region is narrowed (fig. 1).

Conclusion

The analysis of pelvic and hindlimb morphology in rallids shows that *Fulica* possess

Table 2. Relative length of pelvic limbs and its elements

Таблица 2. Относительная длина тазовой конечности и её элементов

Species	Ll	Lf	Lt	Ltm
Crex crex (n = 3)	178.3–182.3 180.5	53.3–55.3 54.3	72.8–76.8 74.9	54.5–57.7 56.1
Rallus aquaticus (n = 2)	245.1; 250.1 247.6	63.8; 69.8 66.8	103.8; 109.8 106.8	62.8; 65.4 64.1
Gallinula chloropus (n = 2)	215.5; 217.3 216.4	59.5–61.8 60.4	95.7–97.2 96.7	58.5–59.4 59.0
Fulica atra (n = 4)	159.1–163.4 160.8	37.5–41.8 39.4	70.8–73.6 71.8	42.0–44.7 43.2
Anas querquedula (n = 2)	118.9; 119.3 119.1	35.2; 35.6 35.4	62.3; 62.7 62.5	28.5; 29.7 29.1
Aythya ferina (n = 2)	120.3; 122.1 121.2	33.8; 34.1 34.0	58.4; 58.9 58.7	27.9; 28.9 28.4
Phasianus colchicus (n = 3)	218.0–223.1 220.4	66.9–70.1 68.5	95.1–96.0 95.5	61.2–65.2 63.2

Note. Lc — length of pelvic limb (% from the length of the body); Lf — femur length (% from the leg length); Lt — tibiotarsus length (% from the leg length); Ltm — tarsometatarsus length (% from the leg length).

a number of specialized features due to macrogenesis (Iordansky, 2004), which led to the appearance of the new genus. Terrestrial *Crex* and *Rallus* stay definitely closer to the type, from which *Fulica* locomotor adaptations to swimming and diving in the water have started. Coot still resembles its terrestrial relatives by the alternate movements of the legs during the swimming, unlike simultaneous stroke in specialized divers, such as loons, grebes and diving ducks (Kurochkin, 1971). Belonging to the group, initially adapted to forest environments (Olson, 1973), *Crex* and *Rallus* mastered a new adaptive zone (sensu Severtzov, 1984) — wetlands near the water. *Fulica* shows the latest rallid adaptation on this way — the adaptation to swimming and diving. Specialized enough, *Fulica*, nevertheless, did not lose the plasticity (*sensu* Severtzov, 1984), like some other species (Shtegman, 1960; Bogdanovich, 1991). Unlike Anatidae, it retained relatively long hind limbs with only slightly shortened tarsometatarsus (table 2), which allowed efficient terrestrial locomotion. Lobbed fingers (in contrast with webbed feet) do not preclude the climbing (Kurochkin, Vasiliev, 1966).

Retaining a certain degree of evolutionary plasticity, expressed in universalism of locomotor appatatus, *Fulica*, nevertheless, is the most specialized genus in Rallidae. This places genus *Fulica* in the rank of the tribe within the subfamily Fulicinae, which correspond to the other studies (Verheyen, 1957; Brodcorb, 1967). In this context, *Gallinula* holds a position between *Rallus* and *Crex*, from the one side, and *Fulica,* from the other.

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