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ЗООЛОГИЯ

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BIPEDAL HOPPING IN BIRDS AND RODENTS: MORPHOLOGICAL AND EVOLUTIONARY ASPECTS

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Hopping in birds is confined exclusively to the perching birds, belonging to the order Passeriformes. Being an adaption to move in canopies, it resulted in the reduction of certain muscles and structures acting in the single support phase of the locomotor cycle. These muscles and structures are not regained by passerines which switched to running (larks, pipits, wagtails). Passerines also lost most of the intrinsic muscles of the foot as they brought digits into the parasagittal plane to ensure the firmer grip of the perch. Bipedal saltation in rodents evolved as an adaptation to escape from predators in sparsely vegetated areas. It has resulted in morphological changes, convergent to those of hopping birds. Muscles responsible for any other movements of the limb segments than flexion-extension are underdeveloped. The reduction of digits and fusion of metatarsalia reach their extreme in *Jaculus orientalis*, which lost all the intrinsic muscles of the foot.

Keywords: *birds, rodents, convergence, hind limbs, hopping, musculature.*
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Introduction. Hopping on two legs in birds and mammals has been studied both energetically and morphologically (Alexander, Vernon, 1975; Clark, 1979; Alexander, 1980; Thompson et al., 1980; Hayes, Alexander, 1983; Moore et al., 2017). This type of locomotion in rodents has resulted not only in the convergent evolution within the group (Berman, 1985) but in certain convergence with hopping birds (Zinoviev, Kalyakin, 2018). Here we analyze common morphological modification in hindlimb muscles of hopping passerines and mammals within the evolutionary context.

Materials and Methods. We used the original data on the hindlimb musculature of the hopping passerines summarized in the monograph (Zinoviev, 2010). Personal anatomical observations and a number of literature sources (Berman, 1985; Moore et al., 2017) were used to assess the hopping rodents' hindlimb musculature.

Anatomical terms follow the *Nomina Anatomica Avium* (Baumel et al., 1993) and *Nomina Anatomica Veterinaria* (ICVGAN 2017).

Results and Discussion. Hopping birds. Hopping in birds is confined exclusively to the perching birds, belonging to the order

Passeriformes. Leg-muscle formula, created by Alfred H. Garrod (1874), and later expanded (Hudson, 1937; Berger, 1959; Kurochkin, 1982; Zinoviev, 2007 a), was proved to be valuable in assessing basic locomotor specializations of birds on the level of family (Zinoviev, 2007 a). Most of the passerine birds have a surprisingly complete leg-muscle formula, which only lacks *m. iliofemoralis externus*, *m. ambiens*, *m. popliteus*, and *vinculum tendinum flexorum*. Lacking components of formula reveal basic locomotor adaptation of the group. All the lacking structures are acting during the single support phase. *M. iliofemoralis externus* prevents the passive adduction of the femur by the force of gravity acting on the body (Zinoviev, 2007 a). *M. ambiens* is energetically efficient in keeping the leg's pose in the middle stage of a single support phase (Kuznetsov, 1995). *M. popliteus* adds to the inward-rotation of the tibiotarsus during single support phase (Zinoviev, 2007 a). And, finally, *vinculum tendinum flexorum* unites *m. fibularis longus, m. flexor perforates digiti III*, and *m. flexor perforans and perforatus digiti III* in one system, which resists overextension of the third toe at the end of single support phase (Zinoviev, 2007 a). The absence of the aforementioned components characterizes passerine birds as adapted to the type of locomotion with no single support phases, namely to the hopping. So-called "running passerine birds" (e.g. Menurae, Pittidae, Alaudidae, Motacillidae) still lack the discussed components, indicating their ancestry among hopping passerines. Hopping adaptation of passerines is also related to the reduction of the intrinsic muscles of the foot. Responsible for individual movements of the digits (mainly adduction and abduction), they are not needed in passerine birds which keep digits as close to the parasagittal plane as possible to ensure the firm grip of the perch.

Bipedally hopping rodents. As I have no purpose to describe in detail the morphological adaptations of all the hopping (or saltating) rodents treated substantially elsewhere (Berman, 1985) I would specifically mention those, related to the absence of single support phases. Most of the muscles, or, rather, muscle complexes (e.g. *m. quadriceps femoris* complex) important in producing the take-off velocity are enlarged, while many of the muscles and muscle groups responsible for movements other than the parasagittal plane have undergone reduction (Berman, 1985). This is strikingly similar to hopping passerines, which show well-developed shank and tarsometatarsus extensors, while adductors and pronators are underdeveloped or altogether absent. The similarity is going even further. Hopping rodents lack many of the intrinsic muscles of the foot, with *Jaculus orientalis* lacking them all (Berman, 1985). As most of the intrinsic flexors and extensors have large synergists on the shank, their reduction is expected in animals with elongated metatarsals and requirements to lighten the foot. Digits, brought in *J. orientalis* together into the parasagittal plane do not require abduction and adduction, as this jerboa is moving primarily on the firm ground.

Conclusion. Hopping passerines and rodents show certain similarities in the hindlimb morphology. Most of the similarities are related to the absence of the single support phase in hopping. This brings the reduction of muscles responsible for any other movements than flexion-extension. The reduction of many intrinsic foot muscles in birds and rodents is related to the restriction of the digital movements by the parasagittal plane. Similar changes are brought to life by different actors. These are hopping in canopies in passerine birds and hopping on the ground in rodents.

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ДВУНОГИЕ ПРЫЖКИ У ПТИЦ И МЛЕКОПИТАЮЩИХ: МОРФОЛОГИЧЕСКИЕ И ЭВОЛЮЦИОННЫЕ АСПЕКТЫ

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Птицы, передвигающиеся при помощи прыжков. принадлежат исключительной к отряду Воробьинообразные. Будучи адаптацией к передвижению в кронах, двуногие прыжки связаны с редукцией ряда мускулов, использующихся во время одноопорных фаз локомоторного цикла. Эти мускулы и структуры отсутствуют даже у воробьиных, вторично перешедших к передвижению с одноопорными стадиями (жаворонки, коньки, трясогузки). Воробьиные птицы также утратили большинство мускулов цевки, максимально приведя пальцы в плоскость, перпендикулярную оси насеста (различные варианты синдактилии). У млекопитающих двуногая локомоция при помощи прыжков возникла как адаптация к уходу от хищников на открытых пространствах. При этом прослеживается ряд конвергентных черт в прыгающими птицами. Мускулы, ответственные за движения вне парасагиттальной плоскости, у прыгающих млекопитающих развиты слабее. Редукция пальцев и слияние плюсневых костей достигает своего максимума у восточного тушканчика (*Jaculus orientalis*), утратившего все дистальные мускулы стопы.
Keywords: *birds, rodents, convergence, hind limbs, hopping, musculature.*

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