APPARATUS OF BIPEDAL LOCOMOTION OF CUCULIFORMS (AVES, CUCULIFORMES): SCENARIO OF AN ADAPTIVE EVOLUTION[1]

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A scenario of an adaptive evolution of cuculiforms' apparatus of bipedal locomotion is revealed on the basis of morpho-ecological analysis of an extensive comparative data on the morphology of hind limbs of Cuculiformes. Hoatzin demonstrates a possible ancestral state; its hind limbs have the most complete number of muscles, although showing some traces of specialization to the transverse grasping of branch. Turacos illustrate the next stage; despite pronounced arboreality, they retain more or less ancestral morphology of hind limbs. Only their feet underwent an adaptation for running along branches – the fourth digit can be moved laterally for better grip. Cuculids show an adaptation to the locomotion in canopies with simultaneous transverse grip of the perch with subsequent reaching of the food item while sitting. This caused an obligate caudal reversion of the fourth toe and disappearance of certain muscles, used in one-leg-supported stage of locomotion. Despite the return to the ancestral type of locomotion, the so-called "running cuckoos" of Old and New World retained major features of cuculids' arboreal adaptation.

Order Cuculiformes, according to the most widely accepted classifications (Peters, 1940; Wetmore, 1960; Morony et al,. 1975; Howard, Moore, 1991), includes two families – touracos (Musophagidae) with 20 species of 6 genera and cuckoos (Cuculidae) with 129 species of 38 genera. An enigmatic hoatzin (*Opisthocomus hoazin* Müller), a sole representative of Opisthocomidae, is also often united with cuculiforms (Hedges et al., 1995; Mindell et al., 1997; Sibley, Ahlquist, 1990). Debates on the systematics of the order reflect a search for the natural classification in which a number of various characters is used. While early classifications were based on a few characters (Nitzsch, 1840; Lilljeborg, 1886; Goodchild, 1891), recent ones include hundreds of them; thanks to the development of computer technologies (see Hughes, 2000 for overview). Cladograms thus obtained serve as valuable sources of information for the study of avian adaptive evolution. Despite functional background being used for polarization of characters, entire picture of the adaptive evolution of cuculiforms remains unrevealed.

Reconstruction of such a picture is possible only on basis of functional elaboration of highly informative skeleton-muscular complexes, such jaw apparatus and limb girdles. Morpho-functional approach to the analysis of these complexes with an aid of biomechanical model has been successfully applied in studying the adaptive evolution of certain groups (Yudin, 1957, 1965; Kurochkin, 1968; Dzerzhinsky, 1972, 1977; Sych, 1999; Zinoviev, 1999, 2006; Dzerzhinsky, Korzun, 2004 etc.). Present paper follows this tradition in revealing adaptive evolution of cuculiforms' hind limbs.

MATERIALS AND METHODS

Original and literature data on hindlimb osteology and musculature of Cuculiformes has served as the material for the study. Data on hindlimb morphology of other groups has been used for the comparative analysis. Due to large number of literature sources, we do not cite all of them here; the entire list is provided elsewhere (Zinoviev, 1999).

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We used a traditional and widely accepted classification of Morony et al. (1975). The cladogram by Hughes (2000) has been used for the analysis of an adaptive evolution of cuculiforms. Mentioned cladogram, on our opinion, is the most compromise one in showing phylogenetic history of Cuculiformes. Names of anatomical structures follow Nomina Anatomica Avium (1993) and rules of Latin grammar. Russian names of birds are given according Boeme and Flint (1994).

RESULTS AND DISCUSSION

To start adaptive analysis of Cuculiformes, we have to prove, that the mentioned group is monophyletic, or at least comprised of sister groups. Although classifications (Peters, 1940; Wetmore, 1960; Howard, Moore, 1991) in which touracos and cuckoos are combined in one order are the most widely excepted, this unification is disputable. Based of DNA-DNA hybridization, touracos and cuckoos have been placed in different orders and supraorders (Strigimorphae and Cuculimorphae, respectively) inside of the Parvclassis Passerae, with hoatzin residing in Cuculiformes (Sibley, Ahlquist, 1990). Methods, used by Sibley and Ahlquist, are not ideal (for critique notes see Mayr, Bock, 1994); its results should be used with caution. By far more suitable classification for cuckoos and their allies has been proposed by Hughes (2000). He put touracos and hoatzin to different families inside order Opisthocomiformes, whereas Cuculidae he places within Cuculiformes. This particular classification in graphic interpretation (fig. 1) we have used in our study.

A vast amount of data on hindlimb morphology of hoatzin, touracos and cuckoos has been collected for more than 140 (Garrod, 1873, 1874, 1875; Beswick, 1976; Beddard, 1885, 1898, 1901; Shufeldt, 1886, 1886a, 1901, 1909; Pycraft, 1903; Larson, 1930; Hudson, 1937; Engels, 1938; Lowe, 1943; Berger, 1952, 1953, 1954, 1955, 1960; Verheyen, 1956; Seibel, 1988; Sych, 1988; Hedges et al., 1995; Hughes, 2000). Mentioned sources cover 33 out of 38 genera of cuckoos, 6 out of 8 genera of touracos and a solitary genus *Opisthocomus*. The data is rich and sufficient to reconstruct an adaptive evolution of hindlimb apparatus of cuckoos and their allies.

Zygodactyly

One of the characteristic features of cuckoos is zygodactyly. In zygodactylous foot second and third toes are directed forward, while first and fourth backward. This configuration can also be seen in other groups such as Psittaciformes and Piciformes. There is no doubt, that zygodactylous foot has derived from anysodactylous one (II, II and III toes are directed forward, I – backward), the most widespread in classis Aves and characteristic for the majority of the ancestral forms (Bock, Miller, 1959; Raikow, 1985). Zygodactyly is undoubtedly an adaptation for grasping the perch. Similar number of opposite toes provides a sure grip in parrots, cuckoos and primitive piciforms. Such a grip is necessary to reach for the food item (fruit, insect etc.) while sitting on the branch (Zinoviev, 1999). Zygodactyly is by no means and adaptation for tree trunk climbing, as it has been proposed earlier. Backwardly directed toes do not give any profit to climbing bird, since the force vector which pulls the bird away from the trunk, goes through forward toes. In this case backwardly directed toes are either secondarily rotated forward to help other toes (piciforms and *Micropsitta*) or undergo the reduction until the complete disappearance of the first toe (*Picoides, Dinopium, Geniculus, Sasia*) (Zinoviev, 1999).

Interestingly, but to some extent turacos show a possible way in which cuckoos have acquired the zygodactyly. Touracos have so called semizygodactylous foot, in which the fourth toe can shift its position from forward to lateral direction. This allows the bird to use two configurations thus increasing the functional potential of the foot. The fourth toe, directed laterally, provides a better grip while touraco moves along the branch (Zinoviev, 1999) (fig. 2).

Hoatzin, in turn, provides an insight on how might have looked like the foot of the remote ancestor of Cuculiformes. Hoatzin has been initially placed in Galliformes (Müller, 1776) as a member of monotypic family Opisthocomidae (Peters, 1934). However, data on osteology
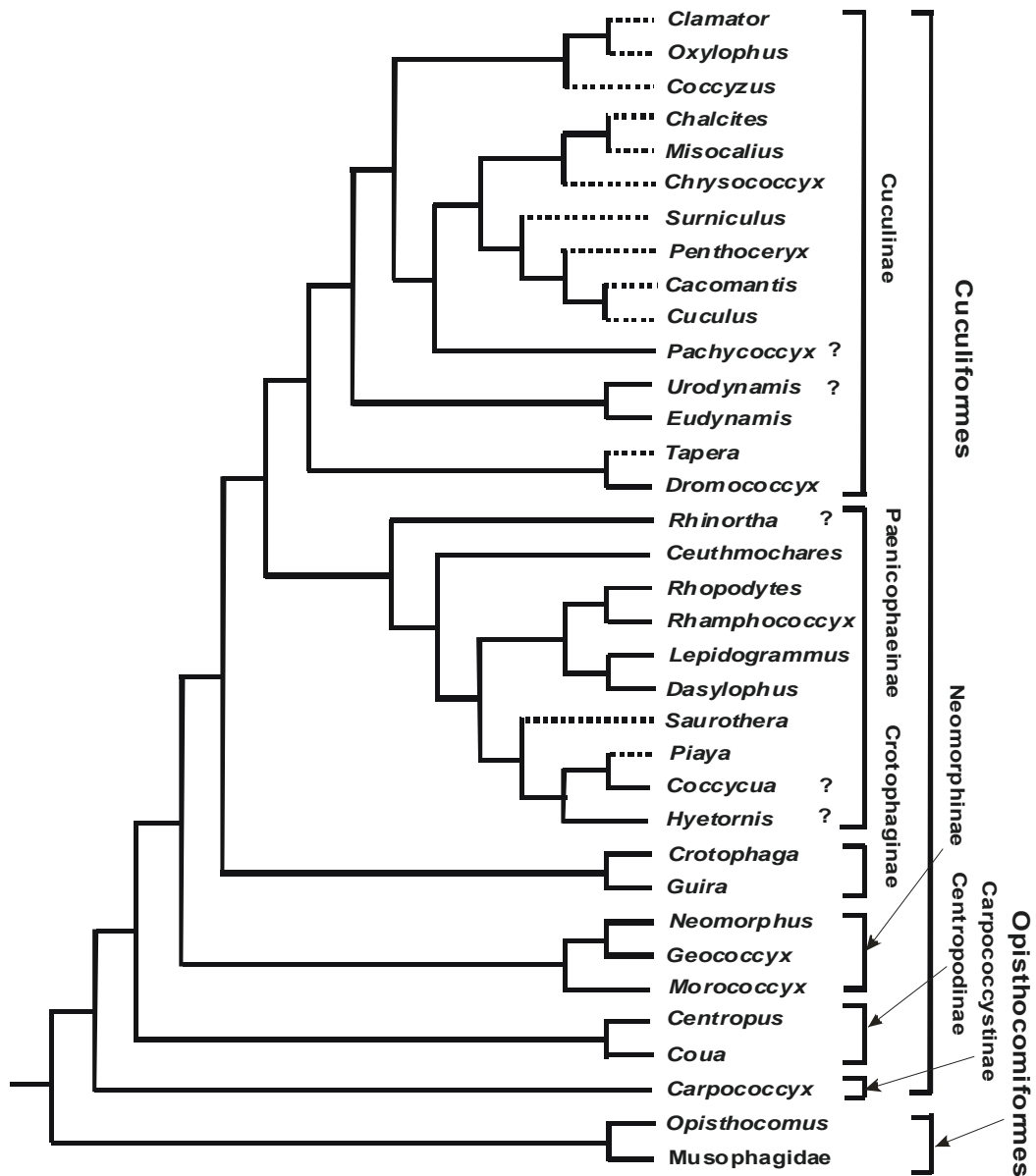
Fig. 1. A condition of m. iliofemoralis in cuckoos and their allies. Data in superimposed on the phylogeny cladogram (Hughes, 2004), based on 135 osteological characters with hoatzin and touracos as outgroups. Dash lines show genera lacking m. iliofemoralis; question marks indicate the lack of information.

(Verheyen, 1956; De Queiroz, Good, 1988), myology (Stegmann, 1978; Sych, 1988; McKitrick, 1991; Korzun et al., 2003) and biochemistry (see Hughes, 2000 for the review) of this bird supported its closer affinity with cuculiforms, touracos in particular. Hoatzin's anysodactylous foot, which had long been one of the main obstructions from placing it close to cuckoos, is, in fact, an ideal ancestral state for the entire order, where zygodactyly has been acquired though the semizygodactylous stage. Interestingly, that *Foro panarium* from the Lower Miocene of Wyoming has a skull, resembling that of the hoatzin, whereas its postcranial skeleton is close to that of touraco (Olson, 1992).

Skeleton and musculature

If our assumption on the origin of zygodactyly through the semizygodactylous stage is true, hind limbs of hoatzin and touracos should retain traces of this process.

As a highly specialized form (adapted to folivory), hoatzin can not be treated as a direct ancestor of touracos and cuckoos. However, its hind limbs are really close to those of proposed ancestor (fig. 2A). Being strictly arboreal, hoatzin, nevertheless, retained almost all hindlimb
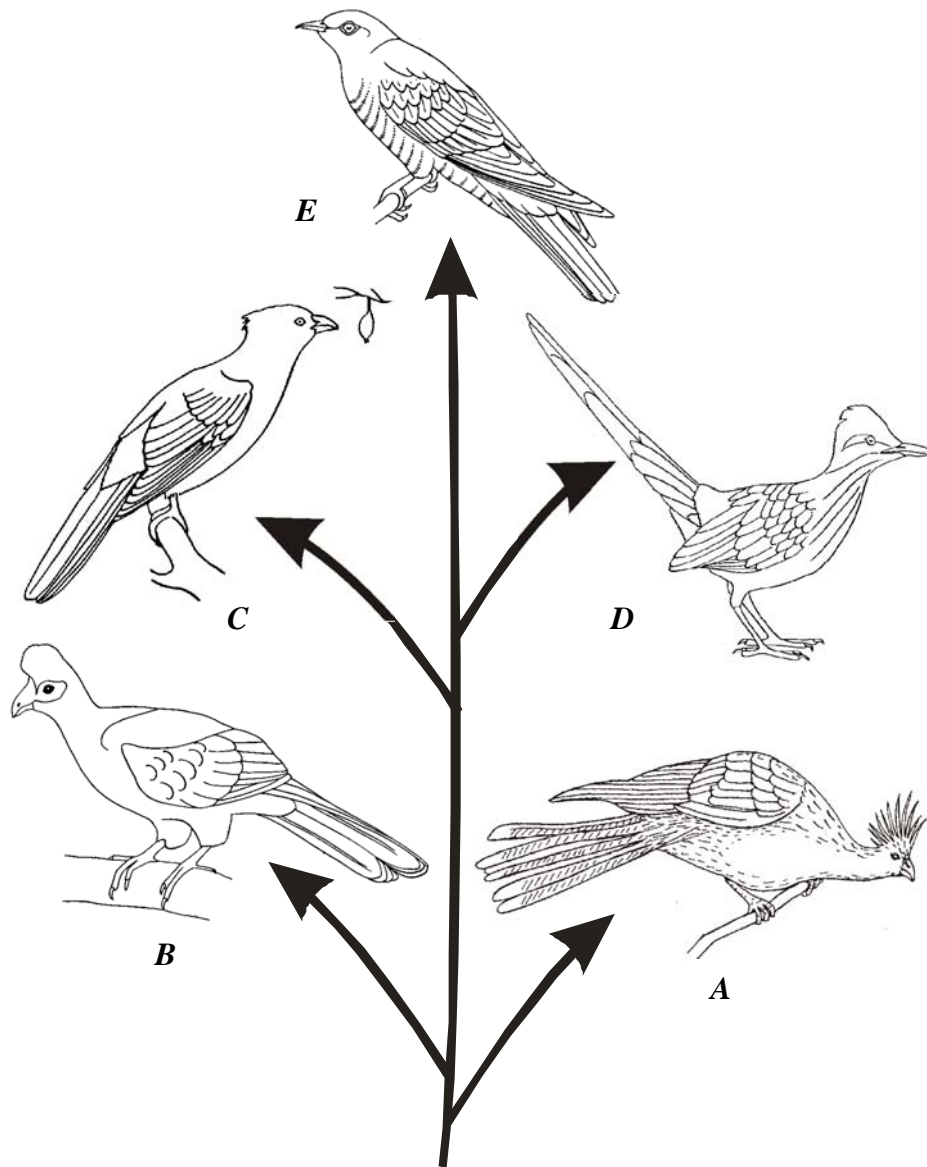
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Fig. 2. A scenario of adaptive evolution of terrestrial locomotor apparatus in cuckoos and their allies, proposed in this paper: A – hoatzin-like stage, B – touraco-like stage, C – common ancestor of cuckoos, D – ground cuckoos of Old and New World, E – Cuculinae (see text for comments).

muscles, a state, generally characteristic for ancestral, less specialized forms (Hudson, 1937). Hoatzin though has lost vinculum tendinum flexorum, which connects terminal tendons of m. flexor perforatus digiti 3 and m. flexor perforans et perforatus digiti 3 (table). Its disappearance allows independent flexure of second and third phalanges of the third toe, important feature for better transverse grip on the perch (Zinoviev, 1999, 2006). This is truly arboreal adaptation of hoatzin. At the same time, the presence in hoatzin's leg of muscles used to control one-leg-supported stages (Zinoviev, 1999) points on the retention of an ancestral type of locomotion. Indeed, it actively moves in canopies alternately using each hind limb (Beswick, 1876).

If hoatzin shows the way in which ancestors of cuckoos became arboreal retaining an ancestral full set of hindlimb muscles, touracos reveal one of the successive stages of arboreal adaptation (fig. 2B) (support for the profound morphological similarity between hoatzin and touraco see in Hughes, 2000: 287). Table shows that touracos have lost two out of 14 components of the extended muscular formula of Garrod. These are m. iliotrochantericus medius and m. iliofemoralis internus. Both muscles are weak and play a minimal role in controlling the hind limb even in the primitive Galliformes. Thus their disappearance in touracos does not point to any specific adaptation. Moreover, m. iliotrochantericus medius s often fuses with its powerful

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Extended Muscular Formula of Garrod for Hoatzin. Touracos and Cuckoos

Family	Muscular Formula													
	A	B	C	D	E	F	G	M	M1	N	X	Y	Am	V
Opisthocomidae	+	+	+	+	+	+	+	+	+	+	+	+	+	-
Musophagidae	+	+	-	+	-	+	+	+	+	+	+	+	+	+
Cuculidae	+	+-	-	-	-+	+	+	+	+	+	+	+	+	-

Abbreviations. A - m. caudofemoralis, B - m. iliofemoralis, C - m. iliotrochantericus medius, D - m. iliofemoralis externus, E - m. iliofemoralis internus, F - m. plantaris, G - m. popliteus, M - m. fibularis longus, M1 - tendo cranialis m. fibularis longi, N - m. fibularis brevis, X - m. flexor cruris lateralis, Y - pars accessoria m. flexoris cruris lateralis, Am - m. ambiens, V - vinculum tendinum flexorum: «+» - present, «-» - absent, «+-» - present in the majority of species, «-+» - absent in the majority of species.

synergist m. iliotrochantericus caudalis, so its presence or absence in touracos is a matter of discussion. Hindlimb musculature of touraco does not really show any big differences from those of hoatzin. We even find a vinculum, which has been lost by hoatzin. This fact points on hoatzin as more specialized arboreal bird, while touracos still retain in canopies an ancestral type of locomotion with alternately used hind limbs. In this case vinculum is very important to coordinate flexors of the third toe to counteract its overextension during contact phase (Zinoviev, 1999). Field observations support these conclusions: locomotion of touracos along branches is identical to that utilized them on the ground (L.P. Korzoun, pers. comm.). Major changes have influenced touracos' foot, which became semizygodactylous.

A table graph, relating to Cuculidae, shows the lack of m. iliofemoralis externus, which has been preserved in other groups. Relatively weak and often fused with more powerful m. iliotrochantericus caudalis, this muscle abducts the femur. That makes it a good indicator of certain aspects in specialization of hind limbs (Zinoviev, 1999). We have shown biomechanically (Zinoviev, Dzerzhinsky, 2000), that abduction of femur is necessary to counteract the force of gravity, which adducts the femur during one-leg-supported stage. M. iliofemoralis externus disappears in species, which do not use one-leg-supported stages in locomotion (Zinoviev, 1999). This happens in many arboreal forms, using in canopies two legs simultaneously (Accipitridae, Strigiformes, Trogoniformes, Coraciiformes, Piciformes, Passeriformes). Species, which have lost m. iliofemoralis externus, still retain the ability to walk and run with one-leg-supported stages. Abducing effect on femur, in this case, is provided by m. iliotibialis lateralis, mm. puboischiofemorales, mm. flexores crures, m. iliofemoralis and m. caudofemoralis. Running passeriforms (Menuridae, Pittidae, Alaudidae and Motacillidae) is good example. No bird acquires this muscle after reduction. It rarely may appear as an anomaly of development (Raikow, 1975; Raikow et al., 1979).

All the mentioned above is definitely true for cuckoos. The absence of m. iliofemoralis externus shows cuculids as specialized perchers, which use both legs simultaneously (fig. 2C). This ancestral specialization did not prevent some representatives from returning to the locomotion with one-leg-supported stages. This happened soon after the acquisition of arboreal specialization (fig. 2D). Hughes (2000) showed, that Old (*Carpococcyx, Centropus, Coua*) and New World ground cuckoos (*Morococcyx, Geococcyx, Neomorphus*) have a number of morphological characters, lost by modern arboreal species. Hughes concluded, that the ancestral form to arboreal cuckoos (similar to that, proposed in our study: fig. 2C) can not be called a cuckoo. We believe that the nominative debates of this kind are not constructive. Our studies, like those of other authors (Korzun et al., 2003), point on the ancestral form, utilizing the movement in canopies with one-leg-supported stages and feeding on fruits, reached from transversely gripped perch. All the modern cuckoos retained to various extent features of this ancestor. Thus we do not think it should be named anything other than cuckoo.

Curiously, the disappearance of m. iliofemoralis externus in the ancestral arboreal form is manifested by modern terrestrial cuckoos. Pycraft (1903) first, and later Berger (1952) have noted interesting tendency in pelvic morphology of cuckoos. The further we follow the row from
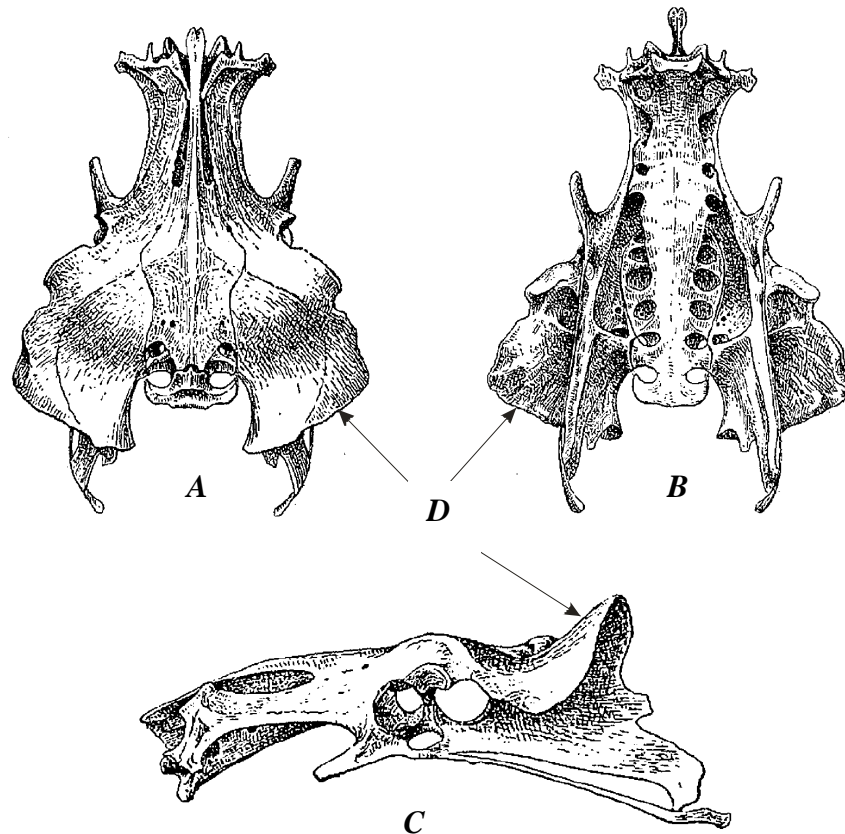
Fig. 3. Pelvis of Greater Roadrunner (*Geococcyx californianus*): A – dorsal aspect, B – ventral aspect, C – lateral aspect, D – lateral saddle-shaped expansion of postacetabular pelvis (according Pycraft, 1903, with changes).

arboreal to terrestrial cuckoos, the wider becomes a saddle-shaped postacetabular ilium (fig. 3D). Pycraft correctly connected this peculiarity to the terrestrial adaptations (he found a similar tendency in able runners, Rallidae). The widening of pelvis moves the origins of femoral retractors (mainly m. flexor cruris lateralis and m. iliofemoralis) laterally, thus increasing their abducing component. This changes along with caudal migration of m. iliotrochantericus caudalis (Berger, 1952) (its posterior portion substitutes the lost m. iliofemoralis externus) show, that the problem of balancing the body during one-leg-supported stages has been solved by ground cuckoos secondarily.

The other muscle, which, however, is not always absent in cuckoos (table), m. iliofemoralis, shows one of the patterns in cuculids' locomotor adaptation. Fig. 1 displays, that muscle is present in basal, terrestrial species (Carpococcystinae, Neomorphinae, Crotophaginae), while absent in the progressive arboreal. This is, from the one side, is connected to the history of the group. From the other, absence of the muscle shows the loss of active locomotion in canopies. The mentioned tendency reaches its peak in subfamily Cuculinae, comprised of strictly arboreal species. They use hind limbs almost exclusively for transverse grip of the perch (fig. 2C). Genus *Cuculus* has further moved in this direction, showing progressive reduction of other hindlimb muscles, f.i. the postacetabular m. iliotibialis lateralis and m. fibularis longus (Berger, 1960).

The absence of vinculum and the separation of terminal tendons of deep digital flexors in hypotarsus' channels allowing them to move more independently are additional evidences of the ancestral adaptation of cuckoos to the transverse grip of the perch. Mentioned vinculum does not reappear in terrestrial cuckoos, where it could be of an advantage in coordinating the action of muscles-flexors of the third toe.

CONCLUSION

Morpho-functional analysis of cuculiforms' hind limbs enables us to reconstruct the following scenario of their evolution (fig. 2).

The ancestral form had a most complete set of hindlimb muscles along with anysodactylous foot. Although quite specialized to the transverse grip of the perch, hoatzin illustrates how this form might have looked like (fig. 2A).

Touracos, despite their arboreality, retain almost complete set of hindlimb muscles. They show the next stage in the evolution of cuckooliforms' locomotor apparatus – the acquisition of semizygodactyly. Laterally moved fourth toe enables a better grip for locomotion along branches (fig. 2B).

The next step is an adaptation for reaching the food item while transversely gripping the perch (fig. 2B). Fourth toe at this stage has been moved backward to be a valuable aid in keeping the balance. A number of muscles, utilized in one-leg-supported stage, have disappeared. This, however, did not prevent the return of some forms to the terrestrial locomotion of an ancestral type. Return happened quite early in the evolutionary history of the group and led to the appearance of ground cuckoos of Old and New World (fig. 2D). Although acquiring typical cursorial features (elongation of distal limb elements, powerful retractors and protractors, concentration of muscles closer to the center of gravity (Berger, 1952), these birds, nevertheless, retained features of an ancestral arboreal adaptation (zygodactyly, absence of specific muscles). They compensated the lack of specialized femoral abductor with lateral shift of retractors' origins. Other cuckoos moved further in the arboreal way, losing the ability to run. This resulted in reduction of some muscles (fig. 2E). These cuckoos have chosen a special hunting tactics, when food item is visually detected and picked from the perch. This tactics is effective in sparse forests with abundant and uniform food (Malchevsky, 1987).

ACKNOWLEDGEMENTS

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