

NOTES ON THE HIND LIMB MYOLOGY OF THE OSTRICH (*STRUTHIO CAMELUS*)

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Introduction

Ostriches (*Struthionidae*), which belong to the taxonomical order *Struthioniformes* along with the flightless *Rheae*, *Casuarii* and *Apteryges*, have been drawing the attention of morphologists for almost two centuries (Meckel, 1825). Besides being attractive in the evolutionary sense (there is still controversy as to whether or not their ancestors were able to fly (Steiner, 1949) or they branched so early in avian history that their ancestors did not yet acquire flight (Lowe, 1928; 1942)) ostriches also become increasingly interesting as farm meat animals. The muscles of the hindlimbs are mainly used for meat production (Jost, 1993).

The first studies of hindlimb myology of the **Ostrich** (*Struthio camelus*) are dated back as early as the first half of the nineteenth century (Meckel, 1828). Many of the following studies also were conducted in the same century (Haughton, 1865; Macalister, 1865; Garrod, Darwin, 1872; Gadow, 1880). In the following centuries a number of works dealing with the hindlimb myology of the ostrich has also appeared (Sudilovskaya, 1931; Cho et al., 1984; Mellet, 1985, 1994; Fowler, 1991; Hopkins and Constantinescu, 1995; Pavaux and Lingereux, 1995; Liswaniso, 1996; Liswaniso et al., 1996 a,b, 1997; Bezuidenhout, 1999; Zinoviev, 1999; Chow et al., 2000; Gangl, 2001; Weissengruber et al., 2002, 2003). Despite such a broad array of works, many of the studies are either too old to follow modern nomenclatural rules or are restricted to certain parts of the limb. Gangl et al. (2004) recently tried to resolve the situation by providing an updated description of hindlimb

muscle topography, names and morphology, based on the dissection of 12 specimens of the African Ostrich and available citations synthesis. However, their work was not without some discrepancies. Since morphological characters are now extensively used in phylogenetic reconstructions, including those of avian hind limbs (McKittrich, 1991), one should be very cautious in describing new structures or changing names of known ones. Thus, the aim of the present study is to point out certain discrepancies in previous descriptions of hindlimb muscles of the Ostrich.

Materials and methods

The hindlimbs of two formalin-fixed adult male Ostriches the collection of the Zoological Museum of Moscow State Lomonosov University have been dissected following standards of gross anatomical methodology. Investigations have been performed at the Department of Vertebrate Zoology, Moscow State Lomonosov University, Moscow, Russia, and at the Department of Zoology, Tver State University, Tver, Russia. Stages of dissection have been documented by multiple original pencil drawings, several of which have been redrawn in ink for this publication.

Results

As in previous studies (Mellet, 1994; Gangl et al., 2004) we found 36 hindlimb muscles in the Ostrich (table).

Table
Таблица

Overview of the hindlimb muscles of the Ostrich according to previous and present studies.
Names and details in bold print indicate the changes, proposed and discussed in this paper.

Список мускулов задней конечности африканского страуса в соответствии с предыдущими и настоящими исследованиями. Жирным шрифтом выделены изменения, предложенные в настоящей работе.

Gangl et al., 2004		This study / Данная работа	
Muscles / Мускулы	Parts, heads and tendons of insertion / Порции, головки и конечные сухожилия	Muscles / Мускулы	Parts, heads and tendons of insertion / Порции, головки и конечные сухожилия
<i>M. iliotibialis cranialis</i>	Cranial and caudal part	<i>M. iliotibialis cranialis</i>	Cranial and caudal part
<i>M. iliotibialis lateralis</i>	<i>Pars preacetabularis</i> <i>Pars intermedia</i> <i>Pars postacetabularis</i>	<i>M. iliotibialis lateralis</i>	<i>Pars preacetabularis</i> <i>Pars acetabularis</i> <i>Pars postacetabularis</i>
<i>M. iliobularis</i>	Tendon of insertion: <i>Crus craniale</i> <i>Crus caudale</i>	<i>M. iliobularis</i>	Tendon of insertion: <i>Crus craniale</i> <i>Crus caudale</i>
<i>M. ambiens</i>		<i>M. ambiens</i>	
<i>M. pectineus</i>			
<i>M. iliotrochantericus caudalis</i>		<i>M. iliotrochantericus caudalis</i>	
		<i>M. iliotrochantericus medius</i>	
<i>M. iliotrochantericus cranialis</i>		<i>M. iliotrochantericus cranialis</i>	
<i>M. iliofemoralis externus</i>	Tendon of insertion: <i>Crus craniale</i> <i>Crus caudale</i>	<i>M. iliofemoralis externus</i>	
<i>M. iliofemoralis internus</i>		<i>M. iliofemoralis internus</i>	
<i>M. femorotibialis externus</i>	Additional tendon on the medial surface of the end-tendon	<i>M. femorotibialis externus</i>	<i>Pars proximalis</i> <i>Pars distalis</i>
<i>M. femorotibialis medius</i>	<i>Caput proximale</i> <i>Caput distale</i>	<i>M. femorotibialis medius</i>	<i>Pars proximalis</i> <i>Pars distalis</i>
<i>M. femorotibialis internus</i>	<i>Caput mediale</i> <i>Caput laterale</i>	<i>M. femorotibialis internus</i>	<i>Pars medialis</i> <i>Pars lateralis</i> <i>Pars pectineus</i>
<i>M. femorotibialis accessorius</i>			
<i>M. flexor cruris lateralis</i>	<i>Pars pelvica</i> <i>Pars accessoria</i>	<i>M. flexor cruris lateralis</i>	<i>Pars pelvica</i> <i>Pars accessoria</i>
<i>M. flexor cruris medialis</i>		<i>M. flexor cruris medialis</i>	
<i>M. caudofemoralis</i>	<i>Pars caudalis</i> <i>Pars pelvica:</i> <i>Caput craniale</i> with intermediate tendon <i>Caput caudale</i>	<i>M. caudofemoralis</i>	<i>Pars caudalis</i> <i>Pars pelvica:</i> <i>Caput craniale</i> with intermediate tendon <i>Caput caudale</i>
<i>M. ischiofemoralis</i>		<i>M. ischiofemoralis</i>	

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Table continued
Таблица (продолжение)

Gangl et al., 2004		This study / Данная работа	
Muscles / Мускулы	Parts, heads and tendons of insertion / Порции, головки и конечные сухожилия	Muscles / Мускулы	Parts, heads and tendons of insertion / Порции, головки и конечные сухожилия
<i>M. obturatorius lateralis</i>	<i>Pars dorsalis</i> <i>Pars ventralis</i> : two tendons do insertion	<i>M. obturatorius lateralis</i>	<i>Pars dorsalis</i> <i>Pars ventralis</i> : two tendons do insertion
<i>M. obturatorius medialis</i>		<i>M. obturatorius medialis</i>	
<i>M. pubo-ischio-femoralis</i>	<i>Pars lateralis</i> <i>Pars medialis</i> : <i>Caput dorsale</i> <i>Caput ventrale</i>	<i>M. pubo-ischio-femoralis</i>	<i>Pars lateralis</i> <i>Pars medialis</i> : <i>Caput dorsale</i> <i>Caput ventrale</i>
<i>M. tibialis cranialis</i>	<i>Caput femorale</i> <i>Caput tibiale</i>	<i>M. tibialis cranialis</i>	<i>Caput femorale</i> <i>Caput tibiale</i>
<i>M. extensor digitorum longus</i>	<i>Crus laterale</i> : <i>Tendo lateralis</i> <i>Tendo medialis</i> <i>Caput mediale</i> : <i>Pars superficialis</i> <i>Pars profunda</i>	<i>M. extensor digitorum longus</i>	<i>Crus laterale</i> : <i>Tendo lateralis</i> <i>Tendo medialis</i> <i>Caput mediale</i> : <i>Pars superficialis</i> <i>Pars profunda</i>
<i>M. fibularis longus</i>	<i>Tendo cranialis</i> <i>Tendo caudalis</i>	<i>M. fibularis longus</i>	<i>Tendo cranialis</i> <i>Tendo caudalis</i>
<i>M. fibularis brevis</i>		<i>M. fibularis brevis</i>	
<i>M. gastrocnemius</i>	<i>Pars lateralis</i> <i>Pars intermedia</i> <i>Pars medialis</i> <i>Pars supramedialis</i>	<i>M. gastrocnemius</i>	<i>Pars lateralis</i> <i>Pars intermedia</i> <i>Pars medialis</i>
		<i>M. plantaris</i>	
<i>M. popliteus</i>		<i>M. popliteus</i>	
<i>M. flexor perforans et perforatus digiti III</i>	<i>Caput femorale</i> <i>Caput tibiale</i>	<i>M. flexor perforans et perforatus digiti III</i>	<i>Caput femorale</i> <i>Caput tibiale</i>
<i>M. flexor perforatus digiti III</i>	<i>Caput laterale</i> <i>Caput caudale</i>	<i>M. flexor perforatus digiti III</i>	<i>Caput laterale</i> <i>Caput caudale</i>
<i>M. flexor perforatus digiti IV</i>	<i>Caput laterale</i> <i>Caput caudale</i> Tendon of insertion: <i>Crus proximale</i> <i>Crus intermedium</i> <i>Crus distale</i>	<i>M. flexor perforatus digiti IV</i>	<i>Caput laterale</i> <i>Caput caudale</i> Tendon of insertion: <i>Crus proximale</i> <i>Crus intermedium</i> <i>Crus distale</i>
<i>M. flexor hallucis longus</i>		<i>M. flexor hallucis longus</i>	
<i>M. flexor digitorum longus</i>		<i>M. flexor digitorum longus</i>	
<i>M. extensor proprius digiti III</i>		<i>M. extensor proprius digiti III</i>	
<i>M. extensor brevis digiti III</i>		<i>M. extensor brevis digiti III</i>	
<i>M. extensor brevis digiti IV</i>		<i>M. extensor brevis digiti IV</i>	
<i>M. abductor digiti IV</i>		<i>M. abductor digiti IV</i>	
<i>M. lumbricalis</i>		<i>M. lumbricalis</i>	

However, as seen in the table, we discarded two muscles (*M. pectineus* and *M. femorotibialis accessorius*) revealing two others instead (*M. iliotrochantericus medius* and *M. plantaris*). We also made certain changes in muscles' heads and parts list. As a number of previous works contain a substantial morphological description of the hindlimb muscles of the Ostrich (see Introduction), we do not see any reason to provide a new one here (that is why our Results part appears unusually short). Instead, in the Discussion, using the most recent description of Gangl et al. (2004) as a reference, we point out the differences and support them by drawings whenever necessary. Like our predecessors, we have continued to use anatomical names listed in the NAA (Vanden Berge, Zweers, 1993). In case of the structures which are not in the NAA, we used names proposed by the previous authors, favoring either the earliest or more appropriate. Only in a few cases did we propose new names as the most logical and suitable.

Discussion

Despite the fact that the previous study (Gangl et al., 2004) was based on representative anatomical material and extensive literature review, we still found some differences in presence and topography of the hindlimb muscles of the Ostrich. Some of them are only slight and can be interpreted as individual variations; we do not discuss them here. However we could not fail to note several others due to their importance as characters used in cladistic analyses.

The first edition of the NAA (Vanden Berge, 1979) does not contain information on names of the parts of *M. iliotibialis lateralis*. In the second edition (Vanden Berge and Zweers, 1993), however, two subdivisions are recognized, *Pars preacetabularis* and *Pars postacetabularis*, which may be continuous or separated by the gap *Hiatus acetabularis*. In case of the continuity of one head of the muscle into the other, a third, acetabular part of the muscle is usually considered. Gangl et al. (2004) named this part *Pars intermedia*. There already have been several names used for this part of the muscle prior to this work. We do not think that the mentioned part merits being named as a separate muscle, as it has been by early authors: *M. tensor fasciae latae* of Meckel (1830) and Gadow (1880); *M. rectus femoris* and *M. tensor va-*

ginae of Owen (1849) and de Man (1873); *M. gluteus maximus* of Macalister (1865) and Beddard (1896); *M. tensor fasciae* of Garrod (1877); *M. tensor fasciae femoris* of Watson (1883); *M. ilio-tibialis medius* of Gadow (Gadow and Selenka, 1891) and Dement'ev (1940). However, there is an appropriate name for this part, given by Vanden Berge as early as 1975 — *Pars acetabularis*. Since this name has been used in number of subsequent works (e.g.: Swierczewski and Raikow, 1981; Raikow, 1987, Zinoviev, 1999), we do not think it should be changed.

Gangl et al. (2004) described *M. iliofemoralis externus* as having its origin along almost the entire dorsal part of the *Ala preacetabularis ilii* just below those of the *Mm. iliotibiales*. They also found two tendons of insertion of this large muscle belly, which they named *Crus craniale* and *Crus caudale*. If we accept such an expansion of the muscle, it will be unique for birds. However, if we take a closer look at this muscle mass we will see that there are two muscles in fact — *M. iliotrochantericus caudalis* and *M. iliofemoralis externus* in their normal position (fig. 1a). *M. iliotrochantericus caudalis* originate from almost entire length of *Ala preacetabularis ilii* just below *M. iliotibialis lateralis*, caudally to *M. iliotibialis cranialis* and dorsally to *M. iliofemoralis internus*. Its tendon of insertion is nothing else but *Crus craniale* of Gangl et al. (2004), which inserts laterally on the *Trochanter femoris* (fig. 1b). *M. iliofemoralis externus* arises fleshy caudally to the mentioned muscle from the *ilium* just above *acetabulum* and below *M. iliotibialis lateralis pars acetabularis*. It inserts to trochanter femoris distally by the attachment of the terminal tendon of *M. iliotrochantericus caudalis* by the tendon (fig. 1b), which Gangl et al. (2004) named *Crus caudale* of *M. iliofemoralis externus*. Bellies of *M. iliotrochantericus caudalis* and *M. iliofemoralis externus* are fused to a large extent, which is not unusual for birds (Gadow and Selenka, 1891; Hudson, 1937; Wilcox, 1952; Kurochkin, 1968; Klemm, 1969; etc.). This muscle was found in the Ostrich by Gadow (1880) (*M. gluteus anterior*) and Sudilovskaya (1931). Even Gangl et al. (2004) noticed that their *M. iliofemoralis externus* could possibly consist of two partly fused individual muscles.

Gangl et al. (2004) claimed *M. iliotrochantericus medius* was absent in the Ostrich. In fact,

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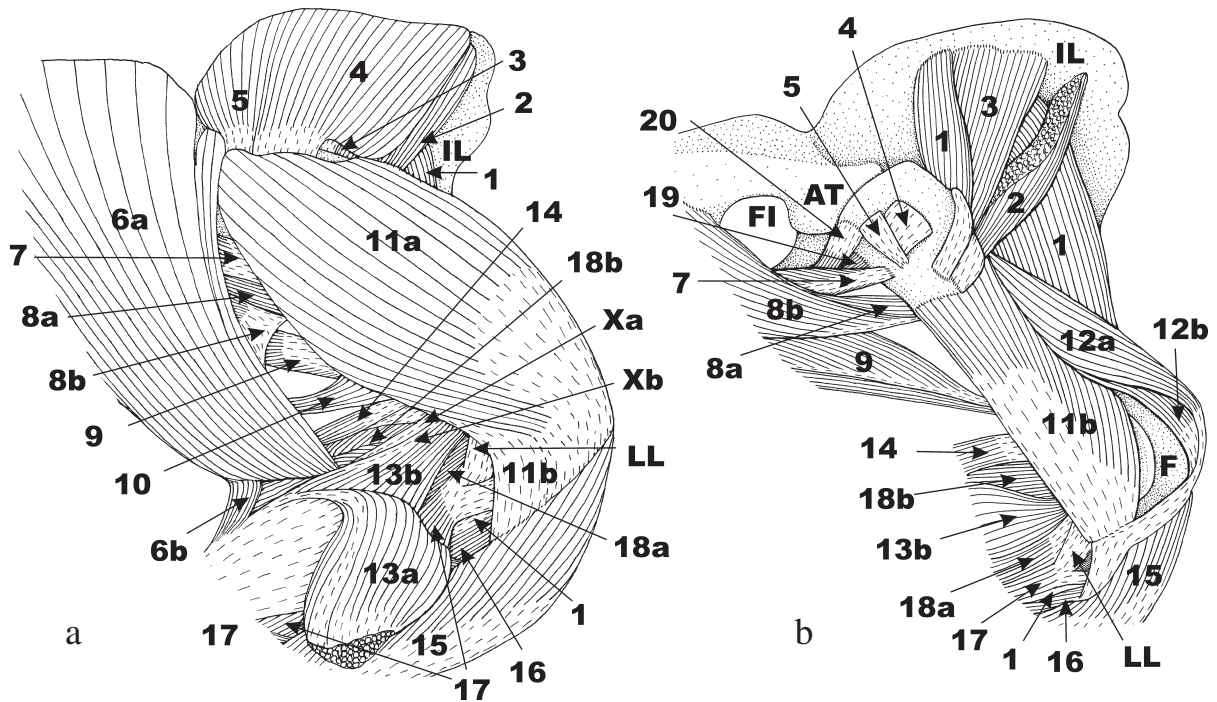


Fig. 1

Some muscles of the pelvis, thigh and shank of the Ostrich. Right hindlimb, lateral view, middle layer (a) and deep layer (b). I — ilium; AT — antitrochanter; FI — fenestra ischiopubica; F — femur, LL — ligamentum collaterale laterale genus; X — ansa m. iliofibularis; Xa — its pars proximalis; Xb — its pars distalis. 1 — m. ambiens; 2 — m. ilioprochantericus cranialis; 3 — m. iliofemoralis internus; 4 — m. ilioprochantericus caudalis; 5 — m. iliofemoralis externus; 6 — m. iliofibularis; 6a — its crus caudale; 7 — m. ischiofemoralis; 8 — m. caudofemoralis; 8a — its pars caudalis; 8b — its pars pelvica; 9 — m. pubo-ischio-femoralis; 10 — m. flexor cruris lateralis pars accessoria; 11 — m. femorotibialis externus; 11a, — its pars proximalis; 11b — its pars distalis; 12 — m. femorotibialis medius; 12a — its pars proximalis; 12b — its pars distalis; 13 — m. gastrocnemius lateralis; 13a — its beginning from the patellar ligament (folded back); 13b — its beginning from pars femoralis distalis ansae m. iliofibularis; 14 — m. gastrocnemius pars intermedia; 15 — m. fibularis longus; 16 — m. tibialis cranialis caput femorale; 17 — m. flexor perforans et perforatus digiti III caput femorale; 18 — m. flexor perforatus digiti IV; 18a — its caput laterale; 18b — its caput caudale; 19 — m. obturatorius lateralis pars ventralis; 20 — m. obturatorius medius.

Рис. 1

Некоторые мускулы таза, бедра и голени африканского страуса. Правая конечность латерально, средний (a) и глубокий (b) слои мышц. I — ilium; AT — antitrochanter; FI — fenestra ischiopubica; F — femur, LL — ligamentum collaterale laterale genus; X — ansa m. iliofibularis; Xa — ee pars proximalis; Xb — ee pars distalis. 1 — m. ambiens; 2 — m. ilioprochantericus cranialis; 3 — m. iliofemoralis internus; 4 — m. ilioprochantericus caudalis; 5 — m. iliofemoralis externus; 6 — m. iliofibularis; 6a — ego crus caudale; 7 — m. ischiofemoralis; 8 — m. caudofemoralis; 8a — ego pars caudalis; 8b — ego pars pelvica; 9 — m. pubo-ischio-femoralis; 10 — m. flexor cruris lateralis pars accessoria; 11 — m. femorotibialis externus; 11a, — ego pars proximalis; 11b — ego pars distalis; 12 — m. femorotibialis medius; 12a — ego pars proximalis; 12b — ego pars distalis; 13 — m. gastrocnemius lateralis; 13a — ego начало на пателлярной сухожилью (отвернуто); 13b — ego начало на pars femoralis distalis ansae m. iliofibularis; 14 — m. gastrocnemius pars intermedia; 15 — m. fibularis longus; 16 — m. tibialis cranialis caput femorale; 17 — m. flexor perforans et perforatus digiti III caput femorale; 18 — m. flexor perforatus digiti IV; 18a — ego caput laterale; 18b — ego caput caudale; 19 — m. obturatorius lateralis pars ventralis; 20 — m. obturatorius medius.

it is present in the Ostrich, being *M. ilioprochantericus caudalis* of the mentioned authors. The place of its insertion fully corresponds to that of *M. ilioprochantericus medius* in other birds. In those which possess this muscle, it inserts proximally to the insertion of *M. ilioprochantericus cranialis* on *Trochanter femoris*, with its terminal tendons often intimately associated with that

of *M. ilioprochantericus cranialis* (fig. 1b). This muscle has been correctly identified by several previous authors. Hans Gadow (1880: *M. iliacus externus medius*) pointed out that this muscle is quite variable in ostriches and can either arise from the *Ala preacetabularis ilii* between places of origin of *M. iliofemoralis internus* and *M. ilioprochantericus caudalis*, as was the case

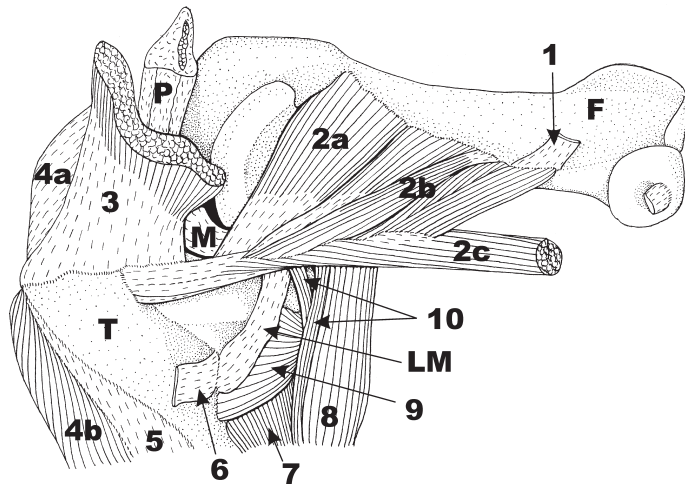


Fig. 2

M. femorotibialis internus and adjacent muscles of the Ostrich. Right hindlimb, medial view. F — femur; T — tibiotalus, P — patella proximalis, imbedded in the tendon of insertion of *M. femorotibialis medius pars distalis*; M — meniscus medialis genus, LM — ligamentum collaterale mediale genus. 1 — tendon of insertion of *m. iliofemorialis internus*; 2 — *m. femorotibialis internus*; 2a — its pars medialis; 2b — its pars lateralis; 2c — its pars pectineus (cut); 3 — *m. iliotibialis cranialis* (cut); 4 — *m. tibialis cranialis*; 4a — its caput femorale; 4b — its caput tibiale; 5 — *m. extensor digitorum longus*; 6 — common tendon of insertion of *mm. flexores crures lateralis et medialis* (folded back); 7 — *m. flexor digitorum longus*, 8 — *m. gastrocnemius pars intermedia*; 9 — *m. popliteus*; 10 — *m. plantaris*.

Рис. 2

M. femorotibialis internus африканского страуса и прилегающие мускулы. Правая конечность медиально. F — femur; T — тибиталус, P — пателла проксималис в конечном сухожилии *M. femorotibialis medius pars distalis*; M — meniscus medialis genus, LM — ligamentum collaterale mediale genus. 1 — конечное сухожилие *m. iliofemorialis internus*; 2 — *m. femorotibialis internus*; 2a — его pars medialis; 2b — его pars lateralis; 2c — его pars pectineus (отрезана); 3 — *m. iliotibialis cranialis* (отрезана); 4 — *m. tibialis cranialis*; 4a — его caput femorale; 4b — его caput tibiale; 5 — *m. extensor digitorum longus*; 6 — общее конечное сухожилие *mm. flexores crures lateralis et medialis* (отогнуто); 7 — *m. flexor digitorum longus*, 8 — *m. gastrocnemius pars intermedia*; 9 — *m. popliteus*; 10 — *m. plantaris*.

in specimens dissected by Haughton (1865: *M. gluteus minimus*), Macalister (1865: *M. gluteus minimus*), Zinoviev (1999) and Gangl et al. (2004), or just caudally to the origin of *M. iliotrochantericus cranialis*, being fused to a varying extent with the belly of the mentioned muscle, as Sudilovskaya (1939) observed.

Gangl et al. (2004) pointed out certain problems with scientific names of *Mm. femorotibiales externus* and *medius* existing in the literature, finally following the picture from Hudson et al. (1969) used in the NAA (Van den Berge and Zweers, 1993: fig. 6.16). There we see a short *M. femorotibialis externus*, which lies distally on the lateral surface of the femur, covered by *M. femorotibialis medius*. However, the description, provided in the NAA is quite different from the drawing. Van den Berge and Zweers, in fact, name the mentioned short muscle as *Pars distalis* of *M. femorotibialis externus*, while the lateral part of the muscle, which covers the previous head defined as *M. femorotibialis externus pars proximalis*. *M. femorotibialis medius*, thus, lies on the cranial surface of the femur and is fused laterally with *M. femorotibialis externus*. This is the traditional definition of these muscles, widely used in literature (Gadow, 1891; George and Berger, 1966; Raikow, 1985;

etc.). Therefore we do not see any reason to follow the works of Hudson et al. (1959; 1969), since in his early work Hudson (1937) himself follows the traditional classification. Thus, the muscle, which Gangl et al. (2004) described as *M. femorotibialis medius* is, in fact, *Pars proximalis* of *M. femorotibialis externus* (fig. 1a), with initial *M. femorotibialis externus* being only *M. femorotibialis externus pars distalis* (fig. 1b). This part is present in many other birds (Owen, 1849; Beddard, 1899; McGowan, 1979; Zinoviev, 1999; etc.) but not as well developed as in the Ostrich, being either confined to the distal ventrolateral surface of the femur or totally fused with *Pars proximalis*. The real *M. femorotibialis medius* thus will be *M. femorotibialis accessorius* of Mellet (1994) and Gangl et al. (2004). According to these authors, it covers the cranial surface of the femur, originating in two heads. First, *Caput craniale* arises distally of the *Trochanter femoris* from the middle part of the cranial femoral shaft. The larger *Caput mediale* originates proximomedially from the previous head, and the proximal patella seems to be embedded in the distal extension of the latter head. Covering the cranial surface of the femur, it has the same subdivision as in many other birds. Such a subdivision is not mentioned

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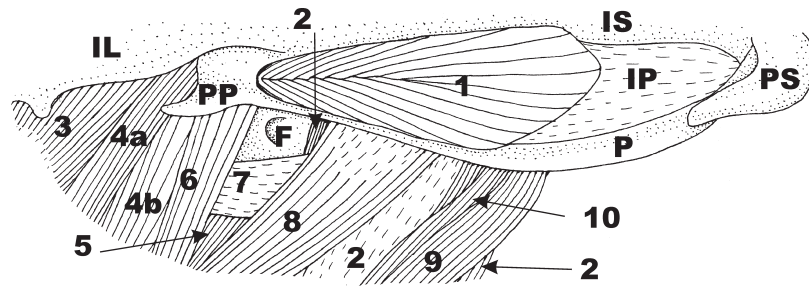


Fig. 3

M. obturatorius medialis and adjacent muscles of the Ostrich. Right limb, superficial layer, medial view. IL — ilium; IS — ischium, P — pubis, PP — processus pectinealis, PS — pubic symphysis, IP — membrana ischiopubica. 1 — *m. obturatorius medialis*; 2 — *m. iliofibularis*; 3 — *m. ambiens*; 4 — *m. femorotibialis medius*; 4a — its pars proximalis; 4b — its pars distalis; 5 — *m. femorotibialis internus pars medialis*; 6 — *m. femorotibialis internus pars pectineus*; 7 — *m. caudofemoralis*; 8 — *m. pubo-ischio-femoralis*; 9 — *m. flexor cruris lateralis*; 10 — *m. flexor cruris medialis*.

Рис. 3

M. obturatorius medialis африканского страуса и прилежащие мускулы. Поверхностный слой, правая конечность, медиально. IL — ilium; IS — ischium, P — pubis, PP — processus pectinealis, PS — pubic symphysis, IP — membrana ischiopubica. 1 — *m. obturatorius medialis*; 2 — *m. iliofibularis*; 3 — *m. ambiens*; 4 — *m. femorotibialis medius*; 4a — ego pars proximalis; 4b — ego pars distalis; 5 — *m. femorotibialis internus pars medialis*; 6 — *m. femorotibialis internus pars pectineus*; 7 — *m. caudofemoralis*; 8 — *m. pubo-ischio-femoralis*; 9 — *m. flexor cruris lateralis*; 10 — *m. flexor cruris medialis*.

in the NAA since the distal part of this muscle is generally minute, poorly separated from the proximal part and easily overlooked by anatomists. However, in the majority of birds which we dissected or reviewed in an extensive literature (Zinoviev, 1999), we found *Pars distalis*, generally represented by a number of muscular fibers, running from craniodistal femur to the proximal surface of patella to insert there fleshy and only slightly contributing to the patellar ligament. This is, as we see, also the case in the Ostrich (fig. 1a, 2), in which, however, the distal part of the muscle simply expands proximally, with its tendon still embedding the part of patella (Weissengruber et al., 2002). For the *M. iliotibialis internus* Gangl et al. (2004) report only two heads — *Caput mediale* and *Caput laterale*, treating the belly, which starts on the pectineal process and adjacent area of pubis, as a separate muscle — *M. pectineus* (in naming such muscle, the authors mention Mellet (1994) as a source; in fact, Haughton (1865) was the first to name this muscular belly *M. pectineus*). We do not see any reason to treat it as a separate muscle. Its close association with *Caput mediale* (fig. 2) allows us to name it as a third part, *Pars pectineus* (traditionally, names Partes rather than Capita are used for subdivisions of *M. femorotibiales*) of *M. femorotibialis internus*, as was already noted by Gadow (1880) and Sudilovskaya (1934).

In the work of Gangl et al. (2004) a tendinous structure to which terminal tendons of *Mm. flexores crures caudalis et medialis* insert is named a quadrifascial tendinous sheet. It is also serves as a place of insertion for *M. cruris lateralis pars accessoria*, while tendon-like *Pars supramedialis m. gastrocnemii* (see below the discussion on this Pars), which runs from the tibiotarsus to the tendon of the *Pars medialis m. gastrocnemii*, forms its ventral part. However, from the descriptions provided by the mentioned authors it is not clear whether this sheet is connected with tibiotarsus or not. If not, as it actually appears from their work, *M. flexores crures* do not have an insertion to the crus. It would have been a unique feature for birds if not for the fact that these muscles in the Ostrich do have a normal insertion on the caudomedial surface of proximal tibiotarsus by the common, although weak tendon (fig. 2). This insertion has been reported by many previous authors (Haughton, 1865; Macalister, 1865; Gadow, 1880; Sudilovskaya, 1931; Zinoviev, 1999).

Authors (Gangl et al., 2004) describe *M. obturatorius medialis* as a muscle which originates primarily on the ventral border of Ischium and the dorsal border and lateral surfaces of the Pubis. In fact, the majority of muscle fibers originate from the lateral surface of the *Membrana ischiopubica* (fig. 3), ending on the aponeurosis, covering almost the whole lateral surface of the

muscle. It is worth mentioning here that most of the belly of *M. obturatorius medialis* has a unique lateral position in the Ostrich, whereas in other birds it is entirely confined to the medial (inner) surface of the pelvis.

Gangl et al. (2004) have also reported an absence of *M. plantaris* in all 12 dissected Ostriches. We cannot agree with them; this muscle, although greatly reduced, is always present in this species. Hans Gadow already pointed out (Gadow, 1880; Gadow and Selenka, 1891) that this muscle in the Ostrich shows several stages of reduction from having a minute belly to being represented by an entire tendinous structure. Gangl et al. (2004) actually found this muscle, but took it for the fourth part of *M. gastrocnemius* — *M. gastrocnemius pars supramedialis*. The tendinous structure which they thus described fully corresponds in position with *M. plantaris* of other birds. In our Ostriches this muscle, which originated tendinously by two heads from the lateral meniscus of the knee and the adjacent caudomedial surface of the tibiotarsus near *Lig. collaterale mediale* genus, had a minute unipennate belly (fig. 2). Its thin terminal tendon fused with that of *M. gastrocnemius pars intermedia* near the middle of the shank, although Sudilovskaya (1931), who also found a minute belly of this muscle, has traced the tendon down to the *Cartilago tibialis*.

Since *M. extensor proprius digiti IV* was found only in Coliiformes, a group with highly specialized manipulative hind limbs (Berman and Raikow, 1982), we do not think it makes sense to mention its absence in the Ostrich on the sole basis that this muscle was listed in the NAA. The fact of the matter is that extensors of foretoes in birds show a high degree of variation (Zinoviev, 2003). If we follow the authors, we also should have mentioned that the Ostrich lacks *M. proprius digiti III accessorius*, reported by Berman (1984) for *Amazona albifrons* and found by Gadow (Gadow and Selenka, 1891) in a number of other parrots, and *M. extensor brevis digiti II*, described for *Numida meleagris* by Hudson et al. (1959).

Thus, our study showed that the hindlimb musculature of the Ostrich is not as unique as it appears from the studies of Mellet (1994) and Gangl et al. (2004). A number of muscles and heads which have been reported as peculiar to the Ostrich, on closer inspection turned out not

to be such, whereas muscles mentioned as absent are indeed present. This shows that one who describes new structures for a given species of birds should be very cautious and use extensive comparative data from the entire class Aves.

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References

- Beddard F.E. 1896. A note upon *Dissoura episcopus* with remarks upon the classification of the Herodiones. — Proc. Zool. Soc. Lond., 231–235.
- Berman S.L. 1984. The hindlimb musculature of the White-fronted Amazon (*Amazona albifrons*, Psittaciformes). — Auk, 101: 74–92.
- Berman S.L., Raikow R.J. 1982. The hindlimb musculature of the mousebirds (Coliiformes). — Auk, 99: 41–57.
- Bezuidenhout A.J. 1999. Anatomy. — The Ostrich. Biology, Production and Health. D.C. Deeming (ed.). Wallingford, Oxon: CABI Publishing: 13–49.
- Cho P., Brown R., Anderson M. 1984. Comparative gross anatomy of Ratites. — Zoo Biol., 3: 133–144.
- Chow H.M., Huang Y.S., Hong W.S. 2000. Anatomization and identification of ostrich hind limb muscles. — Rep. Taiwan Sugar Inst., 169: 31–49.
- Dement'ev G.P. 1940. [Integument, skeleton, musculature, locomotion. — Zoological Manual. Vertebrates. Birds. B.S. Matveev (ed.)]. Moscow-Leningrad: USSR Academic Press, Vol. 6: 19–151 (in Russian). [Демет'ев Г.П. 1940. Покровы, скелет, мускулатура, движение. — Руководство по зоологии. Позвоночные. Птицы. Б.С. Матвеев (ред.). М.-Л.: 19–151].
- Fowler M.E. 1991. Comparative clinical anatomy of ratites. — J. Zoo Wildlife Med., 22: 204–227.
- Gadow H.F. 1880. Zur vergleichenden Anatomie der Muskulatur des Beckens und der Hinteren Gliedmasse der Ratiten. Jena: Gustav Fischer, 56 S.

HIND LIMB MYOLOGY OF THE OSTRICH

- Gadow H.F., Selenka E. 1891. Vögel. I. Anatomischer Teil. — Bronn's Klassen und Ordnungen des Tierreichs. Bd. 6, H.G. Bronn (ed.). Leipzig: CF Winter, 1008 S.
- Gangl D. 2001. Die Muskeln der Hinterextremität des Straußes (*Struthio camelus* LINNÉ 1758). PhD thesis, Veterinärmedizinische Universität, Wien.
- Gangl D.G., Weissengruber E., Egerbacher M., Forstenpointner G. 2004. Anatomical description of the muscles of the pelvic limb of the Ostrich (*Struthio camelus*). — Anat. Histol. Embryol., 33: 100–114.
- Garrod A.H. 1877. Notes on the anatomy of passerine birds. Part II. — Proc. Zool. Soc. Lond., 447–453.
- Garrod A.H., Darwin F. 1872. Notes on an Ostrich lately living in the Society's collection. — Proc. Zool. Soc. Lond., 356–363.
- George J.C., Berger A.J. 1966. Avian myology. New York: Academic Press.
- Haughton S. 1865. Notes on animal mechanics. No. III: On the muscular mechanism of the leg of the Ostrich. — Proc. Roy. Irish Acad., 9: 50–61.
- Hopkins B.A., Constantinescu G.M. 1995. Anatomy of ostriches, emus, and rheas. — The Ratite Encyclopedia: Ostrich, Emu, Rhea. C. Drenowatz (ed.). San Antonio: Ratite Records Inc.: 30–61.
- Hudson G.E. 1937. Studies on the muscles of the pelvic appendage in birds. — Am. Midl. Nat., 18: 1–108.
- Hudson G.E., Lanzilotti P.J., Edwards G.D. 1959. Muscles of the pelvic limb in galliform birds. — Am. Midl. Nat., 61: 1–67.
- Hudson G.E., Hoff K.M., Vanden Berge J.C., Trivette E.C. 1969. A numerical study of the wing and leg muscles of Lari and Alcae. — Ibis, 111: 459–524.
- Jost R. 1993. Über den Strauß (*Struthio camelus*) und seine kommerzielle Nutzung. Diss. Fachber. Vet. Med. Univ., Gießen.
- Klemm R.D. 1969. Comparative myology of the hind limb of procellariiform birds. — South. Illinois Univ. Monogr. Sci., Soc. Sci. Human., Sci. Ser., 2: 1–269.
- Kurochkin E.N. 1968. [Hindlimb morphology and locomotion of swimming and diving birds]. PhD thesis, Paleontological Institution, Moscow, Russia, 256 p. (in Russian). [Курочкин Е.Н. 1968. Локомоция и морфология задних конечностей плавающих и ныряющих птиц. Дисс. ... канд. биол. наук. М., 256 с.].
- Liswaniso D.M. 1996. A morphological and diagnostic imaging study of the distal pelvic limb of the Ostrich (*Struthio camelus*). MSc thesis, University of Glasgow, UK.
- Liswaniso D.M., Purton D., Boyd J.S., Deeming D.C. 1996a. Morphology of the distal region of the pelvic limb of the Ostrich. — Improving our understanding of Ratites in farming environment. D.C. Deeming (ed.). Univ. Manchester: Oxford Print Centre: 9–10.
- Liswaniso D.M., Purton M.D., Boyd J.S., Deeming D.C. 1996b. An ultrasound examination of the distal region of the pelvic limb of the Ostrich. — Improving our understanding of Ratites in farming environment D.C. Deeming (ed.). Univ. Manchester: Oxford Print Centre: 7–9.
- Liswaniso D.M., Purton M.D., Boyd J.S., Deeming D.C. 1997. Topographical anatomy of the distal pelvic limb of the Ostrich (*Struthio camelus*). — Zimbabwe Vet. J., 28: 35.
- Lowe P.R. 1928. Studies and observations bearing on the phylogeny of the Ostrich and its allies. — Proc. Zool. Soc. Lond., 1: 185–247.
- Lowe P.R. 1942. Some additional anatomical factors bearing on the phylogeny of the struthionines. — Proc. Zool. Soc. Lond., 112: 1–20.
- de Man J.C. 1873. Vergelijkende myologische en neurologische Studien over Amphibien en Vogels. Leiden: Acad. Proefschrift., van Doesburgh, 254 S.
- Macalister A. 1865. On the anatomy of the Ostrich (*Struthio camelus*). — Proc. Roy. Irish Acad., 9: 1–24.
- McGowan C. 1979. The hind limb musculature of the Brown Kiwi, *Apteryx australis mantelli*. — J. Morph., 160: 33–73.
- McKittrick M.C. 1991. Phylogenetic analysis of avian hindlimb musculature. — Misc. Publ. Mus. Zool. Univ. Michigan, 179: 1–85.
- Meckel J.F. 1825. System der vergleichenden Anatomie. Vol. 2, 2. Halle: Renger. 638 S.
- Meckel J.F. 1828. System der vergleichenden Anatomie. Vol. 3. Halle: Renger. 670 S.
- Meckel J.F. 1830. Beiträge zur Anatomie des indischen Ka-suars. In: Meckel's Archiv Anat. Phys. Leipzig: 200–217.
- Mellet F.D. 1985. The Ostrich as meat animal — anatomical and muscle characteristics. MSc thesis, University of Stellenbosch, South Africa.
- Mellet F.D. 1994. A note on the musculature of the proximal part of the pelvic limb of the Ostrich (*Struthio camelus*). — J. S. Afr. Vet. Assoc., 65: 5–9.
- Owen R. 1849. On the anatomy of the Southern *Apteryx*, Shaw. Part II. (Myology). — Trans. Zool. Soc. Lond., 3: 277–301.
- Pavaux C., Lignereux Y. 1995. Une dissection myologique de la Jambe et du Pied de l'Australopé (*Struthio camelus*). — Anat. Histol. Embryol., 24: 127–131.
- Raikow R.J. 1985. Locomotor system. — Form and Function in Birds. A.S. King, J. McLelland (eds.). London: Academic Press: 57–147.
- Raikow R.J. 1987. Hindlimb myology and evolution of the Old World Passerine birds (Acanthisittidae, Pittidae, Philepittidae, Eurylaimidae). — Ornith. Mon., Wash. D.C., 41: 1–82.
- Steiner H. 1949. Zur Frage der ehemaligen Flugfähigkeit der Ratiten. — Rev. Suisse Zool., 56: 364–370.
- Sudilovskaya A. 1931. [Comparative anatomical studies of pelvic and hindlimb musculature and innervation of Ratitae (*Struthio*, *Rhea*, *Dromaeus*). Leningrad: USSR Academic Press: 1–84. (in Russian). [Судиловская А. 1931. Сравнительно-анатомическое изучение мускулатуры и иннервации тазовой области и задних конечностей Ratitae (*Struthio*, *Rhea*, *Dromaeus*). Л.: 1–84].
- Swierczewski E.V., Raikow R.J. 1981. Hind limb morphology, phylogeny, and classification of the Piciformes. — Auk, 98: 466–480.
- Vanden Berge J.C. 1975. Aves myology. — Sisson and Grossman's The anatomy of the domestic animals. Getty (ed.). Philadelphia, London, Toronto: W.B. Saunders Co.: 1802–1848.
- Vanden Berge J.C. 1979. Myologia. — Handbook of Avian Anatomy: Nomina Anatomica Avium. J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, J.C. Vanden Berge (eds.). London: Academic Press: 175–219.
- Vanden Berge J.C., Zweers G.A. 1993. Myologia. — Handbook of Avian Anatomy: Nomina Anatomica Avium. J.J. Baumel, A.S. King, J.E. Breazile, H.E. Evans, J.C. Vanden Berge (eds.). Cambridge, MA: Publications of Nuttall Ornithological Club: 189–247.

- Watson M. 1883. Report on the anatomy of Spheniscidae. — Zoology of the Voyage of HMS Challenger, 18: 1–244.
- Weissengruber G.E., Gangl D., Forstenpointner G., Probst A. 2002. Morphological Features of the Patellae in the Ostrich (*Struthio camelus* LINNÉ 1758). — Proc. XXIV Congr. Europ. Assoc. Vet. Anat. Brno, Czech Republic, P. 1–166.
- Weissengruber G.E., Forstenpointner G., Gangl D. 2003. Gut zu Fuß — funktionell-anatomische Aspekte des bipeden Laufens beim Afrikanischen Strauß (*Struthio camelus* Linné, 1758). — Wien. Tierärztl. Mschr., 90: 67–78.
- Wilcox H.H. 1952. The pelvic musculature of the loon, *Gavia immer*. — Am. Midl. Nat., 48: 513–573.
- Zinoviev A.V. 1999. [Avian hind limbs as an organ of bipedal locomotion]. PhD thesis, Moscow State University, Moscow, Russia. 271 p. (in Russian). [Зиновьев А.В. 1999. Задняя конечность птиц как орган двуногой локомоции. — Дисс. ... канд. биол. наук. М., МГУ, 271].
- Zinoviev A.V. 2003. [About terminology of the short extensor muscles of the avian foretoes]. — Ornitologia, 30: 127–131 (in Russian). [Зиновьев А.В. 2003. К вопросу о терминологии коротких разгибателей передних пальцев стопы птиц. — Орнитология, 30: 127–131].

Замечания по миологии задних конечностей африканского страуса

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Резюме

Отпрепарирована мускулатура задних конечностей двух зафиксированных в формалине **африканских страусов** (*Struthio camelus*). И хотя нами отмечено 36 мышц — число, определенное недавними исследованиями (Mellet, 1994; Gangl et al., 2004), серьезные замечания должны быть сделаны по их составу и терминологии. В противоположность данным указанных исследований, *M. iliotrochantericus medius* и *M. plantaris* всегда присутствуют у страуса, хотя брюшко последнего может быть сильно или даже полностью редуцировано, так что его ошибочно принимают за дополнительную головку (*pars supramedialis*) икроножного мускула. Как и у большинства птиц, *M. femorotibialis externus* страуса состоит из двух частей, *proximalis* и *distalis*, которые были описаны предыдущими авторами как новый мускул. *M. femorotibialis accessorius*. *M. femorotibialis internus* состоит у страуса из трех головок — латеральной, медиальной и пектинеальной, а большинство волокон *M. iliotrochantericus medialis* берут начало на латеральной поверхности лобково-седалищной мембраны — черты уникальные для класса Aves. Нет необходимости, на наш взгляд, указывать на отсутствие у страуса *M. extensor proprius digiti IV*, поскольку мускул этот найден только у Coliiformes, где он, вероятно, появился для обслуживания специфической вариодактильной стопы. Таким образом, наши исследования показали, что мускулатура задних конечностей африканского страуса не настолько отлична от таковой других птиц, как это может показаться на основе ряда современных исследований. Это необходимо помнить при использовании миологических признаков, например, для популярного в настоящее время кладистического анализа.