

with fine rootlets and small pieces of dry leaves. The remainder of the nest was coarsely fashioned of small twigs (15%), leaves and leaf pieces (35–40%), and rootlets and fibers (45–50%). The nest was completely covered from above and sides by a curled heliconia leaf and other vegetation, making it almost invisible from any outside view. The adults always entered the nest from behind the large buttresses of the nearby tree.

The two blind, nearly naked young, about two days old on 12 February, weighed 6.0 and 6.3 g respectively. On 15 February one chick disappeared. By 23 February the remaining chick weighed 21.5 g and was largely feathered although it retained considerable body down and the primaries were still one-half sheathed. The juvenile already resembled the adults but with paler gray upperparts and the feathers of the crown and mantle heavily edged rusty buff presenting a scaled appearance. On 24 or 25 February the young fledged and remained with the adults throughout March and early April. On 6 April all three birds foraged in the undergrowth less than 5 m from the nest. This juvenile, last seen on 11 April and still with the adults, was distinguishable by a duller coloration, pale horn-colored legs, and only a trace of the broad silvery eye stripe.

Distraction behavior at the nest site does not seem to be well developed. When a human approached the nest both adults *chek* called, wing-flicked, and fluttered from perch to perch nearby but never far from concealing vegetation.

The present range of the Chestnut-crowned Gnat-eater in Colombia is reduced due to habitat destruction, particularly in the Central Andes. Colombia

is presently making remarkable efforts to preserve interesting and unique habitats through a national park system, and there is promise that this interesting little gnat-eater may be spared from the growing list of disappearing species.

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THE EVOLUTIONARY REAPPEARANCE OF ANCESTRAL MUSCLES AS DEVELOPMENTAL ANOMALIES IN TWO SPECIES OF BIRDS

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In the course of a survey of the hind limb muscles in the order Passeriformes, I have discovered two examples of the apparent reappearance of ancestral muscles occurring as individual anomalies in two species. Although numerous species have been studied (George and Berger 1966, Berger 1969, Gaunt 1969, Raikow unpublished studies), these two muscles have never been found in any passerine bird, and indeed their absence constitutes part of the technical diagnosis of the order Passeriformes. Because these structures are present in a variety of other avian orders but absent in Passeriformes, we may suspect that they were lost somewhere in the history of this order. The occurrence of such a structure as an individual anomaly would then represent the reappearance of an ancestral feature. I will first describe the anomalies, then explain why they may represent ancestral reversions, and finally will speculate on the possible genetic mechanism that could produce them.

DESCRIPTION OF FINDINGS

M. iliofemoralis externus is present in many non-passerine orders, and is designated by the letter "D"

in the leg-muscle formulas that have been used by avian taxonomists. It is absent in the Coraciiformes and Piciformes, which are generally regarded as being close to the ancestry of the Passeriformes. It is called *M. gluteus medius et minimus* by George and Berger (1966: 393) who listed the groups in which it occurs.

In a Common Myna, *Acridotheres tristis* (Sturnidae) from Hawaii, I discovered what appears to be a perfectly distinct and normally developed *M. iliofemoralis externus* in the left hind limb (fig. 1A). The muscle has a fleshy origin 4 mm wide from the iliac crest just caudal to *M. ilirotrochantericus caudalis*. The fibers of the fan-shaped belly converge at the level of the cranial edge of the antitrochanter onto a flat tendon 0.6 mm wide and 4 mm long. The tendon passes distad, superficial to the tendon of *M. obturatorius medialis* and inserts on the femur just proximal to the tendon of *M. ischiofemoralis*. Its origin, insertion, and structure are perfectly normal, and its size and position relative to surrounding muscles are comparable to those in species in which it occurs normally. Unfortunately I was unable to examine the other limb of the specimen because it was incomplete when I obtained it, having been originally collected for other purposes. In six other specimens from the same population, I found no trace of this muscle in either limb (fig. 1B). Thus its presence is clearly an individual anomaly and not a species characteristic.

M. caudiliofemoralis pars iliofemoralis is designated by the letter "B" in muscle formulas. Its occurrence in birds is listed by George and Berger (1966: 407–408), where it is called *M. piriformis pars iliofemoralis*.

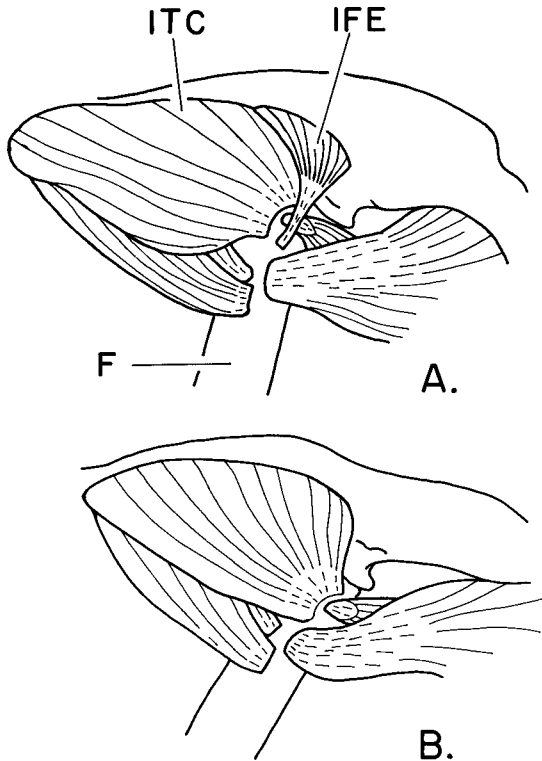


FIGURE 1. Camera lucida drawing of the deep muscles of the hip in two specimens of the Common Myna, *Acridotheres tristis*. a. Abnormal individual showing the presence of *M. iliofemoralis externus* (IFE). b. Normal individual in which this muscle is absent. F, femur; ITC, *M. iliотrochantericus caudalis*.

In a Fox Sparrow, *Passerella iliaca* (Fringillidae) I found this muscle in the left hind limb (fig. 2). It arises by a short, flat aponeurosis from the caudal margin of the pelvis at the region of ilioischial fusion. The aponeurosis is 1.9 mm long and 1.1 mm wide. The belly of the muscle is parallel-fibered and 10.0 mm long. It inserts by a narrow tendon 1.2 mm long onto the caudolateral surface of the femur in common with the dorsal edge of the tendon of insertion of *M. caudiliofemoralis pars caudofemoralis*. By its origin and insertion, this muscle is clearly identified as *M. caudiliofemoralis pars iliofemoralis*, although it is narrower here than in species where it normally occurs. I found no trace of this muscle in the right limb of the same specimen, nor in either limb of two others of the same species. Zusi and Jehl (1970) reported the apparently anomalous occurrence of this muscle in one limb of *Aechmorrhynchus cancellatus* (Scolopacidae), and its absence in the other limb of the same specimen and in both limbs of a second specimen.

I have given names to the anomalous muscles because I consider them to be homologous to the same muscles in taxa where they normally occur. This judgement of homology is based upon the structure, attachments, and relative size and position of the anomalous muscles. Without reference to a theoretical definition of homology, these are the usual operational criteria utilized in comparative myological studies. If these same structures occurred in

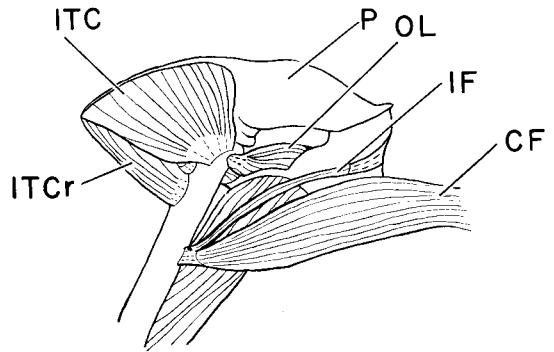


FIGURE 2. Muscles of the hip region in a Fox Sparrow, *Passerella iliaca*, showing the anomalous occurrence of *M. caudiliofemoralis pars iliofemoralis* (IF). CF, *M. caudiliofemoralis pars caudofemoralis*; ITC, *M. iliотrochantericus caudalis*; ITCr, *M. iliотrochantericus cranialis*; OL, *M. obturatorius lateralis*; P, pelvis.

taxa where they are usual, no question of homology would arise.

DISCUSSION

Anomalies are fairly common in vertebrates. Arey (1954: 183–184) listed the following ways by which anomalies may develop: developmental failure, arrest, or excess; fusion or splitting; failure to subdivide; failure to atrophy; failure to consolidate; incorrect migration; misplacement; atypical differentiation; and atavism. Most of these involve deviations from the normal course of development, but atavism is defined as “ancestral recurrences,” and examples in humans are given. Evans (1959) described anomalies in the hyoid muscles of the domestic dog (*Canis familiaris*) and interpreted them as recapitulations of ancestral conditions. Huntington (1903) discussed myological anomalies in primates and considered a major type to be “atavial reversional variations.” These examples show that there are conceptual, comparative anatomical, and developmental bases for a belief that some myological anomalies in vertebrates arise as the reappearance in abnormal individuals of structural features found in ancestral forms.

Insight into the origin of the anomalies described above may be gained by a consideration of how they may have developed in the embryogeny of the abnormal individuals. Romer (1927) described the ontogeny of the thigh muscles in the domestic fowl (*Gallus gallus*), a species in which both *M. iliofemoralis externus* and *M. caudiliofemoralis pars iliofemoralis* occur normally. The muscles arise by the progressive subdivision of an originally homogeneous mass of embryonic mesenchyme. Initially, there is merely a dorsal muscle mass. This divides into a superficial layer and a deep dorsal mass, the latter located around the head of the femur. The deep dorsal mass then further subdivides into the iliотrochantericus muscles and the *M. iliofemoralis externus*. The latter differentiates by splitting away from the *M. iliотrochantericus caudalis*. Its developing muscle fibers grow distally to establish an attachment (insertion) on the femur distinct from those of the iliотrochantericus group. The positions of these muscles are shown in figure 1. It is reasonable to speculate that the evolutionary loss of *M. iliofemoralis*

externus may have resulted from a failure in the developmental mechanism that controls the separation of the anlage of this muscle from the deep dorsal mass of the embryo. An alternative process of loss might be through the gradual size reduction of the muscle in succeeding generations, but then one would not expect an anomalous reappearance of the full-sized muscle. Such a reductional loss might, however, be involved in the case of *M. caudiliofemoralis pars iliofemoralis*, which was of relatively small size in its anomalous form. Romer (1927) described the origin of this muscle (which he termed *M. coccygeo-femoralis brevis*) in terms similar to those described above.

On the basis of the above discussion, I conclude that the occurrence of the anomalies that I have described may be the result of either (1) an atavistic or reversional event, or (2) the production of a neomorph that resembles but is not genetically related to an ancestral structure. The first possibility implies that an ancestral genetic mechanism was retained in the genome in an inactive state since the time that the ancestral muscles were lost. The second suggests that a developmental accident could produce a structure closely mimicking an ancestral condition. Which is more likely?

It is difficult to believe that a developmental accident could produce a structure that so closely resembles an ancestral condition. A new genetic change could conceivably cause a split in the premuscle mass, leading to a new muscle belly resembling another muscle, but only a more complex and integrated mechanism could cause it to establish an insertion exactly like that of a known muscle. For this reason I reject the neomorph hypothesis. This is admittedly a subjective opinion, but particularly in the case of *M. iliofemoralis externus*, the perfection of the anomalous muscle is so exact that I am convinced it must have developed under control of a well-integrated genetic mechanism, and not by an accidental breakup or malpositioning of the developing tissue.

There is no way of knowing just when in passerine history these muscles were first lost, but their absence in all the diverse forms that have been studied suggests that it was at an early stage, and an estimate of at least several million years is reasonable. Apparently during this period of time a genetic mechanism was retained in the genome in an inactive state without undergoing disorganization through the accumulation of mutations or other disruptive events. While this may seem unlikely, there is both direct evidence and a theoretical explanation for such a conservation mechanism.

Kollar (1972) reported experiments in which the oral epithelium of chicks exerted an organizing effect on mouse dental mesenchyme, leading to the deposition of dentin matrix. Kollar suggested (1972: 134) the possibility that "During evolution, the ability to make teeth may have been lost—not the genetic information; perhaps some subtle change in the timing of developmental events may be responsible for toothlessness in birds." H. E. Evans has informed me (pers. comm.) that he has found small upper incisor or canine teeth in the malformed skulls of two cyclopic lambs. Both examples were from range ewes in Idaho and presumed to be due to the ingestion of plant teratogens. No living sheep (*Ovis*: Caprini) has upper incisor or canine teeth.

Little is known about the organization of the genetic basis of the embryogenesis of specific organs

in higher organisms. On the basis of general genetic principles, we may expect that the mechanism probably involves a number of different genes coordinating in a specific temporal sequence. It is furthermore probable that, like most genes, these are pleiotropic in their action. The mechanism controlling the development of a single muscle should not be regarded as existing in isolation, but is most probably a functionally integrated component of a more complex system that has remained functional during the period that the specific mechanism in question has been inactivated. For example, the control of the development of *M. iliofemoralis externus* is part of a system controlling the differentiation of the entire deep dorsal mass. As such, it is subject to the selection pressures acting on the larger system, and might therefore be expected not to undergo disorganization through the accumulation of random disruptive events.

On the basis of the foregoing evidence and discussion, I hypothesize that the occurrence of ancestral muscles as developmental anomalies may be due to the reactivation of a genetic mechanism that was suppressed but conserved in a potentially functional state for millions of years. This mechanism consists of a complex of pleiotropic genes acting in temporal sequence. Its inactivation as far as the suppressed structure is concerned could have resulted from a simple change, perhaps a single gene mutation. Such a modification could also account for the reversional atavisms reported by other workers. It could explain, for instance, why some humans possess a palmaris longus muscle in the forearm while others lack it. In this case the variation is perhaps better regarded as a polymorphism rather than as a simple anomaly. In any event, many structural anomalies have been described in vertebrates, but usually have been vaguely ascribed to developmental errors of various sorts. Consideration of such cases in terms of ancestral-derived character sequences may in the future provide additional examples of suppressed but conserved developmental mechanisms, which may help illuminate the genetic basis of evolutionary change.

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COMMON RAVEN AND STARLING RELIANCE ON SENTINEL COMMON CROWS

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During January, February and March, 1973 we observed interactions of three avian species on 20 days at the Montgomery County sanitary landfill near Blacksburg, Virginia. Sixty-two hours of observation at the landfill were made from the concealment of a blind located on the edge of the landfill trench. On a typical day, Common Crows (*Corvus brachyrhynchos*), the first species to arrive, appeared at the landfill shortly after dawn around 06:30 EST. Common Ravens (*C. corax*) were the next species to arrive, followed later by Starlings (*Sturnus vulgaris*). The number of individuals per species varied from day to day: 35 to 90 crows, 2 to 25 ravens, and 50 to 150+ starlings.

Four to seven sentinel crows always were in position before the appearance of the majority of the flock and before any crows entered or fed in the landfill trench. It was common to see several sentinel crows post themselves in trees near the trench while others stood on high points of the earthen berms on both sides of the trench. The sentinel crows called frequently from their perches, even in the absence of any threat. Common Ravens never entered the trench unless the sentinel crows were in position and the other crows were actively feeding within the trench. These conditions met, ravens would first fly over the trench, land on high ground up from the trench, and after surveying the landfill, fly or walk into it to feed. Neither raven nor starling sentinels were ever observed, though on occasion, a raven gave a low-

pitched, stacatto alarm call while flying over the landfill. Such calling induced all the ravens in the trench to fly out abruptly, but only about half the crows would leave. This sequence also occurred when a raven feeding in the trench gave an alarm call in response to an audible stimulus such as the sound of a diesel engine on a main highway about 350 m away from the landfill. Most often, the three species would flush when sentinel crows intensified their "cawing" in response to their detection of an approaching hazard. All the ravens and most of the crows and starlings flushed in these instances.

Another corvid, perhaps inadvertently, augmented the sentinel system at the landfill. Whenever Blue Jays (*Cyanocitta cristata*) issued alert calls in the woods adjacent to the landfill, all the corvids in the trench promptly became alert, especially the sentinel crows and the ravens. On no occasion did Blue Jay alert calls elicit an immediate flight response by any species in the trench.

After the three species were flushed from the landfill trench, we noticed a definite reinvasion sequence. Starlings were invariably the first species to return, followed by the sentinel crows. With the sentinels in position, other crows began descending into the trench. The ravens waited until crow sentinels were in position and crows were actively foraging before flying to the trench or descending into it. Since starlings entered the trench prior to the arrival of the sentinel crows, they apparently depended less on the corvid warning system, or were less cautious than the ravens.

Behavioral adjustments of ravens and possibly starlings by depending on crow sentinels perhaps enables them to exploit more safely a potentially hazardous food source, and possibly increases overwinter survival of participating individuals for the next breeding season.

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