THE EVOLUTIONARY RE-ESTABLISHMENT OF A LOST ANCESTRAL MUSCLE IN THE BOWERBIRD ASSEMBLAGE

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The loss of anatomical structures during the course of evolution is a common phenomenon, and has elicited much discussion (see Regal 1977 for a review of various theories of causation). Many cases have been reported in which lost ancestral structures have re-appeared as developmental anomalies, but it is less often suggested that such ancestral characters can become re-established as normal components of descendant groups, long after their original loss. Such reversional phenomena have been attributed vaguely to the reversibility of mutations (e.g., Rensch 1959:124), but advances in our understanding of how genes control development offer insight into possible mechanisms for such events. We report herein the apparent re-establishment of a lost ancestral muscle in birds and speculate on the possible genetic basis for it.

M. iliofemoralis externus (IFE), a small, fan-shaped muscle of the hip in many non-passerine birds, arises on the ilium and inserts on the femur. In a group of related Australasian oscines there exists a muscle with the form and position of the IFE, though this muscle has been found absent in other Passeriformes (George and Berger 1966:393; in that work the muscle is named M. gluteus medius et minimus). In the bowerbirds (Ptilonorhynchidae), wattlebirds (Callaeidae), and two species of sickle-billed birds-of-paradise (*Epimachus* spp.; Paradisaeidae) this muscle arises fleshily from the caudal portion of the cranial iliac fossa and the caudal edge of the cranial iliac crest dorsal to the antitrochanter (Fig. 1). It is fused with the caudal edge of M. iliotrochantericus caudalis dorsally, but separates completely from that muscle a few millimeters proximal to the antitrochanter. The fleshy fibers of the IFE pass over the head of the femur and give rise to a short tendon that inserts on the caudolateral surface of the trochanter just proximal to the insertion of M. obturatorius lateralis pars dorsalis and caudal to the insertion of M. iliotrochantericus caudalis. In Loria's Bird-of-paradise (*Loria loriae*) and the New Zealand Thrush (*Turnagra capensis*; Turnagridae), the bellies of the IFE and M. iliotrochantericus caudalis are completely fused over most of their length and are separate only at their insertions (Borecky 1977).

We can offer three possible explanations for the presence of this muscle in the bowerbird group. None of them can be either totally refuted or verified, but we believe that one hypothesis is by far the most likely for the reasons given below. These explanations follow.

(1) *Ancestral retention.* It is possible that the IFE was never lost in the history of the bowerbird group, and that its presence is merely the retention of an ancestral character. This appears unlikely, however, because the muscle is lost in nearly all passerines, at least as far as their myology is currently known, as well as in several other groups of birds generally considered to be closely related to the Passeriformes, namely the Piciformes (Swierczewski 1977), the Coraciiformes and Trogoniformes (Maurer 1977), and the Cuculidae (George and Berger 1966:393). Certainly the most parsimonious explanation for this distribution is that the IFE was lost
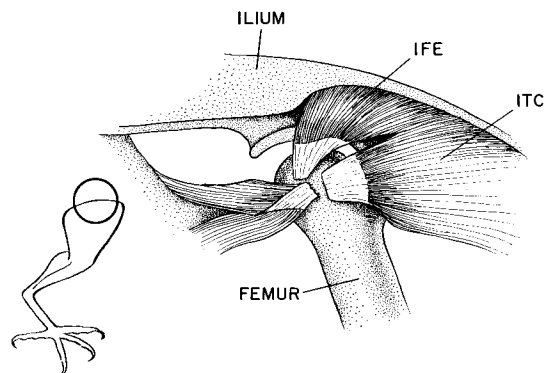

FIGURE 1. Deep muscles of the hip in a bowerbird, *Chlamydera nuchalis,* showing the relationship of M. iliofemoralis externus (IFE) to M. iliotrochantericus caudalis (ITC) characteristic of the bowerbird assemblage. Compare with Figure 3.

in the common ancestor of this passerine and near-passerine assemblage.

(2) *Convergence.* The muscle in the bower-bird group may be a newly evolved structure that mimics but is not homologous to the IFE of other groups. That is, it could be an independently evolved structure whose ontogeny is not controlled by a system of genes derived from that which controlled the development of the true IFE in ancestral forms. We consider this possibility unlikely because of the remarkable similarity in structure, position, and attachments of the muscle in the bowerbird group and in other birds.

(3) *Re-establishment.* We favor the hypothesis that when the muscle was "lost" in the ancestry of the passerines, its loss was limited to its expression in the phenotype; the genetic mechanism controlling its ontogenesis was retained though not expressed. We present four arguments in support of this hypothesis:

(a) *Similarity.* As noted above, the similarity of the muscles in the bowerbird group and various nonpasserines is so great that the control of its development by totally unrelated genetic systems appears very unlikely. If such a great taxonomic gap in its occurrence did not exist, no question of homology would arise.

(b) *Inactivation.* The mechanisms controlling loss and reappearance of structures such as those reported herein and in the literature reviewed below are, ultimately, genetic in nature. We cannot present a specific explanation on this level for such phenomena, because the present understanding of the genetic control of development is still rudimentary. It is possible, however, to speculate briefly within the context of current genetic theory. There is ample evidence that genetic mechanisms can be inactivated during the course of development. Indeed, current models of the genetic control of development in eukaryotes invoke the mechanism of specific temporal patterns of gene activation and deactivation in differentiating cell lineages (see Caplan and Ordahl 1978, and references therein for discussions of various models). The details of such speculative models need not be reviewed here; it is sufficient for the present purpose to highlight the critical idea that functionally related structural genes are controlled by families of regulatory genes, and that much of the morphological change that occurs in the evolution of animals can be ascribed to changes in the
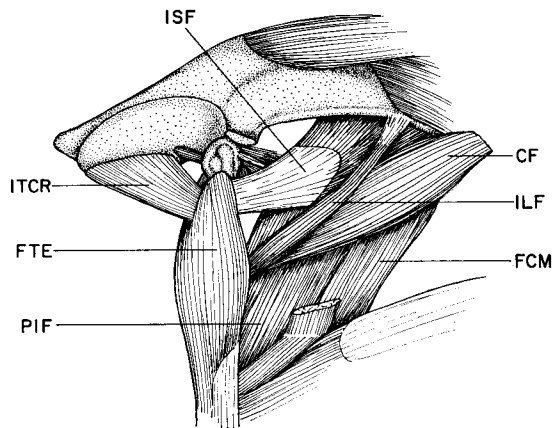

FIGURE 2. Lateral view of deep thigh musculature of a woodswallow, *Artamus leucorhynchus*, showing the anomalous (unilateral) presence of M. iliofemoralis. Abbreviations: CF, M. caudofemoralis; FCM, M. flexor cruris medialis; FTE, M. femorotibialis externus; ILF, M. iliofemoralis (anomaly); ISF, M. ischiofemoralis; ITCR, M. iliotrochantericus cranialis; PIF, M. pubo-ischiofemoralis.

regulatory systems rather than in the structural genes (e.g., Wilson 1976). The existence of developmental anomalies which revert to an ancestral structure supports this concept. Some examples were discussed previously (Raikow 1975), including myological atavisms in mammals, the occurrence of upper incisors or canines in sheep, the retention of capabilities for directing tooth formation in the domestic chicken, and anomalous reappearances of muscles in birds. After that paper was written, we discovered the following additional cases of the anomalous reappearance of ancestral muscles in individual birds and mammals.

M. iliofemoralis (caudiliofemoralis pars iliofemoralis). This thin, strap-shaped muscle was found on the left side of one specimen of a White-breasted Woodswallow (*Artamus leucorhynchus*; Artamidae; Fig. 2). It arose by a thin aponeurosis from the lateral surface of the dorsolateral iliac crest just cranial to the caudal margin of the origin of M. ischiofemoralis. The parallel-fibered belly passed craniodistally to insert tendinously on the caudolateral surface of the femur lateral to the insertion of M. caudofemoralis. The muscle did not occur on the other side of this specimen, or on either side of another specimen of the same species. It is normally absent in passerines. Another anomalous occurrence of this muscle was previously reported in a Fox Sparrow (*Passerella iliaca*; Raikow 1975).
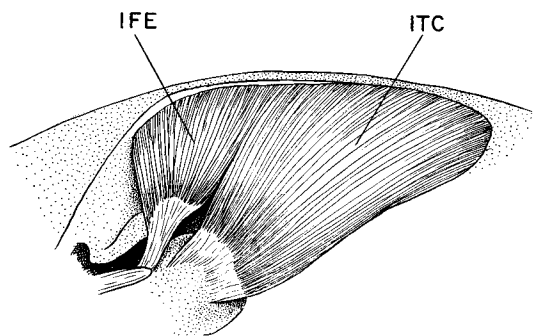
M. iliofemoralis externus. We examined the

FIGURE 3. Muscles of the hip in a specimen of a starling, *Leucopsar rothschildi*. The M. iliofemoralis externus (IFE) is an anomaly, and was absent on the other side of the specimen. ITC, M. iliotrochantericus caudalis. Compare with Figure 1.

FIGURE 4. Muscles of the back in a Yellow-rumped Cacique (*Cacicus cela*) showing the presence of M. latissimus dorsi pars caudalis on the left side and its absence on the right side. The asymmetrical appearance is due to an oblique angle of view. LDC, M. latissimus dorsi pars caudalis; LDCR, M. latissimus dorsi pars cranialis.

limb muscles of 20 genera of Sturnidae (Borecky 1977) and found that the IFE is normally absent in this family. However, in a Rothschild's Myna (*Leucopsar rothschildi*), we found, on one side of the body, an anomalous IFE of the form normally present in the Australasian families described above, i.e., partially fused to the iliotrochantericus caudalis (Fig. 3). An anomalous occurrence of this muscle was previously described in another sturnid, the Common Myna (*Acridotheres tristis*; Raikow 1975).

M. abductor cruris caudalis. In a study of the hind limb of bipedal rodents, this muscle was found unilaterally in one of 18 specimens of the Egyptian Jerboa (*Jaculus jaculus*; Dipodidae) (Berman, unpubl. data). It was also absent in 25 specimens in three genera of other bipedal dipodoids. The origin, insertion, and relationships of the muscle were similar in this specimen to the condition in other rodents. It originated from the deep fascia in the posterior sacral region, just caudal to the fascia of M. gluteus superficialis and deep to the origin of M. femorococcygeus. It first crossed the underside of M. femorococcygeus and then that of M. biceps femoris, to insert on the fascia of the lateral shank just beneath the distal border of M. biceps femoris.

(c) *Bilateral asymmetry.* M. latissimus dorsi pars caudalis is a strap-shaped muscle of the forelimb in birds; it arises from the dorsal midline and inserts on the humerus. We discovered asymmetry in the presence of this muscle in two passerine species (Raikow 1978). Two Palm Tanagers (*Thraupis palmarum*) showed the muscle on both sides, while a third specimen had it on one side only. Similarly, in a Yellow-rumped Cacique
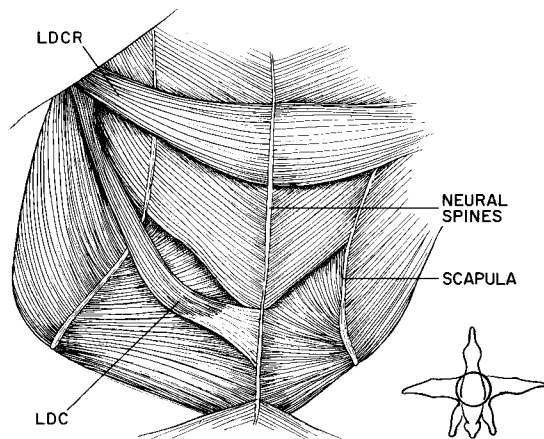
(*Cacicus cela*) the muscle was present bilaterally in one specimen and unilaterally in another (Fig. 4). These observations support the idea that the appearance or nonappearance of a muscle may depend on a relatively easily perturbed developmental event; in terms of current theory this may be attributable to the switching on or off of a regulatory gene.

(d) *Anomalies in sturnids.* We noted above two occurrences of the anomalous presence of the IFE in different genera of the family Sturnidae. This suggests that the developmental information for the growth of this muscle is present in an inactive state in this family, occasionally being expressed in anomalous individuals. In a study of the phylogenetic relationships of the "corvid assemblage," Borecky (1977) concluded that the Ptilonorhynchidae, Paradisaeidae, Callaeidae, and probably the Turnagridae together form a radiation whose sister group is the Sturnidae. That is, these families share their most recent common ancestry with the Sturnidae, which family is the primitive sister group of the rest of the assemblage. On this basis, it is reasonable to speculate that passerines possess unexpressed genetic information for the development of the IFE, and that this is sometimes reactivated anomalously in individual sturnids. This characteristic was perhaps also present in the common ancestry of the Sturnidae and the bowerbird assemblage. After separation from its common ancestor with the Sturnidae, the lineage leading to the bowerbird group could have

reactivated the mechanism in question so that the IFE was once again expressed in the phenotype.

The idea that an organized system of developmental genetic information may be retained in the genome without being expressed phenotypically has been suggested by other studies. Kurtén (1963) reported the evolutionary reappearance of teeth and tooth structures in cats; he attributed this to the progressive reactivation of a growth field controlling tooth development. A more specific example of developmental control was given by Jannett (1975) who discussed "hip glands" in voles (*Microtus*). These are patches of skin glands that develop under the stimulus of male sex hormones in some species, but are absent in others. However, in the latter, their appearance may be induced experimentally by the administration of hormones in excess of normal physiological levels. Jannett suggested that these findings indicate that the ancestors of the species without hip glands possessed them, and that the experiment "illustrates how structures are evolutionarily either gained or lost in steps." If the assumption that these species evolved from forms possessing hip glands is correct, then the loss of these structures appears to be the result of a modification of the reactivity of the presumptive glandular tissue to the normal hormone level of the species. In any event, the response to increased hormones demonstrates the presence of genetic information for the development of structures not normally expressed in the phenotype.

If, as we suggest, the phenotypic expression of certain genetic information can be interrupted for significant periods of time, then one may ask whether a structure in its second appearance should be considered homologous to the structure in its earlier manifestation. This appears to be largely a matter of definition. So many meanings have been given to homology that it is necessary to specify what is intended in any discussion. The most widely accepted idea of homology today is that it is based on descent from a corresponding condition in a common ancestor. This implies continuity of developmental genetic control. If this definition of homology is accepted, it would appear that re-established characters should be considered homologous, in a special sense, to their corresponding ancestral features.

We have shown that there is reason to believe that the loss of a structure in the phenotype does not necessarily mean that the genetic information controlling its development has also been eliminated from the genome. This hypothesis is based on the existence of reversional anomalies and the asymmetry of structures. It is consistent with current ideas of developmental genetics, especially in relation to the possible temporary inactivation of regulatory genes. If the premise is accepted, then the concept of subsequent reactivation of genetic mechanisms, resulting in the re-establishment of "lost" structures such as the IFE in the bowerbird assemblage, is a reasonable hypothesis.

ACKNOWLEDGMENTS

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