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Hind Wings in Basal Birds and the Evolution of Leg Feathers

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Recent discoveries of large leg feathers in some theropods have implications for our understanding of the evolution of integumentary features on the avialan leg, and particularly of their relevance for the origin of avialan flight. Here we report 11 basal avialan specimens that will greatly improve our knowledge of leg integumentary features among early birds. In particular, they provide solid evidence for the existence of enlarged leg feathers on a variety of basal birds, suggest that extensively scaled feet might have appeared secondarily at an early stage in ornithomorph evolution, and demonstrate a distal-to-proximal reduction pattern for leg feathers in avialan evolution.

A bizarre hind wing formed by large pennaceous feathers (feathers with stiff vanes) along the metatarsus is known in several non-avian dinosaurs (1–4) and may have played an important role in the evolution of flight on the line to birds (1–7). However, no examples of this unusual structure have so far been reported in basal birds, although *Archaeopteryx* and one enantiornithine specimen have been reported to have large pennaceous feathers along the tibiotarsus (8, 9), and the relevance of large leg feathers to the early evolution of flight has been questioned on this basis (10, 11). Here we describe 11 specimens of different avialan taxa that preserve exceptional integumentary structures associated with the hindlimb (Figs. 1 to 3 and figs. S1 to S8) (12). These specimens demonstrate the presence of hind wings in basal birds. All 11 specimens are from the Lower Cretaceous Jehol Group (13) and are housed in the Shandong Tianyu Museum of Nature (STM).

Among these specimens, STM16-18 and STM16-19 (Fig. 1) are referable to the basal avialan *Sapeornis*, because the elements preserved in these individuals are nearly identical in morphology to those of previously described specimens of this genus (12, 14). STM16-18 is a nearly complete articulated skeleton lacking the pectoral girdle and forelimbs. STM16-19 is a partial skeleton preserving only the pygostyle, the two pubes, and the left hindlimb.

In STM16-18, a series of parallel pennaceous feathers is preserved along the distal half of the tibiotarsus and nearly the whole length of the metatarsus in each hindlimb (Fig. 1, A to C). The longest ones exceed 50 mm in length and appear to be located close to the distal end of the tibio-

tarsus, whereas the metatarsal feathers are shorter but still measure more than 30 mm. The lengths of the tibiotarsus and metatarsus themselves are 65 and 33 mm, respectively. Leg feathers of similar morphology can also be recognized on both the tibiotarsus and the metatarsus of STM16-19 (Fig. 1D). The pennaceous feathers attached to the hindlimbs of these two specimens have rachises that are significantly curved and appear to have symmetrical vanes. The feathers are nearly perpendicular to the tibiotarsus and metatarsus in orientation

and form a planar surface as in some basal deinonychosaurs with large leg feathers (1–4).

The leg integument is poorly known in confuciosornithids (15, 16), but five confuciosornithid specimens housed in the STM (STM13-32, STM13-44, STM13-55, STM13-57, and STM13-331) contribute significant new information (Fig. 2A and figs. S1 to S5) (12). In these specimens, large pennaceous feathers occur along nearly the whole length of the tibiotarsus and are individually more than half as long as this bone (Fig. 2B). Most interestingly, some feathers occur on the proximal half of the left metatarsus in STM13-32, though these feathers are insufficiently well preserved for it to be possible to determine whether they are pennaceous.

STM7-50, STM7-161, and STM7-215 (Fig. 2C and figs. S6 to S8) are referable to the Enantiornithes and probably belong to two different taxa (12). Regularly arranged large feathers are preserved along the whole length of the tibiotarsus in each of these specimens (Fig. 2D). The feathers measure more than half of the tibiotarsal length, have curved rachises, and are nearly perpendicular to the tibiotarsus. These specimens provide further support for the existence of a reduced hind wing in enantiornithines (8). As in most bird specimens from Liaoning, no integumentary structures are preserved in association with the feet.

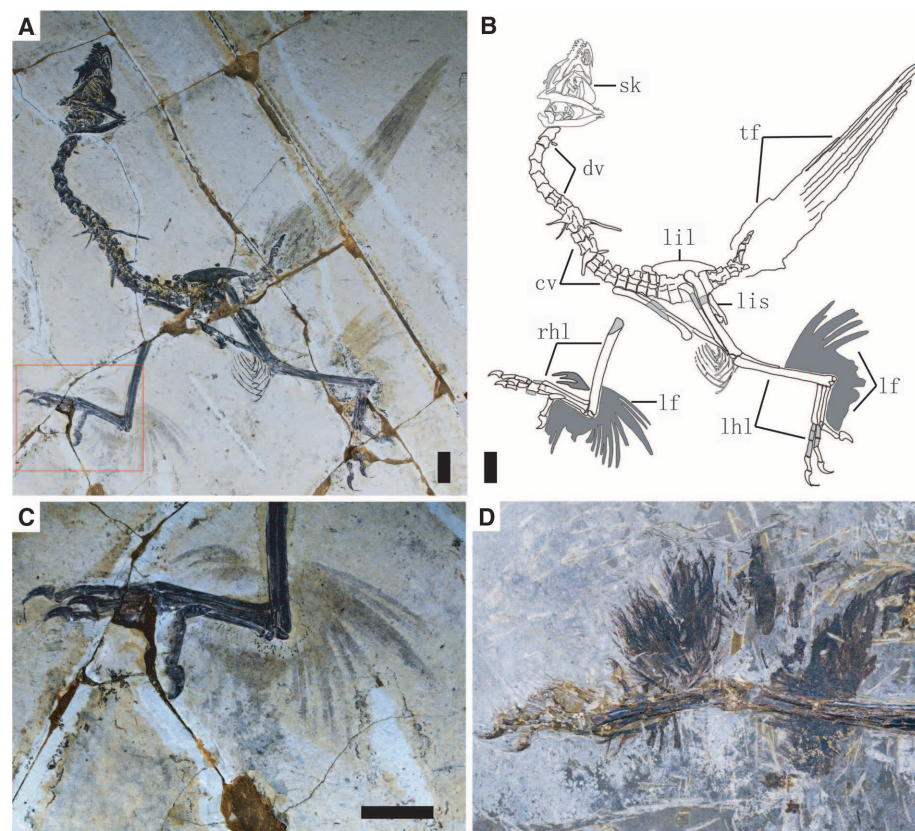


Fig. 1. Leg feathers in the basal avialan *Sapeornis*. Photograph (A) and drawing (B) of STM16-18; and close-up photographs of leg feathers of STM16-18 (C) and STM16-19 (D). Abbreviations: cv, cervical vertebrae; dv, dorsal vertebrae; lf, leg feathers; lhl, left hindlimb; lil, left ilium; lis, left ischium; rhl, right hindlimb; sk, skull; tf, tail feathers.

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STM9-5 (Fig. 3A), referable to *Yanornis* (12, 17, 18), is the first known basal ornithuromorph specimen in which both feathers and scales are well preserved on the legs. The femoral and crural feathers are short and plumulaceous (soft and downy), and the latter appear not to extend to the distal end of the tibiotarsus (Fig. 3, B and C). This is in stark contrast to the condition in other basal paravians, including basal deinonychosaurs (4), the basal avialan *Epidexipteryx*, *Sapeornis*, confuciusornithids, and enantiornithines (8, 19). In these taxa, the femoral and crural feathers are large, and in most cases they are pennaceous feathers that have curved rachises and extend nearly perpendicular to the limbs to form a planar surface.

However, STM9-5 differs from known specimens of the aforementioned taxa in having large scales that cover the anterior surfaces of the digits, including the fused metatarsals (Fig. 3, D and E). There appears to be a single row of large rectangular plates on the metatarsus, with a similar row extending along the phalangeal series of each of the three main digits. Each row of large plates is flanked by smaller scales. Tubercular skin, possibly representing interdigital telae (webs), is preserved between the pedal digits. However, this skin appears to be variable in extent: The putative web between digits III and IV extends close to the distal end of ungual III, whereas the one between digits II and III appears to extend only to the midpoint of digit III. The presence of webbing in this taxon will require confirmation on the basis of a better-preserved specimen.

The specimens described here collectively provide important new information about avialan hindlimb integumentary features, particularly in that they confirm the presence of a four-winged condition in basal birds. Large metatarsal feathers were first discovered in the basal dromaeosaurids *Microraptor* and *Sinornithosaurus* (1, 20–22), were subsequently reported in the enigmatic *Pedopenna* and the basal deinonychosaurs *Anchiornis* and *Xiaotingia* (2–4, 23), and can now also be definitively said to occur in the basal avialan *Sapeornis*. The morphology of the metatarsal feathers shows considerable variation among taxa known to possess these structures. In *Microraptor*, the metatarsal feathers are proportionally large with highly asymmetrical vanes (1), whereas in *Pedopenna*, *Anchiornis*, and *Sapeornis* they are proportionally smaller and have nearly symmetrical vanes (2, 3). In all cases, however, the metatarsal feathers are similar in general arrangement (nearly perpendicular to the metatarsus, forming a large flat surface) and in having stiff vanes and curved rachises. These features suggest that the metatarsal feathers were aerodynamic in function (12), providing lift, creating drag, and/or enhancing maneuverability, and thus played a role in flight (1–7, 24, 25). The presence of metatarsal feathers with a probable aerodynamic function in both deinonychosaurs and avialans strongly supports the interpretation that leg feathers were an important factor in the origin of avialan flight,

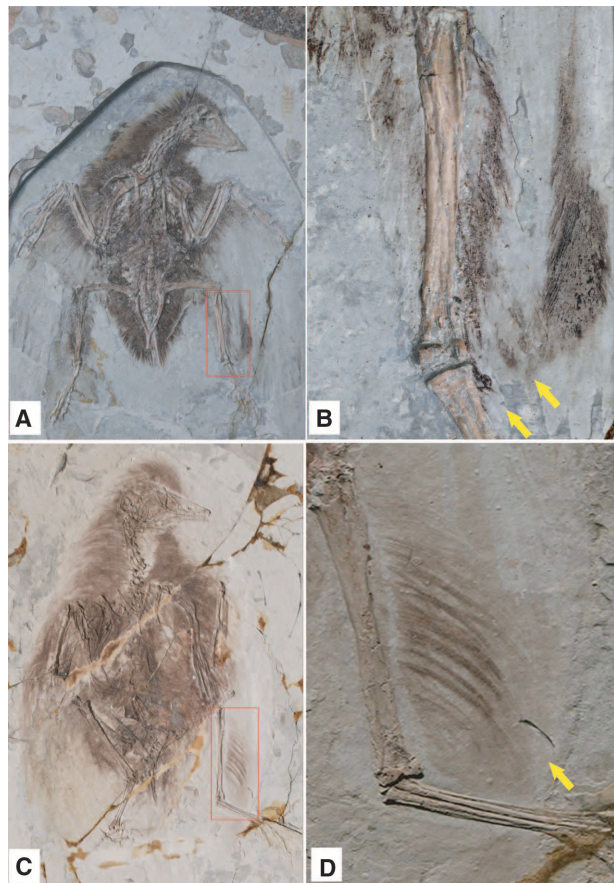
although the nature of their biomechanical contribution to flight ability in taxa that possessed them is debated (1–7, 24–26). It should be noted that preservational limitations make it difficult to reconstruct the precise location and orientation of the leg feathers in these basal paravians, including basal birds. Some limited evidence suggests that the large leg feathers of these taxa attach to the anterolateral margins of the hindlimb bones and are laterally directed (Fig. 4), but other possibilities exist (12).

Metatarsal feathers are also known in several other coelurosaurian dinosaurs, although in these cases they take the form of short filaments rather than large pennaceous feathers (27, 28). Short filamentous feathers have been reported to cover the metatarsus of the compsognathid *Sinocalliopteryx* (27), and similar feathers are also seen near the metatarsus of one specimen of the tyrannosauroid *Yutyranus* (28). Metatarsal feathers are unknown in some other coelurosaurians that clearly bear femoral and crural feathers (8, 19), such as the therizinosauroid *Beipiaosaurus* (29), the oviraptorosaurians *Protarchaeopteryx* (30) and *Caudipteryx*, and enantiornithines. However, extensively scaled feet are unknown in any non-ornithuromorph coelurosaurian specimen, including the aforementioned taxa. Therefore, the lack in these taxa of known pedal feathers, including metatarsal ones, may be best regarded as a case of absence of evidence (perhaps resulting from the

vagaries of preservation) rather than evidence of absence. The point is underscored by the fact that the preservation of integumentary structures is typically inconsistent even within a given taxon. For example, of 273 confuciusornithid and 1065 enantiornithine specimens in the STM that preserve feathers on some part of the body, only 8 of the former and 143 of the latter preserve feathers on one or both hindlimbs. Consequently, the discovery of STM9-5, in combination with data from other recently reported coelurosaurian fossils (27, 28), implies that feathered feet might be primitive for the Coelurosauria, and extensively scaled feet might have appeared secondarily at an early stage of ornithuromorph evolution.

In almost all cases, the leg feathers of modern birds are less well developed than the arm feathers, and the difference is especially clear on the distal limb segments. The leg feathers of extant birds are generally small and fluffy, as in the basal ornithuromorph *Yanornis* (STM9-5), but differ considerably from the relatively large sheet-forming feathers seen in basal paravians, including such basal birds as sapeornithids, confuciusornithids, and enantiornithines (1–7, 24). Large contour feathers are present on the crural segment in some birds, especially predatory ones (31), but they are bunched and extend distally to lie at a low angle to the skin of the lower leg. A featherless pes is characteristic of most extant

Fig. 2. Leg feathers in the basal avialan *Confuciusornis* and the enantiornithine *Cathayornis*. (A) *Confuciusornis*, STM13-32. (B) Close-up of leg feathers of STM13-32. (C) *Cathayornis*, STM7-50. (D) Close-up of leg feathers of STM7-50. Yellow arrows indicate the distalmost preserved points on individual leg feathers.



birds, although some species (such as the golden eagle) have extensively developed fluffy pedal feathers (31). The probable function of leg feathers, including pedal feathers, in extant birds is to protect and/or insulate the leg (31, 32).

We incorporated information from the new specimens described in this paper into an analysis (12) that aimed to reconstruct the ancestral states of two key pedal integumentary characters for the major nodes across coelurosaurian phylogeny. The analysis was performed using Mesquite, a software package that offers a variety of functions for ancestral state reconstruction and other phylogeny-based analyses (33). Although the results are admittedly tentative because of the paucity of data available from the poorly known integuments of early birds and other extinct coelurosaurians, the analysis does suggest an interesting evolutionary pattern (Fig. 4). Short pedal filamentous feathers appeared early in the evolution of coelurosaurian dinosaurs (27), and the presence of extensively feathered feet is likely to be a diagnostic feature for Coelurosauria or a slightly more exclusive clade. Large femoral, crural, and pedal feathers are primitively present in the

Paraves. Large pedal feathers were lost early in avialan evolution, but large femoral and crural feathers persisted in derived non-ornithuromorph avialans and formed a reduced hind wing. Early in ornithuromorph evolution, extensively scaled feet appeared, and femoral and crural feathers became much smaller. The pedal scales of ornithuromorphs represent either a reversal to the pre-coelurosaurian primitive condition or novel structures that are not fully homologous to typical reptilian scales.

The evolution of leg feathers parallels that of arm feathers in basal paravians, which is not surprising given that forelimbs and hindlimbs share fundamental similarities both developmentally and morphologically (34). However, leg feathers were gradually reduced in a distal-to-proximal direction in avialan evolution, with eventual loss of the distal feathers and appearance of pedal scales in ornithuromorphs. The interpretation that the pedal scales of ornithuromorph birds are a secondarily derived feature is consistent with the fact that scale formation in extant birds requires inhibition of feather formation that would otherwise occur, and with developmental

evidence from the feathered feet of the scaleless (High-line) and Silkie strains of chicken (35). In the ontogenetic development of a modern bird, feathered feet can be changed into scaled feet or vice versa by changing the expression pattern of either one gene or a set of genes (36–38). A similar genetic change might have occurred early in avialan evolution.

Changes in the extent and morphology of the leg feathers were probably linked to the evolution of paravian locomotion in that the distribution and structure of leg feathers would have affected the aerodynamic properties of the limb (1, 4). Although early bird flight might initially have involved four wings, as strongly indicated by the basal avialan specimens STM16-18 and STM16-19, the locomotor system of ornithuromorph birds is characterized by a combination of flight using feathered arms and bipedal terrestrial locomotion using the legs. The reduction and loss of distal feathers on the legs reflect decoupling of the forelimbs from the hindlimbs in the locomotor system of ornithuromorph birds, in which the arms became specialized for flight and the legs for terrestrial locomotion (39).

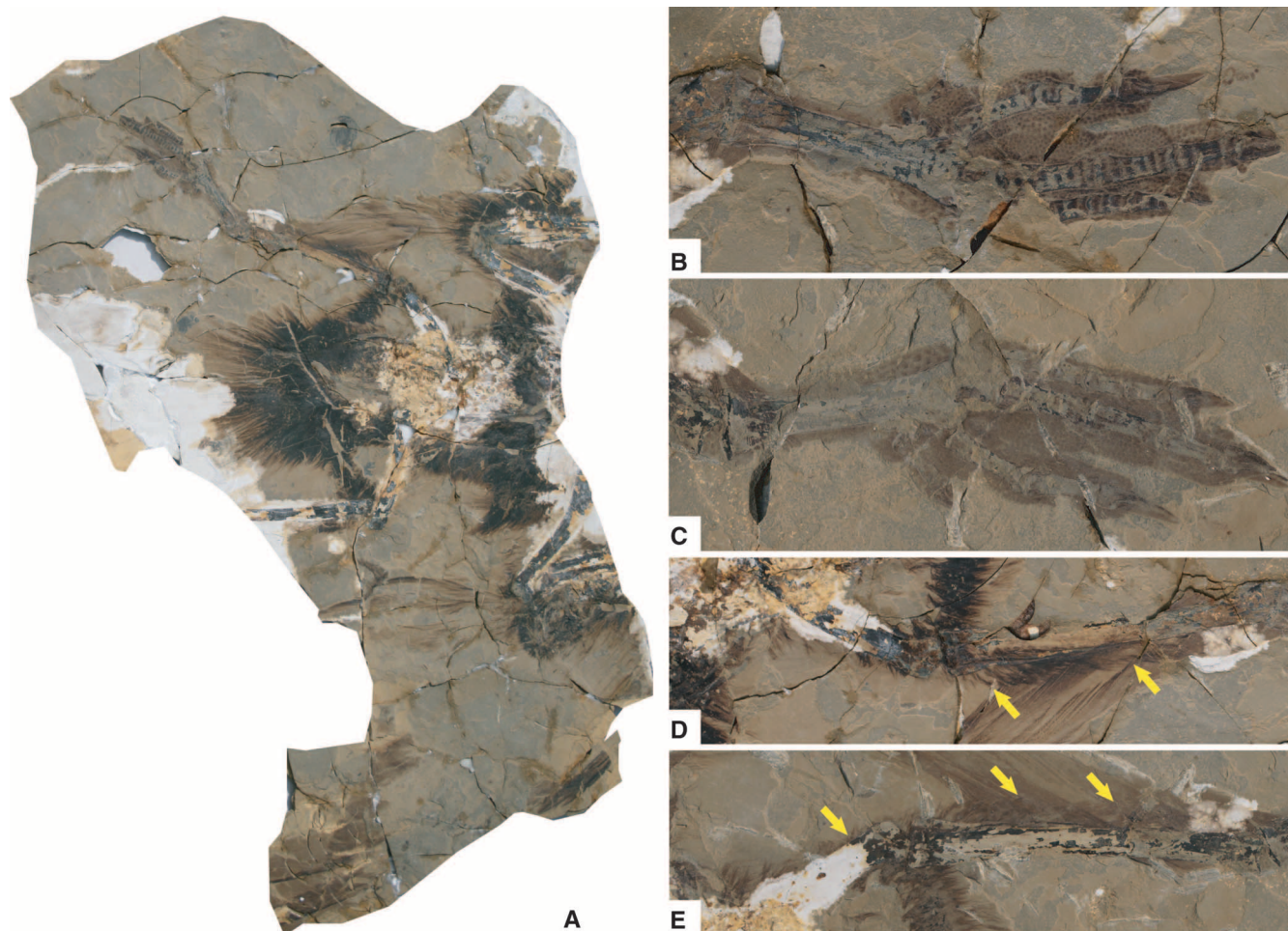
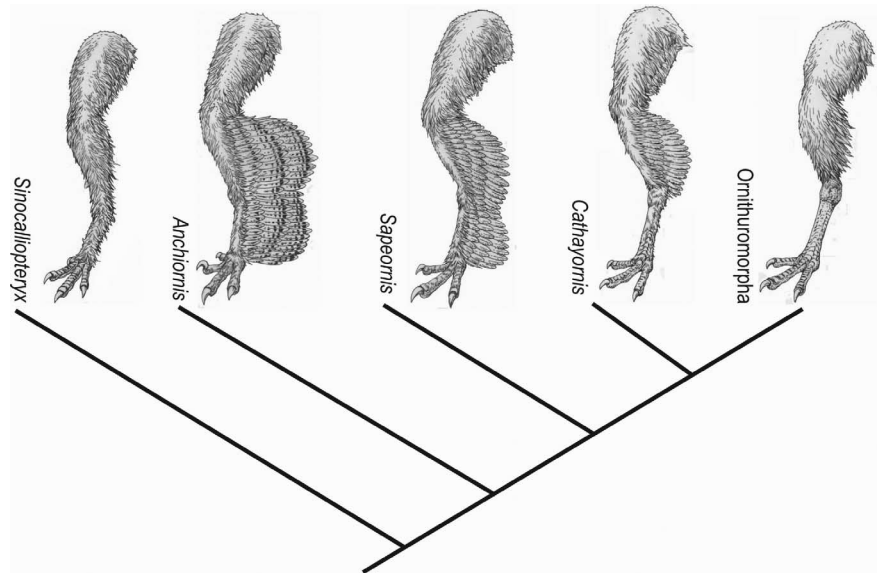


Fig. 3. Integumentary features of the hindlimb in the basal ornithuromorph *Yanornis*. (A) Photograph of STM9-5. Pedal integument of STM9-5 as seen in the slab (B) and counter slab (C). Femoral and crural feathers of STM9-5 as seen in the slab (D) and counter slab (E). Yellow arrows indicate the distalmost preserved points on individual leg feathers.

Fig. 4. Evolution of leg feathers in coelurosaurian dinosaurs. Four major stages in the evolution of integumentary structures on the hindlimb are represented by the compsognathid *Sinocalliopteryx* (short filamentous feathers covering legs, including feet); the basal deinonychosaurian *Anchiornis* and the basal avialan *Sapeornis* (large pennaceous feathers on legs, including feet, forming a winglike structure); the enantiornithine *Cathayornis* (large femoral and crural feathers forming a reduced winglike structure); and ornithuromorphs (small femoral and crural feathers and featherless feet).



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Supplementary Materials

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Supplementary Text
Figs. S1 to S10
Tables S1 to S3
References (40–60)

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Adaptive Evolution of Multiple Traits Through Multiple Mutations at a Single Gene

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The identification of precise mutations is required for a complete understanding of the underlying molecular and evolutionary mechanisms driving adaptive phenotypic change. Using plasticine models in the field, we show that the light coat color of deer mice that recently colonized the light-colored soil of the Nebraska Sand Hills provides a strong selective advantage against visually hunting predators. Color variation in an admixed population suggests that this light Sand Hills phenotype is composed of multiple traits. We identified distinct regions within the *Agouti* locus associated with each color trait and found that only haplotypes associated with light trait values have evidence of selection. Thus, local adaptation is the result of independent selection on many mutations within a single locus, each with a specific effect on an adaptive phenotype, thereby minimizing pleiotropic consequences.

Darwin believed that adaptation occurred through “slight successive variations” (1). Fisher later elaborated on this idea by proposing the geometric model of adaptation (2), which assumes that most mutations are pleiotropic and therefore that mutations of small phenotypic effect are more likely than those of large effect to bring a population closer to its fitness optimum. To test

Fisher’s model, we must identify individual mutations and assess both their phenotypic effects and their degree of pleiotropy. Although recent years have seen considerable progress in identifying loci or genes underlying adaptive phenotypes [reviewed in (3, 4)], few have genetically dissected these loci to the level of individual mutations [but see (5–8)], and none have examined multiple traits at this level