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Diagrams from the study

LEGS WITH UPDATE WINGS


Hind wings...

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Imagine your'd never seen the whole variety of chicken breeds and you only know the iconic picture of a chicken as you can find everywhere, like on food products, during Easter etc. Imagine you see a Cochin or Brahma for the first time in your life, and you see no legs under the chicken. What you see is hind wings instead of legs! Can you imagine how strange this is?

Fossils have been found from dinosaurs (2003) on which you can see prints of feathers in the stone. Before the dead animal fossilised, the sediment was shaped after its contours and therefore we know that certain dinos had feathers. These microraptors had just like Brahma also feathers on the legs. The evolution of the leg and arm feathers looks very much the same and over time the leg feathers disappeared and were replaced by scales depending on the environment of the animal

change from feathered to scaled legs is caused by genes r chickens and it is likely this happened the same way in toric times. (2)

So, ahmas and Cochins are theropod (two legged) microraptors. Yes? No? Yes.

Why are there hard feathers, some as stiff as wing- and tail feathers on legs? This question has been answered a lot of times, depending on the latest insights in evolution of the birds,

Brahma leg feathers Pti-2... and vulture hocks.

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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First this. In this article, only the things are selected of interest to us. It is a summary of outcomes and conclusions of the study and not written in narrative form, therefore it comes across as somewhat chunky.

Remember that crest is actually saddle feathers moved to the top of the head?
It is a kind of feather-relocation.
Feathered legs are wing feathers that have moved to the legs and this has been proven to be true.
Chickens are strange.
No, they are amazing...

Brachydactyly, or short outer toe is a pleiotropic or by-effect of Pti-1 Langshan. It is not a separate gene.

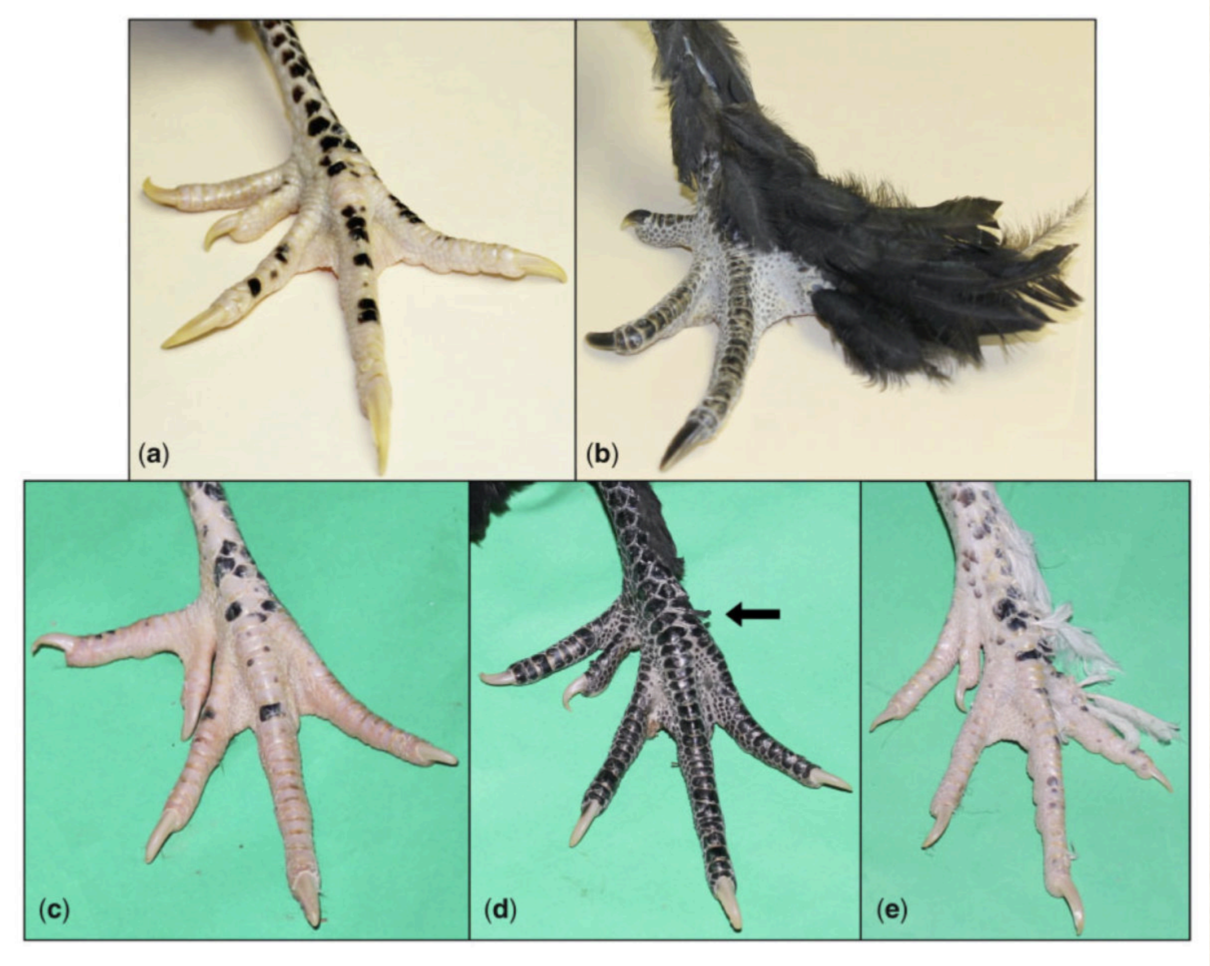
Leg feathers consist of two factors
TBX5 is an arm, so wing specific mutation, located on the forelimb gene on chromosome 15. PITX1 is a mutation on the hindlimb gene on chromosome 13. So much for the simple description.

The action is as follows: the TBX5 wing mutation is activated and at the same time the PITX1 hind limb mutation is suppressed in expression. What actually happens is that the identity shifts from the front limbs to the hind in terms of appearance. So they are literally wing legs.

Initially, the ancestors of chickens had scales, so clean legs. Mutations also created feathered legs (ptilopody). Legs without leg feathers are a derivative of feathered legs of the '4-winged' dinos, as previously described in my article 'Hind Wings' you find it on my website in the E-zine (Articles).

Short history
It was Somes who came up with two independent dominant mutations that cause leg feathers, as you know they are Pti-1 and Pti-2.
Pti-1 is also called Langshan leg feathers, these chickens are homozygous for Pti-1 and homozygous wildtype for pti-2+/pti-2+ or not present Pti-2.
Brahma is homozygous for Pti-1 and Pti-2.
Pavlovskaya has pti-3 a recessive leg feather gene according to Somes in 1990.
Dorshorst found Pti-1 and Pti-2 in Silkies in 2010 and later Sun et al found ditto mutations on the above two chromosomes in Beijing You chickens in 2015.

(The simple overview and implications can be found in Genetics of Chicken Extremes, editions in Dutch, English, Italian.)



This new study on leg feathers
This recent 2020 study is about what exactly happens. A three-generation population was established by crossing Langshan (Pti-1) with Houdan (wild-type [+] no leg feathers). The aim was to find casual mutations that cause leg feathers.

The set-up was as follows: Following Houdan (no leg feathers +, +) x Langshan (TBX5 Pti-1, pti-2+), there were 25 F1 hens and 222 backcrossed hens by crossing F1 hens with Houdan cocks. All F1 hens had feathered legs.

From the cross F1 leg feathered hens x Houdan cock, the segregation was: 82 clean legs (37%), 44 intermediate (20%) and 96 with leg feathers (43%).
The backcrossed hens that had light leg feathering had significantly less feathering than Langshan, see fig.1 This indicates incomplete dominance of Pti-1 Langshan.
The backcrossed hens were divided into two lines, with leg feathers (Langshan) and without (Houdan) leg feathers. The intermediate chickens did not participate.

A test was also done on the two mutations by looking at the F2 of Houdan (clean legs, +, +) and Silkie (leg feathers TBX5 Pti-1 and PITX1 Pti-2) for the relationship between phenotype and genotype.
From the 194 F2, the leg feather score was recorded at birth and from 174 F2 also at adulthood (a few died).
The length of the fourth toe was also scored relative to the leg length because there is a relationship between brachydactyly (short outer toe) and leg feathers.
There were 9 different genotype combinations, TBX5 (Pti-1) x PITX1 (Pti-2) had leg feathers.

Figure 4 on the next page includes the length of the fourth toe of the F2 at birth and as an adult.
The phenotype at birth and as an adult chicken show the same genotypes, and in both Pti-1 and -2 and both at the same time, there is heavier feathering.
Both mutations show incomplete dominance. There was one exception in Pti-1/Pti-1 and that was heavily feathered legs at birth. It may have been down feathers, which would later be suppressed. Therefore, it is not possible to determine that Pti-1 and -2 leads to heavier leg feathers at birth because Pti-1/Pti-1 also has heavy leg feathers at birth.
Another thing: Pti-2 shows in (eventually) adult chickens a recessive inheritance in chickens without Pti-1 (TBX5) (fig 4b), i.e. those that have wild-type clean legs.

Fig. 1. Feathered-leg phenotypes in the mapping population of Houdan (clean leg) x Langshan (feathered leg) cross.
a, purebred Houdan.
b, purebred Langshan.
c, backcross individuals with clean leg
d, intermediate feathered leg
e, feathered leg
The feather stubs commonly observed in the intermediate phenotype are indicated by an arrow. Photo: Jingyi Li.

On outer toe length
Pti-2 genotypes do not significantly correlate with toe length (fig 4c), while on the contrary, Pti-1 is significantly associated with shorter toe length (fig 4b) and is incompletely dominant (4d).
For both leg feathering and toe length, no effect of sex was seen, both genes being fully autosomal. For the results, this allowed the hens and cocks to be merged.

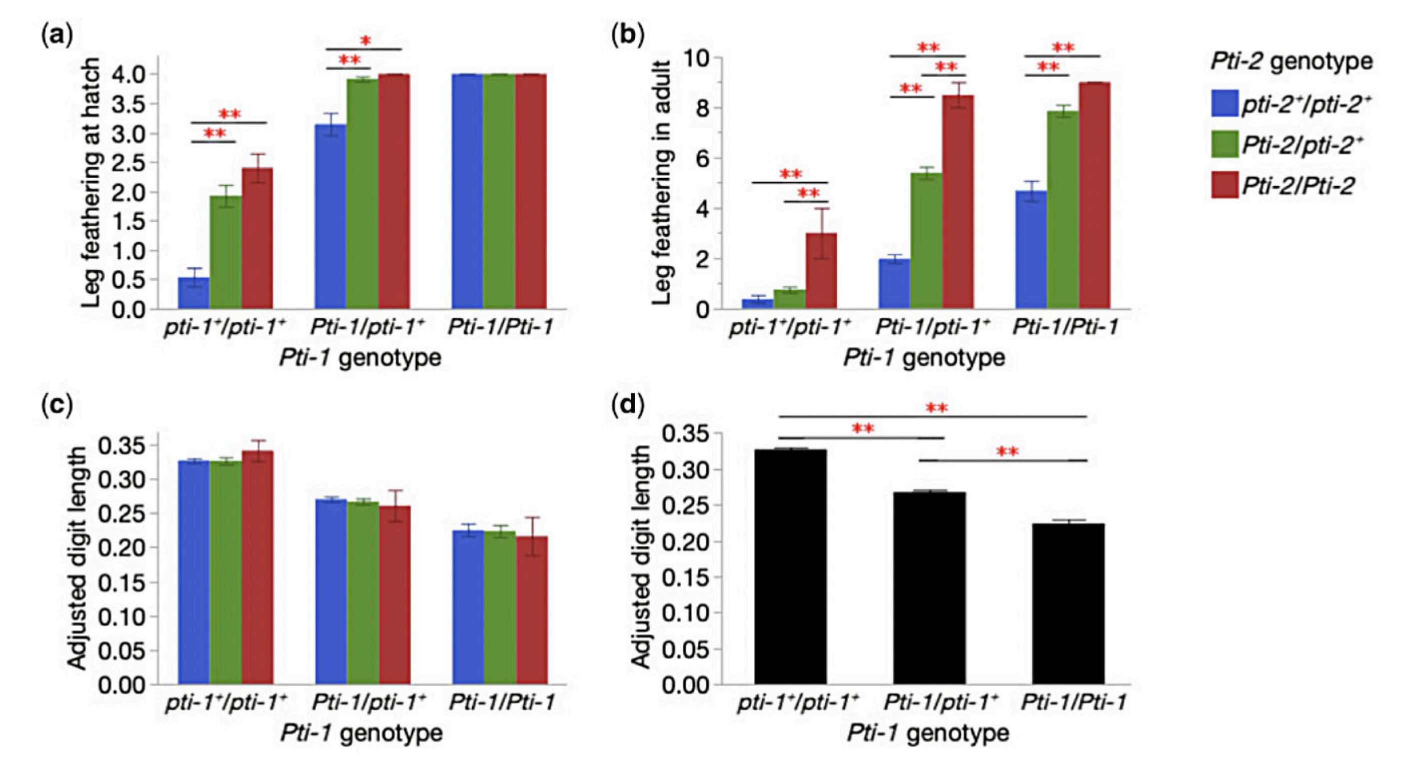


Fig. 4. Phenotypic effects of *Pti-1* (*TBX5*) and *Pti-2* (*PITX1*) genotypes in an F_2 intercross between Silkie (*Pti-1/Pti-1*, *Pti-2/Pti-2*) and Houdan ($pti\text{-}1^{+}/pti\text{-}1^{+}$, $pti\text{-}2^{+}/pti\text{-}2^{+}$) chicken. The error bars represent SD. Significant differences are indicated by "*" ($P < 0.05$) or "**" ($P < 0.01$). Leg feathering scores at hatch (*a*) and at 27 weeks of age (adult) (*b*) are plotted for the nine different genotype combinations. Higher scores indicate heavier feathered leg. Adjusted digit length, calculated by the length of the fourth digit divided by the length of the shank from the same individual, was plotted for the nine different genotype combinations (*c*) as well as for the *Pti-1* genotypes only (*d*).

Leg feathers without leg feather genes?
Somes (1992) was correct that there were two dominant genes for leg feathers. Somes showed that the heavy leg feathers were caused by Pti-1 and Pti-2 together, and Langshan was only Pti-1 and wild-type for pti-2+.
It is possible that there is a third leg feather gene because 29 of 44 backcrosses in Langshan/Houdan had intermediate feathering while they were wildtype for both genes, i.e. had no leg feather genes. It has been proposed that the cause may be that there is a third gene after all with a modest effect on phenotype or a combination of several other genes selected over time to make the leg feathers on the Langshan somewhat heavier.

Somes found a 15:1 split between feathered and clean legs in F2 in the cross between Cochin/Leghorn and Sultan/Leghorn. He suggested that there were two dominant genes for leg feathering that inherited independently in F2 resulting in extra leg feathers when combined.

Source: Mutations Upstream of the TBX5 and PITX1 Transcription Factor Genes Are Associated with Feathered Legs in the Domestic Chicken, 2020

This study also revealed that both genes were incompletely dominant. Also in this study in the cross Silkie/Houdan, leg feathers were seen on chickens that were wildtype and should actually have clean legs. So that third leg feather gene must exist and that is what they are going to look for.

Furthermore, it became clear that TBX5 (Pti-1) affects feather length and PITX1 (Pti-2) affects feather location. This works exactly identically in domestic pigeons so they are very old mutations evolutionarily (to be precise for who wants to know:17.7kb deletion in chickens, 44kb deletion in pigeons 200kb upstream of PITX1). It is TBX5 (Pti-1) that shifts the feather expression from the leg to an expression of the wing. The pleiotropic effect of this is brachydactyly, a shortened outer toe.
This is attached to Pti-1. In humans, something similar can happen (TBX5 shortening) but the other way around in terms of limbs and there are a few more differences. In humans it is called Liebenberg syndrome.

Another interesting thing is that the study also found that in both Cochin and Silkie, PITX (Pti-2) was not fixed (firmly established) in these breeds

Liebenberg syndrome, the human version of the short outer toe.

Table 1. Genotype Distributions in Feathered-Leg and Clean-Leg Chickens Analyzed by Whole-Genome Sequencing or a Diagnostic Test.

Breed	Genotype of *Pti-1* (*TBX5*)			Genotype of *Pti-2* (*PITX1*)		
	Pti-1/Pti-1	*Pti-1/pti-1*$^{+}$	*pti-1*$^{+}$*/pti-1*$^{+}$	*Pti-2/Pti-2*	*Pti-2/pti-2*$^{+}$	*pti-2*$^{+}$*/pti-2*$^{+}$
Feathered-leg chickens						
Beijing You	1	0	0	1	0	0
Booted Bantam	1	0	0	1	0	0
Brahama	9	2	2	4	1	8
Cochin	15	2	0	11	3	3
D'Uccle Belgiana	2	0	0	2	0	0
Faverolle	8	1	0	0	0	9
Langshan	5	0	0	0	0	5
New Hampshire × Silkie	0	2	0	0	1	1
Marans	2	4	0	0	0	6
Silkie	19	0	0	7	10	2
Sultan	5	2	0	6	1	0
Sundheimer	1	0	0	0	0	1
Clean-leg chickens[a]	0	0	379	0	0	379

[a]These 379 individuals lacking feathered legs represent 85 different breeds of chicken.

(table 1). In another study (2020), PITX1 (Pti-2) was strongly down regulated in HH35 (embryo stage) and not in HH39 in chickens that had PITX1 (Pti-2).

The current study also showed that the same favoured mutations can be found in different populations where strong phenotypic expression is liked.

Yep, we cross everything to everything to jack up a certain trait or even transfer it from one population (breed) to another. These practices have been taking place since we started breeding chickens for their beauty. It is to be expected that scientists will start having more and more problems with 'pure breeds' as we mix everything. Indeed, another consequence is that certain traits are not all strongly inherited as they once were without mixing genes from other breeds. Think of Silkies, they have long since ceased to look the way they once did in the USA. In Europe, this trend is somewhat less because there they are not really fond of extreme traits which are often also associated with reduced animal welfare.
Hopefully this stripped down verson of the study helps you better understand the leg feather genes.
It should make a lot of things clear you had questions about if you crossed clean x feather legged and didn't always get the results you anticipated. You can incorporate the findings here in your expectations. Don't start to cry too fast when things don't look 100% immediately. And don't panic when your just hatched chicks of your Langshans, Faverolles or Marans have massive leg feathers, it will be okay when they get their grown up chicken feathers.
Studies like this, done with 'our' chickens instead of laboratory lines of Leghorns are the most fun because we can recognise the variable outcomes.

Why you don't always get much expression when you cross a Pti-1 Langshang, Pti-2 Brahma with a wildtype clean legged is because Pti-2 behaves recessive when crossed to clean legged (wildtype) and Pti-1 is incomplete dominant.

The resulting chicken from for example on the photo Orpington x Silkie, only shows half Pti-1/pti-1+ while it does have Pti-2/pti-2+ invisibly.

Don't despair if you if your F1 of heavily feather legged x clean legged has very little leg feathers, in the F2 it will be okay again for 50% if crossed to the feather legged parent and 25% when F1 x F1.

Don't despair either if you notice a shorter outer toe, it is part of Pti-1. You can only regulate the expression by selection or not at all, that's not clear. However, it also explains why you still get chickens without a toe nail or with super short outer toes from 'okay' parents.