ARE 5 E-ALLELES TOO MANY? HOW ABOUT 14!??!?

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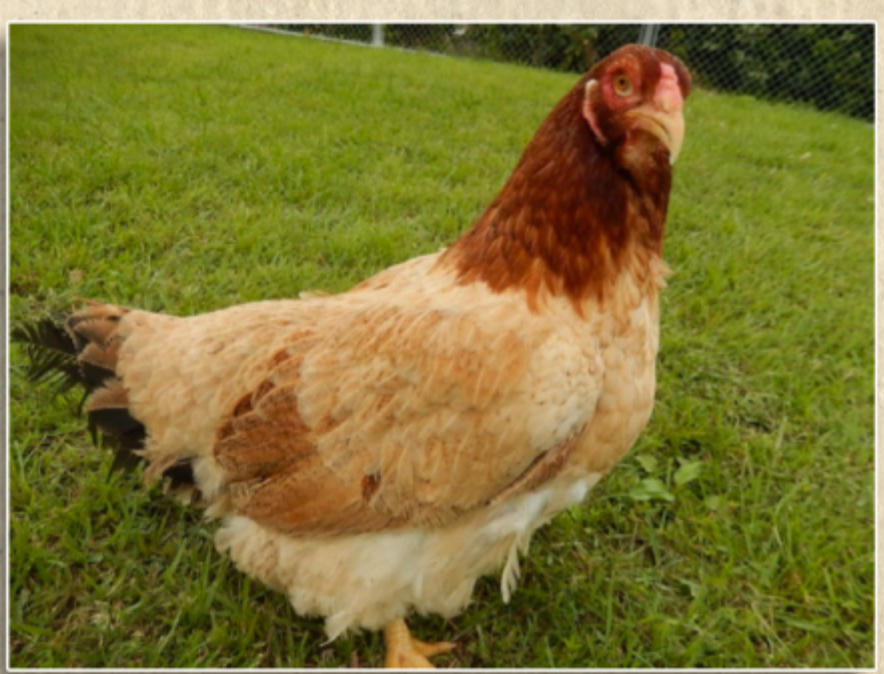
FROM TRADITIONAL E-ALLELE NAMES TO MC1R HAPLOTYPES

Molecularly, we go from 5 to 14 e-alleles
For decades, chicken breeders have used the E-locus notation (E, ER, e+, eb, eWh) to describe plumage colour inheritance. A 2020 Japanese study has now mapped exactly what these traditional alleles look like at the molecular level, and uncovered some surprises along the way.

What is MC1R and why should you care?
The MC1R gene (Melanocortin-1 Receptor) is what geneticists call the E-locus. It's the gene that controls whether feathers produce black pigment (eumelanin) or red/yellow pigment (pheomelanin). Different versions of this gene, called haplotypes, are what we've been calling E, ER, e+, eb, eWh years.

The Japanese researchers examined 732 native Japanese chickens, some you might know, and 155 non-Japanese breeds, sequencing their MC1R genes and comparing them to their actual plumage colours. Here's what they found....

The paper's sloppy use of 'wt' wild-type
What you should know when reading the original paper is their confusing use of 'wt' (wild-type). In standard genetics literature, 'wild-type' specifically means e+ - the Red Junglefowl genotype with duckwing pattern (males with black breast, females with salmon breast). However, this Japanese paper uses 'wt' loosely to describe any male that looks like it has a black breast, regardless of whether it's actually e+, eb, or eWh. Since all three alleles produce identical-looking males, this creates confusion. The only way to know the true genotype is to look at the



*The colour of the Hinaidori female homozygous for **e^m** H5 haplotype. The feather colour is similar to that of wheaten.*

THE E-LOCUS MOLECULAR TRANSLATION GUIDE

1 Extended Black (E)
Called H7, H8, H9, H10, H11, or H12 depending on exact variations. All share the critical amino acid change at position 92 (Glu->Lys). Produces solid black plumage in both sexes, yet not always. Most common in Japanese breeds: H7, H8, and the newly discovered H9.

2 Birchen (ER)
Called H4 in molecular terms. Traditionally described as 'dark wild-type'. Interestingly, the Japanese study found solid black plumage, not the expected dark wild-type pattern with crow wing. The key change: amino acid swap at position 133

3 Duckwing (e+)
Called H0 and H1 in molecular terms. Males: black breast, red/gold hackles and saddle. Females: salmon coloured breast, brown body with stippling (the paper mentions 'pencilling' however we use that when Pg is included). Found in Red Junglefowl and most 'natural' coloured breeds.

4 Brown/Asiatic Partridge (eb)
Called H6 in molecular terms. Males: look exactly like wild-type (can't tell them apart from e+ males). Females: brown/partridge throughout. No salmon breast (slightly lighter on breast for camouflage).
Important discovery: eb and ebc (buttercup) are molecularly identical. The pencilling in buttercup comes not from MC1R. The key changes: three amino acid swaps at positions 71, 92, and 215.

5 Wheaten (eWh)
Called H2 (and H3 variant) in molecular terms.
Males: look like wild-type, lack a shaft stripe in hackle and saddle. Females: uniform wheaten colour (no salmon breast). The key change: one amino acid swap at position 143.
Wheaten (em) H5, substitution A644C (His215Pro), phenotype similar to eWh H2, H3, male wild-type, female wheaten.

females: e+ females have salmon breasts (true duckwing), whilst eb and eWh females do not. So when reading this paper, don't trust the 'wt' label for the e-allele, check what the females actually look like.

A few interesting things...

1. Some alleles look identical molecularly: Wheaten (eWh) and recessive wheaten (ey) can't be distinguished by MC1R sequence.
Brown (eb) and buttercup (ebc) are identical at MC1R; the pencilling comes from elsewhere.

2. A new wheaten-like allele (proposed symbol: em): Called H5 in the study. Females show wheaten-like plumage (no salmon breast). Males look wild-type. Found in some Hinaidori and Mie-Jidori breeds

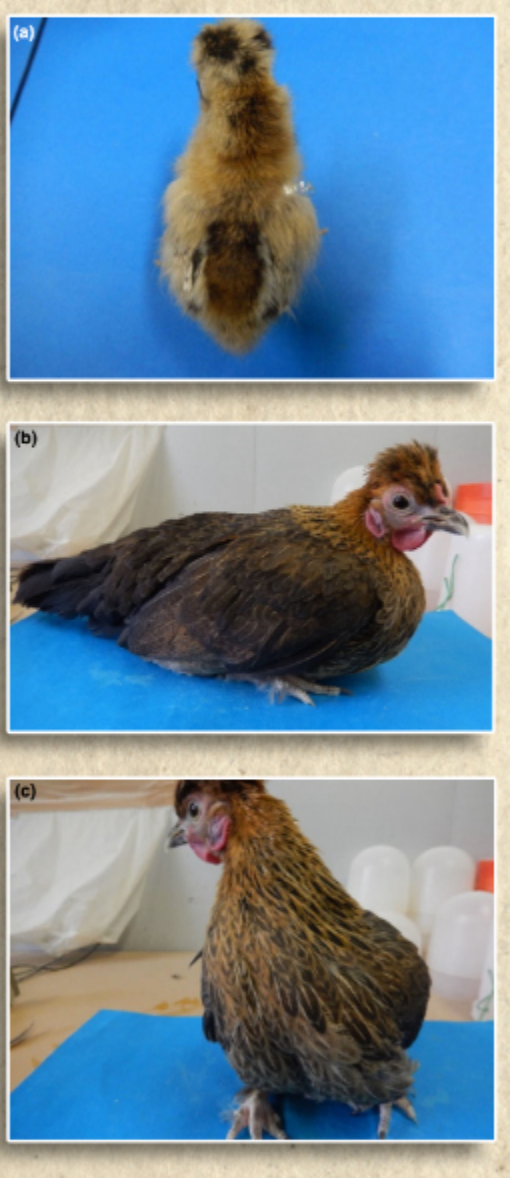
3. Males can be deceptive: You cannot tell e+, eb, or eWh apart by looking at males alone. They all show the same 'black-breasted red' colour. Only females reveal the genotype. E and ER males are distinguishable from the other e-alleles by their crow wing (black secondaries).

4. The buttercup mystery solved: The beautiful pencilling in buttercup is not part of the E-locus. It's a separate modifier working on top of eb. This explains why some eb birds have pencilling and others don't.

The Satsumadori in this paper
The Satsumadori (v) comes in different varieties. Looking at the photograph and phenotype: The 'wild-type' variety female shows no salmon breast, she's uniformly coloured throughout (slightly lighter breast due to camo).
This is the classic eb (asiatic partridge) female phenotype, known in Japan as 'shirosasa' (white hackled). It is also described as such in the EU standard. We mostly know eb in combination with Pg, which gives pencilled patterns/colours. (See 'eb Asiatic 'wildtype' partridge, Sept 2022 www.chickencolours.com).

The Satsumadori is eb without Pg, so it is surprising that the Japanese paper considers eb pg+ Satsumadori to be new. The molecular data also shows H6 (the eb- 'c' in the paper was probably added when they mentioned black on the breast of the eb hen; this is inconsistent with the use of 'wt'). Males look eb wild-type, as expected. This illustrates an important point we as breeders already know, you must look at the sisters to properly identify the e-allele. It is funny to read, while these Satsumadoris are for decades in the fancy. Some languages call it 'wild partridge' because of the coarse nature of the stippling, it is plain Asiatic partridge (without pencilled or multiple laced).

On the eb Satsumadori they write: *"This is the first finding in this breed. Precise observation revealed that the females of this variety have a large number of minute black speckles on the breast, which are in contrast with the completely black-breasted white variety females (e.g. those observed in Onagadori and Shôkoku breeds) that lack such speckles on the breast."*



*The chick (a) and adult (b and c) plumage of the female homozygous for the (new) **H14** haplotype. The chick has stripes on its back similar to those of the wt (black-breasted red). The adult plumage is also similar to but darker than the wt, with the breast possessing black markings that are not seen in the real wt.*

New Haplotypes H13 and H14: mysteries yet to solve

The study discovered two new haplotypes, H13 and H14, both found exclusively in the Ukokkei. Unfortunately, the researchers were unable to assign traditional E-locus names to these variants because their effects remain unclear or unknown.

H13 - Unknown Phenotype
H13 contains a newly discovered substitution *C919G* (Arg307Gly), along with the *G274A* substitution that normally causes *black* plumage. However, H13 was only found in white Ukokkeis that were recessive white (c/c), which masks all colour making it impossible to

see what feather colour H13 would actually give. Although H13 was also detected in black Ukokkei, it only appeared in two heterozygous birds, never homozygous, so the true effect of H13 remains a mystery.

H14 - Wild-type-like despite carrying a "Black" mutation

H14 also contains the new *C919G* substitution plus *G274A* like the white Ukokkei (which normally causes black plumage). The researchers were able to test H14 by crossing a white Ukokkei to wild-type Tosa-Jidori. Surprisingly, birds homozygous for H14 showed wild-type-like plumage, not black. This suggests that other substitutions in H14 (either G409A or C919G, or both) suppress the black effect that G274A normally produces. Males showed the standard wild-type pattern, whilst females showed wild-type-like feathers but slightly darker with some black markings on the breast, not quite true wild-type, but certainly not black.

Because the phenotypes remain unclear (H13) or unusual (H14), the researchers chose not to propose E-locus abbreviations and names for these haplotypes. They remain simply H13 and H14 in the molecular nomenclature, awaiting further breeding experiments to clarify their true effects and inheritance patterns.

The bottom line

Modern molecular genetics confirms what experienced breeders have known for generations, now with added precision. The traditional e-alleles notation still works perfectly well for breeding purposes. What's changed is our understanding of what's actually happening at the DNA level, and the discovery that some 'different' alleles are actually the same gene with different modifier genes acting on them. And those new modifiers don't have to change the feather colour.

Based on comments I've received in the past: before you jump to conclusions and assign a new haplotype to your chicken simply because you don't understand its colour based on the parents, remember that it's highly unlikely to be one of these new e-alleles. Without a laboratory in your shed and similar Japanese breeds, there are more common reasons for unexpected colours: you may have coded the egg incorrectly, the parents might not be the actual parents, the parents may have the same colour but express it much less obviously (especially regarding black pigmentation in hens), a neighbouring cock may have jumped the fence, modifier genes you weren't aware of could be at play, etc. It's far more likely that your unexpected colour has a simpler explanation than a novel mutation. For most breeding decisions, you can continue using the traditional notation because most breeds are not these Japanese ones. The molecular haplotype information (H0-H14) is simply the same thing described in a different language, useful for research, the old notation remains perfectly valid for practical backyard breeding. Trust your eyes, especially when looking at the sisters of the cocks. They'll tell you what you need to know about the e-allele, regardless of whether you call it eb or H6.

HAPLOTYPE PRIMER

Duckwing (e+) H0,H1
Wheaten (eWh) H2, H3
Wheaten (em new) H5
Birchen (ER) H4
Asiatic Partridge (eb) H6
Extended Black (E) H7, H8, H9 new, H10, H11, H12 leghorn
Unassigned: H13, H14

If you need to know the nucleotides (amino acids) see the scheme on page 8 of the Japanese paper.

(a) **Chabo** [white columbian female (left) and male (right)] - H0, H2, H8 (we call 'white columbian' black tailed white', the researchers don't know the names we use, svd).

(b) **Gifu-Jidori** [wt male (middle), wheaten female (left) and wt female (right)] - H0, H2

(c) **Hinaidori** [wt males (left) and wheaten females (right)] - H0, H1, H2, H5, H6

(d) **Ingie** (mahogany male) - H2

HAPLOTYPE PRIMER

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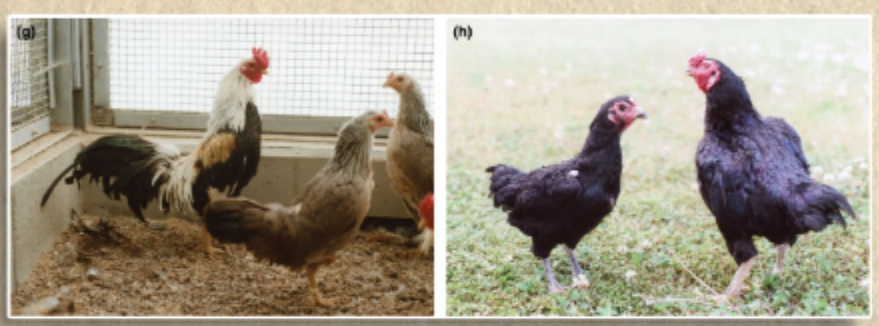
Extended Black (E) H7, H8, H9 new, H10, H11, H12 leghorn
Unassigned: H13, H14

(e) **Iwate-Jidori** (black-breasted white males) - H0 (e+)
(f) **Jitokko** [wt male (left) and female (right)] - H0, H1, H2, H5 (e+, eWh, em < new wheaten allele)



(g) **Kawachi Yakko** [black-breasted white-like male (left) and female (right)] - H0 (e+)

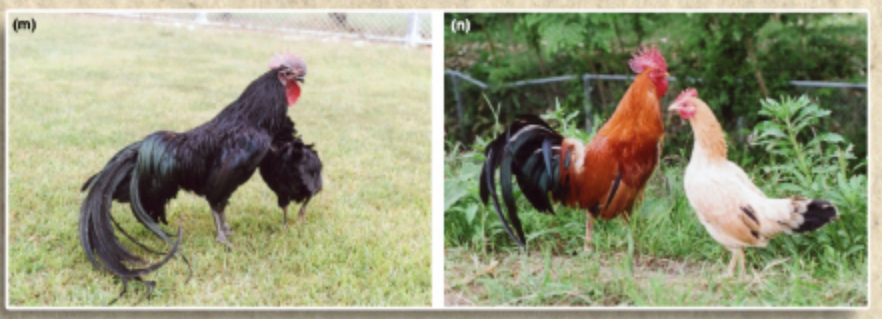
(h) **Kinpa** [black female (left) and male (right)] - H7, H8, H9 is new, H11 (E)

(i) **Koeyoshi** [black-breasted white-like male (left) and female] - H0 (e+)

(j) **Ko-Shamo** [wt male (left) and wheaten female (right)] - H2 (eWh)

(k) **Kumamoto** [buff male (left) and female (right)] - H2, H6 (eWh, eb)

(l) **Kurekodori** [black female (left) and black-breasted silver male (right)] - H0, H4, H6, H7 (e+, ER, eb, E)

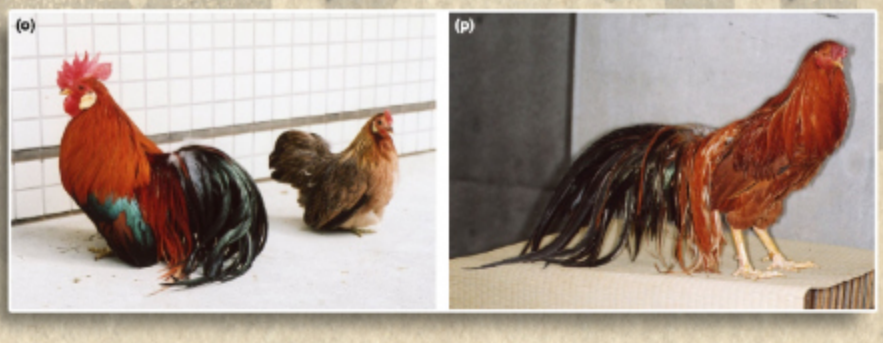


(m) **Kurokashiwa** [black male (left) and female (right)] - H1, H6, H7 (e+, eb, E)

(n) **Mie-Jidori** [buff columbian male (left) and female (right)] - H5 (em < new wheaten).

HAPLOTYPE PRIMER

Duckwing (e+) H0,H1 **Wheaten (eWh)** H2, H3
Wheaten (em new) H5
Birchen (ER) H4
Asiatic Partridge (eb) H6
Extended Black (E) H7, H8, H9 new, H10, H11, H12 leghorn
Unassigned: H13, H14



(o) **Minohiki Chabo** [wt male (left) and female (right)] - H0 (e+)
(p) **Minohikidori** (buff columbian male) - H0, H5 (e+, em < new wheaten)

(q) **Miyadidori** [black female (left) and male (right)] - H1, H6, H7, H9 (e+, eb, E, new E)

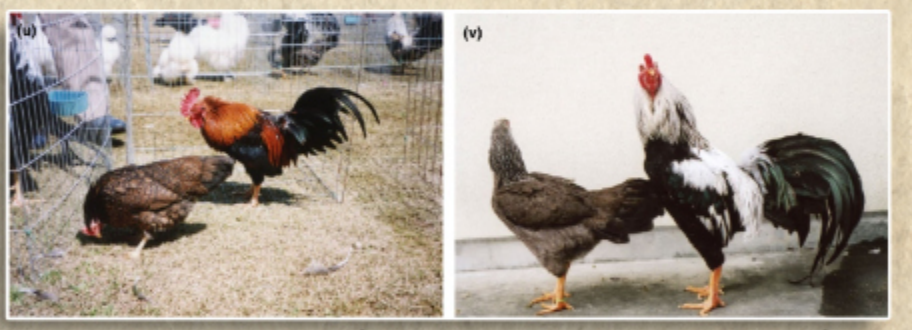
(r) **Nagoya** [buff columbian male (left) and female (right)] - H2 (eWh)

(s) **Onagadori** (black-breasted white male) - H0 (e+)

(t) **O-Shamo** [black male (front) and female (back)] - H0, H1, H4, H5, H6, H8, H9 (e+, ER, em < new wheaten, eb, E)

(u) **Ryujin-Jidori** [wt-like female (left) and wt male (right)] - H0, H1 (e+)

(v) **Satsumadori** [black-breasted female (not, she is eb, svd) (left) and male (right)] - H0, H6 (e+, eb)



(w) **Shôkoku** [black-breasted male (left) and female (right)] - H0, H12 (e+, E from Leghorn)

(x) **Tômaru** (black male) - H4, H7, H11 (ER, E)

HAPLOTYPE PRIMER

Duckwing (e+) H0,H1
Wheaten (eWh) H2, H3
Wheaten (e^m new*) H5
Birchen (ER) H4
Asiatic Partridge (eb) H6
Extended Black (E) H7, H8, H9 new, H10, H11, H12 leghorn
Unassigned: H13, H14

(y) **Tosa-Jidori** [wt male (left) and female (right)] - H0, H1, H6 (e+)
(z) **Tosa Kukin** [buff Columbian female (left) and male (right)] - H2, H3 (eWh)

(a1) **Tôtenkô** (wt male) - H0 (e+)

(b1) **Ukokkei** [white male (left) and female (right)] - H6, H13, H14 (eb, 0, 0) (white variety) or H6, H7, H8, H10, H13 (black variety - not shown) (eb, E, 0)

(c1) **Uzura Chabo** [wt female (left) and male (right)] - H0 (e+)

(d1) **Yakido** [black female (left) and male (right)] - H5, H6, H7, H8, H9 (e^m new wheaten, eb, E)

BREEDS WITHOUT A PHOTO:
Australorp [black] H7 (E)
Barred Plymouth Rock [barred] H4, H8 (ER, E)
Black Minorca [black] H1, H4, H8 (e+, ER, E)
Brown Leghorn [wt] H0, H1 (e+)
Fayoumi [autosomal barring] H4, H8 (ER, E)
Rhode Island Red [mahogany] H2 (eWh)
White Leghorn [white] H10, H12 (E)
White Plymouth Rock [white] H2, H4, H6, H7, H10 (eWh, ER, eb,

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Following: the Discussion of the paper in normal breeder's speak because it might be interesting to some...

Wild-type and wt-like plumage (page 10-11)
The breeds showing true wild-type or wild-type-like plumage patterns (such as Iwate-Jidori, Kawachi Yakko, Koeyoshi, Minohiki Chabo, Onagadori, Ryujin-Jidori, Satsumadori, Tosa-Jidori, Shōkoku, Tōtenkō, Uzura Chabo, and Brown Leghorn) all had the same haplotypes (H0 and H1) as previously reported for e+ in the literature, confirming earlier studies to be true.
Some of the following I already described in the short version at the start of this article:
However, there was one notable exception: the black-breasted white variety of Satsumadori did not possess the wild-type haplotypes (H0 or H1, e+), but was instead fixed with haplotype H6 (buttercup, ebc < note the scientists don't know the difference between the 'old' ebc and the modern eb, they call every haplotype where

the female has black stippling [as used by us to create pencilling when adding Pg], 'ebc', you should read eb because also in this example the Satsumadori hen does NOT have the ebc pattern as in the English Buttercup breed that gave the name 'ebc', svd), even though this variety showed a wild-type feather colour. This was the first discovery of this in the breed. Females have numerous minute black speckles on the breast (we call that stippling or peppering), which distinguishes them from truly clean black-breasted white females (such as those in Onagadori and Shōkoku < referring to e+ salmon breasts see photo w) that lack such speckles.
Moreover, in the Tosa-Jidori, which is assumed to have wt plumage, the H6 haplotype (ebc) was present alongside H0 and H1. This is the first time of finding H6, eb, in this breed as well.
In the majority of native Japanese breeds with a wild-type or wild-type-like feather colour, the H0 e+ haplotype was either fixed or present in high frequency. In contrast, only Ryujin-Jidori, which also has a wild-type-like plumage pattern, carried the H1 haplotype with high frequency. This indicates the specificity of this breed amongst native Japanese chicken breeds with wild-type or wild-type-like feather colour, suggesting a distinct breeding history from the other native Japanese breeds.

Brownish plumage (page 11)
Ko-Shamo wheaten-coloured females were wheaten H2, supporting previous reports that A427G enhances pheomelanin production leading to wheaten. The Nagoya breed, which is buff columbian, is also wheaten (H2). The Tosa Kukins with the same feather colour, too.
In the Chabo, H2 eWh was also seen in buff columbian and white columbian varieties (buff and black tailed white [eWh s+ or S, Db] the scientists don't know the hobby colour names). The white plumage of the white columbian variety is presumed to result from the effect of the silver (S) gene.
Furthermore, Ingie and Rhode Island Red with mahogany plumage and columbian pattern were also wheaten and the majority of Kumamotos who have buff plumage. These facts confirmed that the A427G substitution (H2) in the MC1R gene contributes to expression of brownish plumage.

Ko-Shamo and Gifu-Jidori wheaten (H2, eWh) males expressed wild-type feather colour, supporting traditional genetics. In addition to the A427G substitution observed in wheaten (H2), an additional non-synonymous substitution (T398C; H3, eWh) was discovered in the study. This substitution was found only in Tosa Kukin breed, which has buff columbian plumage, so this substitution (H3 eWh) is presumed to affect the expression of brownish plumage similarly to A427G (H2). This paper calls wheaten: brownish.

The Mie-Jidori (photo: n) also has a buff columbian feather colour and had the A644C substitution (therefore H5, em < new wheaten), so A644C was assumed to lead to brownish (read: wheaten) plumage. The effect of A644C (H5, em < new wheaten) could not be determined from only Mie-Jidori because they also carried columbian (Co). Fortunately, a Hinaidori female was homozygous H5(em). This female had a wheaten feather colour, similar to the usual wheaten (H2) plumage.Two O-Shamo males were homozygous for H5 and had the wild-type feather colour. The feather colour of H5 homozygous birds was revealed in this study. The researchers propose the gene symbol 'em' for H5.
The birds showing columbian or buff plumage were eWh (H2), em (H5) or ebc (H6): however the majority of the Minohikidori having a buff columbian feather colour were e+ (H0)!!!. This was a surprise, because they preassumed that all Minohikidori would be eWh (H2).

Regarding birchen ER (H4), traditional genetics states it does not exhibit solid black feathers but dark a wild-type-like colour. In this study, birds with the birchen allele (H4, ER, for example, Tômaru and Black Minorca) showed solid black feathers, this is different from traditional genetics. Additionally, this study revealed that ER birchen is not basically distributed amongst native Japanese chickens, with only Tômaru having ER.
(I want to add, that ER needs Ml melanotic to be solid black, see an article I wrote on Ml on the website, which is in this study, not expressed by the MC1R gene of course.)

Black plumage (page 12)
The substitution G274A (Glu92Lys) is known to cause solid black feathers. In this study, birds showing black feathers (such as Kinpa, Kurokashiwa, Miyadidori, and Australorp) possessed this substitution (H7–H12).
But, birds carrying G274A along with A644C (H6) never showed solid black feathers. Because A644C (H5) itself causes a wheaten colour, the A644C substitution is assumed to suppress the effect of G274A and prevents a black feather expression.
In addition to the known haplotypes for black plumage (H7, H8, and H10–H12), a new e-allele (H9) was discovered in this study. However, no substitution was found in H9, suggesting it has no effect on the feather colour. In general, H9 birds (Kinpa, O-Shamo, and Yakido) showed black feathers. The H9 haplotype was discovered only in native Japanese chickens.

According to traditional genetics, E/E birds show solid black feathers. In this study, almost all breeds with E/E were solid black (such as Kinpa, Kurokashiwa, Miyadidori, Tômaru, and Yakido). However, all Kurekodori males showed numerous whitish (silver) feathers in hackle and saddle while being E/E, this is different from the usual theory (no it is not, we know that solid black regardless the e-allele needs additional melanisation to be solid black, the Cemani is a nice example when there are not enough melanisers present, or they are ER from an early cross to Ardenner for hybridisation to get the breed going). The reason why Kurekodori males do not exhibit solid black plumage under the E/E condition requires further investigation.

For solid white (recessive or dominant plus additions) birds, the effect of the MC1R gene aka e-allele aka haplotypes on feather colour isn't visible. In this study was found that a lot of White Leghorns carry H12 (causing with black feathers). Across all native and non-Japanese breeds, only White Leghorns had this haplotype that often. Despite this, some of the white Shôkoku, a native Japanese breed, also had this unique haplotype, similar to White Leghorn, in relatively high frequency. Presumably, some of the white variety of Shôkoku comes from a cross between White Leghorn and Shôkoku. (It would be interesting whether the white Shôkoku carries dominant white and all the other black inhibitors or transformers to splash and cuckoo, or recessive white that doesn't need those because it doesn't leak black and red like homozygous dominant white does.)

That's it folks, for additional information, read the original paper.

Below some Ukokkei (Japanese Silkie) photos from my archive

You see that the comb colour depends on the feather colour beneath because not all are hypermelanised like (Chinese) Silkies (carrying Fm, fibromelanosis).










Based on: Kabir et al. (2020) Discovery of a new nucleotide substitution in the MC1R gene and haplotype distribution in native and non-Japanese chicken breeds, Animal Genetics and Ellett & Okimoto (2000) Melanocortin 1-receptor (MC1R) gene polymorphisms associated with chickens E locus alleles.