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Review

Fibromelanosis in domestic chickens

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Abstract. *Fibromelanosis is a mutation in domestic chickens (Gallus gallus domesticus) known for centuries in Southeastern Asia and Europe, expressed with abnormal accumulation of the dark pigment melanin in the dermis and connective tissue formations of the avian body. Fibromelanosis (Fm) is due to a dominant autosomal gene(s) whose expression is influenced by various modifying genes. The mutation is mainly seen in some Asian breeds, with the exception of Svart Höna and the Argentina Tuzo type. The usage of the breeds with fibromelanosis is different depending on the social and geographical spread. According to Asian beliefs, these birds possess a healing potential and are used in religious rites and folk medicine. In the other parts of the world, the most popular and most encountered breed with hyperpigmentation is the Silkie, bred only for decorative and exhibition purposes.*

Keywords: fibromelanosis, melanin, endothelin 3, Silkie

Introduction

The term fibromelanosis or dermal hyperpigmentation is used to designate a mutation in domestic chickens (*Gallus gallus domesticus, Linnaeus, 1758)*, determining dermal and visceral melanisation (Hutt, 1949; Crawford, 1990; Dorshorst et al., 2011; Shinomiya et al., 2011). The description of this phenotype as fibromelanosis (Fm) was proposed by Hutt (1949). Hyperpigmentation is manifested with dark, grey-black coloration of the skin, eyes, serosas, muscles and nervous connective tissue sheaths, gonads, trachea and periosteum of birds due to abnormal accumulation of eumelanin in tissues (Hutt, 1949; Smyth, 1976, 1990, 1994; Muroya et al., 2000; Stevens, 2005; Dorshorst et al., 2011). Chickens carrying this mutation have been called „black-boned chickens" or „wu gu ji" due to the dark periosteal coloration. It is assumed that in domestic chickens, this phenotype has emerged in China together with the silky mutation of the feathering. India and Java are also considered possible sites of origin of fibromelanosis (Ekarius, 2007). The Chinese Silkie (*Gallus gallus domesticus Brisson*) is the oldest chicken breed with fibromelanosis, mentioned by Marco Polo during his Asian trip by the end of the 13th century (Haw, 2006; Scrivener, 2009). Later, hens with the exterior of the Silkie were described by Aldrovandi in 1600 (Aldrovandi and Lind, 1963; Scrivener, 2009). Information about birds with black skin and fluffy feathering is encountered in old Chinese texts from the time of the Tang dynasty (Wandelt and Wolters, 1996**;** Dorshorst et al., 2010). The Silkie is the most studied among all known breeds carrying the Fm mutation (Dorshorst et al., 2011). The first investigations of the genetic origins of the mutation and the pigmentation mechanisms in Silkies date back to the beginning of the last century (Bateson, 1909; Bateson and Punnett, 1911; Kuklenski, 1915; Dunn and Jull, 1927). Despite the numerous researches on the origin and molecular mechanisms of expression of fibromelanosis, many issues still remain unclear (Shinomiya et al., 2012).

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Today, more than 25 breeds and breed groups with fibromelanosis expression are known, and almost all of them originate from southeastern Asia (Dorshorst et al., 2011). The breed variety in this part of the world is understandable as hens with dark bones play an important role in Chinese folk medicine, religious rites of inhabitants of the Malay Archipelago and Asian cuisine (Tian et al., 2007a; Tian et al., 2007b; Li and Luo, 2003; Dorshorst et al., 2011; Shinomiya et al., 2012). In industrial poultry breeding, the expression of the phenotype is undesirable due to common consumers' attitude. Nevertheless, the phenomenon could be observed in commercial chicken breeds, and Crespo and Pizarro (2006) described the emergence of fibromelanosis in a broiler flock.

Melanin and melanogenesis

Melanin-producing cells in vertebrates, called melanocytes, originate from the neural crest cells, located at the end of the neural tube, part of embryonic ectoderm (Le Douarin, 1982, 2004; Dorshorst et al., 2011). For the neural tube, undifferentiated melanoblasts migrate in the body where they differentiate into melanocytes (Lucas and Stettenheim, 1972; Smyth, 1976, 1994; Bowers, 1988; Nordlund et al., 2006; Gunnarsson, 2009). The migration of melanoblasts in mammals and birds occurs via the so called dorsal pathway. In lower vertebrates, the migration and differentiation of nervous cells, glial cells and melanoblasts follows the ventral (ventrolateral) pathway (Le Douarin, 1982; Serbedzija et al., 1989; Ericson et al., 1992; Faraco et al., 2001; Shinomiya et al., 2012). In chicken breeds with fibromelanosis, melanoblasts migrate not only via the dorsolateral pathway to the skin, but also through the ventral pathway, and are stored in the internal organs (Ericson, 1993; Lecoin et al., 1994, 1995; Muroya et al., 2000; Faraco et al., 2001; Shinomiya et al., 2012).

Melanocytes located in internal organs and tissues of chickens with fibromelanosis contain melanosomes in a different stage of maturity (mainly stage III and IV) like dermal ones (Faraco et al.,

2001; Ortolani-Machado et al., 2007; Ortolani-Machado et al., 2009). Brumbaugh (1971) distinguishes two types of melanocytes: eumelanin-synthesizing (eumelanocytes) and pheomelanin-synthesizing (pheomelanocytes). In birds, melanocytes produce two types of melanin pigments: eumelanin and pheomelanin (Hutt, 1949; Smyth, 1990; Prota, 1988, 1995; Ito et al., 2000; Stevens, 2005; Simon et al., 2009). Eumelanin is the dark (dark-brown to black) pigment, of dihydroindole carboxylic acid and/or dihydroindole polymers, responsible for the expression of fibromelanosis. Pheomelanin is present only in the feathering of birds (Smyth, 1990, 1994) and represents cysteine-containing benzothiazine polymer with red to yellow colour. The deposition of both pigments in a specific body area/feathering is determined by several genes and their interaction (Hutt, 1949; Smyth, 1990; Stevens, 2005). The two melanin types act in opposite directions, eumelanin being a photoprotective and antioxidant pigment, while pheomelanin is phototoxic and with prooxidant activity (Chedekel et al.,1980; De Leeuw, 2001; Simon et al., 2009).

The process of melanin synthesis is termed melanogenesis (Figure 1). Both pigment forms of melanin are synthesized by oxidation of the amino acid L-tyrosine to 3,4-dihydroxyphenylalanine (DOPA) and dopaquinone by tyrosinase (TYR) (Lerner and Fitzpatrick, 1950; Simon et al., 2009). Apart from tyrosinase, eumelanin production (Hearing, 2005; Gunnarsson, 2009; Olivares and Solano, 2009) occurs also through tyrosinase-like proteins: $TYRP_1$ and $TYRP_2$ (DCT). By the same pathway, ortho-quinone playing a role in melanogenesis, is also formed (Cooksey et al., 1997). According to the type of the pigment produced, dopaquinone is consequently converted in cyclodopa, dopachrome, dihydroindole carboxylic acid (DHICA) or dihydroindole (DHI), and finally into eumelanin (Körner and Pawelek, 1982; Palumbo et al., 1987, 1991; Land and Riley, 2000; Simon et al., 2009). The pheomelanin is synthesized through conversion of dopaquinone into cysteinyldopa (5-S- cysteinyldopa or 2-S- cysteinyldopa) by addition of cysteine. Cysteindopa interacts with dopaquinone to yield cysteindopa-quinone and DOPA. Cysteindopa-quinone is then dehydrated and transformed into ortho-quinonimine, which is then converted (with or without decarboxylation) into pheomelanin precursors benzothiazine (BT) and benzothiazine carboxylic acid (BTCA) (Thomson, 1974; Smyth, 1990, 1994; Prota et al., 1998; Napolitano et al., 1999; Ito et al., 2000; Simon et al., 2009). When tyrosinase activities are low, pheomelanin synthesis could occur from cysteine to dopaquinone.

Melanin synthesis events occur in membrane-bound

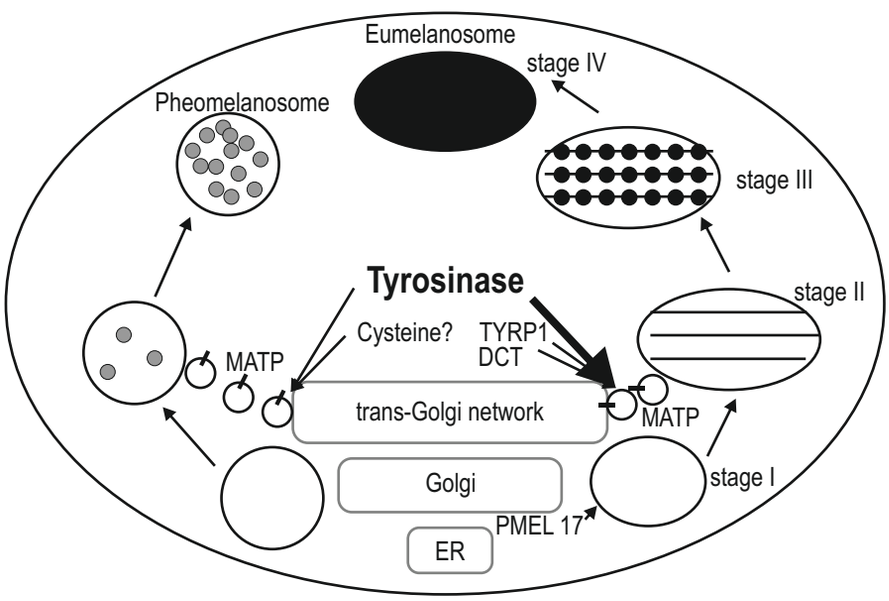

Figure 1. Stages of pheomelanosome and eumelanosome formation in the melanocyte (according to Hearing, 2005)

organelles of melanocytes, called melanosomes (Smyth, 1990, 1994; Liu and Simon, 2003; Gunnarsson, 2009; Simon et al., 2009). Melanosomes are melanocytic lysosome-like cell organelles. They are thought to originate from melanocytic endoplasmatic reticulum as primary melanosomes. The formation of melanosomes occurs through four stages: stage I melanosome – stage II melanosome (premelanosome) – stage III melanosome – stage IV melanosome (melanin granules) (Figure 1). Depending on the synthesized pigment, eumelanosomes and pheomelanosomes are distinguished (Brumbaugh, 1968; Hearing, 2005;Gunnarsson, 2009; Patrick and Borovansky, 2011).

Melanin role is diverse. It is responsible for the typical protective feathering coloration aiding the mimicry of the Red Junglefowl (*Gallus gallus*, *Linnaeus*, 1758) and freely living domestic chickens (*Gallus gallus domesticus, Linnaeus,* 1758) with wild-type feathering colour. According to Smyth (1994) melanin is important during the embryonic life and the first days after the hatching of chicks. The presence of eumelanin in the skin provides a natural protection from solar UV radiation. The antioxidant function of eumelanin helps the reduction of systemic levels of free radicals. The lack or reduced melanin levels during the embryogenesis could result in impaired relationships between the visual receptor and the brain (Smyth, 1994).

Genetic features of fibromelanosis

This mutation is determined by a dominant autosomal gene conditionally termed *Fm*/*EDN3* (Fibromelanosis) interacting with the

sex-linked recessive wild type *id*$^{+}$ gene and possibly, the *W*$^{+}$ gene that determines the white colour of the skin. Recent researches (Dorshorst et al., 2010, 2011; Shinomiya et al., 2012) and the new gene terminology points out the Fm locus in chromosome 20, with the *EDN3* gene as the main factor provoking fibromelanosis. The attractiveness of these birds has raised the interest of both poultry breeding amateurs and geneticists. Fibromelanosis is one of the first phenotype signs in chickens subject to genetic analysis as early as the early 20th century (Bateson, 1909; Bateson and Punnett, 1911; Punnett, 1923; Hutt, 1949; Smyth, 1976; Smyth, 1990; Stevens, 2005; Dorshorst et al., 2010).

The first investigations on the mechanism of fibromelanosis inheritance were performed by Bateson and Punnett (1911) on Silkies and brown Leghorns. They describe two factors, responsible for hyperpigmentation: pigmentation factor (*P*) and inhibition factor (*I*). According to authors, only birds with the *P/P/i/i* phenotype are completely pigmented, the genotype *P/p/I/i* determines a slight pigmentation whereas birds with genotypes *p/p/i/i*, *p/p/I/i* and *p/p/I/I* are not pigmented. Bateson and Punnett (1911) established a sex-linked inheritance of the trait and assumed the existence of a third element – *F,* linked with sex and influencing the expression of fibromelanosis. The research of Bateson and Punnett (1911), and then of Dunn and Jull (1927) showed the mode of trait inheritance and its relationship with other genes. Until recently, the gene responsible for the expression of fibromelanosis was labelled as *Fm* (Hutt, 1949; Smyth, 1976; Smyth, 1990; Stevens, 2005; Mishra et al., 2008; Dorshorst et al., 2010). Today, we speak about a Fm locus with a main fibromelanosis *EDN3* gene (Dorshorst et al., 2010, 2011; Shinomiya et al., 2012).

On the basis of earlier studies Dorshorst et al.(2010), Dorshorst et al. (2011) and Shinomiya et al. (2012), used PCR and microsatellite markers to localise the Fm locus in chromosome 20 (10.2–11.7 Mb). According to Dorshorst et al. (2011) fibromelanosis is due to two duplicated regions in chromosome 20 (10,717,600–10,842,919 bp and 11,264,226–11,432,336 bp). The size of these areas is over 100 kb, the first coding for endothelin 3 (*EDN3*), *ATP5E* (ATP synthase epsilon subunit), *TUBB1* (tubulin, beta 1) and *SLMO2* (slowmo homolog 2). The same authors proved the presence of the *EDN3* sequence in the genome of four studied breeds with fibromelanosis: Silkie, Ayam Cemani, Svart Höna and Black Hmong, as well as increased expression of *SLMO2* and *TUBB1* in the fibromelanosis phenotype.

Endothelin 3 (*EDN3*) is a gene with acknowledged role in enhancing the proliferation of melanoblasts and melanocytic regulation (Lahav et al., 1996; Dupin et al., 2000; Garsia et al,. 2008; Aoki et al., 2009; Dorshorst et al., 2010; Dorshorst et al., 2011; Shinomiya et al., 2012). *EDN3* possesses a mitogenic effect against melanoblasts (Lahav et al., 1996; Lahav et al., 1998). According to numerous authors (Nataf et al., 1998; Nagy and Goldstein, 2006; Dorshorst et al., 2010) *EDN3* is established in the chick embryo mesenchyme in melanoblastic migration. Shinomiya et al., (2012) report for the presence of five specific genes in this locus: *EDN3*, *HIVEP1*, *SLMO2*, *F1ATPase-e* and *TUBB3* in the Silkie chicken breed (Figure 2). *EDN3* together with other three genes (except for *HIVEP1*) are detected in Silkies × Minorca crosses.

The other primary gene influencing the expression of

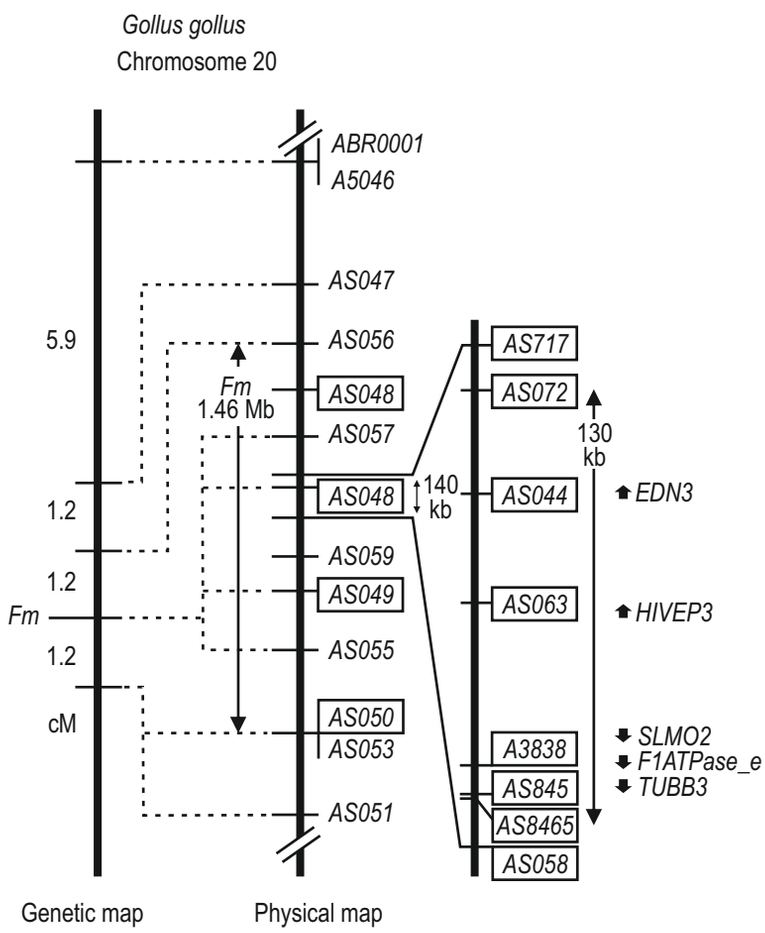

Figure 2. Fm locus of the chromosome 20 in Gallus gallus (according to Shinomiya et al., 2012)

fibromelanosis is the incomplete dominant, sex-linked *Id* or sex-linked dermal melanin inhibitor (Bateson and Punnett, 1912; Dunn and Jull, 1927; Hutt, 1949; Smyth, 1990; Stevens, 2005; Dorshorst et al., 2010). The effect of the dermal melanin inhibiting gene against Fm is modifying. The *Id* allele exhibits an inhibiting activity, whereas the wild type recessive allele (id^+) potentiates the expression of fibromelanosis. Many authors (Bitgood, 1985, 1988; Levin et al., 1993; Dorshorst and Ashwell, 2009; Dorshorst et al., 2010) established the localisation of the Id locus in the sex Z chromosome. Through modern methods, specific nucleotide sequences are determined in a region, several Mb of size, in the Id locus (Dorshorst et al., 2010; Shinomiya et al., 2012). According to Dorshorst et al. (2010) genes that are potential inhibitors of dermal melanin are *B4GALT1* (beta 1,4-Galactosyltransferase, polypeptide 1) and *VCAN* (chondroitin sulfate proteoglycan versican), localised in the sex Z chromosome. The role of B4GALT1 in neural crest cells (NCCs) migration along the ventral pathway during the embryogenesis is acknowledged (Hathaway and Shur, 1992**;** Appeddu and Shur, 1994). *B4GALT1* is detected in the *Id* locus (67.1–72.3 Mb) at 68.7 Mb, immediately close to the *B* (Barring) gene (Dorshorst et al., 2010). The second candidate *Id* gene in the view of the same team – *VCAN* – in located outside the Id region of the Z chromosome at 61.3 Mb. It exhibits an inhibiting effect on NCCs migration along both the dorsal and the ventral pathways during the embryogenesis (Landolt et al., 1995). The dominant wheaten allele (e^{Wh}) from the E locus could have a suppress id^+ with regard to shanks and fascial pigmentation (Smyth, 1990).

Smyth (1990) affirms that the expression of dermal melanosis is determined by the lack of the dominant white allele in homozygous state (*I*), due to melanin-inhibiting effect (Smyth, 1990; Gunnarsson, 2009; Stevens, 2005). In the presence of the *E* allele from the E locus determining the black colour of feathering, the inhibiting effect of the *I* gene on id^+ is reduced (Smyth, 1990, 1994). The pigmentation of fascias is enhanced in the presence of allele *c* (locus C of chromosome 1), determining the recessive white colour of feathering in a homozygous state (*c/c*).

There are other dermal inhibitors, which could enhance or reduce the expression of Fm. A typical inhibitor of melanin is the sex-linked barring gene *B/* (*Barring*), which determines the barring and cuckoo feathering pattern in chickens (Spillman, 1908; Punnett, 1923; Hutt, 1949; Jaap , 1955; Bitgood, 1985; Schreck and Bowers, 1989; Smyth, 1990; Dodgson, 2003; Dorshorst and Ashwell, 2009). Dorshorst and Ashwell (2009) established the *B* gene at 71.8 Mb in the sex Z chromosome. Due to its presence, only cuckoo type Silkies with genotypes *B/B/Fm/Fm* or *B/-/Fm/Fm* are without phenotypically expressed fibromelanosis depending on the sex. The barring gene *B/* reduces at a lesser extent the deposition of melanin in the presence of e^+ or e^b alleles in the E locus combined with Columbian feathering *Co* (Smyth, 1994). Some alleles related to feathering colour from the E locus (*E, ER*) could, together with id^+, influence the accumulation of dermal melanin and provoke hyperpigmentation on the face. They also enhance the expression of the *Fm* gene (Brumbaugh, 1967; Smyth, 1976, 1990).

In several European breeds predominantly, a mutation resembling fibromelanosis called „gypsy face" is encountered. It affects only the face and some formations of the head (comb, wattles, earlobes). Here, the melanin pigmentation is superficial, affecting only the skin of the head, not well studied and probably with polygenic inheritance. Most commonly, birds with markedly dark face have also dark feathering (black, birchen, blue birchen, yellow birchen etc.) indicating an association of this phenotype trait with *E* and *ER* alleles of the E locus (Brumbaugh, 1967; Smyth, 1976, 1990). It is thought that sex-linked melanin-inhibiting gene is essential for the appearance of dark face (id^+) in birds. In female birds, the dark face is better expressed, with well-pigmented fleshy facial growths. Breeds carrying this mutation are Ardennes chickens, Bruges game, Liège game, European Sumatra type, Tomaru, Modern English game fowl bantam, some lines European Australorps and Tuzo. It is interesting to note that a similar mutation appears in some representatives of the Black Shumen chicken breed, well manifested in female birds due to the sex-linked inheritance of the id^+ gene and hemizygosity (Figure 3). According to us, this phenotype expression is due to the effect of the *E* allele for black feathering, the wild recessive form of the melanin-inhibiting gene (id^+) and the gene determining the white colour of the skin (W^+). The iris pigmentation is not altered in Black Shumen chickens with a dark face, unlike other breeds, where it is hyperpigmented.

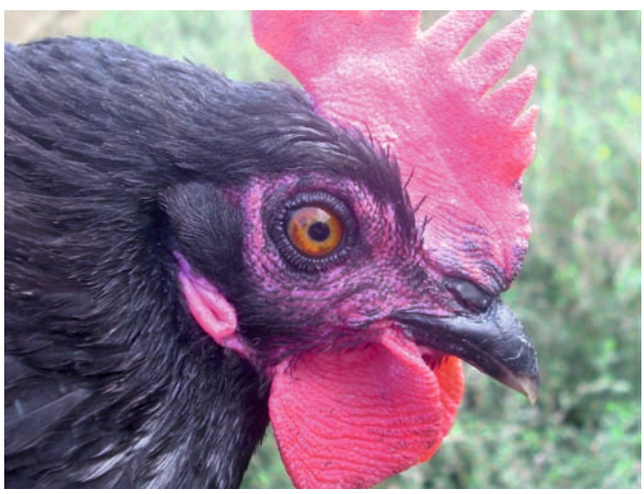

Figure 3. Black Shumen hen with melanosis on the facial skin and part of the comb (original photo)

Poultry breeds with fibromelanosis

Poultry breeds with fibromelanosis (DAD-IS Database, FAO) are: Silkie (Japan/Europe), Silkie Bairiong (China), Dongxiang (China), Emei Black (China), Jianghan (China), Jiangshan Silkie (China), Jiuyuan Black (China), Lueyang (China), Muchuan Silkie Black (China), Tengchongxue (China), Wumeng blacked-boned chicken (China), Xingwen black boned chicken (China), Yanjin blacked-boned chicken (China), Yugan black-boned chicken (China), Yunyang white silked black boned chicken (China), Zhuxiang (China), Ga ac (Vietnam), Black Hmong chicken (Vietnam), Oke (Vietnam), Svart Höna (Sweden), Ayam Cemani (Indonesia), Sumatra (Indonesia), Kadaknath (India), Ogol chicken (Korea), Argentinean Tuzo type (Argentina).

The Silkie is the most popular chicken breed with fibromelanosis (Figure 4). It has a number of mutations responsible for its unique exterior and genome: characteristic fluffy plumage (*h*), fibromelanosis (*Fm* in association with id^+ and W^+), crest (*Cr*), beard (*Mb*), feathered legs (*Pti-1; Pti-2*), five toes (*Po*), walnut comb (*P/_/R/_*) and bluish-white earlobes (Kuklenski, 1915; Hutt, 1949; Smyth, 1990; Stevens, 2005; Ekarius, 2007; Dorshorst et al., 2010; Shinomiya et al., 2012).

Another attractive breed is the Chinese Dongxiang, which apart from fibromelanosis is distinguished with its eggs with blue-greenish shells (Zhao et al., 2006; Gao et al., 2008; Wang et al., 2008;

Figure 4. White non-bearded Silkie hens (original photo)

Figure 5. Ayam Cemani rooster (courtesy by Paulina Ivanova, 2011)

Lukanov et al., 2012).

During the last years, a number of studies on genetic features and productive traits have been conducted on Kadaknath (Chatterjee et al., 2007; Ahlawat et al., 2008; Mishra et al., 2008; Arora et al., 2011; Haunshi et al., 2012), Dongxiang (Zhao et al., 2006; Wang et al., 2007; Gao et al., 2008; Wang et al., 2009) and Ayam Cemani breeds (Łukasiewicz et al., 2009; Joanna and Monika, 2010; Dorshorst et al., 2011; Shinomiya et al., 2012).

Economic, social and exterior-related significance of fibromelanosis

Chickens with fibromelanosis are especially valued in China, Vietnam, Thailand, India, Indonesia, Malaysia and Korea, due to their involvement in religious beliefs of southeastern Asian people, their folk medicine and cuisine. These chickens are used in Chinese folk medicine as it is believed that they contain unknown helpful substances (Li and Luo, 2003; Dorshorst et al., 2011; Shinomiya et al., 2012). Many products originating from Fm chickens are prescribed for enhancement of patient's immunity and systemic anabolic processes. Also, they are used to treat diabetes, anaemia, dysmenorrhoea, postparturient disorders (Tian at al., 2007a, b). The comparative studies in Silkie Bairiongs and White Plymouth Rock chickens reared under identical conditions showed significantly higher levels of carnosine in the meat of Silkies (0.45%) than in Plymouth Rocks (0.22%). Carnosine is a natural dipeptide acting as a physiological buffer in muscles, antioxidant, neurotransmitter and antiglycating agent (Hipkiss and Brownson, 2000; Guanghong, 2001; Tian at al., 2007a, b).

Black-boned chickens are frequently encountered in Asian cuisine recipes and are renowned as a valuable, easily digestible healthy food rich in carnosine (Tian at al., 2007; Shinomiya et al., 2012). One of the most popular dishes prepared with meat from these chickens is the "black-boned chicken soup". Chickens are sought-after at the Asian market and by South Asia immigrants all over the world. Danny Wu, owner of K. K. Live Poultry reported for the sale of more than 3000 "black-boned" chickens per week for Chinatown restaurants in New York (Louie, 2007). Therefore, the production of meat from Fm chickens is a large, still unoccupied production niche for restaurants offering original Chinese cuisine.

Fibromelanosis chickens as Ayam Cemani, have been used for centuries in some religious rites. They are believed to possess mystic forces (Figure 5). For the first time, they are described by Dutch colonists having visited the Java island in the beginning of the 20th century (Steverink, The Cemani site).

Outside Asia birds with dark skin, muscles and bones are accepted as something mystic, strange and exotic and are not popular for consumption. Nevertheless, they have found its place in exotic poultry breeding due to their unique appearance, Silkies are now among the most popular exotic chicken breeds in the world (Ekarius, 2007; Scrivener, 2009; Dorshorst et al., 2010, 2011), widespread in Europe, North America, Australia and Japan (Scrivener, 2009; Dorshorst et al., 2011).

Conclusion

Fibromelanosis is a mutation in domestic chickens (*Gallus gallus domesticus, Linnaeus, 1758*), emerging most probably in the first years AD in southeastern Asia. It is manifested with dark, bluish-black coloration of the skin, eyes, serosas, muscles and nervous connective tissue sheaths, gonads, trachea and periosteum of birds due to abnormal accumulation of eumelanin in tissues. The phenotype expression is determined by a group of genes within the Fm locus in chromosome 20 (10.2–11.7 Mb), together with the modifying action of genes from the Id locus of the sex Z chromosome. According to contemporary research, the *EDN3* gene is the primary gene responsible for the appearance of the mutation. A number of other genes-modifiers (intensifiers or inhibitors) could influence the expression of the main Fm genes.

This unique mutation is known in more than 25 breeds, the major part of which are found in southeastern Asia. This is associated with traditional Chinese folk medicine, and the religious and culinary traditions of Asian peoples. At a worldwide scale, some of breeds with fibromelanosis are reared as exotic birds. The Silkie chickens are examples for the various aspects of use of these birds in eastern and western cultures. It gained a global popularity as a decorative breed, while in Asia, it is nowadays used in folk medicine and culinary. A future increasing interest to these birds from poultry hybrid industry could be anticipated considering the increasing Asian population throughout the world and the million fans of Asian cuisine.

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CONTENTS 1 / 2

Review

Genetics and Breeding

Nutrition and Physiology

CONTENTS 2 / 2

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