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MECHANISM AND FUNCTIONS OF IDENTIFIED miRNAs IN POULTRY SKELETAL MUSCLE DEVELOPMENT – A REVIEW

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Abstract

Development of the skeletal muscle goes through several complex processes regulated by numerous genetic factors. Although much efforts have been made to understand the mechanisms involved in increased muscle yield, little work is done about the miRNAs and candidate genes that are involved in the skeletal muscle development in poultry. Comprehensive research of candidate genes and single nucleotide related to poultry muscle growth is yet to be experimentally unraveled. However, over a few periods, studies in miRNA have disclosed that they actively participate in muscle formation, differentiation, and determination in poultry. Specifically, miR-1, miR-133, and miR-206 influence tissue development, and they are highly expressed in the skeletal muscles. Candidate genes such as *CEBPB*, *MUSTN1*, *MSTN*, *IGF1*, *FOXO3*, *mTOR*, and *NFKB1*, have also been identified to express in the poultry skeletal muscles development. However, further researches, analysis, and comprehensive studies should be made on the various miRNAs and gene regulatory factors that influence the skeletal muscle development in poultry. The objective of this review is to summarize recent knowledge in miRNAs and their mode of action as well as transcription and candidate genes identified to regulate poultry skeletal muscle development.

Key words: poultry, skeletal muscle development, miRNAs, genes, proliferation, differentiation

Abbreviations:
miRNA – Micro RNA
MRFs – Muscle regulatory factors
MYOD – Myoblast determination protein
MRF4 – Muscle-specific regulatory factor 4
MYOG – Myogenin
MYF5 – Myogenic factor 5
MEF2C – Myocyte enhancer factor 2C
Hox-A11 – Homeobox protein

ROCK1 – Rho-associated coiled-coil containing protein kinase 1
MUSTN1 – Musculoskeletal embryonic nuclear protein 1
MSTN – Myostatin
IGF – Insulin-like growth factor
FOXO3 – Forkhead Box 03
mTOR – Mammalian target of rapamycin
HDAC4 – Histone deacetylase
SRF – Serum response factor
PI3K – Phosphoinositide-3-kinase
ANXA2 – Annexin A2
TPM3 – Tropomyosin 3
EIF2AK3 – Eukaryotic translation initiation factor 2 alpha kinase 3

Skeletal muscle development is a complex and tightly developmental process comprising differentiation of myoblast from the mesodermal precursor cells fused to form mature myotubes. The myotubes also differentiate to form myofibres during embryogenesis (Buckingham, 2006; Luo et al., 2013; Velleman et al., 2010; White et al., 2010). Genetic factors such as transcription factors, gene polymorphism, DNA methylation, and non-coding RNAs work together to control the development of muscle fiber formation from the mesodermal precursor cells (Berkes and Tapscott, 2005; Clop et al., 2006; Luo et al., 2013; Saccone and Puri, 2010). Myoblast formation, determination, and differentiation are regulated by four main muscle-specific regulatory factors (*MRFs*) which are myoblast determination protein (*MYOD*), muscle-specific regulatory factor 4 (*MRF4*), myogenin (*MYOG*), and myogenic factor 5 (*MYF5*) (Braun and Gautel, 2011; Wood et al., 2013). Myocyte enhancer factor 2C (*MEF2C*), sine oculis homeobox homolog (*SIX1-SIX6*), and eyes absent (*EYA*) are other genes that also control skeletal myogenesis (Grifone et al., 2007; Potthoff and Olson, 2007; Wang et al., 2016). The members of *MRFs* are essential in embryonic muscle development because they control genes expressly involved in muscle growth, differentiation, morphogenesis, and contractility (Braun and Gautel, 2011; Wood et al., 2013).

Poultry is an essential agricultural organism that serves as a primary source of protein worldwide and bridges the evolutionary gap between mammals and other vertebrates (Hillier et al., 2004).

Owing to the high demand of poultry, several genes associated with skeletal muscle development have been identified to enhance its production (Chen et al., 2015; Xu et al., 2017, 2015, 2013 a, b; Zhu et al., 2017).

Recently, extensive studies have shown that miRNAs play vital roles in skeletal muscle development (van Rooij et al., 2008; Luo et al., 2013). Several discovered miRNAs including miR-1, miR-133, and miR-206 are broadly studied to express in muscle tissue. MiRNA-1 and miRNA-133, which are from the same miRNA cistrons are involved in the development and differentiation of skeletal and cardiac muscle (Chen et al., 2006; Gu et al., 2014; Wu et al., 2019) whereas miR-206 precisely expresses in the skeletal muscle (Hak et al., 2006). Also, miR-181 down-regulates the homeobox protein *Hox-A11* which inhibits myogenesis to promote myogenesis

whereas miR-486 is revealed to induce myoblast differentiation by inhibiting *Pax 7* while miR-206 regulates embryonic myogenesis by targeting the deleterious controllers of *MYOD*, *MYFS*, and *MYOG* in muscle development stages and miR-27b ensures myogenic differentiation by modulating *Pax 3*. More so, miR-148a downregulates an inhibitor of myogenesis known as Rho-associated coiled-coil containing protein kinase 1 (*ROCK1*) and regulates muscle differentiation (Crist et al., 2009; Dey et al., 2012; Kablar and Rudnicki, 2000; Naguibneva et al., 2006). Therefore, the aim of this review was to explore the miRNAs and their mode of action, related transcription and candidate genes identified to regulate poultry skeletal muscle development.

Transcription factors and candidate genes identified in poultry skeletal muscle development

The muscle development process is regulated by several genes which coordinate and complement with each other in every stage. Amongst them are the two most important transcription factors: muscle regulatory factors (*MRF*) and myocyte enhancer factor 2 (*MEF2*) families which help in the formation and differentiation of muscles (Berkes and Tapscott, 2005; Braun and Gautel, 2011). These two families jointly regulate and essentially express in embryonic muscle development and control the transcription of various myogenic-specific genes involved in muscle development (Braun and Gautel, 2011; Wood et al., 2013). The *MRF* family which is basic helix-loop-helix (*bHLH*) proteins includes *MYOD*, *MYOG*, *MRF4*, and *MYF5* while the *MEF2* family which is MADS-box transcription factors consists of *MEF2A*, *MEF2B*, *MEF2C* and *MEF2D* (Potthoff and Olson, 2007; Wood et al., 2013). Except for *MYF5,* the others play the central role in the muscle differentiation, that is, myogenin and *MRF4* promote myogenic differentiation during myogenesis (Sumariwalla and Klein, 2001; Wood et al., 2013); *MYOD* plays the determining role for myoblast formation (Ishibashi et al., 2005) whilst differentiation is enhanced through *MEF2* interactions with members of the *MRF* family and other myogenic factors (Potthoff and Olson, 2007).

Apart from the two families mentioned above, several studies have been made to discover genes and molecular mechanisms involved in the increase in skeletal muscle development in poultry which include *MUSTN1*, *MSTN*, *IGF1*, *FOXO3*, *mTOR*, *NFKB1*, and *CEBPB* (Chen et al., 2015; Xu et al., 2017, 2015, 2013 a, b; Zhu et al., 2017). Musculoskeletal embryonic nuclear protein 1 (*MUSTN1*) gene, identified in rats in 2002, was mainly found in skeletal muscles and tendons (Hadjiargyrou et al., 2002; Liu et al., 2010). Myostatin (*MSTN*), otherwise known as growth differentiation factor 8 (*GDF-8*), significantly expresses in the development and growth of cardiac muscle and skeletal muscle (Hennebry et al., 2008; Mendias et al., 2008). In chicken, it is revealed that the polymorphisms of *MSTN* gene have an impact on several traits and their changes are related to regulating abdominal fat weight, birth weight and breast muscle weight (Gu, 2004). It is also reported that the variations of *MSTN* affect breast meat percentage and multiple traits in duck (Junqing et al., 2011; Xu et al., 2013). The insulin-like growth factor (*IGF*) system categorized as an indispensable regulatory system controls cell proliferation and differentiation in many poultry and mammalian tissues such as muscle, bone, liver, reproductive organs, and

the central nervous system (Castigliego et al., 2010; Dupont and Holzenberger, 2003; Harris and Westwood, 2012; Richards et al., 2005; Song et al., 2012; Xu et al., 2012). Forkhead box 03 (*FOXO3*) is an essential transcriptional regulator that regulates cell proliferation, differentiation, metabolism, apoptosis, and transformation (Accili and Arden, 2004; van der Horst and Burgering, 2007). Overexpression of *FOXO3* down-regulated the expression of *MRFs* (*MYOD*, *MYOG*, *MRF4*, and *MYF5*) which also enhances skeletal muscle proliferation and differentiation suggesting that *FOXO3* may play a vital role in myoblast proliferation and differentiation in poultry (Gan et al., 2016; Yin et al., 2014). Mammalian target of rapamycin (*mTOR*) through Akt/mTOR pathway and nuclear factor kappa-B, subunit 1 (*NFKB1*) are essential for regulating muscle fiber growth and skeletal mass development, thus inhibiting atrophy in muscles (Bodine et al., 2001; Hunter and Kandarian, 2004). *CEBPB* regulates multiple genes in response to growth hormones and activates adipogenesis to inhibit myogenesis (Cui et al., 2011; Hache et al., 2007). Several other candidate genes regulate skeletal muscle development; more research should be made to confirm those that function significantly in the development of poultry skeletal muscle.

MicroRNAs identified in poultry skeletal muscle development

Skeletal muscle development involves several complex processes from the embryonic stage through to the postnatal muscle fiber hypertrophy. During the early stage, mesodermal precursor cells resulting from somites produce the myoblast which fuses to form mature myotubes. The proliferation of myotubes causes it to differentiate into myofibres (Buckingham, 2006; Luo et al., 2013; Velleman et al., 2010; White et al., 2010). After birth, muscle fibers resulting from satellite cell fusion resize to promote muscle growth (Moss and Leblond, 1971). Different studies have been made to identify and characterize several miRNAs related to skeletal muscle development (Andreote et al., 2014; Li et al., 2018), embryo development (Glazov et al., 2008; Hicks et al., 2008), lipogenesis and cell proliferation (Hicks et al., 2010), lung in response to *Mycoplasma gallisepticum* HS (Zhao et al., 2017) among others in chicken.

Several miRNAs have been established to regulate skeletal muscle development at each step of the developmental process. Some of them individually expressed in skeletal muscle cells whiles others showed during differentiation progress implying that miRNAs specifically target tissue gene expression pattern (Luo et al., 2013). With regards to poultry growth and development, much attention is drawn to different miRNAs found at different periods in the embryo and muscle development. Comparatively, for embryo development and tissue-specific maintenance, most miRNAs are substantially expressed in embryos rather than adults (Huang et al., 2008; Li et al., 2011; Liang et al., 2007). Using Solexa sequencing, 42 new miRNA candidates were identified in chicken embryos (3, 4, and 5 days old) from 651,273 reads obtained from dissected somite tissue. Eighteen miRNAs were confirmed of which novel miR-10a (28,660) and miR-10b (113,106) were confirmed to have a high number of reads and most abundant respectively indicating that these two miRs are involved in somite development (Rathjen et al., 2009). It was revealed that from stage

14 of chicken embryo incubation, miR-1 was identified in the somatic myotome which matches with the beginning of skeletal muscle differentiation (Hamburger and Hamilton, 1951); miR-133 from (at stage 15) and miR-206 (at stage 20) were identified in the myocardium and myotome, and somites respectively for fast development of limbs (Darnell et al., 2006). Jebessa et al. (2017) identified several miRNAs in the embryonic stages (E11, E16, and P1). Respectively, 214, 225 and 255 novel miRNAs from 390, 418 and 375 known miRNAs were characterized in chicken skeletal muscle development (Jebessa et al., 2017). The most relatively expressed miRNAs in all the periods were miR-10b-5p, miR-148a-3p, miR-22-3p and miR-133a-3p whereas miR-133a/b, miR-206, miR-486, miR-26a, miR-27b, miR-378, miR-148a, and miR-181 (muscle-specific) which play substantial regulatory roles in skeletal muscle and metabolism were extremely present in skeletal muscle (Jebessa et al., 2017; McCarthy and Esser, 2006). In broilers and layers, miR-125b, miR-221, and miR-206 expressions were confirmed in three developmental stages (9e, 17e, and 21a) (Andreote et al., 2014). Each miRNA exhibited a specific expression pattern during muscle development, but the general model of all miRNAs showed similar expression between the two chicken lines. MiR-125b, miR-221, and miR-206 had the same expression levels at stage 9e; miR-125b and miR-206 had a higher expression at stage 17e than 9e whereas miR-221 had lower expression. The expression level of miR-125b was maintained at stage 21a similar to that observed at 17e, and miR-221 expression was again reduced, while miR-206 resumed to the expression level that was observed at 9e (Andreote et al., 2014).

The miRNA transcriptome of broilers and layers revealed 15 differentially expressed miRNAs involved in skeletal muscle growth of which nine were shown in the broilers and six expressed in females (Li et al., 2011). Also, a study in the breast muscle of pedigree male (PeM) broiler and Barred Plymouth Rock (BPR) chicken lines revealed 38 abundantly expressed mature miRNAs (Khatri et al., 2018). In the Pekin duck, a study identified and validated 15 miRNA using qRT-PCR analysis. By comparing the expression profiles among tissues, three muscle-specific miRNAs (-1, -133, and -206) were highly expressed in the leg, breast and heart muscles; six (6) were related in myogenesis (miR-103a-3p, miR-107, miR-26a-5p, miR-10a-5p, miR-181a-3p and miR-222a); two (2) miRNA (miR-152 and miR-143) were found in all tissues while the remaining four (4) miRNAs (let-7i, miR-23a, miR-24, and miR-214) could be found in either liver or kidney (Gu et al., 2014). In quails, 32 miRNAs were expressed at different periods of the early embryo development. After 24 and 30 h of incubation, expression pattern of 14 of the miRNAs which included let-7a, let-7b, mir-24-3p, mir-26a, mir-122, mir-126, mir-10b decreased in numbers whereas mir-10b, mir-20, mir-103, and mir-196a increased numerically. Finally, the qPCR analysis revealed that seven miRNA: let-7a, let-7b, mir-10b, mir-26a, mir-122, mir-125b, and mir-126 were differentially expressed during early quail embryo development (Schellander et al., 2013).

Table 1. Target genes and functions of miRNAs identified in poultry skeletal muscle

miRNAs	Muscle-specific	Target genes	Functions	References
miR-1	Yes	*HDAC4, YY1, Pax3, Pax7 Cx43*	Muscle differentiation and development	(Chen et al., 2006; Koutsoulidou et al., 2011; McCarthy and Esser, 2006; Wu et al., 2019)
miR-133	Yes	*IGF-1R, nPTB, MAML1*	Muscle differentiation and development	(Chen et al., 2006; Koutsoulidou et al., 2011; McCarthy and Esser, 2006; Wu et al., 2019)
miR-206	Yes	*Pola1, Cx43, Pax3, Pax7*	Muscle differentiation and cell proliferation	(Hak et al., 2006; Jia et al., 2016; Koutsoulidou et al., 2011; McCarthy, 2008)
miR-148	No	*ROCK1*	Promotes muscle differentiation	(Gu et al., 2014; Kablar and Rudnicki, 2000; Zhang et al., 2012)
miR-125b	No	*IGF-II*	Regulates calcification of vascular smooth muscle cells, myoblast differentiation *in vitro*, muscle regeneration *in vivo*, target *IGF*	(Ge et al., 2011; Goettsch et al., 2011; Khatri et al., 2018)
miR-221/222	No	*p27*	Myocyte development into phenotype differentiation	(Cardinalli et al., 2009; Khatri et al., 2018; Liu et al., 2009)
miR-101	No	*MYCN*	Organ establishment and gonad development	(Buechner et al., 2011; Cutting et al., 2012)
miR-181b	No	*Hox-A11*	Establish muscle phenotype during differentiation	(Gu et al., 2014; Naguibneva et al., 2006)
miR-24	No	*Glypican-1*	Enhance proliferation and differentiation	(Gu et al., 2014; Harding and Velleman, 2016; Sun et al., 2008)
miR-214	No	*Ezh2, N-ras*	Promotes muscle cell proliferation and differentiation	(Feng et al., 2011; Flynt et al., 2007; Gu et al., 2014; Juan et al., 2009; Liu et al., 2010)
miR-26a	No	*Ezh2, Smad1, Smad4*	Promotes myogenic differentiation	(Chung and Tellam, 2008; Dey et al., 2012; Gu et al., 2014)
miR-29b	No	*YY1*	Differentiation of muscle progenitor cells (MPCs)	(Gu et al., 2014; Wang et al., 2011)
miR-128	No	*Sp1*	Muscle satellite cell proliferation and myogenic differentiation	(Eun et al., 2008; Gu et al., 2014; Guo et al., 2003)
miR-10a	No	–	Somite development, muscle development, and myogenesis	(Hu et al., 2014; Huang et al., 2010; Khatri et al., 2018)
miR-146b	No	–	Myoblast differentiation and muscle regeneration	(Khanna et al., 2014; Khatri et al., 2018)
miR-126	No	–	Mediates vascular integrity and angiogenesis; regulates skeletal muscle growth; activates *IGF-1*	(Khatri et al., 2018; Rivas et al., 2014; Wang et al., 2008)

Classification of miRNAs

All the identified miRNAs can be classified as muscle-specific (myomiRs), and non-muscle specific (non-myomiRs) and each has a particular role it plays in the skeletal muscle development process (Table 1). To study and understand miRNAs in proliferation and differentiation, the C2C12 mouse myogenic cell line model which mimics several conditions that occur *in vivo* in skeletal muscle development was used (Burattini et al., 2004). Earlier studies *in vitro* have established that, in the presence of myogenin, myosin, differentiation genes and under low serum conditions, culture of C2C12 myoblast could effectuate myoblast to differentiate to form myotubes (Yaffe and Saxel, 1977). However, this C2C12 mainly affected the expression of miRNA in the cell such that seventy-seven miRNAs were up-regulated whereas sixty-eight were down-regulated in differentiation and proliferation stages (Lu et al., 2012). Studies have confirmed that miR-1, miR-133, and miR-206 which were most expressively up-regulated were exceptionally involved in differentiation of skeletal muscle (Chen et al., 2006; Hak et al., 2006). Except for miR-699a which was found to impede muscle differentiation, miR-9-2, miR-122a, miR-703, and miR-805 which were highly down-regulated were seldom found to involve in muscle differentiation (Crippa et al., 2011).

Muscle-specific miRNAs (myomiRs)

As discovered in humans and mouse, this class of miRNAs has also been implicated in the skeletal muscle development in poultry (Gu et al., 2014; Jebessa et al., 2017; Khatri et al., 2018; Wu et al., 2019). MyomiRs are the miRNAs that solely express in striated muscle and presently comprise miR-1, miR-133, miR-206, miR-208a, miR-208b, miR486 and miR-499 (McCarthy, 2008; O'Rourke et al., 2010; van Rooij et al., 2007). However, only three of them (mir-1, mir-133, and mir-206) have been severally studied, recognized and proven in poultry (Jebessa et al., 2017; Wu et al., 2019). Except for miR-206 which is only specific in skeletal-muscle, the other myomiRs express in both skeletal and cardiac muscles (Lagos-Quintana et al., 2002). The expression of the myomiRs is controlled by *MRFs* (*MYOD*, *MYOG*, *MRF4*, *MYF5*), *MEF2s*, *SRF* and several transcriptional factors which play crucial roles in each stage of the muscle development process (Braun and Gautel, 2011; Chen et al., 2006; Potthoff and Olson, 2007; Sweetman et al., 2008; Wood et al., 2013; Wu et al., 2019).

Mechanism and functions of miR-1

MiRNA-1 is associated with the differentiation and development of skeletal muscle. Significantly, researches have proven that miRNA-1 functions in the initial stage through to the later stages in skeletal myocyte development and the homeostatic maintenance of skeletal muscle (Chen et al., 2006). It is also revealed that miR-1 regulates the generation of cardiac muscle and its related diseases (Townley-Tilson et al., 2010). However, these essential functions of miR-1 are regulated and inhibited by several transcription factors. It is revealed that *mTOR* signaling regulates the expression of miR-1 by controlling *MYOD*, a transcriptional factor that promotes the expression of miR-1 (Sun et al., 2010). Activation of miR-1 inhibits the expression

of target genes which suppress muscle development. Histone deacetylase (*HDAC4*) is a transcriptional repressor which hinders *MEF2* protein expression that enhances muscle development (Chen et al., 2006). MiR-1 is capable of constraining the expression of *HDAC4* by binding to its 3UTR, thus promoting muscle cell differentiation (Chen et al., 2006; Wu et al., 2019). Also, miR-1 can inhibit the expression of a zinc-finger transcription factor, *YY1* which negatively regulates muscle gene regulation and *PAX7* which up-regulates *ID2* (inhibitor of DNA binding 2) to repress *MYOD* regulation (Chen et al., 2010; Lu et al., 2012). More so, miR-1 regulates myogenesis through PI3K/Akt signaling pathway which contributes to muscle growth and hypertrophy (Figure 1) (Bassel-Duby and Olson, 2006; Egerman and Glass, 2014). When Akt phosphorylates, it decreases *FOXO3a* (a transcription factor that adversely controls protein synthesis and muscle growth) and regulates miR-1 promoter activity. When the expression of miR-1 decreases, *IGF-1* and *IGF-1R* expression increases because they are target genes to miR-1 (Elia et al., 2009).

Mechanism and functions of miR-133

MiR-1 and miR-133 have similar regulatory functions and transcription factors because they are all transcribed from the same bicistronic transcripts. miRNA-133 (miR-133a/b) functions early in the myogenic stem cells differentiation into myoblast and the growth of complex muscle tissues (Baquero-Perez et al., 2012; Hak et al., 2006; Koomkrong et al., 2015; Takaya et al., 2009). MiRNA-133 promotes myoblast proliferation and regulates the growth and function of myocardium and bone by inhibiting the activity of *SRF* and *TGFBRI* (Wu et al., 2019; Yin et al., 2013; Zhao et al., 2005). It is established that miR-133 repressor decreased the overexpression of miR-133 but greatly increased the expression of *SRF* and *TGFBRI* which suggests that overexpression of miR-133 negatively regulates *SRF* and *TGFBRI* which control the development of skeletal muscles in ducks (Wu et al., 2019). Also, miR-133 inhibits the expression of *IGF-1R*, *nPTB*, and *MAML1*. *MAML* regulates the connection of Notch and *MEF2* to arouse muscle differentiation; *IGF-IR* contributes to embryonic and postnatal development and growth of muscle cell whereas pre-mRNA splicing is controlled by nPTB in muscle and neuron differentiation (Boutz et al., 2007; Huang et al., 2011; Shen et al., 2006). MiR-133a/b regulates MAPK pathway via down-regulation of its transducers (*FFGFR1* and *PP2AC*) to promote differentiation and suppress myoblast proliferation (Feng et al., 2013; Liu et al., 2011). Similar to miR-1, when the expression of myogenin increases, it activates the expression of miR-133 which blocks *IGF-IR*, thereby decreasing the regulation of Akt phosphorylation (Figure 1) (Huang et al., 2011).

Mechanism and functions of miR-206

As described earlier in the above myomiRs, miR-206 which plays similar roles is also a recognized myogenic miRNA which has significant functions during muscle development, and they are abundantly expressed in the skeletal muscle of many animals including poultry (Liang et al., 2007; McDaneld et al., 2009). However they are not always high because its pattern of expression is temporal. Studies have shown that miR-206 inhibited Pola 1 which is the largest subunit of DNA polymerase A

(DNA pol a) for DNA synthesis in myoblast differentiation (Hak et al., 2006). The expression of *Pax3* and *Pax7* (Figure 2) which prevented early differentiation of myoblast is hindered when miR-206 is overexpressed (Chen et al., 2010; Hirai et al., 2010). Overexpression of miR-206 in chicken myoblast increased the expression of myogenin and muscle creatine kinase which are essential genes for muscle differentiation (Jia et al., 2016). A study reported that in the P38 MAPK, ERK1/2, PI3K, and insulin signaling pathways, *ANXA2*, *TPM3*, and *EIF2AK3* genes are up-regulated when miR-206 is suppressed (Khatri et al., 2018). It is established that *ANXA2* (annexin A2) regulates proliferation, migration and cytoskeletal formation in muscle cells (Chen et al., 2014; Draeger et al., 2002); *TPM3* (tropomyosin 3) links with actin filament in muscle cells and troponin complex to regulate contraction of the striated muscle in vertebrates (Lawlor et al., 2010) and *EIF2AK3* (eukaryotic translation initiation factor 2 alpha kinase 3) controls mitochondrial morphology and function (De Mario et al., 2017). Khatri and colleagues proposed that the quick myogenesis displayed in the breast muscle of PeM chickens was due to miR-206 and its own targets interaction (Khatri et al., 2018).

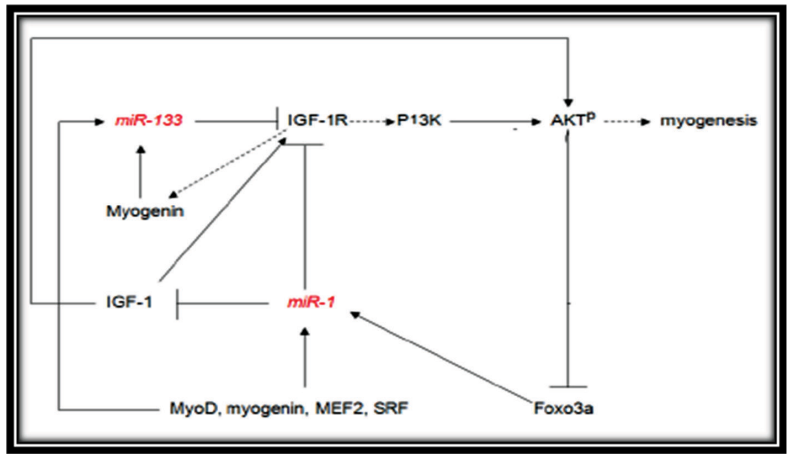

Figure 1. MicroRNAs regulating myogenesis via PI3K/Akt signaling. The dash arrows show the pathway not verified. *MYOD* (myogenic differentiation); *MEF2* (myocyte enhancer factor 2); *SRF* (serum response factor); *AKTP* (phospho-AKT); *Foxo1a* (forkhead box O1); *Foxo3a* (forkhead box O3); *IGF-1* (insulin-like growth factor 1); *IGF-1R* (insulin-like growth factor 1 receptor); PI3K (phosphoinositide-3-kinase) (Xu et al., 2013 b)

Non-muscle-specific miRNAs (Non-myomiRs)

Apart from the muscle-specific identified in poultry skeletal muscle, other miRNAs which are non-muscle specific have also been discovered and proven to play vital roles in the muscle development process. Some of the non-myomiRs identified in the poultry skeletal muscle include: let 7, miR-10, miR-21, miR-22-3p, miR-24, miR-26, miR-27, miR-107, miR-125, miR-126, miR-148, miR-181, miR-196, miR-221, miR-222, and miR-214. Some of the miRNAs promote muscle proliferation and differentiation whereas others negatively regulate muscle differentiation.

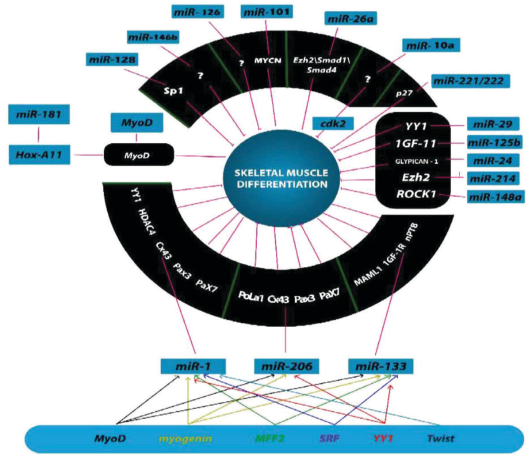

Figure 2. miRNAs regulation in skeletal muscle differentiation in poultry. The figure shows miRNAs (in blue) associated with skeletal muscle differentiation and their mRNA targets (in the black box) and some transcription factors (in the blue box found at the bottom) that control the expression of three muscle-specific miRNAs

Mechanism of non-myomiRs that promote muscle proliferation and differentiation

Among the miRNAs discovered in the poultry, miR-24, miR-26a, miR-181, miR-214, and miR-148 are proven to enhance skeletal muscle differentiation. The overexpression of these miRNAs increases the appearance of the *MRFs* to enhance myoblast differentiation. In C2C12 myoblast differentiation, the levels of miR-24, miR-26a and miR-148a were expressly up-regulated compared to undifferentiated cells. This implies that overexpression of the mentioned miRNAs enhances myogenic differentiation. The high levels of miR-24, miR-26a and miR-148a, could directly inhibit the appearance of their target genes *TGF-β1*, *Ezh2* and *ROCK1* respectively which suppress muscle differentiation (Dey et al., 2012; Sun et al., 2008; Zhang et al., 2012). A study revealed that the expression of glypican-1, a target gene of miR-24 increased significantly at 24 hours then declined at 72 hours of muscle proliferation and differentiation when miR-24 was inhibited (Harding and Velleman, 2016). Creatine kinase, an enzyme which increases during myogenesis was induced when miR-26a was highly expressed (Chung and Tellam, 2008). The muscle phenotype is established upon the up-regulation of miR-181 during myogenic differentiation by inhibiting the expression of *HoxA11*, a target gene that represses the differentiation processes (Naguibneva et al., 2006). In the embryonic stem cells, miR-214 increases muscle cells differentiation and stimulates the transcription of developmental regulators by downregulating PcG proteins which repress this progress in the embryonic stem cells. MiR-214 controls the PcG proteins by targeting the *Ezh2* 3'UTR during transcription (Juan et al., 2009). It also down-regulates N-ras level (proto-oncogene) which inhibits muscle differentiation (Liu et al., 2010). Again, miR-214 promotes

muscle proliferation. To prove this, C2C12 cells were transfected with miR-214 inhibitor and cultured in a growth medium which hindered myoblast proliferation. This shows that miR-214 promotes both muscle differentiation and proliferation (Feng et al., 2011). Overexpression of miR-128 inhibited Sp1 expression, an activator of MyoD which regulates cell proliferation and differentiation. MiR-128 was expressively increased in the brain and skeletal muscles (Guo et al., 2003).

Mechanism of non-myomiRs that negatively regulate muscle differentiation

MiR-221/222 and miR-125 are examples of identified miRNAs in poultry which have been reported to regulate myogenic differentiation negatively (Cardinalli et al., 2009; Ge et al., 2011). A study reported after Northern blot analysis that miR-221/222 acts contrary to miR-133 because they were highly expressed in myoblast to inhibit proliferation and differentiation (Cardinalli et al., 2009). Ras-MAPK signaling pathway down-regulates the expression of miR-221/222 during myogenesis in poultry and mammals (Cardinalli et al., 2009). Even though myoblast proliferation was not altered when miR-125 levels declined, differentiation was negatively regulated in C2C12 myoblast differentiation. MiR-125 targeted *IGF-II* which importantly regulates skeletal myogenesis in the myocytes (Ge et al., 2011).

Conclusion

Skeletal muscle development is a multi-step process regulated by several genetic factors of which miRNAs play an essential role. Two most important transcription factors; the muscle regulatory factors (*MRF*) and myocyte enhancer factor 2 (*MEF2*) families help in the formation and differentiation of muscles. The discovery of miRNAs enhances our understanding of the regulatory roles and mechanisms of these miRNAs which are essential for the skeletal muscle differentiation. These miRNAs can be muscle-specific (miR-1, miR-133, and miR-206) and non-muscle specific (miR-24, miR-181, miR-128, and others). The vital functions of miR-1, miR-133 and miR-206 in myogenesis aid us to comprehend the significance of tissue-specific miRNAs. However, the regulatory functions of non-myomiRs in myogenesis cannot be overlooked. Each of the muscle-specific miRNAs has their mRNA target: miR-1 targets and inhibits *HDAC4*, *YY1*, *Pax 3* and *Pax 7*; miR-133 targets *MAML1*, *IGF-IR*, *nPTB*; and miR-206 targets *Pola 1*, *Pax3*, *Pax 7*. Little is known about the target genes of the other miRNAs. It is projected that several miRNAs control about one-third of mammalian and poultry genes, but the specific targets and roles of most miRNAs have not been discovered which might be helpful in poultry breeding industry.

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Competing Interests

Conflict of Interest: The authors declare that there is no conflict of interest

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