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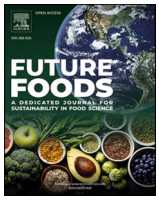

The roles of media ingredients in muscle cell culture for cultured meat production—A mini-review

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ABSTRACT

This review was conducted to provide basic knowledge in developing new culture media for cultured meat production by compiling research on how the main media components affect cell proliferation and muscle differentiation. The culturing process can be divided into five processes: cell acquisition, cell proliferation, cell differentiation, myotube formation, and muscle maturation. To date, cultural media research has shown that amino acids, fatty acids, and carbohydrates mainly act as energy and nutrient sources for cell proliferation and muscle production, and minerals mainly play roles as regulators of cell proliferation and muscle production. Vitamins not only protect cells from oxidative stress but also promote cell growth and regulate cell growth-related genes. Additionally, cytokines play a role in regulating genes related to muscle proliferation and regeneration, and hormones, such as growth factors, insulin, and thyroid hormones, benefit muscle growth and regulation.

1. Introduction

In order to cultivate cells acquired from livestock and prepare them as cultured meat, technologies for culturing them in large quantities at a low cost must be developed. However, there are still many technical challenges in the mass production of industrialized cultured meat (Lee et al., 2021; Lee et al., 2023a). To accomplish full-scale industrialization, studies on the components of the culture media as well as basic studies on the cells themselves are urgently needed. Currently, the development of more effective cell culture media is difficult because information about the roles of media components in cell and muscle growth is very scarce. For example, fetal bovine serum (FBS)—the most important component, accounting for a large portion of the cost—is prepared with a serum extracted from pregnant cows, and despite controversies related to animal welfare, few materials have been developed to replace it (Chelladurai, 2021). In addition, the roles of the other main components constituting the basal media have not been properly studied (Liu et al., 2023). Before the demand for cultured meat, industrialized production of media components was not an issue. There was little need to mass-produce cell culture media at a low cost and there was no regard for food safety, so commercial culture media were used, and there was little need for research on the components.

To successfully industrialize cultured meat production, the ingredients of the culture media must be food safe, low cost, and able to proliferate cells in large quantities or induce differentiation. Since thorough research on the commercial materials currently used for industrialized meat culturing is needed, the purpose of this study is to provide foundational information to aid in developing new cell culture media by reviewing and compiling previous research on how the main cell culture media components affect the cell culture and myogenesis.

2. Essential media ingredients for the culturing of cultured meat

In this study, we identify and classify the main components of the media used at each stage of the cell culturing process. Each classified component may be included in multiple media or as an additional supplement depending on the function of the medium or serum. In some cases, we only know the role of the ingredient and not its exact composition (i.e., FBS, horse serum, etc.). However, understanding the role of specific ingredients and the interactions that occur when they are

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used together is essential for accurately and efficiently mimicking the body's muscle-building process. Currently, there is a lack of systematic research on the roles and efficacies of many cell culture media components, so this review describes only components that have been the focus of published research.

Fig. 1 provides an overview of the meat culturing process. The process can be divided into six stages: cell acquisition, cell proliferation, muscle differentiation, myotube formation, muscle maturation, and cultured meat development. Muscle satellite cell proliferation occurs during the transformation of muscle satellite cells into myoblasts and myocytes, and muscle is created through the formation, differentiation, and maturation of myotubes through the fusion of multiple muscle progenitor cells (Fukada et al., 2022; Dayanidhi and Lieber, 2014). This muscle cell growth process requires specific signaling mechanisms for each stage (Sousa-Victor et al., 2022; Choi et al., 2021, 2020). It is known that when the basal lamina is destroyed by muscle damage, initially dormant muscle satellite cells are activated through interactions with signaling molecules (Grabowska et al., 2013; Kann et al., 2021). Subsequent proliferation and differentiation into muscle fibers are regulated by myogenic regulatory factors expressed in activated muscle satellite cells, and the distance between cells may be important for this interaction (Tavi et al., 2010; Kann et al., 2021). In addition, myogenic differentiation and myoblast fusion occur through signaling by cytokines and hormones (Hindi et al., 2013). This overall process of muscle production can be regulated by components in the medium such as amino acids, growth factors, vitamins, and fatty acids. An investigation was conducted on muscle cells derived from edible meat species, including the mouse myoblast cell line (C2C12), and the media and additives used in each cell culture step and their resulting effects were investigated. The effects of ingredients used in culturing different types of cells have not been clearly compared, and the appropriate dosage for each cell and their effects may be different. Nevertheless, the media used in these stages have many overlapping components, and there are few studies providing clear reasons for their inclusion, assessing their efficacies, or assessing the negative effects of overlapping use. Therefore, the systematic study of each component would be highly beneficial to the production of cultured meat.

2.1. Amino acids

Table 1 summarizes the components contained in basal media used in cultured meat and their roles. Glycine is used in the biosynthesis of glutathione, heme, creatine, nucleic acids, and uric acid and promotes protein synthesis and wound healing (Wang et al., 2013a). In addition, it can be effective in treating muscle-wasting diseases by increasing mammalian target of rapamycin complex 1 (mTORC1) activation, proliferating muscle satellite cells by replenishing the one-carbon unit pool, and regenerating muscle (Lin et al., 2020). Similarly, lysine supplementation is known to be effective in satellite cell proliferation and regulated muscle growth through the mTORC1 pathway (Jin et al., 2019)

Cysteine is an amino acid that promotes cell differentiation, and cystine, which is two cysteine molecules linked by a disulfide bond, has been found to increase the expression of factors involved in neural differentiation (Elkafrawy et al., 2021; Wang et al., 2013b). Cysteine is also used in the synthesis of glutathione, an antioxidant, and can thus protect cells from oxidative stress (Kranich et al., 1998; Elkafrawy et al., 2021).

Gheller et al. (2021) administered serin and glycine together, showing that they sustained the proliferation of muscle stem/progenitor cells. When C2C12 cells, a mouse myoblast cell line, were treated with alanine and glutamine, cell differentiation was promoted in both single (alanine or glutamine) and mixed (alanine and glutamine) treatments, and mixed treatments promoted the proliferation of damaged cells (Liu et al., 2018). Adding glutamine and aspartic acid together led to increased cell growth compared to treatments without glutamine, and these results were confirmed in treatments with L-glutamic acid or glutamic acid alone (Xu et al., 2014; Yamauchi et al., 2002; Jara et al., 2021). Including glutamic acid in the medium also increased glutamine production, and this glutamine promoted cell proliferation in actual piglet muscle and in vitro myogenic cell cultures in a dose-dependent manner (Rubin, 2019; Zhao et al., 2021). Since L-glutamine in a liquid state is unstable in the medium, it is usually added in larger amounts

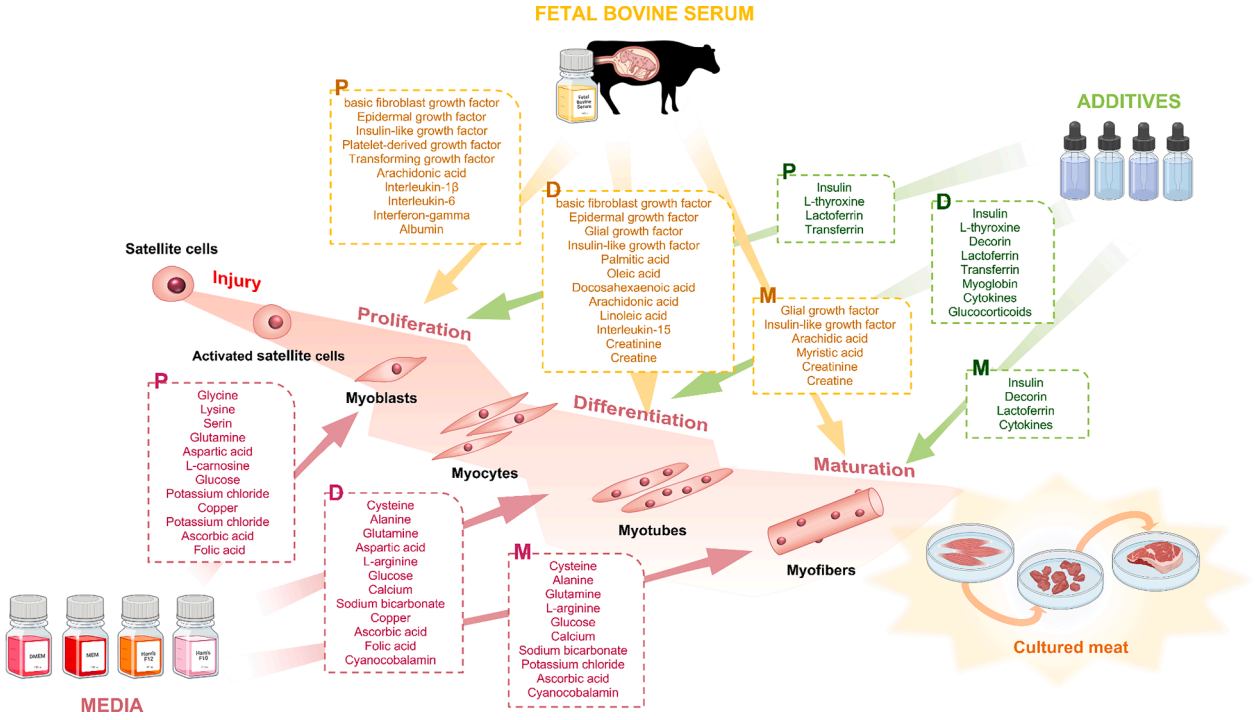

Fig. 1. An overview of the meat culture process showing the culture materials that can be used at each step: proliferation (P), differentiation (D), and maturation (M). Each ingredient can be applied as an overlapping component in MEDIA (pink), FBS (yellow), ADDITIVES (green), or any combination thereof.

Table 1
Overview of the roles of basal media components for the cultured meat.

	Basal media components		Cell Proliferation		Muscle Differentiation		Muscle Maturation		Reference
			Addition	Deficiency	Addition	Deficiency	Addition	Deficiency	
Amino acids	Glycine	Non-essential amino acid synthesized by animals, microorganisms, and plants	+						Gundersen et al., 2005
	Lysine	Essential amino acid which, is play an essential role in the production of carnitine	+						Mountsinai, 2005
	Cysteine	Nutritionally semi essential amino acid and is present mainly in the form of L-cystine in the extracellular space			+				Yin et al., 2016
	Serine	One of the so-called non-essential amino acids, which plays a central role in cell proliferation	+						De Koning et al., 2003
	Alanine	Non-essential amino acid that occurs in high levels in its free state in plasma	+		+				NCBI, 2024a
	Glutamine	The most abundant free amino acid in the body, known to play a regulatory role in several cell specific processes	+ +		+				Curi et al., 2005
	Glutamic acid	Glutamic acid is a ubiquitous amino acid combined with peptides and proteins	+						Garattini et al., 2000
	Aspartic acid	Endogenous amino acid present in vertebrates and invertebrates Playing an important role in the neuroendocrine system, as well as in the development of the nervous system	+						D'Aniello, 2007
	L-Arginine	Precursor of nitric oxide, an endogenous messenger molecule involved in a variety of endothelium-mediated physiological effects in the vascular system	+*						Böger and Bode-Böger, 2001
	L-Carnosine (β-alanyl-L-histidine)	Histidine-containing dipeptide with potent antioxidant properties Exhibiting both pro-oxidant and antioxidant activities	+*						Mahomoodally andKhadaroo, 2022
	Leucine	Through target of rapamycin (mTOR) pathway, leucine increases protein anabolism	+*						Coëffier et al., 2011
	Isoleucine	Isoleucine is BCAAs called branched chain amino acids which play important roles in cellular metabolism and stress responses			+				Wu et al., 2022
	Valine	Valine is one of branched chain amino acids and is considered to be a potent arginase inhibitor			+				Selamnia et al., 1998
Carbohy-drates	Glucose	Ubiquitous source of energy for nearly all living things	+, – –		+				Y. Liu et al., 2022
	Glycogen	Highly branched polymer of glucose found in the liver and muscle, forming distinct cellular organelles and particles	+				+		Mandl et al., 2023
Minerals	Potassium chloride	Mineral used in the management of potassium-chloride cotransport	+		+				Dunham and Logue, 1986
	Calcium	Important mineral which plays a crucial part in cell cycle control			+	–			Whitaker et al., 1990
	Phosphate	Essential nutrient, plays a crucial role in various physiological functions which are enzyme activation and cellular signaling	+		+, – –*				García, 2023
	Sodium bicarbonate	Monosodium salt of carbonic acid with alkalinizing and electrolyte replacement properties			+				NCBI, 2024b
	Copper	Essential trace element crucial for various biological processes, acting as a cofactor in enzymes involved in cellular respiration, connective tissue formation	+	–	+	–			Linder, 2013
	Zinc	Vital micronutrient crucial for the development and functioning of living organisms, playing essential roles in gene expression, enzyme actions, and immune system enhancement	+		+		+		Ozturk et al., 2023
	Magnesium	Essential cation for all living cells, including skeletal myocytes, plays key role in myofiber relaxation	+						Zocchi et al., 2021
Vitamins	Ascorbic acid	Essential water-soluble vitamin, known as vitamin C Acts as antioxidant, protects tissues, cell membranes, and deoxyribo nucleic acid	+*		+				Mittu et al., 2022

(*continued on next page*)

Table 1 (*continued*)

Basal media components		Cell Proliferation		Muscle Differentiation		Muscle Maturation		Reference
		Addition	Deficiency	Addition	Deficiency	Addition	Deficiency	
Folic acid	Crucial micronutrient with significant impacts on human health, known as vitamin B9	+	–	+				Kurowska et al., 2023
Cyanocobalamin	Crucial cobalt corrin complex essential for various biological functions known as vitamin B12			+*				Mantareva et al., 2023
Pyridoxine	Essential for amino acid metabolism, vital member of the vitamin B6 family		–*		–*			Bibi et al., 2024; Tazuya et al., 1993
Riboflavin	Essential nutrient acting as coenzymes in flavoproteins involved in biochemical pathways, known as vitamin B2		–					Nani et al., 2020
Vitamin D3	Secosteroid hormone that has immunomodulatory, antioxidant, and anti-inflammatory effects	+						Tripathi and Mishra, 2023

+: positive effects of content, ++: positive effects of excessive content, –: negative effects of contents, – –: negative effects of excessive content.
* : results of animal experiment.

than other amino acids. In the culture medium, L-arginine is oxidized to CO_2 and ammonia and can act as an energy source for cells.

Yao et al. (2008) showed that feeding diets supplemented with L-arginine to piglets stimulated protein synthesis in skeletal muscle by improving the levels of mTOR and 4E-binding protein-1 (4E-BP1). The amino acid L-carnosine (β-alanyl-L-histidine) is a natural dipeptide that exists in relatively high concentrations in skeletal muscle. When fed to pigs, it activates the Akt/mTOR/S6K signaling pathway and promotes the proliferation of muscle satellite cells, ultimately improving muscle growth (J. Liu et al., 2022).

Among these amino acids, L-arginine has been shown to stimulate the growth and proliferation of pre-adipocytes, while leucine, isoleucine, and valine have been shown to stimulate adipocyte differentiation through acetyl-CoA production (Ma et al., 2017; Green et al., 2016; Lee et al., 2023b).

Taken together, the research has shown that amino acids play important roles in cell culture media, including roles in muscle protein synthesis, muscle regeneration, protecting cells from oxidative stress, and promoting cell proliferation and cell differentiation. Additionally, they may act as an energy source for muscle cells. Therefore, they are thought to be very important in the cell culture medium, and studies on the individual effect of each amino acid on cell growth, muscle production, and development are needed.

2.2. Carbohydrates (sugars)

Glucose is an important component of the basal medium and acts as another major energy source in cells (Furuichi et al., 2021). Normal proliferating cells prefer a high glucose content, but Furuichi et al. (2021) showed that glucose actually reduced Pax7 expression in skeletal muscle satellite cells at too high a concentration (19 mM). Glucose supplementation at a 20–25 mM level increased the differentiation of muscle satellite cell cultures into adipocytes and dramatically increased intracellular lipid accumulation (Aguiari et al., 2008; Yue et al., 2010). Conversely, the addition of 2 mM glucose or 15 mM glucose combined with insulin (50 nM) was found to favor skeletal muscle growth, regeneration, or differentiation (Grabiec et al., 2014; Furuichi et al., 2021). This glucose, along with galactose, also helps in adipogenesis, while sucrose is also used as an energy source by adipocytes (Krishna et al., 2020). It was also found that FABP4, a marker of adipogenesis, was highly expressed (Delcourt et al., 2020).

Since glucose in the blood and glycogen in the muscle are the only carbohydrates in animal cells, they can be expected to play significant roles as energy sources in the cell culture process. However, it has also been reported that excess glucose negatively affects the cell culture process because it can affect osmotic pressure in the cell medium and promote cell death by affecting the overexpression of excessive cell proliferation-related genes (Federici et al., 2001; T. Liu et al., 2022). Therefore, it will be necessary to study the optimal amount of carbohydrates in cell culture media.

2.3. Minerals

Potassium chloride can activate insulin-like growth factor (IGF)−1 and increase myoblast proliferation through a paracrine mechanism (Kravchenko et al., 2019). Myoblasts may influence muscle hypertrophy. Sufficiently differentiated muscle cells can perform muscle contraction. Potassium chloride, which is also released from contracting myotubes, likely stimulates the development of muscle hypertrophy, acting through a paracrine mechanism to activate IGF-1 and increase myoblast proliferation (Kravchenko et al., 2019). Calcium and phosphate both induce muscle contraction, and tissue movement can be observed when the myotubes are well-formed (Porter et al., 2002; Chung et al., 2020). Calcium is released by the action potential, enabling cross-bridges between myosin and actin and causing muscle contraction. Additionally, lowering the calcium concentration in C2C12 cells decreased myogenin (Myog) expression and increased Myf5 expression, inhibiting skeletal myoblast differentiation (Porter et al., 2002). According to Yamaguchi et al. (2013), sodium bicarbonate is involved in the differentiation of human skeletal muscle myoblasts under mild heat stress, increasing mRNA levels of MyHC type I while decreasing MyHC IIx mRNA levels. It has been shown to upregulate factors involved in MyHC I regulation, thereby influencing muscle fiber type during cell differentiation (Yamaguchi et al., 2013). On the other hand, high phosphate (Na_2HPO) levels inhibit muscle differentiation by reducing myotube size, the fusion index, and myogenin expression in C2C12 skeletal muscle cells (Chung et al., 2020). The addition of high phosphate reduced the expression of myogenin even when mice were simply fed a high-phosphate diet (Chung et al., 2020). Additionally, the intracellular concentration of copper directly affects the proliferation, differentiation, and death of mammalian cells, with deficiencies and excesses producing negative effects (Agarwal et al., 1989). Zinc promotes not only myoblast proliferation and differentiation but also the maturation of muscle fibers by increasing the activity of the PI3K/Akt pathway (Mnatsakanyan et al., 2018).

Additionally, various trace minerals such as copper, zinc, and iron regulate the growth of adipocytes, and calcium in adipocytes regulates lipid metabolism and induces adipogenesis (Winiarska-Mieczan et al., 2021; Karava et al., 2021 Karava et al., 2021). In addition, studies have been conducted to show that phosphate limitation promotes adipocyte differentiation by interfering with mTORC1 signaling (Ko et al., 2020).

Thus, to summarize the main findings of research on minerals in cell

culture media, potassium acts on cell proliferation, and calcium not only acts as a trigger for the contraction of muscles but also appears to influence cell proliferation and differentiation. Phosphate and zinc are also reported to play roles in controlling cell proliferation and expression. Therefore, minerals are thought to play a role in regulating not only muscle contraction but also cell proliferation and differentiation.

2.4. Vitamins

In C2C12 cells, ascorbic acid (Vitamin C) phosphate induced thick and long myotube formation and increased the expression levels of myosin heavy chain (MYH) 1/2 and *Myh1, Myh4*, and *Myh7* (Diao et al., 2021). Although only studied in fish (*Piaractus mesopotamicus*), the addition of ascorbic acid increased myoblast proliferation and mRNA expression of myog and *mtor*, markers associated with skeletal muscle myogenesis and protein synthesis (Duran et al., 2019; Zanella et al., 2021). These results suggest that ascorbic acid's role in preventing oxidative stress can have a meaningful effect on muscle satellite cells. Folic acid (Vitamin B9) enhances the differentiation of C2C12 cells and the expression of myogenin, and when deficient, it can affect skeletal muscle development by inhibiting proliferation and inducing cell cycle disruption (Li et al., 2018; Hwang et al., 2018). Cyanocobalamin (Vitamin B12) is the only mineral vitamin that animals cannot produce. In cell cultures, it promotes the differentiation of C2C12 cells and thickens the diameter of the resulting muscle fibers through the transforming growth factor (TGF)-β signaling pathway (Li et al., 2022). Pyridoxine (Vitamin B6) deficiency impairs muscle formation by reducing the number of quiescent satellite cells and producing defects in the proliferation of activated satellite cells (Komaru et al., 2021). It can also adversely affect the viability and function of satellite cells by reducing the levels of muscle amino acids and peptides, such as carnosine and anserine, in muscle cells (Komaru et al., 2021). Similarly, riboflavin (Vitamin B2) deficiency can affect cell growth and development by disrupting the normal progression of the cell cycle (Powers et al., 2012; Mazur-Bialy and Pocheć, 2017). Molinari et al. (2021) confirmed that the addition of vitamin D3, magnesium, potassium, and curcumin can increase C2C12 cell viability when added in combination to the culture medium. This combination potentially improves muscle recovery after intense activity and ultimately may prevent a loss of muscle mass (Molinari et al., 2021).

In the case of adipocytes, L-ascorbic acid-2-phosphate increased cell growth at a concentration of 250 mM, but exhibited cytotoxicity at high concentrations, showing dose-dependent cell death, and pyridoxine deficiency led to decreased adipogenesis (Wu et al., 2020; Mascolo and Verni, 2020). In addition, various studies have been conducted on the effects of vitamins such as folic acid and cyanocobalamin deficiency leading to lipid accumulation and differentiation of pre-adipocytes (Yu et al., 2014; Chan et al., 2022; Boachie et al., 2020).

Looking at the main known effects of vitamins in the cell culturing process, ascorbic acid (Vitamin C) has been shown to promote muscle production by increasing the expression of muscle protein-related genes as well as preventing cell oxidative stress by acting as an antioxidant, and folate has been reported to promote muscle development. Pyridoxine deficiency has been shown to affect muscle growth and development because it reduces the number of cells and the levels of amino acids and peptides in the muscle. Since most vitamins can play an important role in cell growth and development, further studies on the use of each for the production of cultured meat are needed.

3. Important FBS ingredients for the culturing of cultured meat

3.1. Growth factors

Table 2 summarizes the FBS components and their roles, excluding other components already covered in Table 1. A number of growth factors known to affect muscle cell differentiation and growth are present in FBS. When mouse myoblasts were co-cultured with basic fibroblast growth factor (bFGF), myoblast viability was significantly improved compared to the control group, and significantly higher *myogenin* and lower *MyoD1* expression levels were detected during differentiation (Hagiwara et al., 2016), indicating that myoblasts differentiated into the myotubes. Epidermal growth factor (EGF), developed by D'Andrea et al. (2019), reportedly increased the number of mouse muscle satellite cells, and affected protein synthesis by increasing the expression of creatine phosphokinase, an indicator of muscle-specific differentiation in sheep muscle satellite cells (Roe et al., 1989). Fibroblast growth factor (FGF), which is involved in the proliferation of satellite cells in muscle tissue, is necessary for the maintenance and repair of skeletal muscle (Sheehan and Allen, 1999; Pawlikowski et al., 2017). Among the FGF family proteins, FGF1, 2, 4, 6, and 9 stimulated the proliferation of muscle satellite cells in mice, surpassing that of the control group, and when administered together with hepatocyte growth factor (HGF), FGF2, 4, 6, and 9 each produced higher satellite cell proliferation than HGF alone (Sheehan et al., 1999). Syndecan—a member of the heparan sulfate proteoglycan (HSPG) family of proteins, required for FGF and HGF to signal to their receptors—is closely associated with muscle tissue growth and differentiation, and syndecan-3 and syndecan-4 are expressed in all satellite cells for at least 96 h. Considering that, it is believed that HSPG plays an important role in muscle regeneration (Cornelison et al., 2001). However, Yamada et al. (2010) reported that high concentrations of hepatocyte growth factor (HGF) inhibit the proliferation of skeletal muscle satellite cells by inducing the expression of myostatin. Glial growth factor (GGF) 2 stimulated myogenesis in a long-term perspective, stimulating cell fusion and increasing creatine kinase, while the effects of IGF on myogenesis of myoblast were also confirmed (Florini et al., 1996). The latter is an important component in muscle development and growth, and IGF-I and IGF-II are regulated through interactions with IGF binding protein (IGFBP) to promote the appropriate proliferation and differentiation of satellite cells and myoblasts (Stewart and Rotwein, 1996; Oksbjerg et al., 2004; Wildemann et al., 2007; Aboalola and Han, 2017). More specifically, IGF-I affects early-stage muscle formation, and IGF-II enhances muscle differentiation through the expression of muscle differentiation markers MyoD, MyoG, and MHC (Aboalola et al., 2017). Platelet-derived growth factor (PDGF) stimulates mouse myoblast proliferation (Wildemann et al., 2007), while TGF inhibits the progression of muscle precursor cells, cell proliferation, and differentiation because it delays skeletal muscle formation by inhibiting Myf5 and MyoD induction (Syverud et al., 2016). However, in another study, culturing primary muscle cells with TGF-β1 stimulated the synthesis of collagen type I and led to the formation of denser myofiber (Weist et al., 2013).

Al-Mansoori et al. (2022) revealed that adipogenesis is regulated by several transcription factors, such as preadipocyte factor-1 (Pref-1) and sterol precursor element binding protein-1 (SREBP-1), which stimulate the differentiation of mesenchymal stem cells and preadipocytes to produce mature adipocytes (Al-Mansoori et al., 2022). IGF-1 is directly involved in the differentiation and growth of immature adipocytes, and vascular endothelial growth factor regulates the morphological characteristics and function of fat (Al-Samerria and Radovick, 2021; Jin et al., 2018; Song et al., 2010).

Growth factors are important components of FBS that affect muscle satellite cell proliferation and differentiation, and the combinations of growth factors and their interactions can be powerful inducers of satellite cell proliferation and differentiation. However, because the types, amounts, and effects of all growth factors in serum have not been completely elucidated, we believe that further research would improve our control of the muscle development process through advancements in the composition and content of the cell culture medium.

3.2. Fatty acids

Triglyceride, a form of fat, is stored in lipid droplets in skeletal

Table 2
Overview of the roles of FBS components for the cultured meat.

FBS components			Cell Proliferation		Muscle Differentiation		Muscle Maturation		Reference
			Addition	Deficiency	Addition	Deficiency	Addition	Deficiency	
Growth factors	Basic fibroblast growth factor (bFGF)	Multifunctional protein that in promoting muscle regeneration, glucose uptake, and muscle mass maintenance in various physiological conditions	+*		+*				Jin et al., 2022
	Epidermal growth factor (EGF)	Crucial stimulatory growth factor in the human body, belonging to the receptor tyrosine kinase family, and is involved in cell proliferation, differentiation, and growth	+*		+*				Salajegheh, 2016
	Fibroblast growth factor (FGF) 1, 2, 4, 6, 9	Diverse family of polypeptide specific cell-surface receptors, influencing cell proliferation, migration, differentiation, and survival	+*						Ornitz and Itoh, 2001
	Hepatocyte growth factor (HGF)	Multifunctional cytokine that plays a crucial role in cell growth, motility, and morphogenesis	– –		+				Salajegheh, 2016
	Glial growth factor (GGF) 2	Cytokine known as glial cell line-derived neurotrophic factor (GDNF)			+		+		Xu et al., 2023
	Insulin-like growth factor (IGF)	Single-chain polypeptides with proinsulin homology Promote mitogenesis, cell differentiation, and prevent cellular apoptosis			+		+		Winston and Arora, 2006
	Insulin-like growth factor-I (IGF-I)	Produced by liver in response to growth hormone Involved in promoting growth and various physiological processes		+		+			Livingstone, 2013
	Insulin-like growth factor-II (IGF-II)	Peptides involved in various physiological processes and stimulate cell proliferation		+		+			Janssen, 2020
	Platelet-derived growth factor (PDGF)	Crucial mitogen with trophic effects on various cell types, stored in platelet α-granules and produced by different cells		+*					Heldin and Westermark, 1999
	Transforming growth factor (TGF)	Small, single-chain polypeptide expressed by developing and adult tissues Stimulates growth, repair, or migration of neighboring epithelial cells		–*		–*			Hsuan, 2004
	Transforming growth factor-β1 (TGF-β1)	Prototype of the TGF-β superfamily, an evolutionary conserved family of structurally related dimeric cytokines with representatives in organisms					+		Janssens et al., 2005
Fatty acids	Lauric acid	Primary fatty acid coconut oil reported many metabolic benefits			+				Alfhili and Aljuraiban, 2021
	Myristic acid	Straight-chain, fourteen-carbon, long-chain saturated fatty acid mostly found in milk fat			+				European Bioinformatics Institute, 2021
	Palmitic acid	Common 16-carbon saturated fat that represents 10–20% of human dietary fat intake	No Effect		No Effect, –		–		Cayman Chemical, 2019a
	Oleic acid	Unsaturated fatty acid that is the most widely distributed and abundant fatty acid in nature	+, –		No Effect, +				Drugbank, 2021
	Docosahexaenoic acid	Long-chain, highly unsaturated omega-3 (n-3) fatty acid			+				Calder, 2016
	Linoleic acid	The most highly consumed PUFA found in the human diet	+, –		+				Whelan and Fritsche, 2013
	Arachidonic acid	Integral constituent of biological cell membrane, conferring it with fluidity and flexibility	+		+				Hanna and Hafez, 2018

(*continued on next page*)

Table 2 (*continued*)

FBS components			Cell Proliferation		Muscle Differentiation		Muscle Maturation		Reference
			Addition	Deficiency	Addition	Deficiency	Addition	Deficiency	
	Arachidic acid	Long-chain saturated fatty acid that has been found in peanut butter and anaerobic fungi			+		+		Cayman Chemical, 2019b
	Palmitoleic acid	16-carbon unsaturated fatty acid that mainly originated from de novo lipogenesis	–		–				Frigolet and Gutierrez-Aguilar, 2017
Interleukins and Interferons	Interleukin-15	Pleiotropic cytokine with a broad range of biological functions in many diverse cell types			+				Perera et al., 2012
	Interleukin-1β	Potent pro-inflammatory cytokine that is crucial for host-defense responses to infection and injury	+						Lopez-Castejon and Brough, 2011
	Interleukin-6	Soluble mediator with a pleiotropic effect on inflammation, immune response, and hematopoiesis	+ +						Tanaka et al., 2014
	Interleukin-1α	Comprised of 11 members that have pleiotropic functions in inflammation and cancer			–				Malik and Kanneganti, 2018
	Interleukin-17	Key cytokine that links T cell activation to neutrophil mobilization and activation			–				Zenobia and Hajishengallis, 2015
	Interferon-β	Cytokine that is naturally produced by the immune system in response to biological and chemical stimuli			–				Abdolvahab et al., 2016
	Interferon-γ	Multifaceted cytokine with significant roles in antiviral, antimycobacterial, and antitumor immunity	+				+		Salas et al., 2023
The others	Cholesterol	Chameleon biomolecule in cellular multiplex		–	+				Saxena and Chandra, 2020
	Albumin	Hydrophilic protein synthesized in the liver and catabolized in various tissues, including the kidney	+						Gburek et al., 2021
	Creatine	Waste product that comes from the digestion of protein in your food and the normal breakdown of muscle tissue	+		+				National Kidney Foundation, 2023
	Iron	Critical roles in electron transport and cellular respiration, cell proliferation and differentiation	–		– –				Boldt, 1999

+: positive effects of content, ++: positive effects of excessive content, –: negative effects of contents, – –: negative effects of excessive content.
*: results of animal experiment.

muscle and can be hydrolyzed to produce fatty acids (Watt and Cheng, 2017). Lauric acid increased MHCIIb protein expression and the proportion of IIb muscle fibers in C2C12 cells (Wang et al., 2018). It also increased the mRNA expression of genes involved in glycolysis, such as *HK2* and *LDH2*, and it is presumed that these processes were achieved through the activation of TLR4 signaling (Wang et al., 2018). Myristic acid (14:0) increased the protein level of β-tubulin and increased DGKδ-dependent glucose uptake activity in C2C12 myoblasts (Sakai et al., 2022). Since β-tubulin constitutes microtubules and is related to muscle mass, it is believed that myristic acid may improve skeletal muscle mass (Sakai et al., 2022). Also, in the same study, lauric acid (12:0), palmitic acid (16:0), and oleic acid (18:1) were confirmed to have no such effects (Sakai et al., 2022). In another study, palmitic acid decreased the number and diameter of myotubes in C2C12 cells and impaired myotube formation by reducing protein synthesis, despite having no effect on proliferation (da Paixão et al., 2021). Specifically, a greater number of type II fibers were formed in the treated group than in the non-treated group (da Paixão et al., 2021). Although the conditions were slightly different between studies, palmitic acid, oleic acid, docosahexaenoic acid, and linoleic acid have all been confirmed to promote differentiation by inducing cell fusion in bovine, chick, and mice cells (Sun et al., 2023; Xu et al., 2018; Allen et al., 1985; Hurley et al., 2006). Hurley et al. (2006) also suggested that the presence or absence of cis-9 double bonds in fatty acids may influence muscle cell differentiation. Arachidonic acid has been confirmed to stimulate both proliferation and differentiation in bovine myoblasts (Leng and Jiang, 2019; Leng, 2018), and arachidic acid induced differentiation in C2C12 cells through the COX-2-dependent pathway, increasing myotube size, muscle content, and protein attachment in a dose-dependent manner and resulting in cell hypertrophy (Markworth and Cameron-Smith, 2013).

In bovine skeletal muscle satellite cells, palmitoleic acid down-regulated the expression of the *Pax3, Pax7*, and *myogenin* genes, which are related to muscle fiber development, and it was confirmed that muscle fiber development was reduced (Zhang et al., 2021). In another study, linoleic acid and oleic acid promoted cell proliferation without the death or necrosis of satellite cells and upregulated the expression of *PPARγ*, a gene related to lipid metabolism (Belal et al., 2018). Conversely, the expression of adipocyte transcription factors increased, allowing some of the bovine skeletal muscle satellite cells to be converted into adipocytes, which significantly increased the triacylglycerol

content and the size of lipid droplets in the cultured cells (Zhang et al., 2021). Similarly, oleic acid induced lipid droplet formation in satellite cells (Sun et al., 2023). Choi et al. (2015) studied the effects of various saturated and unsaturated fatty acids using bovine semimembranosus satellite cells and intramuscular preadipocytes. Saturated fatty acids, particularly stearic acid and palmitic acid, promoted lipogenesis and lipid gene expression, while conversely, unsaturated fatty acids, especially oleic acid and linoleic acid, decreased the expression of genes related to fatty acid metabolism (Choi et al., 2015). These fatty acids have also been shown to affect the growth and development of adipocytes. Docosahexaenoic acid, which belongs to the omega-3 fatty acid family, is known to inhibit adipocyte differentiation and induce cell death, and long-chain saturated fatty acids and polyunsaturated fatty acids can affect adipocyte growth by regulating transcription factors of adipocytes (Kim et al., 2006; Azain, 2004). In addition, oleic acid and stearic acid have been shown to affect the production and maturation of adipocytes (Malodobra-Mazur et al., 2020).

Taking the previous research as a whole, fatty acids have been shown to be involved in the production of muscle fibers through muscle protein expression during cell and muscle production, and it has been reported that they not only affect the absorption of glucose in muscle cells but also promote cell differentiation. However, there are studies showing that palmitoleic acid reduces muscle development-associated gene expression. Additionally, saturated fatty acids promote lipid gene expression, while unsaturated fatty acids reduce it. The addition of fatty acids may contribute to increasing the fat content of the final meat product by increasing lipid droplets. Therefore, it is considered necessary to control the fatty acid composition in the cell culture medium.

3.3. Interleukins and interferons

Interleukin (IL)−15— a myokine, that is a hormone produced in muscles—promoted the differentiation of pig muscle satellite cells (Li et al., 2014). Otis et al. (2014) suggested that increased IL-1β expression after muscle injury increases NF-κB activity, which may affect the proliferation of skeletal muscle satellite cells, and although this paper found no effect, higher concentrations of IL-6 promoted myoblast proliferation in cell cultures (Wang et al., 2008). However, Li et al. (2009) showed that exposure to IL-1α or IL-1β stimulates NF-κB signaling but ultimately reduces myofibrillar proteins in terminally differentiated myotubes. Additionally, IL-17 induces osteogenic differentiation by activating the ERK1,2 mitogen-activated protein kinase signaling pathway in C2C12 myoblasts and inhibits myogenic differentiation by downregulating the expression of myogenin and MyHC (Kocić et al., 2012). In contrast to their effects on muscle, previous studies have shown that IL-6, IL-15, and IL-17, as well as IL-18, IL-33, IL-1β, and IL-1F6, all impair or reduce adipogenesis (Al-Mansoori et al., 2022; Fuster et al., 2011; Quinn et al., 2005).

Among type 1 interferons, interferon-β affects the differentiation ability of mouse myoblasts (C2C12) and impairs myotube formation (Franzi et al., 2013). Conversely, interferon-γ, the only type 2 interferon, promotes muscle regeneration by promoting the proliferation of mouse skeletal muscle cells and also reduces fibrosis by inhibiting signaling of TGFβ1, a fibrotic stimulant (Cheng et al., 2008; Kelić et al., 1993; Foster et al., 2003).

3.4. Other FBS components

In the study of Hana et al. (2021), treating C2C12 and HepG2 cells with unconjugated bilirubin slightly increased the absorption of free fatty acids under low blood glucose conditions, an effect absent at higher glucose concentrations. When an environment depleted of cholesterol was created by adding methyl-β-cyclodextrin, the proliferation of chick myoblasts was inhibited and the expression level of p53 increased (Mermelstein et al., 2005). Additionally, when chick myoblasts were differentiated, myotubes formed were about three times thicker than those grown in media that was not depleted of cholesterol, and various related transcription factors were either up- or down-regulated in the muscle cells (Mermelstein et al., 2005; Possidonio et al., 2014). Albumin is effective in satellite cell proliferation to the extent that when only recombinant human albumin is added under serum-free medium conditions, the short-term growth of satellite cells for cultured meat production appears similar to that with the addition of 20% FBS (Stout et al., 2022). Creatine not only promotes protein adhesion, muscle-specific protein synthesis, and growth but also favors myogenesis in cultured muscle cells (Sestili et al., 2016). In C2C12 cells, creatine promoted myoblast fusion and enhanced the expression of myosin heavy chain type II, troponin T, and titin, and it was confirmed that the p38 and Akt/PKB-p70s6k pathways were involved in inducing this differentiation improvement (Deldicque et al., 2007). Conversely, excess iron can have a negative effect on C2C12 cell growth. It not only reduced the expression of satellite cell markers and myoblast differentiation markers but also delayed myogenesis by reducing the size of regenerated muscle fibers and reducing phosphorylation in the MAPK signaling pathway (Ikeda et al., 2019).

4. Important additives for media development of cultured meat

Table 3 summarizes the culture media additives and their roles in cultured meat production. Insulin can promote muscle satellite cell survival and self-renewal, promote myoblast growth, and regulate muscle protein synthesis and hypertrophy (Ahmad et al., 2023). In human embryonic stem cells, insulin can inhibit caspase cleavage and apoptosis and promote cell survival by activating the PI3K/AKT cascade (Godoy-Parejo et al., 2019). Additionally, it was confirmed that cells spread on matrigel exhibited suppressed myosin light chain phosphorylation (Godoy-Parejo et al., 2019). The addition of insulin after the formation of a sufficient amount of satellite cells promoted satellite cell fusion (Allen et al., 1985). Also, the treatment of chick skeletal muscle myoblasts with insulin increased the cell number, the extent of fusion, and creatine phosphokinase activity, but the formed myotubes can rapidly degenerate (Kumegawa et al., 1980). The hormone L-thyroxine, when added alone, had a small effect on myogenesis, but differentiated myotubes were maintained for a relatively long time, and when L-thyroxine and insulin were added together, a synergistic effect on cell proliferation and differentiation was confirmed (Kumegawa et al., 1980). Decorin, a small leucine-rich proteoglycan, up-regulated myogenic genes *Myf5, Myf6, MyoD*, and *myogenin*, and down-regulated *TGF-β1* and *myostatin*, causing C2C12 myoblasts to differentiate into myotubes at a high rate (Li et al., 2007). This effect indicates that decorin not only prevents fibrosis but also improves muscle regeneration (Li et al., 2007).

Lactoferrin is a glycoprotein that promotes the proliferation of C2C12 cells (Kitakaze et al., 2018). Lactoferrin increased the expression of myosin heavy chains and promoted myotube formation and increased their size. This effect may be due to low-density lipoprotein receptor-related protein 1 (Kitakaze et al., 2018). Transferrin, which is found in early chicken muscles during embryonic development, is a glycoprotein involved in iron transport that reduces cell death in neuro-2a cells and favors the neuronal differentiation process (Matsuda et al., 1984; M.J. Pérez et al., 2023). Simsa et al. (2019) cultured bovine myosatellite cells with hemoglobin or myoglobin proteins from bovine blood or equine muscle. While hemoglobin had no effect or a slight negative effect, myoglobin significantly increased proliferation and metabolic activity. Fibro-adipogenic progenitor cells within the muscle support muscle regeneration by releasing cytokines that stimulate the differentiation of muscle stem cells (Cerquone Perpetuini et al., 2020). Additionally, glucocorticoids have shown an effect on myogenesis by inhibiting the adipogenesis of muscle fiber-adipose progenitor cells and promoting the terminal differentiation of satellite cells (Cerquone Perpetuini et al., 2020). In the case of adipocytes, insulin has been shown to increase the amount of GLUT4 glucose transporter to enhance glucose

Table 3
Overview of the roles of additives for the cultured meat.

Additives		Cell Proliferation		Muscle Differentiation		Muscle Maturation		Reference
		Addition	Deficiency	Addition	Deficiency	Addition	Deficiency	
Insulin	Polypeptide hormone mainly secreted by β cells in the islets of Langerhans of the pancreas	+		+				Rahman et al., 2021
L-thyroxine	Synthetic T4 hormone that is biochemically and physiologically indistinguishable from the natural one	+		+				Colucci et al., 2013
Decorin	Small leucine-rich proteoglycan involved in extracellular matrix interactions and signaling			++*		+*		Kubo et al., 2022
Lactoferrin	Glycoprotein that promotes the proliferation of C2C12 cells	+*		+*		+*		Kitakaze et al., 2018
Transferrin	Iron-binding glycoprotein which, is enhances neuronal differentiation by reducing cell death	+*		+*				M.J. Pérez et al., 2023
Hemoglobin	64k Da protein that carries oxygen to cells and tissues in vertebrates	No Effect, –*		No Effect, –*		No Effect, –*		Utsugisawa and Kanno, 2022
Myoglobin	Crucial oxygen-binding protein found in cardiac myocytes and skeletal muscle fibers, traditionally known for its role in oxygen storage and transport	+*		+*		+*		Sarkarati et al., 2023
Glucocorticoids	A class of anti-inflammatory steroids, play anti-inflammatory and immunosuppressive effects			+				Mitre-Aguilar et al., 2022

+: positive effects of content, ++: positive effects of excessive content, –: negative effects of contents, – –: negative effects of excessive content.
*: results of animal experiment.

uptake, and it has been reported that the lactoferrin receptor LRP1 may contribute to adipogenesis (Santoro et al., 2021; Jamka et al., 2020).

To sum up our current understanding of cell culture additives for cultured meat production, insulin is an important additive because it plays an important role in muscle metabolism by converting glucose into glycogen. Thyroid hormones could also be essential for cell growth because they increase the basal metabolic rate of muscles and promote carbohydrate, fat, and protein metabolism as well as oxygen consumption. Lactoferrin promotes muscle tube formation and transferrin is reported to be an important substance in cell cultures because it inhibits apoptosis.

5. Development of media for cultured meat production

Currently, many studies are accelerating the development of media for cultured meat production. According to a study by Kanayama et al. (2022), there was no significant difference in cell growth and differentiation (C2C12 and bovine skeletal muscle-derived primary cell) when the ingredients present in Dulbecco's Modified Essential Medium (DMEM) medium were replaced with food grade ingredients (Kanayama et al., 2022). In addition, FG-DMEM was developed by replacing the composition raw materials of existing DMEM with food grade ingredients, such as adding L-arginine HCl instead of L-arginine or choline chloride instead of glycerophosphatidylcholine, and showed similar effects to DMEM on proliferation and differentiation ability (Kanayama et al., 2022). Stout et al. (2022) developed Beefy-9, which is suitable for culturing bovine satellite cells for cultured meat production, based on serum-free medium (B8) for human stem cell culture. In this process, the addition of recombinant albumin made it possible to grow and maintain cells without FBS, but considerable additional costs were incurred. Afterwards, recombinant albumin was replaced with rapeseed protein isolate (RPI), and Beefy-R was developed, which is effective in reducing unit costs, promoting differentiation, and maintaining cell identity and myogenicity (Stout, 2023). In the study by Yamanaka et al. (2023), *Chlorella vulgaris*-derived nutrient medium (CVNM) was used as a basal medium. Unlike DMEM, CVNM contains nutrients and cell-secreted growth factors, and in particular, the concentration of IGF-2 (insulin--like growth factor-2) is significantly higher, promoting the growth of bovine myoblast cells (Yamanaka et al., 2023). However, since both FG-DMEM and CVNM treatments showed higher cell proliferation efficiency when FBS was added, the use of FBS is still unavoidable. In another study, a serum-free medium for cultured meat production was developed by adding black soldier fly larvae (*Hermetia illucens*) hydrolyzate to B8, a serum-free medium (Garg, 2024). This medium showed excellent proliferation efficiency to the extent that there was no significant difference from the FBS-added medium in the growth of spheroid cells (BSC) (Garg, 2024). Kolkmann et al. (2022) developed chemically defined serum free media (SFM). SFM replaced FBS by adding chemical ingredients such as albumin, α-linolenic acid, GlutaMAX™, and FGF-2 based on DMEM/F12 medium, and was confirmed to maintain 97% growth rate and differentiation ability compared to the existing FBS-added growth medium. (Kolkmann et al., 2022). Multus's Proliferum® M was developed as an FBS substitute and completely replaced FBS during the proliferation of mammalian myoblasts, fibroblasts and adipocytes, showing proliferation efficiency similar to existing FBS-added media. In addition, it is a product that is expected to be used to produce cultured meat for consumption as it is produced in accordance with the ISO22000 food safe manufacturing standard (Multus, 2024). IntegriCulture's CulNet® system is a unique method that promotes the growth of target cells by circulating the culture medium of various types of 'Feeder cells' (cells that secrete serum components suitable for the cells). When using this system, it was confirmed that the proliferation efficiency of duck and chicken liver cells was superior to the culture medium with FBS added without FBS based on I-MEM, a basal medium (IntegriCulture, 2022). This is predicted to be the effect of serum-like components such as albumin and transferrin secreted from feeder cells (Yuki and Ikko, 2016; IntegriCulture, 2022). Research on media for cultured meat is being conducted based on various materials, but there are still not many products that are commercially available. A critical element in the development of cultured meat media is the replacement of lab-grade cell culture reagents with food grade materials. At the same time, in order to be price competitive with real meat, expensive media components such as FBS and growth factors, must be replaced. Currently, it is still difficult to meet all desired conditions to maximize the efficiency of cell proliferation and differentiation, thus, continuous research and development is needed to fully elucidate media components and their roles to improve culture efficiencies for cultured meat production.

6. Conclusion

In this review, we identified the important culture media components used for cultured meat production and discuss the current knowledge regarding their functions and effects. Amino acids, fatty acids, and carbohydrates mainly supply energy and nutrients for cell proliferation and muscle production, while minerals mainly play as

regulators of cell proliferation and muscle production. Vitamins have been found to not only protect cells from oxidative stress but also promote cell growth and regulate cell growth-related gene expression. In addition, cytokines are known to play roles in regulating genes related to muscle proliferation and regeneration, while hormones, such as growth factors, insulin, and thyroid hormones show beneficial effects towards muscle growth and growth regulation. As mentioned above, given the lack of systematic studies on cell culture components, we could not discuss all media components used for cell culturing nor could we fully characterize the effects of each media component.

One of the main reasons for the delay in the full-scale industrialization of cultured meat is that the culturing technology has not yet been fully established, and one factor in this is the lack of knowledge about the roles of media components. The possibility of reducing the use of livestock and reducing greenhouse gas emissions from livestock played a major role in the rise of the cultured meat industry. However, about 30% of the ingredients mentioned in this paper that are currently used in cell culture media—such as insulin, cholesterol, lactoferrin, transferrin, myoglobin, thyroid hormone, growth factors, cytokines, and testosterone—are substances mainly derived from animals. Therefore, there is no guarantee that cultured meat produced with the current culture technology is 100% animal-free, and research on replacing animal-derived ingredients with plant-derived or synthetic substances will also be essential to the industry. In addition, research on specific roles of media components in myogenesis should persist alongside active research and development of media component alternatives.

Ethics statement

The study did not require special ethical consideration as per the guidelines of IACUC.

CRediT authorship contribution statement

Da Young Lee: Writing – review & editing, Writing – original draft, Investigation, Data curation. **Seung Hyeon Yun:** Investigation, Data curation. **Juhyun Lee:** Investigation, Data curation. **Ermie Mariano Jr.:** Investigation, Data curation. **Yeongwoo Choi:** Investigation. **Dahee Han:** Investigation, Data curation. **Jinmo Park:** Investigation, Data curation. **Jin Soo Kim:** Investigation, Data curation. **Seung Yun Lee:** Writing – review & editing. **Sun Jin Hur:** Writing – review & editing, Supervision, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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