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Abstract

Foodomics is a valuable tool to understand the biochemistry and relevant compounds associated with meat quality traits. This approach is composed of four main strategies (transcriptomics, metabolomics, proteomics and lipidomics) that allow comprehensive and high-throughput characterization of the genetic expression, metabolites, proteins and lipids of meat and meats products to improve the knowledge about the underlying mechanisms and molecules involved in the meat quality traits to produce high-quality cuts. Therefore, this mini review highlights and presents potential biomarkers (RNA, metabolites, proteins and lipids) and the biological processes associated with the main meat quality attributes (such as color, IMF, tenderness and drip loss).

Keywords: omics; transcriptomics; metabolomics; proteomics; lipidomics; fresh meat

Introduction

Meat quality encompasses a complex set of factors that indicate whether a meat cut is suitable for consumption or not [1]. In terms of consumer purchase decision and eating experience, the main factors are the visual identification of color at the point of sale, intramuscular fat (IMF) or marbling, and the water-holding capacity prior to eating whereas the smell, tenderness, juiciness, and flavor play a major role during preparation and consumption [2]. In this sense, accumulating evidence about the importance of factors such as breed [3], rearing conditions [4,5], animal feeding [6], animal characteristics at the moment of slaughter [7,8], pre-slaughter conditions [9], and meat processing conditions [10] were investigated to impact the potential quality of meat.

The effect of these factors and other along the continuum from farm-to-fork have been traditionally explained by a combination of biochemical and mechanical mechanisms, wherein molecules (such as fatty acids) or characteristics (pH and shear force, for instance) have been used as indicators [3,5,6,11]. More recently, the advances in the analytical technologies and bioinformatics tools have enabled a deeper investigation of the biological processes involving the genetic expression, physiological responses, activity of enzymes and other metabolic processes that affect the final quality of meat [3,9,10].

Foodomics is an emerging strategy to obtain comprehensive and high-throughput information of composition, nutritional value, safety, and quality as well as reactions mechanisms, biochemistry, and biological activity of selected compounds [12]. This discipline encompasses transcriptomics, metabolomics, proteomics and lipidomics (Figure 1) among others that have been fast evolving during the last decade [13,14]. Furthermore, foodomics approach has been successfully applied in the investigation of metabolic processes in many fields of food sciences including milk proteins [15], lactic

55 acid bacteria and probiotic activity [16], comprehensive compositional analysis of durum
56 wheat [17], identification of triacylglycerols and polar lipids in olive fruit [18], as well as
57 to understand the effect of emerging technologies [19,20] and quality attributes [21] on
58 meat products.

59 Taking into account the increasing number of publications using transcriptomics,
60 metabolomics, proteomics and lipidomics to study meat quality [22–24], the aim of this
61 mini review is to highlight recent and relevant studies carried out using foodomics
62 approach to select potential biomarkers and biological processes related to meat quality
63 (especially for cattle, pig and lamb). In this mini review, a short description of each omics
64 approach is presented followed by a brief description of recent studies.

65 **Foodomics**

66 Within the omics approaches to evaluate the quality of meat, transcriptomics
67 stands for elucidation of the all the RNA transcripts at a given time of the genome of meat
68 tissue. Moreover, the transcriptomic shed light in the link between the functional elements
69 in DNA and meat quality [25]. As previously indicated, breed is an important factor that
70 can influence meat quality. In this sense, understanding the differences in the expression
71 of genes and the consequent effect on the development of animal and metabolic processes
72 could explain the meat quality attributes obtained from different breeds, muscles, rearing
73 practices, and post-slaughter processing conditions (Table 1). For example, this approach
74 was used by Liu *et al.* [26] to identify potential biomarkers to differentiate between Min
75 (Chinese pig breed) and Large White pigs: *ACSM3*, *HOXC6*, and *ISLR2* as well as the
76 *Longissimus dorsi* muscle from *Biceps femoris*: *CPT1A*, *CPT1B*, and *CRYAB* for Min
77 breed. Similarly, the differences in the fat deposition and the IMF content in the
78 *longissimus dorsi* of Yunling cattle (*PGM1*, *GALM*, *PGM1*, *GPI*, and *LDHA* involved in
79 glucose metabolism) and Chinese Simmental (*ALDH9A1*, *ACSL5*, *ACADM*, *ACAT2*, and

ACOT2 related to lipolysis and oxidative metabolism) were evidenced by Zhang et al. [27]. Tenderness of *longissimus dorsi* obtained from Maremmana and Chianina cattle were also explained in terms of gene expression of several proteins such as *TRIM45* (a protein involved in growth, cell differentiation and apoptosis), *TRIM32* (regulation of skeletal muscle differentiation and the regeneration of adult skeletal muscle), and *PRKAG3* (regulation of energy metabolism) [28]. The authors also indicated that the differences in glycogen storage in skeletal muscle could be explained by diferential abundance of isoforms of *PRKAG3*. Additionally, the effect of diet composition in gene expression and the consequent quality of meat was assessed by Chen *et al.* [29]. In this study, the expression of genes *ACOT4*, *ECHS1*, *HACD1*, *NPR1*, *ADCY2*, *MGLL*, and *IRS1* (fatty acid metabolism), *TNNC1*, *MYL3*, *TCAP*, and *TNNT1* (muscle formation and development) in Landrace × Yorkshire pigs were affected by the amount of mulberry leaves in the feed. Accordingly, the authors suggested that these could explain the differences observed in the drip loss and shear force of *longissimus dorsi*.

From another point of view, the metabolomic can be defined as a comprehensive exploration using qualitative and quantitative assessment of small hydrophilic molecules/metabolites (also known as metabolome) found in a food sample. A food metabolome includes several compounds such as polyphenols, organic acids, amino acids, vitamins, and minerals from the endogenous metabolism or ingestion/exposure to exogenous compounds that directly reflect the present and past metabolic processes in a food matrix [30]. An interesting approach in the use of metabolomics consist in the identification of potential biomarkers to indicate the evolution of meat properties during aging period (Table 1). Accordingly, Lana *et al.* [31] selected potential indicators from the metabolome of *longissimus thoracis* obtained from Piedmontese cull cows. According to these authors, serine and arginine metabolites had the great potential to control the

evolution of WHC, cooking loss (both negative correlations) and shear force (positive correlation). Moreover, the authors also demonstrated that the metabolic processes related to autophagic response and nitrogen metabolism explained the importance of serine and arginine for the quality of Piedmontese cull cow. Similarly, NADH, L-methionine, a sugar phosphate, taurine, guanosine and a malic acid–borate complex were proposed as potential biomarkers to control the changes in color of *longissimus dorsi* in lambs during aging for 1 week or 8 weeks, vacuum or modified atmosphere packaging, and 1 or 7 days of display [32]. Moreover, this study strengthened the role of reactions involving myoglobin and the presence of antioxidant enzymes in the stability of meat color. A recent comprehensive review by Muroya and co-workers [33] in the field of MEATabolomics to study both muscle and meat metabolites summarized all the researchers conducted around the world for the identification of potential biomarkers to control meat quality under several factors.

On the other hand, proteomics is a large-scale study of proteins that gives insights about the structural and functional meat proteins. Moreover, proteomics can also clarify the protein-protein interactions and also their molecular location in the sample [34]. In the case of meat, this approach fits perfectly in the discovery of biological process involving meat quality attributes (Table 1). For example, proteomics data revealed the effect of rearing practices and diet composition (hay, grass, and haylage) on the quality attributes of meat (*longissimus thoracis*) from PDO Maine-Anjou cows [4]. According to this study by Gagaoua and co-workers, different diets induced significant abundance changes of MyHC-IIx (structural function), PGM1, ICDH (energy metabolism), Hsp40, and Hsp70-Grp75 (stress response proteins) that are linked with ultimate pH, color, shear force, sensory attributes, and IMF. Another experiment carried out by Gagaoua *et al.* [35] revealed that MyHC-I, MyHC-IIa, MyHC-IIx (structural proteins); DJ-1, PRDX6

(oxidative stress); and CAPN1 (proteolysis) could be used as biomarkers for tenderness regardless of the end-point cooking temperature (55 *vs* 74 °C), panelists origin (French and UK citizens) as well as cattle breed (Aberdeen Angus, Limousin, or Blond d'Aquitaine). In another experiment related to meat tenderness , López-Pedrouso *et al.* [36] found that IVD, LAMB1, MYL3, SDHC and SDHA could be used as biomarkers for *longisimus thoracis et lumborum* (Iberian wild deer). Additionally, the authors indicated that FABP4, IVD, CRYZ (metabolism), LAMB1 (cell signaling), MYL3 (structural function), and SERPINB6 (regulation of cellular processes) were potential biomarkers for IMF. In the frame of meta-proteomics, a recent integrative and comprehensive study by Picard and Gagaoua [37] allowed to identify among twelve proteomic studies from the same laboratory on two muscles being *longissimus thoracis* and *semitendinosus* a total of 61 putative protein biomarkers resulting an extensive list (among genders, breeds, muscles and evaluation method of tenderness) proposed for validation (Table 1). This meta-proteomics allowed a better understanding of the biological processes underpinning beef tenderness in two muscles of French breeds and their variations according to the main factors underlying this important quality for both consumers and industries. In the case of horse meat, a recent study carried out by della Malva [38] identified 22 proteins specific proteins to follow up the influence of aging time in three muscles (*longissimus lumborum*, *semitendinosus*, and *semimembranosus*). The authors proposed that MYL1 and MYL2 as potential markers for shear force since the accumulation of these proteins were influenced by cut and aging time.

In our quest for biomarkers of beef qualities, especially of bovine tenderness, a recent integromics meta-analysis on 28 proteomics experiments from the literature allowed to identify the main molecular signatures of beef tenderness on *Longissimus thoracis* muscle [39]. This study gathered 128 protein biomarkers from which 64 were

found in a minimum of two studies, allowing then the authors to propose a robust list of 33 biomarkers for future validation. This integromics meta-analysis highlighted the degree of the interconnectedness of the pathways underlying beef tenderness and the relevance in the order of importance of muscle contractile and structure proteins, energy metabolism proteins, heat stress proteins and oxidative stress proteins (Figure 2) in the determination of beef tenderness.

The comprehensive study of lipid components in food samples is known as lipidomics [13]. This approach determines the composition of fatty acids, glycerolipids, glycerophospholipids, polyketides, prenol lipids, saccharolipids, sphingolipids, and sterol lipids [40]. The use of lipidomics in the quality assessment of meat was explored in a recent study that aimed to differentiate cut (loin, rump, shank, shoulder, and belly) and breed (Jilin, Sanmenxia and Tibetan) of pork [41]. According to these authors, the differentiation of cut for Tibetan pigs can be performed with arachidyl carnitine, Jilin black pigs with the diglyceride 14:0/18:1(9Z)/0:0, and Sanmenxia black pigs using diglyceride (14:0/18:1(9Z)/0:0). Regarding the differentiation of breeds, the authors indicated that 100 lipid compounds (such as triglyceride (15:0/18:1(9Z)/18:1(9Z)), phosphatidylserine (O-18:0/16:0), 6-deoxoteasterone, isobutyryl-L-carnitine, artemisinic acid, and arachidyl carnitine) could be selected.

Conclusion

Foodomics approach could improve the knowledge about the gene expression, metabolites (both lipophilic and hydrophilic), metabolic and biochemical processes underlying high quality meat and candidate biomarkers to assess meat quality, regardless of species, breeds, genders and quality trait. Moreover, transcriptomics, metabolomics and proteomics are the most common strategies to investigate meat quality and provide crucial and extensive information. They further allow identification of biomarkers

regarding the underlying processes and molecules that explains differences in tenderness, IMF, and sensory properties among different species, aging conditions or diet composition including the rearing practices and production systems. Further experiments are suggested to strength the connection between these new biomarkers with the preference and acceptance of sensory panels, since the selection of biomarkers can be affected by the origin of panelists, cooking temperature and quality trait. In terms of species, few studies explored the biomarkers and metabolic process in the meat of other animals such as small ruminants (lambs, goats, and sheep), horse and game meat. The field can also progress towards the use of other omics such as miRNomics, epigenomics, and glycomics that can expand and deepen the current knowledge about meat quality.

CRediT authorship contribution statement

Paulo Eduardo S Munekata: Conceptualization, Writing - original draft, Writing - review & editing. Mirian Pateiro: Writing - review & editing. María López-Pedrouso: Writing - review & editing. Mohammed Gagaoua: Writing - review & editing. Jose Manuel Lorenzo: Supervision, Writing - review & editing.

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352 **Table and figure captions**

353 **Table 1.** Foodomics approaches in the selection of biomarkers related to meat quality

354 **Figure 1.** Omics tools allowing to investigate and control meat quality traits through identification
355 of biomarkers

356 **Figure 2.** List of the 33 robust biomarkers of beef tenderness, from 5 main biological pathways,
357 shortlisted with a cut-off ≥ 4 from 124 proteins [39]

358

Table 1.

FoodOmic approach	Muscle/cut (breed)	Selected variable(s)	Quality attributes (selected genes, metabolites, proteins or lipids)	Ref.
Transcriptomics	*Longissimus dorsi* and *biceps femoris* (Min and Large White pigs)	Breed	Breed (*ACSM3*, *HOXC6*, *ISLR2*, *NEFM*, *PLP1*, *SIM1*, *ZIC1*, and *ZNF503*) and muscle/cut differences (*AMD1*, *CPT1A*, *CPT1B*, *CRYAB*, *GPX3*, *HSPB1*, *IRS1*, *PPARA*, *PPARGC1A*, *PYGM*, *RASGRP3*, *UCP3*, and *ZIC1*)	[26]
Transcriptomics	*Longissimus dorsi* (Yunling and Chinese Simmental cattle)	Breed	IMF and fatty acid composition (*ALDH9A1*, *ACSL5*, *ACADM*, *ACAT2*, and *ACOT2* for Yunling breed; *PGM1*, *GALM*, *PGM1*, *GPI*, and *LDHA* for Simmental breed)	[27]
Transcriptomics	*Longissimus dorsi* (Maremmana and Chianina cattle)	Breed	Tenderness (*TRIM45*, *TRIM32*, and *PRKAG3*)	[28]
Transcriptomics	*Longissimus dorsi* (Landrace × Yorkshire pigs)	Diet	Water loss (*ACOT4*, *ECHS1*, *HACD1*, *NPR1*, *ADCY2*, *MGLL* and IRS1) and shear force (*TNNC1*, *MYL3*, *TCAP*, and *TNNT1*)	[29]
Metabolomics	*Longissimus thoracis* (Piedmontese cull cows)	Aging time	WHC, cooking loss, and shear force (serine and arginine)	[31]
Metabolomics	*Longissimus dorsi* (Lamb, breed not indicated)	Aging time and conditions, and display time	Color (NADH, L-methionine, a sugar phosphate, taurine, guanosine and a malic acid–borate complex)	[32]
Proteomics (integrative study)	*Longissimus thoracis* and *Semitendinosus* muscles of different French breeds (steers, bulls, and cows)	Gender, breed, muscle and evaluation method of tenderness	Robust protein biomarkers of beef tenderness whatever the muscle (HSPB1, HSPB6, TPI1, YWHAE, MYH1, MYL1, MYL2, and MYBPH), robust protein biomarkers whatever the gender and muscle (TNNT3), robust biomarker whatever the muscle of toughness in bulls and of tenderness in cows (PGM1), robust biomarker of longissimus thoracis tenderness for different genders (HSPA1B and ACTA1), biomarkers of longissimus	[37]

			thoracis tenderness with similarities among genders (ENO1 and ENO3 between young bulls and cows; HSPA9 and MSRA between steers and cows); major beef tenderness biomarkers of semitendinosus muscle (PVALB)	
Proteomics	*Longissimus thoracis* (PDO Maine-Anjou cows)	Rearing practices	Ultimate pH, color, shear force, sensory attributes, and IMF (MyHC-IIx, PGM1, Hsp40, ICDH, and Hsp70-Grp75)	[4]
Proteomics	*Longissimus thoracis* (Aberdeen Angus, Limousin and Blond d'Aquitaine young bulls)	Breed, cooking temperature, and country origin of panelists	Tenderness (MyHC-I, MyHC-IIa, MyHC-IIx, DJ-1, PRDX6, and CAPN1)	[35]
Proteomics	*Longissimus lumborum, semitendinosus and semimembranosus* (Horse, breed not indicated)	Aging time and cut	Shear force (22 horse-specific proteins; interaction between aging time and cut)	[38]
Proteomics	*Longisimus thoracis et lumborum* (Iberian wild deer)	Tenderness	Shear force (IVD, LAMB1, MYL3, SDHC, and SDHA) and IMF (FABP4, IVD, LAMB1, MYL3, CRYZ, and SERPINB6)	[36]
Lipidomics	Shoulder, rump, loin, shank and belly (Tibetan, Jilin and Sanmenxia pork)	Cut and breed	Cut and breed (several lipid compounds; each cut and breed have specific biomarkers; triglycerides, phospholipids, fatty acids, and polyketides)	[41]

IMF: intramuscular fat; PDO: Protected Designation of Origin; WHC: water holding capacity; *ACADM*: acyl-CoA dehydrogenase medium chain; *ACAT2*: acetyl-CoA acetyltransferase 2; *ACOT2*: acyl-CoA thioesterase 2; *ACOT4*: acyl-coenzyme A thioesterase 4; *ACSL5*: acyl-CoA synthetase long chain family member 5; *ACSM3*: acyl-CoA synthetase medium chain family member 3; ACTA1: Actin, alpha skeletal muscle; ACTN2: alpha-actinin-2; *ADCY2*: adenylyl cyclase type 2; ADSSL1: adenylosuccinate synthetase isozyme 1; *ALDH9A1*: aldehyde dehydrogenase 9 family member A1; *AMD1*: adenosylmethionine decarboxylase 1; CAPN1: calpain 1; CAPZB: capping actin protein of muscle z-line subunit beta; CFH: complement factor H; *CPT1A*: carnitine palmitoyltransferase 1A; *CPT1B*: carnitine palmitoyltransferase 1B; *CRYAB*: alpha-crystallin B chain; DJ-1: protein deglycase; *ECHS1*: enoyl-coa hydratase, short chain 1; ENO1: alpha-enolase; ENO3: beta-enolase; FABP4: fatty acid binding protein 4; FHL1: four and a half LIM domains 1; *GALM*: galactose mutarotase; GAPDH: glyceraldehyde-3-phosphate dehydrogenase; GOT1: aspartate aminotransferase, cytoplasmic; *GPI*: glucose-6-phosphate isomerase; *GPX3*: glutathione peroxidase 3; *HACD1*: 3-hydroxyacyl-CoA dehydratase 1; *HOXC6*: homeobox C6; HPX: hemopexin; Hsp40: heat shock protein 40 (encoded by DNAJA1); HSPA1B : Heat shock 70 kDa protein 1A; Hsp70-Grp75: heat shock protein 70-glucose regulated protein 75 (encoded by HSPA9); *HSPB1*: heat shock protein beta-1; HSPB6: heat shock protein beta-6; ICDH: isocitrate dehydrogenase; *IRS1*: insulin receptor substrate 1; *ISLR2*: immunoglobulin superfamily containing leucine rich repeat 2; IVD: isovaleryl-CoA dehydrogenase; LAMB1: laminin subunit beta-1; *LDHA*: lactate dehydrogenase A; MASP2: mannan-binding lectin serine protease 2; *MGLL*: monoglyceride lipase; MYBPH: myosin-binding protein H; MYH1: myosin-1; MYH7: Myosin-7; MyHC-I: myosin heavy chain I; MyHC-IIa: myosin heavy chain IIa; MyHC-IIx: MHC-IIX: myosin heavy chain IIX (encoded by MYH1); MYL1: Myosin light chain 1/3, skeletal muscle isoform; MYL2: Myosin regulatory light chain 2, ventricular/cardiac muscle isoform; *MYL3*: myosin light chain 3; MSRA: Mitochondrial peptide methionine sulfoxide reductase; *NEFM*: neurofilament medium; *NPR1*: natriuretic peptide receptor 1; OGDH: 2-oxoglutarate dehydrogenase,

mitochondrial; OGN: mimecan; *PGM1*: phosphoglucomutase 1; PLA2G2D5: phospholipase A2; *PLP1*: proteolipid protein 1; *PPARA*: peroxisome proliferator activated receptor alpha; *PPARGC1A*: peroxisome proliferator-activated receptor gamma coactivator 1-alpha; PRDX6: peroxiredoxin-6; PVALB: Parvalbumin; *PRKAG3*: protein kinase amp-activated non-catalytic subunit gamma 3; *PYGM*: glycogen phosphorylase; *RASGRP3*: ras guanyl-releasing protein 3; SDHA: succinate dehydrogenase [ubiquinone] flavoprotein subunit; SDHC: succinate dehydrogenase cytochrome b560 subunit; SERPINB6: serpin B6; SERPINF2: alpha-2-antiplasmin; *SIM1*: single-minded homolog 1; *TCAP*: titin-cap; TNNT3: Troponin T Fast; *TNNC1*: troponin C1, slow skeletal and cardiac muscles; *TNNT1*: troponin T1, slow skeletal type; TPI1: Triosephosphate isomerase; *TRIM32*: tripartite motif containing 32; *TRIM45*: tripartite motif containing 45; *UCP3*: uncoupling protein 3; VCL: vinculin; YWHAE: tyrosine 3-monooxygenase/tryptophan 5-monooxygenase activation protein, 14-3-3 epsilon; *ZIC1*: zic family member 1; and *ZNF503*: zinc finger protein 503. Genes encoding proteins are indicated in italic.

Fig 1.

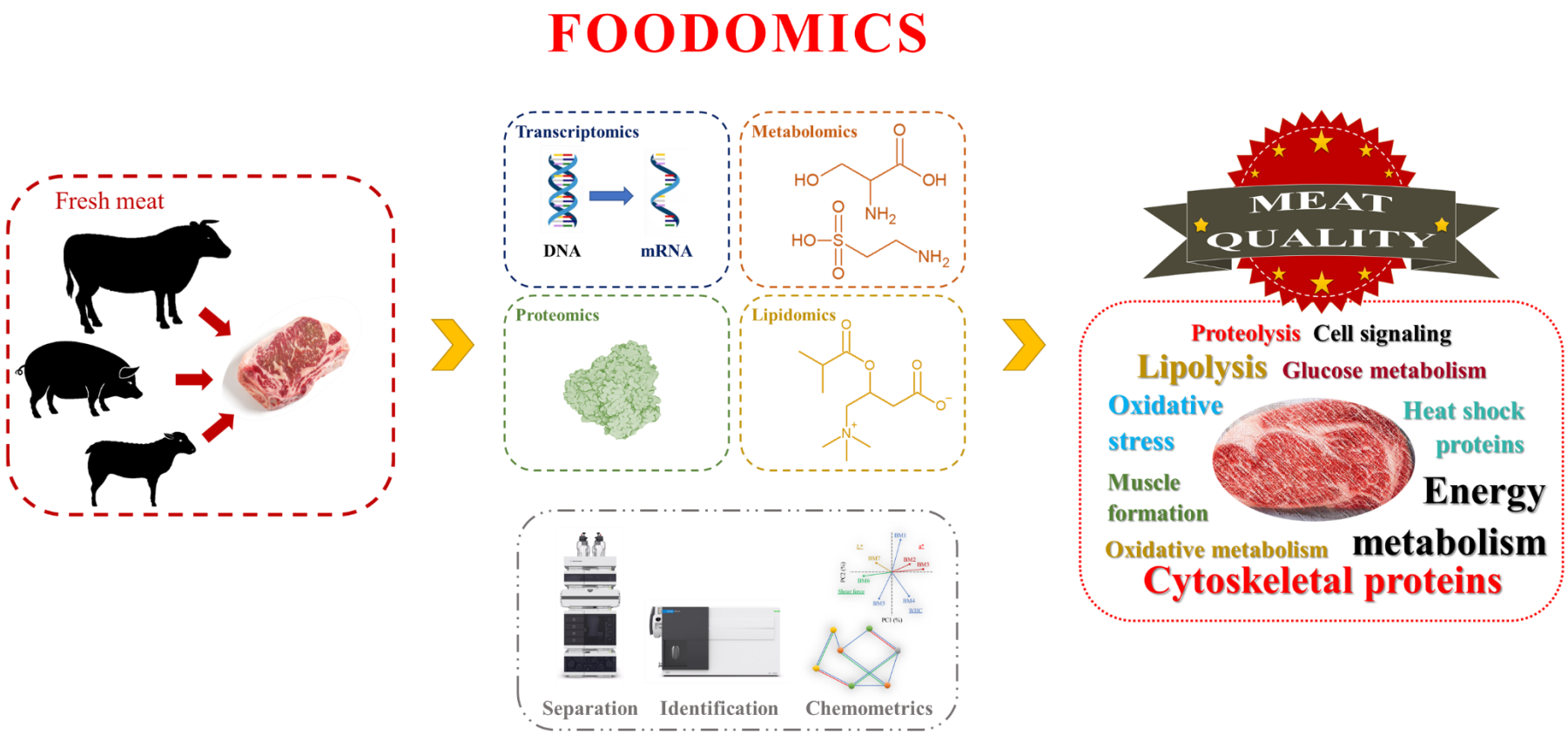
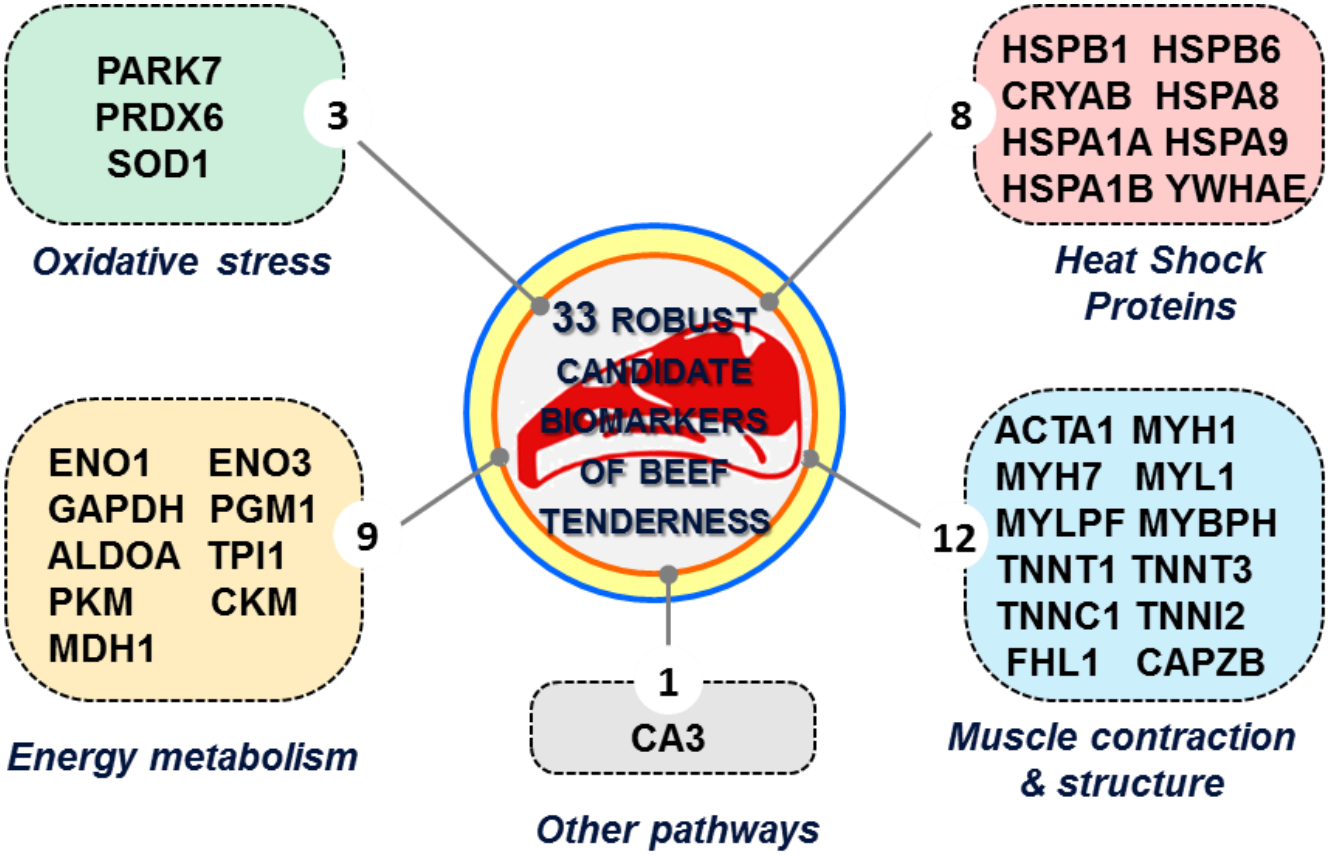

FOODOMICS
Fresh meat
Transcriptomics
DNA
mRNA
Metabolomics
Proteomics
Lipidomics
Separation
Identification
Chemometrics
MEAT QUALITY
Proteolysis
Cell signaling
Lipolysis
Glucose metabolism
Oxidative stress
Heat shock proteins
Muscle formation
Energy metabolism
Oxidative metabolism
Cytoskeletal proteins

Fig 2.


PARK7
PRDX6
SOD1
3
Oxidative stress
HSPB1 HSPB6
CRYAB HSPA8
HSPA1A HSPA9
HSPA1B YWHAE
8
Heat Shock Proteins
33 ROBUST CANDIDATE BIOMARKERS OF BEEF TENDERNESS
ENO1 ENO3
GAPDH PGM1
ALDOA TPI1
PKM CKM
MDH1
9
Energy metabolism
1
CA3
Other pathways
ACTA1 MYH1
MYH7 MYL1
MYLPF MYBPH
TNNT1 TNNT3
TNNC1 TNNI2
FHL1 CAPZB
12
Muscle contraction & structure

Conflicts of Interest

The authors declare no conflict of interest.

Highlights

- Foodomics is expanding the knowledge about meat quality
- Differences in tenderness, IMF and sensory properties can be explained by foodomics
- Underlying biochemistry of meat quality can be studied in-depth with foodomics
- Robust biomarkers can be obtained from proteomics