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Foodomics in meat quality

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16 **Abstract**

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

27

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

29

30 **Introduction**

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

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

48 Foodomics is an emerging strategy to obtain comprehensive and high-throughput
49 information of composition, nutritional value, safety, and quality as well as reactions
50 mechanisms, biochemistry, and biological activity of selected compounds [12]. This
51 discipline encompasses transcriptomics, metabolomics, proteomics and lipidomics
52 (Figure 1) among others that have been fast evolving during the last decade [13,14].
53 Furthermore, foodomics approach has been successfully applied in the investigation of
54 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

80 *ACOT2* related to lipolysis and oxidative metabolism) were evidenced by Zhang et al.
81 [27]. Tenderness of *longissimus dorsi* obtained from Maremmana and Chianina cattle
82 were also explained in terms of gene expression of several proteins such as *TRIM45* (a
83 protein involved in growth, cell differentiation and apoptosis), *TRIM32* (regulation of
84 skeletal muscle differentiation and the regeneration of adult skeletal muscle), and
85 *PRKAG3* (regulation of energy metabolism) [28]. The authors also indicated that the
86 differences in glycogen storage in skeletal muscle could be explained by differential
87 abundance of isoforms of *PRKAG3*. Additionally, the effect of diet composition in gene
88 expression and the consequent quality of meat was assessed by Chen *et al.* [29]. In this
89 study, the expression of genes *ACOT4*, *ECHS1*, *HACD1*, *NPR1*, *ADCY2*, *MGLL*, and
90 *IRS1* (fatty acid metabolism), *TNNC1*, *MYL3*, *TCAP*, and *TNNT1* (muscle formation and
91 development) in Landrace × Yorkshire pigs were affected by the amount of mulberry
92 leaves in the feed. Accordingly, the authors suggested that these could explain the
93 differences observed in the drip loss and shear force of *longissimus dorsi*.

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

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

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

130 (oxidative stress); and CAPN1 (proteolysis) could be used as biomarkers for tenderness
131 regardless of the end-point cooking temperature (55 vs 74 °C), panelists origin (French
132 and UK citizens) as well as cattle breed (Aberdeen Angus, Limousin, or Blond
133 d'Aquitaine). In another experiment related to meat tenderness , López-Pedrouso *et al.*
134 [36] found that IVD, LAMB1, MYL3, SDHC and SDHA could be used as biomarkers
135 for *longissimus thoracis et lumborum* (Iberian wild deer). Additionally, the authors
136 indicated that FABP4, IVD, CRYZ (metabolism), LAMB1 (cell signaling), MYL3
137 (structural function), and SERPINB6 (regulation of cellular processes) were potential
138 biomarkers for IMF. In the frame of meta-proteomics, a recent integrative and
139 comprehensive study by Picard and Gagaoua [37] allowed to identify among twelve
140 proteomic studies from the same laboratory on two muscles being *longissimus thoracis*
141 and *semitendinosus* a total of 61 putative protein biomarkers resulting an extensive list
142 (among genders, breeds, muscles and evaluation method of tenderness) proposed for
143 validation (Table 1). This meta-proteomics allowed a better understanding of the
144 biological processes underpinning beef tenderness in two muscles of French breeds and
145 their variations according to the main factors underlying this important quality for both
146 consumers and industries. In the case of horse meat, a recent study carried out by della
147 Malva [38] identified 22 proteins specific proteins to follow up the influence of aging
148 time in three muscles (*longissimus lumborum*, *semitendinosus*, and *semimembranosus*).
149 The authors proposed that MYL1 and MYL2 as potential markers for shear force since
150 the accumulation of these proteins were influenced by cut and aging time.

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

155 found in a minimum of two studies, allowing then the authors to propose a robust list of
156 33 biomarkers for future validation. This integrative meta-analysis highlighted the
157 degree of the interconnectedness of the pathways underlying beef tenderness and the
158 relevance in the order of importance of muscle contractile and structure proteins, energy
159 metabolism proteins, heat stress proteins and oxidative stress proteins (Figure 2) in the
160 determination of beef tenderness.

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

173 **Conclusion**

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

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

190 **CRedit authorship contribution statement**

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

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324 is the use of deer meat, which support the use of proteomics to select biomarkers
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341 biomarkers after a comprehensive evaluation of more than 100 putative proteins
342 using targeted and untargeted data-independent proteomic methods. This review
343 is also a unique big database of proteomic biomarkers of beef tenderness in the
344 world.
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- 351

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	<i>Longissimus dorsi</i> and <i>biceps femoris</i> (Min and Large White pigs)	Breed	Breed (<i>ACSM3</i> , <i>HOXC6</i> , <i>ISLR2</i> , <i>NEFM</i> , <i>PLP1</i> , <i>SIM1</i> , <i>ZIC1</i> , and <i>ZNF503</i>) and muscle/cut differences (<i>AMD1</i> , <i>CPT1A</i> , <i>CPT1B</i> , <i>CRYAB</i> , <i>GPX3</i> , <i>HSPB1</i> , <i>IRS1</i> , <i>PPARA</i> , <i>PPARGC1A</i> , <i>PYGM</i> , <i>RASGRP3</i> , <i>UCP3</i> , and <i>ZIC1</i>)	[26]
Transcriptomics	<i>Longissimus dorsi</i> (Yunling and Chinese Simmental cattle)	Breed	IMF and fatty acid composition (<i>ALDH9A1</i> , <i>ACSL5</i> , <i>ACADM</i> , <i>ACAT2</i> , and <i>ACOT2</i> for Yunling breed; <i>PGM1</i> , <i>GALM</i> , <i>PGM1</i> , <i>GPI</i> , and <i>LDHA</i> for Simmental breed)	[27]
Transcriptomics	<i>Longissimus dorsi</i> (Maremmana and Chianina cattle)	Breed	Tenderness (<i>TRIM45</i> , <i>TRIM32</i> , and <i>PRKAG3</i>)	[28]
Transcriptomics	<i>Longissimus dorsi</i> (Landrace × Yorkshire pigs)	Diet	Water loss (<i>ACOT4</i> , <i>ECHS1</i> , <i>HACD1</i> , <i>NPRI</i> , <i>ADCY2</i> , <i>MGLL</i> and <i>IRS1</i>) and shear force (<i>TNNC1</i> , <i>MYL3</i> , <i>TCAP</i> , and <i>TNNT1</i>)	[29]
Metabolomics	<i>Longissimus thoracis</i> (Piedmontese cull cows)	Aging time	WHC, cooking loss, and shear force (serine and arginine)	[31]
Metabolomics	<i>Longissimus dorsi</i> (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)	<i>Longissimus thoracis</i> and <i>Semitendinosus</i> 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 (<i>HSPB1</i> , <i>HSPB6</i> , <i>TPI1</i> , <i>YWHAE</i> , <i>MYH1</i> , <i>MYL1</i> , <i>MYL2</i> , and <i>MYBPH</i>), robust protein biomarkers whatever the gender and muscle (<i>TNNT3</i>), robust biomarker whatever the muscle of toughness in bulls and of tenderness in cows (<i>PGM1</i>), robust biomarker of <i>longissimus thoracis</i> tenderness for different genders (<i>HSPA1B</i> and <i>ACTA1</i>), biomarkers of <i>longissimus</i>	[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	<i>Longissimus thoracis</i> (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	<i>Longissimus thoracis</i> (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	<i>Longissimus lumborum</i> , <i>semitendinosus</i> and <i>semimembranosus</i> (Horse, breed not indicated)	Aging time and cut	Shear force (22 horse-specific proteins; interaction between aging time and cut)	[38]
Proteomics	<i>Longissimus thoracis et lumborum</i> (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; *PGMI*: phosphoglucomutase 1; PLA2G2D5: phospholipase A2; *PLPI*: proteolipid protein 1; *PPARA*: peroxisome proliferator activated receptor alpha; *PPARGCIA*: 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; *SIMI*: 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

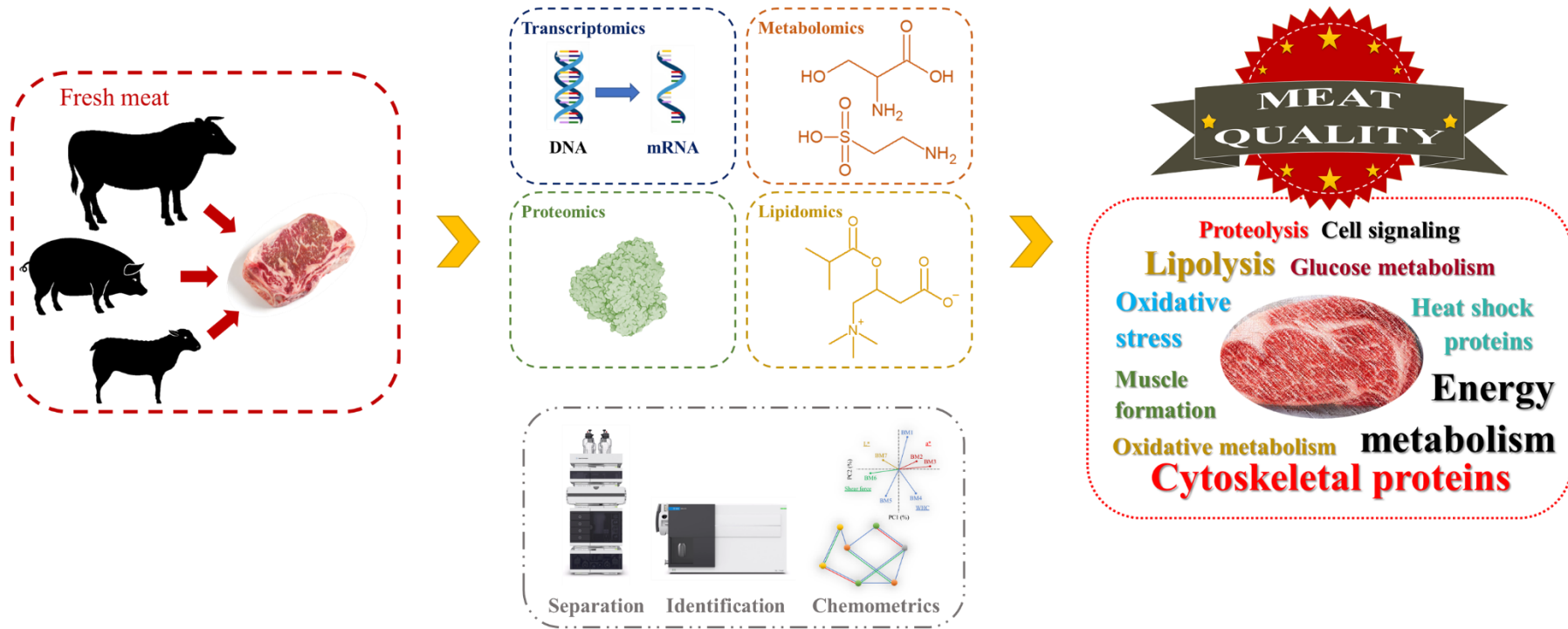
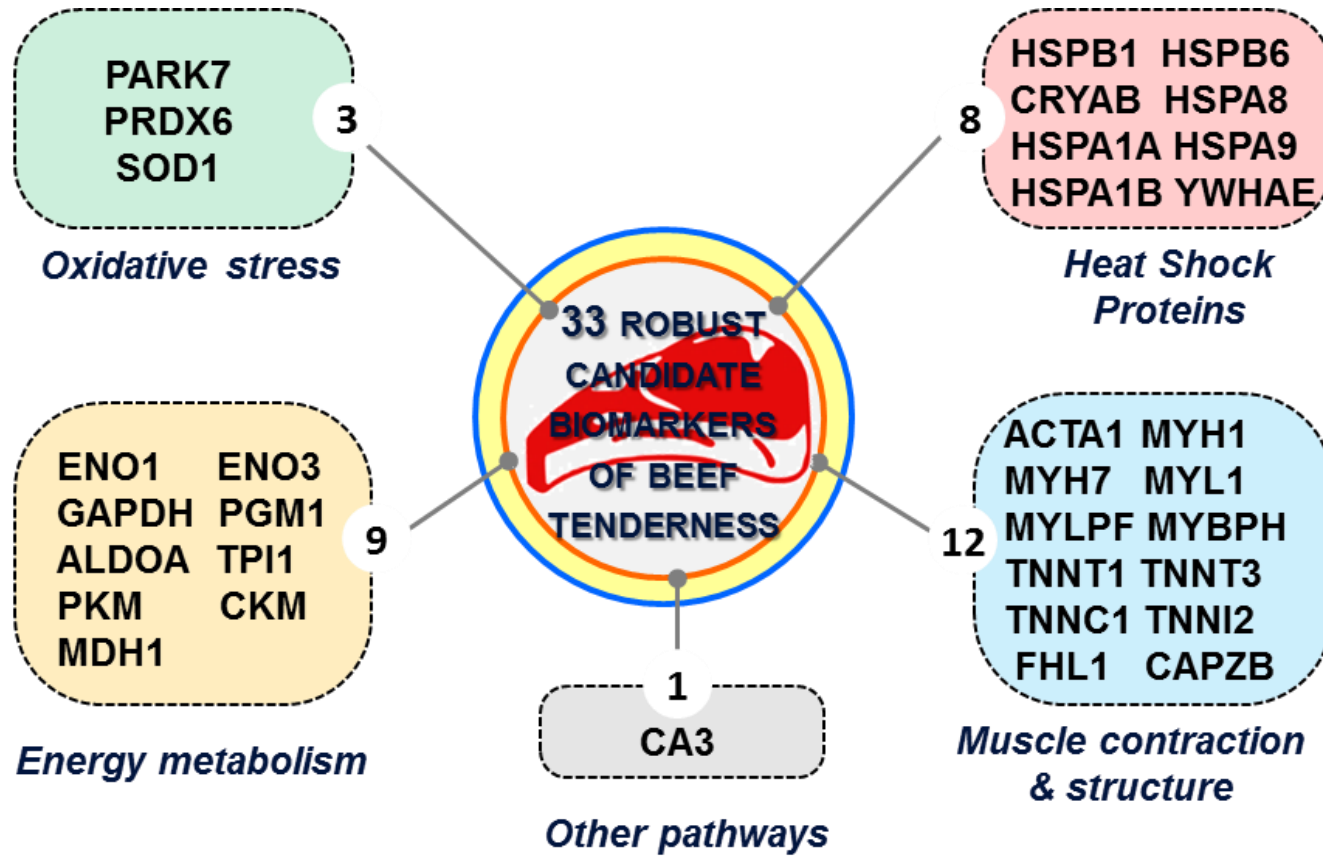


Fig 2.



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