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► **To cite this version:**

Mohammed Gagaoua, Daniel Franco, Ranjith Ramanathan. Meat Omics: Trends and applications of Omics strategies in meat research. *Journal of Proteomics*, 2024, 295, pp.105090. 10.1016/j.jprot.2024.105090 . hal-04415987

**HAL Id: hal-04415987**

**<https://hal.inrae.fr/hal-04415987>**

Submitted on 26 Jan 2024

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# 1 Meat Omics: Trends and applications of Omics strategies in meat research

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8

9 The sustainable production of meat and meat products with consistently high quality is an ongoing challenge  
10 for farmers, meat industry stakeholders, and researchers. To guarantee sustainable and high eating qualities of  
11 meat products to consumers, it is a prerequisite to understand the biological mechanisms underlying the  
12 conversion of muscle into meat, as well as a deeper understanding and control of the impacts of pre- and post-  
13 harvest practices on the *post-mortem* muscle and the determination of the final meat quality traits. Over the past  
14 two decades, considerable advances in high-throughput Omics technologies in the frame of Foodomics (**Fig. 1**)  
15 such as genomics, transcriptomics, proteomics and, more recently, peptidomics, metabolomics, and lipidomics,  
16 together with the considerable development of sophisticated statistical methods/packages and bioinformatics  
17 toolboxes [1, 2], have made it possible to explore meat quality and its determination in unprecedented depth  
18 [3]. In fact, Omics technologies allow the generation of large amounts of biological data about the genomes,  
19 transcriptomes, proteomes, metabolomes, etc. from a wide variety of samples such as tissues (muscle, fat) or  
20 biological fluids (plasma, meat exudate) to relate them with key meat quality parameters and/or animal  
21 performances, and thereby decipher meat quality variation or better understand the development of quality and  
22 its defects (**Fig. 1**).

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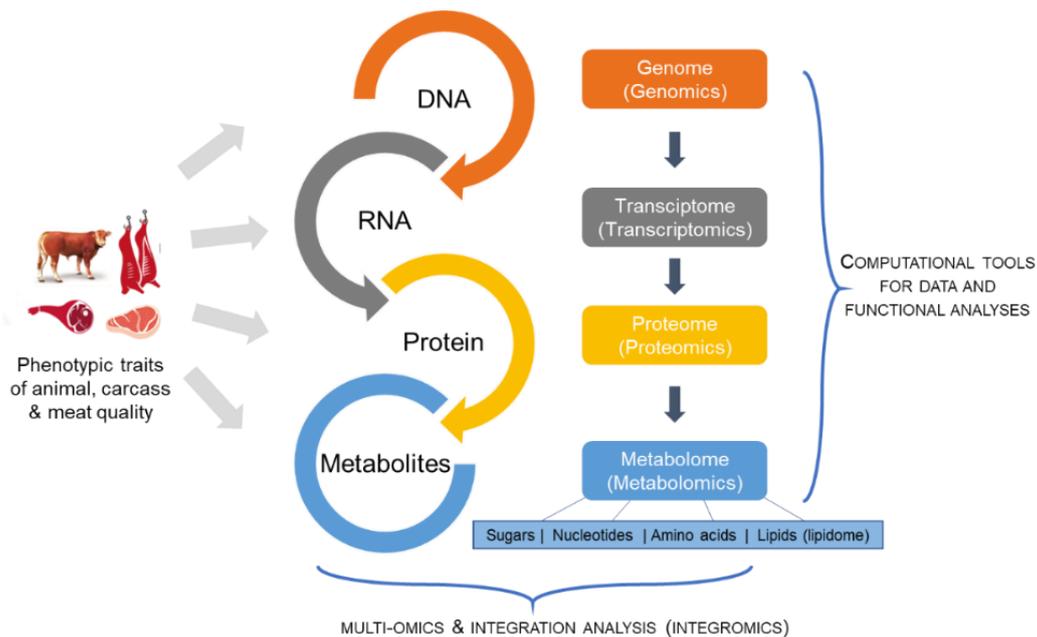
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34 **Fig. 1.** Illustration of the cascade of the big four Omics approaches applied in meat research profiling and beyond.

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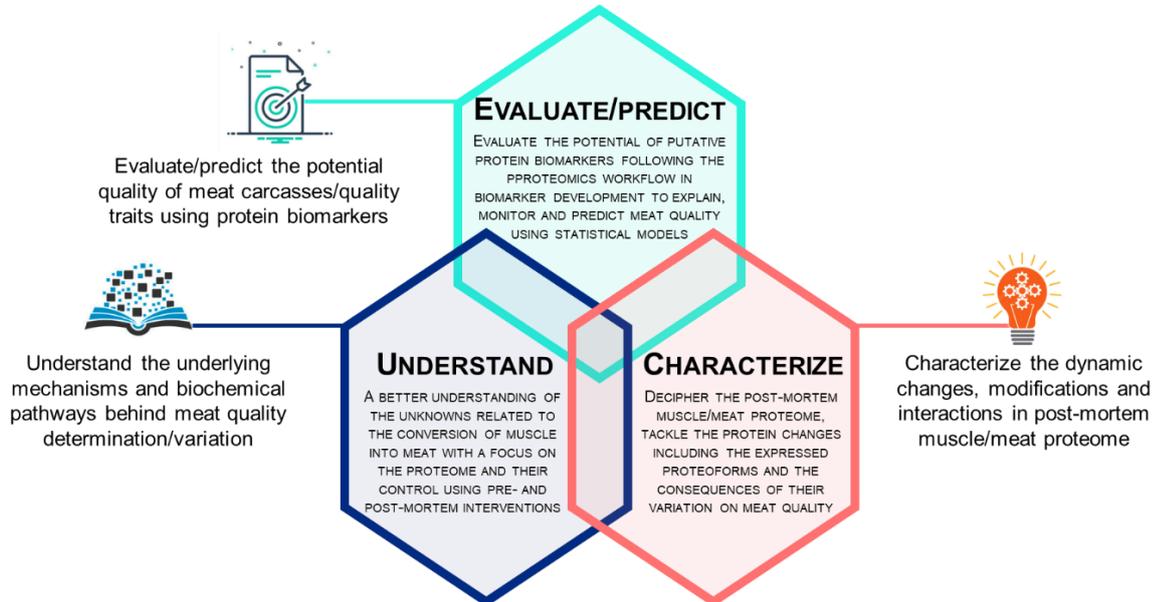
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In this thematic issue, the potential of Omics methods currently applied to meat research have been demonstrated through seventeen papers that grouped seven reviews and ten original research papers. Overall, the papers described cutting-edge Omics methods to study several key aspects of meat quality, which were mainly dominated using proteomics (both traditional and label-free shotgun approaches), followed by metabolomics, lipidomics and new emerging approaches such as Rapid Evaporative Ionization Mass Spectrometry (REIMS) fingerprinting. The dominating use of proteomics in meat research can be for example explained by the substantial improvement of the experimental technology over the past decades as it evolved from conventional methods to high-throughput methods such as tissue microarray, protein pathway array and mass spectrometry in the frame of shotgun proteomics [4]. Notwithstanding, proteomics has been mainly applied

44 for three major objectives (**Fig. 2**) as recently discussed by Gagaoua *et al.* [5], these being (i) to characterize  
 45 the dynamic changes, modifications and interactions in *post-mortem* muscle/meat proteomes; (ii) to understand  
 46 the underlying mechanisms and biochemical pathways underpinning the determination and variation of the  
 47 phenotypes of interest in animal production including meat quality traits; and (iii) to evaluate, predict and monitor  
 48 the potential quality of carcasses and meat quality traits based on candidate biomarkers. This latter was mainly  
 49 conducted in the frame of data-driven approaches (*i.e.*, methods seeking potential putative biomarkers based  
 50 on data modelling) to propose explanatory mechanisms and/or predictive models of the targeted phenotypes.  
 51 Interestingly, similar objectives have been adopted in the current developments and emerging applications of  
 52 metabolomics in meat research [6, 7].



53 **Fig. 2.** The main application objectives of proteomics, as one of the major  
 54 used Omics, in the field of meat research (based on Gagaoua *et al.* [5]).

55 Of the seven reviews, the first one by Mao *et al.* [3] gave an overview of the current applications of Omics in  
 56 elucidating the underlying biological mechanisms and related factors associated with meat safety. Beyond the  
 57 applications of Omics technologies to explore the adaptive mechanisms of microorganisms, the authors further  
 58 emphasized the impact of post-translational modifications (PTMs) in fresh meat. In the frame of chicken meat  
 59 quality defects, Zhang *et al.* [8] explored the etiology of broiler myopathies using several Omics approaches. To  
 60 the best of our knowledge, this is the first review that addressed the applications of genomics, transcriptomics,  
 61 proteomics, metabolomics, lipidomics and metagenomics to evaluate meat quality defects in chicken, also  
 62 referred to as myopathies. The authors described that the different Omics approaches have been used to  
 63 understand the genetic predisposition, the protein expression, and the biochemical pathways that are  
 64 associated with the expression of woody breast meat, white striping, and other myopathies. Ramanathan *et al.*  
 65 [6] provided a comprehensive and updated overview of the trends and challenges of metabolomics and how it  
 66 has been applied in the last seven years in meat research to elucidate quality changes. The authors described  
 67 the importance of metabolites in meat color and its quality defects such as dark-cutting beef, its usefulness to  
 68 monitor muscle- and aging-specific impacts on meat color, its emerging use in meat tenderness and flavor  
 69 research to identify biomarkers or for a better understanding of their determination. Furthermore, the authors  
 70 emphasized the current advances in bioinformatics as key tools to overcome on one hand the challenges of  
 71 data analysis and interpretation and, to gain on the other hand a deeper understanding of the biochemical  
 72 changes within the objectives of metabolite pathway enrichment analysis. In the frame of multi-omics, Zhang *et al.*  
 73 [9] explored the potential of integrating proteomics and metabolomics for deeper molecular insights into the  
 74 pathways underpinning sheep meat quality variation and authenticity. The review highlighted, for instance, that  
 75 the improvement of color stability and tenderness could be associated with changes in glycolysis, energy  
 76 metabolism and endogenous antioxidant capacity of the muscle/meat. They further discussed the conflicting  
 77 roles of proteolysis in meat quality determination, as enhanced proteolysis seemed to be positively related to  
 78 tenderness and flavor, but can negatively impact lamb color stability. Jia *et al.* [10] reviewed for the first time the  
 79 emerging use of lipidomics in meat research, with a focus on goat meat quality. The authors emphasized the  
 80 different applications of lipidomics such as a better understanding of goat meat quality development, and its  
 81 evaluation likely for in-depth characterization of the nutritional and health profiles of goat meat. In the context of  
 82 the nutritional benefits and functional quality of meat, the research paper by Gathercole *et al.* [11] exemplified  
 83 the valuable role of proteomics in analyzing the potential bioactivities of meat during simulated digestion. The  
 84 last two reviews by Agregán *et al.* [12] and Suman *et al.* [13], reviewed the applications of proteomics to study  
 85 processed meat products and to characterize the biochemistry of fresh beef color, respectively. Agregán *et al.*  
 86 [12] evidenced how the knowledge gained by proteomics can be useful for the improvement of both the

87 technological processes in meat and the safety quality. Suman *et al.* [13], reviewed the studies published in the  
88 last decade on the pivotal role of muscle proteome in fresh beef color determination. For example, they  
89 discussed the wide range of factors, including endogenous skeletal muscle components, which can affect  
90 myoglobin biochemistry and color stability in beef. Moreover, the potential use of muscle proteins and PTMs of  
91 myoglobin as candidate biomarkers for fresh beef color have been discussed in detail. Finally, the authors  
92 provided an up-to-date list of candidate protein biomarkers based on what has been recently proposed by  
93 Gagaoua and co-workers thanks to an integromics meta-analysis approach to predict beef color quality  
94 determination [14].

95 In addition to showcasing a range of Omics applications in meat research, proteomics studies in the frame of  
96 the discovery and evaluation of biomarkers especially for beef quality were tremendous. Zhu *et al.* [15] revealed  
97 using for the first time a shotgun proteomics approach the molecular signatures determining multiple beef  
98 sensory traits (tenderness, stringiness, chewiness and flavor) along with the related protein biomarkers. Among  
99 the results, the study reported that precursor metabolites and energy is a key molecular signature of multiple  
100 beef quality traits. Moreover, the authors identified that phosphorylase b kinase regulatory subunit alpha  
101 (PHKA1) and starch-binding domain-containing protein 1 (STBD1) were both correlated with the four quality  
102 traits evaluated and, accordingly these proteins have been proposed as putative biomarkers. Lamri *et al.* [16]  
103 applied for the first time the same shotgun proteomics approach to identify biomarkers of multiple goat meat  
104 quality traits. The authors focused on texture quality traits and found 25 proteins to be differentially abundant  
105 among quality clusters. Thanks to several bioinformatics analyses, the authors evidenced the  
106 interconnectedness of muscle structure, energy metabolism and response to stress as pivotal biological  
107 pathways underpinning the determination of goat meat quality. The study by Santiago *et al.* [17] combined two-  
108 dimensional electrophoresis (2-DE) and mass spectrometry to compare the muscle proteomes of bulls and  
109 steers. It showed that bulls had more key proteins of catabolic processes, oxidative stress, and muscle  
110 contraction compared to steers. For the steers, proteins previously reported as biomarkers of beef tenderness  
111 and marbling were up-regulated in steers. Beldarrain *et al.* [18] used for the first time 2-D DIGE to delve into  
112 proteomic differences between aged and non-aged horsemeat. The authors followed the degradation of  
113 myofibrillar proteins up to 21 days of ageing and validated using western-blotting the proteins of interest as a  
114 way to monitor meat tenderization. The study extended our knowledge of the potentialities of 2-D DIGE to study  
115 meat proteolysis during ageing and to compare divergent muscle/meat samples. Another study on beef quality,  
116 focused on the early *post-mortem* (1 h and 1 day) proteome and metabolome of samples categorized based on  
117 their pH at 6 h *post-mortem* to reveal new insights about beef tenderization [19]. The study revealed greater  
118 potential of protein degradation, and higher amounts of energy production proteins and metabolites to be related  
119 to the higher tenderness at 1 day *post-mortem* of low 6 h pH steaks. The authors proposed potential biomarkers  
120 of more rapid *post-mortem* metabolism to be linked to earlier tenderization in beef that are worthy of validation  
121 using appropriate Omics methods. Likewise and in the frame of beef quality biomarkers evaluation, Picard *et al.*  
122 [20] investigated using univariate and multivariate statistical approaches the relationships of a list of 29  
123 candidate biomarkers quantified in two muscles of cows using Reverse Phase Protein Array (RPPA) assay [21]  
124 with multiple meat and carcass qualities. The authors shortlisted 10 protein biomarkers to be tested in a larger  
125 population to feed the pipeline of biomarker discovery. Currently, progress in meat quality biomarker discovery  
126 (namely for beef), while significant, is still hampered by several technical drawbacks related to the nature of the  
127 muscle structure, such as the recovery of connective tissue and extracellular matrix (ECM) proteins. To shed  
128 light on this aspect, Listrat *et al.* [22] described thanks to a data-mining and bioinformatics approach the first  
129 cattle matrisome repertoire containing 1022 genes. We believe that the integration of matrisome analyses in  
130 meat research would help us in the future to reveal the sophisticated mechanisms underlying meat quality  
131 determination and, accordingly refine the list of biomarkers that will be proposed to the meat industry in  
132 complementary of the recently proposed first repertoire of beef tenderness biomarkers [23].

133 Studies on lamb meat Omics are very scarce in the literature. della Malva *et al.* [24] investigated for the first  
134 time the effects of dietary supplementation with hazelnut skin by-product on both the plasma and muscle  
135 proteomes and the consequences on meat quality. The authors evidenced using 2-DE, LC-MS/MS and  
136 bioinformatics approaches the biochemical pathways at interplay and the potential candidate plasma biomarkers  
137 to predict, in non-invasive way, lamb meat quality early *post-mortem*. Among the proteins influenced by hazelnut  
138 skin by-product supplementation, four of them, these being apolipoprotein A-I (APOA1), prohibitin (PHB), actin,  
139 cytoplasmic 2 (ACTG1) and albumin (ALB) were common to both plasma and muscle proteomes. The authors  
140 suggested a sophisticated biological cross-talk. Furthermore, the four proteins have been proposed as  
141 candidate biomarkers to predict early *post-mortem* lamb meat quality. Zhang *et al.* [25] on another hand  
142 proposed the first REIMS fingerprinting study to accurately discriminate lamb meat aged with different methods  
143 and levels of dehydration. It showed that REIMS is a promising approach for rapid authentication and quality  
144 prediction of ageing methods and flavor potential of lamb meat and other muscle foods.

145 In summary, this thematic issue gathered diverse applications of Omics approaches in meat research and all  
146 highlighted their potential to decipher the unknowns. Nevertheless, comprehensive studies from a systems  
147 biology perspective are needed to integrate information obtained from different Omics methods/data and

148 thereby understand a larger picture beyond quality variations. Further efforts in Omics data sharing among the  
149 meat scientist's community is definitely necessary to advance common scientific and technical questions that  
150 would allow significant developments and consolidation of our current understanding of the mechanisms. Meat  
151 Omics has with no doubts a promising future ahead with key roles in helping achieve the sustainable framework  
152 agenda of livestock and meat production.

## 153 Acknowledgements

154 We are grateful to the support of Brigitte Picard (an imminent meat proteomics researcher at INRAE), Ingrid  
155 Miller (executive editor of animal proteomics at *Journal of Proteomics*), Carly Middendorp (senior editorial  
156 manager at *Journal of Proteomics*) and Juan Calvete (editor-in-chief of *Journal of Proteomics*). We are further  
157 thankful to the reviewers and contributing authors for giving their reflections on, and valuable contributions to,  
158 the Meat Omics field and making this thematic issue possible.

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### Mohammed Gagaoua

Dr. Mohammed Gagaoua is a meat scientist who received his food engineering degree at Constantine University, Algeria. In 2009, Mohammed started a high postgraduate diploma and conducted research on the main endogenous muscle proteolytic systems and serpins inhibitors in the frame of apoptosis as the first step of muscle to meat conversion before receiving his Ph.D. in 2015 on meat and muscle biochemistry at INRA research Centre, France, and Constantine University on biomarkers of sensory qualities of beef: understanding of the biological mechanisms and prediction. He worked as a lecturer at the "Université de Bejaia" from 2011 to 2014, as an associate professor at "University Mentouri Constantine" from 2012 to 2017, before moving to INRA Auvergne-Rhône-Alpes, France to manage a project about the farm-to-fork continuum data in the frame of "big-data" in meat science field to understand meat quality variability using for the first time rearing factors for joint management of meat and carcass quality properties based on metadata. In February 2019, Mohammed moved to the Department of Food Quality and Sensory Science, Teagasc Food Research Centre, Ashtown, Dublin 15 Ireland

234 where he was awarded the prestigious Marie Skłodowska-Curie Career-FIT grant on a research project titled "Omics-Based  
235 Biomarkers for Beef Carcass Quality Management". Since October 2022, Mohammed has been appointed as a permanent  
236 meat scientist at INRAE, France to develop a research program in the frame of sustainable production and consumption  
237 aiming to develop a "One Quality" approach of pork/meat within several farming and production systems. Mohammed's  
238 academic focus is on meat science, meat and meat products, foodomics with expertise on proteomics applied to muscle  
239 foods, and data integration in the frame of "integromics". His main research interests are muscle and meat biochemistry,  
240 Omics in meat science research, novel strategies to improve eating meat quality, biomarkers of meat qualities, and the  
241 integration of intrinsic and extrinsic quality dimensions of meat. As a career achiever, Mohammed was runner-up in 2015  
242 for the International Meat Secretariat Award; he received the ICoMST2018 award by Robin Shorthouse for outstanding  
243 contribution to advancing Meat Science and the ICoMST2018 Meat Science journal award for best presentation in Australia.  
244 He has published more than 130 peer-reviewed papers in international journals, edited 2 books; has 20 book chapters, 60  
245 proceedings, along with numerous contributions in national and international conferences.



### Daniel Franco

Daniel Franco started his career in 1997 at the Chemical Engineering Dept. involved in a European project related to new processes for the extraction of oils and antioxidant molecules from non-conventional oilseeds and vegetables with applications in pharmaceutical and food industries. During his PhD, Daniel acquired knowledge of solid-liquid extraction of oil from vegetable matrices, as well as, in chromatography techniques for determining polyphenolic compounds. From 2005 to 2009, he obtained a postdoctoral position at Agricultural Research Centre and his research was focused on understanding the biochemical mechanisms behind meat ageing and the technological processes applied to meat products in terms of texture, sensorial and nutritional parameters. In this period, he was able to broaden his knowledge about antioxidant natural compounds in the animal production field. From 2009 to 2022, he worked at Meat Technology Centre in projects related to food technology. Daniel completed his analytic training in LC and GC, developing and validating methods to quantify levels of lipid/protein oxidation, fractionation by SPE with HPLC/FD/DAD and GC/MS for volatile

260 compounds. In September 2022, he returned to Chemical Engineering Dept. as Assistant Professor. During these years,  
261 Daniel was involved in the following topics: 1) Extension of food shelf life using natural extracts with antioxidant/antimicrobial  
262 from agricultural by-products using green technologies. 2) Development of novel-healthier meat products based on fat and  
263 salt reduction, replacement of animal fat or incorporating functional compounds. 3) Identifying proteomic and genomic  
264 biomarkers associated with food quality, using molecular techniques for protein separation. 4) Valorisation of meat by-  
265 products using enzymatic process to obtain bioactive peptides.  
266



### Ranjith Ramanathan

Dr. Ranjith Ramanathan is a Professor of Meat Science holding Leo and Kathy Noltensmeyer Endowed Research Chair in the Department of Animal and Food Sciences at Oklahoma State University. Dr. Ramanathan received his Ph.D. and MS degree in Animal Science from the University of Connecticut in 2012. He earned his Bachelor of Veterinary and Animal Science in 2004 from Kerala Agricultural University, India. Since 2012, he has been a faculty in the Department of Animal and Food Sciences at Oklahoma State University. Dr. Ramanathan's research focuses on fundamental and applied factors influencing fresh meat quality, specifically postmortem biochemistry and meat color. In addition, he teaches five different undergraduate and graduate-level food science courses. Dr. Ramanathan has secured a total of \$6.4 million in research grants. In addition, he has published 100 peer-reviewed journal articles and 145 refereed abstracts. Dr. Ramanathan has served on 69 graduate student committees as a chair or committee member. He has been recognized by the USDA-Association of Public Land Grant University Young Educator Award, American Meat Science Association Achievement Award,

281 American Chemical Society Young Scientist Award, Southern Section ASAS Early Career Awards, and NACTA for his  
282 teaching and research excellence.