



**HAL**  
open science

## **Enhanced identification of *Morganella* spp. using MALDI-TOF mass spectrometry**

Mathilde Duque, Cécile Emeraud, Rémy Bonnin, Quentin Gaii-Gianetto, Laurent Dortet, Alexandre Godmer

### **► To cite this version:**

Mathilde Duque, Cécile Emeraud, Rémy Bonnin, Quentin Gaii-Gianetto, Laurent Dortet, et al.. Enhanced identification of *Morganella* spp. using MALDI-TOF mass spectrometry. *Journal of Mass Spectrometry and Advances in the Clinical Lab*, 2025, 37, pp.9-13. <10.1016/j.jmsacl.2025.04.011>. <hal-05132703>

**HAL Id: hal-05132703**

**<https://hal.science/hal-05132703v1>**

Submitted on 30 Jun 2025

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

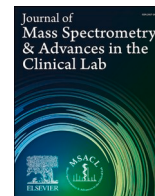


Distributed under a Creative Commons CC BY-NC-ND 4.0 - Attribution - Non-commercial use - No Derivative Works - International License



Contents lists available at [ScienceDirect](https://www.sciencedirect.com)  
**Journal of Mass Spectrometry and  
 Advances in the Clinical Lab**

journal homepage: [www.sciencedirect.com/journal/journal-of-mass-spectrometry-and-advances-in-the-clinical-lab](https://www.sciencedirect.com/journal/journal-of-mass-spectrometry-and-advances-in-the-clinical-lab)



## Short Report

## Enhanced identification of *Morganella* spp. using MALDI-TOF mass spectrometry

Mathilde Duque<sup>a</sup>, Cécile Emeraud<sup>a,b,c</sup>, Rémy A. Bonnin<sup>a,b,c</sup>, Quentin Gaii-Gianetto<sup>d,e</sup>, Laurent Dortet<sup>a,b,c</sup>, Alexandre Godmer<sup>f,g,\*</sup>

<sup>a</sup> Team “Resist” UMR1184 “Immunology of Viral, Auto-Immune, Hematological and Bacterial diseases (IMVA-HB)”, INSERM, Université Paris-Saclay, CEA, LabEx LERMIT, Faculty of Medicine, Le Kremlin-Bicêtre, France

<sup>b</sup> Bacteriology-Hygiene Unit, Bicêtre Hospital, Assistance Publique-Hôpitaux de Paris, Le Kremlin-Bicêtre, France

<sup>c</sup> Associated French National Reference Center for Antibiotic Resistance: Carbapenemase-Producing Enterobacteriaceae, Le Kremlin-Bicêtre, France

<sup>d</sup> Institut Pasteur, Université Paris Cité, Bioinformatics and Biostatistics HUB, Paris, France

<sup>e</sup> Institut Pasteur, Université Paris Cité, Proteomics Platform, Mass Spectrometry for Biology Unit, UAR CNRS 2024, Paris, France

<sup>f</sup> U1135, Centre d’Immunologie et des Maladies Infectieuses (Cimi-Paris), Sorbonne Université, Paris, France

<sup>g</sup> Bacteriology Department, Saint-Antoine Hospital, AP-HP. Sorbonne Université (Assistance Publique Hôpitaux de Paris), Paris, France



## A B S T R A C T

**Introduction:** The genus *Morganella*, including clinically isolated species *M. sibonii* and *M. morganii*, has a still underexplored role in clinical microbiology. Despite the clinical relevance of *Morganella* spp., current MALDI-TOF commercial systems fail to differentiate these species. Whole genome sequencing (WGS) remains the most effective method to distinguish species. However, this method is not adapted for routine lab workflow. Enhancing MALDI-TOF’s accuracy could make it a rapid and effective approach for distinguishing *Morganella* species in routine laboratory diagnostics.

**Objectives:** This study aims to improve the performance of MALDI-TOF for identifying *Morganella* spp. using WGS as the gold-standard reference method.

**Methods:** We applied Machine Learning (ML) algorithms to a collection of 235 clinical *Morganella* spp. strains to develop an optimized identification model. Whole genome sequencing was used to characterize these strains and perform phylogenetic analysis, categorizing 209 strains as *M. morganii* and 26 as *M. sibonii*.

**Results:** The ML-based classifiers showed improved identification accuracy (44 of the 160 designed with accuracy at 1). Also, MS analysis identified 11 peaks able to discriminate between *M. morganii* and *M. sibonii*.

**Conclusion:** Through development of a publicly-available online ML-based classifier, this study has improved the capacity of MALDI-TOF for distinguishing *Morganella* spp., providing a reliable, user-friendly solution suited to routine clinical diagnostics and supporting a better understanding of the roles of *M. morganii* and *M. sibonii* in human pathology.

## Introduction

*Morganella* spp. are facultative anaerobic Gram-negative rods belonging to Enterobacterales. Until recently, the *Morganella* genus comprised two major species: *M. morganii*, a clinically relevant species, and *M. psychrotolerans*, associated with seafood poisoning by histamine production [1]. Recently, *M. sibonii*, formerly a subspecies of

*M. morganii*, has been proposed as a third species [2].

*M. sibonii* differs from *M. morganii* in its biochemical traits, potential virulence factors, and intrinsic resistance features. Notably, *M. sibonii*’s genome contains a trehalose operon (hydrolyzing trehalose as a carbon source), absent in *M. morganii* [3]. Downstream of this operon, a type VI secretion system (T6SS) and a type III secretion system (T3SS) were identified, which may influence pathogenicity [2].

**Abbreviations:**  $\alpha$ -HCCA, Alpha-Cyano-4-Hydroxycinnamic Acid; *bla*DHA, Beta-Lactamase DHA-type; CE-IVD, Conformité Européenne - In Vitro Diagnostic; Kappa, Cohen’s Kappa Coefficient; KPC, *Klebsiella Pneumoniae* Carbapenemase, *M. morganii*, *Morganella morganii*; *M. sibonii*, *Morganella sibonii*; MALDI-TOF MS, Matrix-Assisted Laser Desorption/Ionization Time-of-Flight Mass Spectrometry; *m/z*, Mass-to-Charge Ratio; mda, Mean Decrease Accuracy; ML, Machine Learning; MS, Mass Spectrometry; MSclassifR, Machine Learning Classifier R Package (for mass spectra); multinom, Multinomial Logistic Regression; NDM, New Delhi Metallo-beta-lactamase; NDM-1, NDM-5, NDM-7, Variants of New Delhi Metallo-beta-lactamase; nnet, Single Hidden Layer Neural Network; OXA, Oxacillinase; RF, Random Forest; RFE-RF, Recursive Feature Elimination with Random Forest; SelectionVarStat, Variable Selection Statistic; SVM, Support Vector Machine; T3SS, Type III Secretion System; T6SS, Type VI Secretion System; *tetD*, Tetracycline Resistance Gene D-like; VIM, Verona Integron-encoded Metallo-beta-lactamase; WGS, Whole Genome Sequencing.

\* Corresponding author at: U1135, Centre d’Immunologie et des Maladies Infectieuses (Cimi-Paris), Sorbonne Université, Paris, France.

E-mail address: [alexandre.godmer@aphp.fr](mailto:alexandre.godmer@aphp.fr) (A. Godmer).

<https://doi.org/10.1016/j.jmsacl.2025.04.011>

Received 18 November 2024; Received in revised form 16 April 2025; Accepted 21 April 2025

Available online 3 May 2025

2667-145X/© 2025 THE AUTHORS. Publishing services by ELSEVIER B.V. on behalf of MSACL. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

*Morganella* spp. produce a class C  $\beta$ -lactamase (*bla*<sub>DHA</sub>-like) conferring resistance to amoxicillin as well as first- and second-generation cephalosporins. They are intrinsically resistant to polymyxins, macrolides, and fosfomycin and show decreased susceptibility to imipenem [4]. Interestingly, wild-type *M. sibirica* possesses the *tetD*-like gene resulting in resistance to tetracycline, whereas wild-type *M. morganii* lacks this gene and remains susceptible [2]. *M. morganii* is an opportunistic pathogen involved in various infections [4]. The high mortality rate of these infections highlights the importance of studying *Morganella* spp. [5]. Several studies have shown that *M. morganii* is enriched in the microbiota genome of patients with inflammatory bowel disease and colorectal cancer [6–8]. Cao et al. demonstrated that *M. morganii* can produce indoleamine, exacerbating colon tumorigenesis in gnotobiotic mice [9].

Despite these findings, the epidemiology and pathogenesis of *Morganella* spp. remain poorly understood. Although rapid differentiation of these species in clinical microbiology laboratories does not directly provide additional insights into pathogenicity, it greatly facilitates routine identification and epidemiological surveillance which remain largely unexplored for *Morganella* spp.. Whole genome sequencing (WGS) accurately distinguishes these species and can detail pathogenic differences; however, its complexity and cost limit routine use. In contrast, Matrix-assisted Laser Desorption/Ionization Time-of-Flight Mass Spectrometry (MALDI-TOF) is widely adopted for its speed, cost-effectiveness, and ease of integration into clinical workflows [10,11]. However, commercial MALDI-TOF systems, such as MALDI BioTyper® (Bruker®) and VITEK® MS (bioMérieux), have limitations in distinguishing between *M. morganii* and *M. sibirica*, due to genetic and spectral similarities. Machine learning (ML) algorithms present a promising solution to overcome these limitations by enhancing MALDI-TOF's identification accuracy, expanding its potential as a rapid, low-cost method for routine species differentiation [12–14]. This study aims to improve MALDI-TOF performance in accurately distinguishing clinically relevant *Morganella* species by integrating an ML-based approach, with WGS as the gold standard.

## Materials and methods

A total of 235 *Morganella* spp. strains isolated between 1966 and 2023 were used for this study. From 2020 to 2023, 96 strains were collected from clinical isolates at Kremlin-Bicêtre and Paul-Brousse hospitals in France (Supplemental Table 1). The remaining 137 strains were part of an international study on multi-drug-resistant strains from various European countries between 1966 and 2022 [2]. As only fully anonymized patient samples were used that were not obtained specifically for use in this study through an interaction or intervention with living individuals, neither informed consent nor IRB review were required. WGS was performed using Illumina® technology (HiSeq system), with reads assembled using Shovill v1.1.0 and Spades v3.14.0. Resistome analysis used ResFinder databases, and species determination was performed through phylogeny using reference genomes, visualized with iTOL v6.5.2. Isolates were stored at  $-80^{\circ}\text{C}$  (Microbank, Inc., Canada), thawed, and cultured on Mueller-Hinton agar at  $37^{\circ}\text{C}$  for 18–24 h. Subcultures were performed the next day, with three deposits from each strain using the direct transfer method. Spots were covered with 1  $\mu\text{L}$  of MALDI matrix [ $\alpha$ -HCCA] (Bruker® Daltonics, Bremen, Germany). Mass spectra were acquired with a Microflex® LT instrument (Bruker® Daltonics, Bremen, Germany) using the default CE-IVD (Conformité Européenne – *In Vitro* Diagnostic) method parameters recommended by Bruker®. Post-acquisition signal processing was performed using the MALDIquant R package following a standard pipeline (Supplemental Table 2) [15].

Concerning ML analysis, the spectra were divided into a training dataset (72.8 % of the spectra, 171 strains) for classifier training and a test dataset (21.2 % of the spectra, 64 strains) for performance assessment (Supplemental Fig. 1). Each strain's spectra were exclusive to one

dataset. Sixteen ML-based pipelines were developed using the MSclassifR package to perform ML-based classifiers [15]. Non-informative peaks were removed using three methods: Recursive Feature Elimination with Random Forest (RFE-RF), “SelectionVarStat” for peak selection via multiple hypothesis testing, and “Mean Decrease Accuracy” (mda) using variable importances of random forests [15]. A pipeline without discriminant peak selection was also implemented to evaluate this step's influence. Four ML algorithms were employed: linear logistic multinomial regression (multinom), single hidden layer neural network (nnet), random forest (RF), and support vector machines with linear kernel (SVM).

Each pipeline was characterized by the method used to remove non-informative peaks and the ML algorithm used to classify mass spectra. Performance was measured on the test dataset using Cohen's Kappa coefficient (Kappa) and accuracy.

The mass spectra were processed as described in Supplemental Table 2. Masses were aligned within a 500 ppm tolerance, and peak binning was performed using a maximum deviation of 500 ppm. For each species, peak frequency was calculated as the percentage of mass spectra in which a given peak was detected. This was determined by dividing the number of mass spectra containing the peak by the total number of mass spectra for that species. Peaks were then filtered based on their occurrence across species: only those detected in at least 90 % of the spectra from one species and in no more than 10 % of the spectra from the other species were retained. A tool for viewing the spectra peaks of both species is available at: <https://agodmer.github.io/Morganella/>.

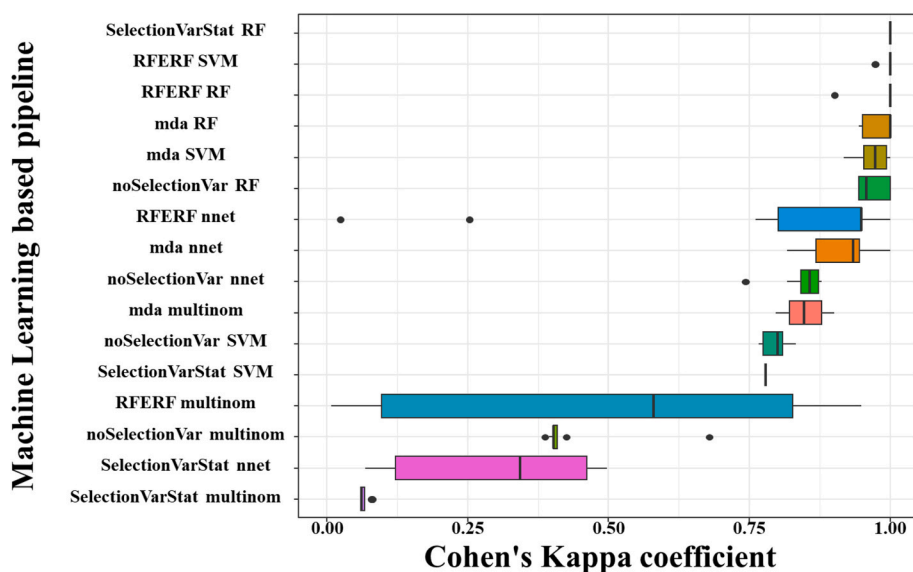
## Results

### ML-based approach

Among the 235 *Morganella* spp. isolates, 209 *M. morganii* and 26 *M. sibirica* were identified by WGS. Resistome analysis detected 102 carbapenemase producers, including 47 NDM-1, 8 NDM-5, 3 NDM-7, 19 OXA-48, 1 OXA-204, 1 OXA-641, 19 KPC-2, 2 VIM-1, 1 NDM-1 + KPC-2, and 1 NDM-1 + OXA-48 (Supplemental Fig. 2). A total of 705 spectra (obtained as triplicates per strain) were generated for the ML-based approach. The 16 ML-pipelines led to the creation of 160 ML-based classifiers. The average Kappa coefficient and accuracy, along with their standard deviation for all classifiers, were  $0.76 \pm 0.31$  and  $0.88 \pm 0.22$ , respectively (Supplemental Table 3). The best pipelines, “SelectionVarStat-RF,” “RFE-SVM,” “RFE-RF-RF,” and “mda-RF,” had Kappa values of  $1 \pm 0$ ,  $1 \pm 0.01$ ,  $0.99 \pm 0.03$ , and  $0.98 \pm 0.03$ , respectively, indicating high agreement with the WGS (Fig. 1, Supplemental Table 4). The RF algorithm showed statistically better Kappa performance across others algorithms ( $p < 10^{-5}$ , Supplemental Table 5). Peak selection methods like “mda” and “RFE-RF” were statistically more efficient than methods without peak selection ( $p < 10^{-2}$ , Supplemental Table 5). Of note, with our methodology, “RFE-RF” selected fewer peaks ( $10 \pm 2.03$ ) compared to “mda” ( $195 \pm 15.4$ ) (Supplemental Table 6). A total of 44 models, 20 using RFE-RF and 29 using the RF algorithm, achieved a Kappa of 1, indicating perfect agreement with the WGS. The most suitable pipelines were “RFE-RF” and “RFE-RF-SVM,” achieving high performance with fewer peaks.

### Peak discriminant analysis

Among the 1297 peaks analyzed, 11 strongly discriminated between the two species (Table 1). For *M. morganii*, peaks at 8979.44  $m/z$ , 4490.09  $m/z$ , 4962.53  $m/z$ , and 9923.59  $m/z$  were detected in 99.84 %, 99.36 %, 95.85 %, and 93.46 % of spectra, respectively, while these peaks appeared in only 3.85 %, 3.85 %, 3.85 %, and 5.13 % of *M. sibirica* spectra. Conversely, peaks at 9006.82  $m/z$ , 6931.90  $m/z$ , 10678.12  $m/z$ , 9451.01  $m/z$ , 9609.74  $m/z$ , 4970.53  $m/z$ , and 9530.61  $m/z$  were observed in more than 91 % of *M. sibirica* spectra and in less than 5.6 % of



**Fig. 1.** Performance of the Machine Learning-based pipelines (each trained 10 times) according to the Kappa coefficient. Notes: mda for “Mean Decrease Accuracy” using variable importances of random forests; multinom: selection linear regression; nnet for single hidden layer neural network; “noSelectionVar” for without selection of discriminant peak; RF: random forest; RFERF for Recursive Feature Elimination with Random Forest; “SelectionVarStat” for peak selection via multiple hypothesis testing; SVM for support vector machines with linear kernel. The effectiveness of Machine Learning (ML)-based pipelines was tested by integrating selected peaks into ML-based algorithms trained via 4-fold cross-validation.

**Table 1**

Discriminant peaks found in this study in order to separate the species *M. morgani* and *M. sibonii*.

Peak ( <i>m/z</i> )	<i>M. morgani</i> *frequency of the peak % (number of times the peak is present / the total spectra)	<i>M. sibonii</i> *frequency of the peak % (number of times the peak is present / the total spectra)
8979.44	99.84 (417/418)	3.85 (3/78)
4490.09	99.36 (415/418)	3.85 (3/78)
4962.53	95.85 (401/418)	3.85 (3/78)
9923.59	93.46 (391/418)	5.13 (4/78)
9006.82	0.80 (3/418)	96.15 (75/78)
6931.90	0.64 (3/418)	92.31 (72/78)
10678.12	0.48 (2/418)	91.03 (71/78)
9451.01	1.91 (8/418)	92.31 (72/78)
9609.74	4.15 (17/418)	93.59 (73/78)
4970.53	3.35 (14/418)	92.31 (72/78)
9530.61	5.58 (23/418)	91.03 (71/78)

\* frequencies were estimated with the total of 418 and 78 spectra of *M. morgani* and *M. sibonii*, respectively.

*M. morgani* spectra. Among these discriminant peaks, one notable mass shift was detected. The peak at 4962.53 *m/z* in *M. morgani* versus the peak at 4970.53 *m/z* in *M. sibonii* shows an 8 Dalton difference, which is within the range typically expected for minor protein variations in MALDI-TOF analyses (Fig. 2).

## Discussion

*Morganella* species play a significant role in human clinical settings, and there may be different levels of virulence between species [2]. Distinguishing between these species is important for monitoring their epidemiological distribution and optimising routine diagnostics, even if detailed analysis of pathogenic differences is still a matter for WGS.

This study aimed to provide a simple, rapid, accurate and cost-effective method to differentiate between the two most common *Morganella* species in human pathology using MALDI-TOF. Two approaches were evaluated: a peak-based approach identified five discriminant peaks accurately distinguishing the species (Table 1), and ML-based classifiers. These classifiers showed promising results, with ML-based

classifiers among the 160 evaluated achieving perfect agreement with the gold standard (Kappa = 1), corresponding to 100 % accuracy on the test set which was fully independent from the training set and composed of 192 unseen spectra corresponding to 64 strains, including 57 strains of *M. morgani* and 7 strains of *M. sibonii*.

Despite the class imbalance with *M. sibonii* representing only 11 % of isolates and *M. morgani* 89 %, our ML-based approach achieved accurate classification. This imbalance is consistent with the low clinical prevalence of *M. sibonii*, which accounts for only about 5 % of the 363 clinical strains, as reported by Chen et al. [16]. The robust generalization performance observed across the 44 ML-based classifiers indicates that the limited representation of *M. sibonii* did not significantly impair overall classifier effectiveness. A plausible explanation for this phenomenon is that the removal of non-informative peaks in the ML-based pipeline resulted in the selection of highly discriminating peaks (as detailed in Table 1) that effectively differentiate the two species.

Notably, classifiers using a limited subset of peaks (“RFERF-RF”, “RFERF-SVM”) identified the same peaks as in Table 1. The ML-based approach streamlined the identification process, eliminating the need for a manual algorithm and offering an accessible online solution for routine use. In addition, the RF algorithm was found to be the most robust and accurate for analyzing spectral data, as previously reported in the literature [13,14]. In addition, these ML-based methods are useful for detecting subtle mass shifts that could reflect minor differences in protein isoforms or post-translational modifications relevant to species differentiation (Fig. 2).

This work represents a significant improvement in the differentiation of *Morganella* species by MALDI-TOF. This advance could improve the clinical diagnosis of *Morganella* spp. and also contribute to a better understanding of the prevalence of *M. sibonii* versus *M. morgani*, as well as their respective involvement in human pathology. However, the study was monocentric, which may introduce bias. A multicentre evaluation will be required to validate the accuracy, sensitivity, and specificity of our ML-based classifier, and to improve its robustness and applicability where necessary. To facilitate this work, an ML-based classifier is publicly available (<https://bigbiomed.shinyapps.io/MorgaMSclassifR/>).

Of note, *M. psychrotolerans*, which is rarely isolated from human samples, was excluded from the analysis [17].

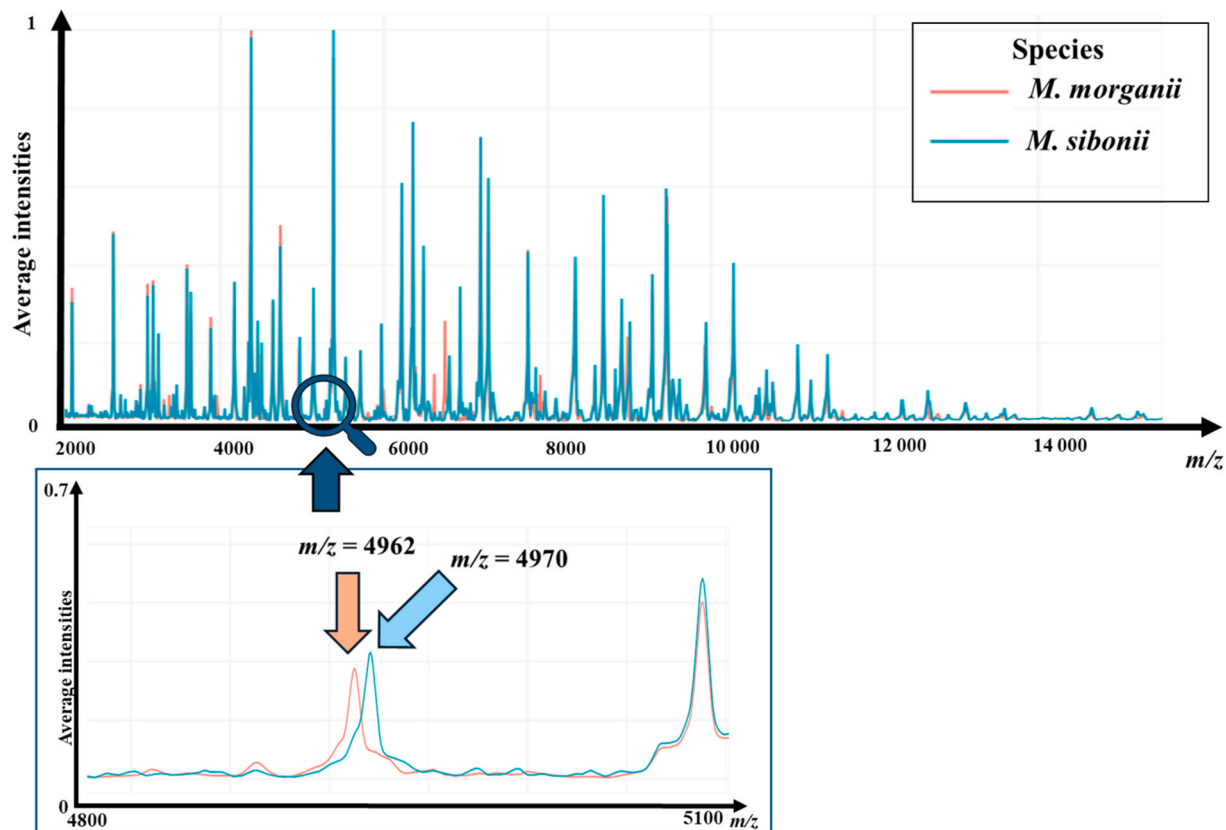


Fig. 2. Visualization of two discriminant peaks able to distinguish *M. morgani* from *M. sibi*. This visualization tool is available at <https://agodmer.github.io/Morganella/>. Notes: *m/z* for Mass-to-Charge Ratio.

## Conclusion

This study improves the capability of MALDI-TOF to distinguish *Morganella* spp., providing a reliable, user-friendly solution suited to routine clinical diagnostics. By accurately identifying *M. morgani* and *M. sibi*, this approach supports better understanding of their roles in human pathology.

## Ethics statement

The study was conducted in accordance with the Declaration of Helsinki and national (France) and institutional (Assistance Publique de Hôpitaux de Paris) standards. As only fully anonymized patient samples were used that were not obtained specifically for use in this study through an interaction or intervention with living individuals, neither informed consent nor IRB review were required.

## Funding sources

Mathilde Duque was supported by a grant from FRM, file number: FDM202306017178.

## CRediT authorship contribution statement

**Mathilde Duque:** Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Cécile Emeraud:** Writing – review & editing, Visualization, Supervision, Methodology, Formal analysis, Data curation, Conceptualization. **Rémy A. Bonnin:** Writing – review & editing, Visualization, Validation, Resources, Investigation, Conceptualization. **Quentin Gai-Gianetto:** Writing – review & editing, Validation, Software, Methodology. **Laurent Dortet:** Writing – review & editing, Validation, Methodology, Data curation, Conceptualization.

**Alexandre Godmer:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Methodology, Investigation, Formal analysis, Data curation, 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.

## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jmsacl.2025.04.011>.

## References

- [1] J. Emborg, P. Dalgaard, P. Ahrens, *Morganella psychrotolerans* sp. nov., a histamine-producing bacterium isolated from various seafoods, *Int. J. Syst. Evol. Microbiol.* 56 (10) (Oct. 2006) 2473–2479, <https://doi.org/10.1099/ijs.0.64357-0>.
- [2] R.A. Bonnin et al., Spread of carbapenemase-producing *Morganella* spp from 2013 to 2021: a comparative genomic study, *Lancet Microbe* 2024, 2024. [Online]. Available: [https://doi.org/10.1016/S2666-5247\(23\)00407-X](https://doi.org/10.1016/S2666-5247(23)00407-X).
- [3] N. Palmieri, C. Hess, M. Hess, M. Alispahic, Sequencing of five poultry strains elucidates phylogenetic relationships and divergence in virulence genes in *Morganella morgani*, *BMC Genom.* 21 (1) (Dec. 2020) 579, <https://doi.org/10.1186/s12864-020-07001-2>.
- [4] H. Liu, J. Zhu, Q. Hu, X. Rao, *Morganella morgani*, a non-negligent opportunistic pathogen, *Int. J. Infect. Dis.* 50 (Sep. 2016) 10–17, <https://doi.org/10.1016/j.ijid.2016.07.006>.
- [5] A. Bandy, Ringing bells: *Morganella morgani* fights for recognition, *Public Health* 182 (May 2020) 45–50, <https://doi.org/10.1016/j.puhe.2020.01.016>.
- [6] W. Chen, F. Liu, Z. Ling, X. Tong, C. Xiang, Human Intestinal Lumen and Mucosa-Associated Microbiota in Patients with Colorectal Cancer, *PLoS One* 7 (6) (Jun. 2012) e39743, <https://doi.org/10.1371/journal.pone.0039743>.
- [7] A.M. Thomas, et al., Metagenomic analysis of colorectal cancer datasets identifies cross-cohort microbial diagnostic signatures and a link with choline degradation,

- Nat. Med.* 25 (4) (Apr. 2019) 667–678, <https://doi.org/10.1038/s41591-019-0405-7>.
- [8] J. Wirbel, et al., Meta-analysis of fecal metagenomes reveals global microbial signatures that are specific for colorectal cancer, *Nat. Med.* 25 (4) (Apr. 2019) 679–689, <https://doi.org/10.1038/s41591-019-0406-6>.
- [9] Y. Cao, et al., Commensal microbiota from patients with inflammatory bowel disease produce genotoxic metabolites, *Science* 378 (6618) (Oct. 2022) eabm3233, <https://doi.org/10.1126/science.abm3233>.
- [10] A. Croxatto, G. Prod'hom, G. Greub, Applications of MALDI-TOF mass spectrometry in clinical diagnostic microbiology, *FEMS Microbiol. Rev.* 36 (2) (Mar. 2012) 380–407, <https://doi.org/10.1111/j.1574-6976.2011.00298.x>.
- [11] M. Welker, A. Van Belkum, V. Girard, J. Charrier, D. Pincus, An update on the routine application of MALDI-TOF MS in clinical microbiology, *Expert Rev. Proteom.* 16 (8) (Aug. 2019) 695–710, <https://doi.org/10.1080/14789450.2019.1645603>.
- [12] C.V. Weis, C.R. Jutzeler, K. Borgwardt, Machine learning for microbial identification and antimicrobial susceptibility testing on MALDI-TOF mass spectra: a systematic review, *Clin. Microbiol. Infect. off. Publ. Eur. Soc. Clin. Microbiol. Infect. Dis.* 26 (10) (Oct. 2020) 1310–1317, <https://doi.org/10.1016/j.cmi.2020.03.014>.
- [13] A. Candela, et al., Automatic Discrimination of Species within the Enterobacter cloacae Complex Using Matrix-Assisted Laser Desorption Ionization–Time of Flight Mass Spectrometry and Supervised Algorithms, e01049-22, *J. Clin. Microbiol.* 61 (4) (Apr. 2023), <https://doi.org/10.1128/jcm.01049-22>.
- [14] A. Godmer, et al., Contribution of machine learning for subspecies identification from *Mycobacterium abscessus* with MALDI-TOF MS in solid and liquid media, *Microb. Biotechnol.* 17 (9) (2024) e14545, <https://doi.org/10.1111/1751-7915.14545>.
- [15] A. Godmer, Q.G. Gianetto, K. Druart, MSclassifR: Automated Classification of Mass Spectra. (Aug. 09, 2023). Accessed: Jul. 29, 2024. [Online]. Available: <https://cran.r-project.org/web/packages/MSclassifR/index.html>.
- [16] J. Chen, et al., Tracing the possible evolutionary trends of *Morganella morganii*: insights from molecular epidemiology and phylogenetic analysis, e00306-24, *mSystems* 9 (7) (Jun. 2024), <https://doi.org/10.1128/msystems.00306-24>.
- [17] W.T. Oh, et al., *Morganella psychrotolerans* as a possible opportunistic pathogen in rainbow trout (*Oncorhynchus mykiss*) fisheries, *Aquaculture* 520 (Apr. 2020) 735021, <https://doi.org/10.1016/j.aquaculture.2020.735021>.