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Review

Specificity database for bacterial pesticidal proteins against invertebrate targets

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ABSTRACT

Bacteria produce a number of proteins with specific biocidal activity against invertebrate pests. These proteins have been employed successfully in biocontrol for decades, by use of microbial sprays and bioengineered crops. While traditionally associated with *Bacillus thuringiensis* (Bt) and other well-characterised bacteria, the protein repertoire has recently been expanded to include novel structural classes and sources. Here we present a database comprising, at the time of writing, 3963 entries drawn from 466 research articles and 174 patents, documenting activity against 253 invertebrate species across 25 taxonomic orders. This resource includes toxicity and non-toxicity data encompassing both single-component and multi-component protein activities, assay methods, and bibliographic references. The dataset reveals a trend in testing priorities, with a focus on pests of agricultural and medical importance from the orders Lepidoptera, Coleoptera, and Diptera. This focus, however, highlights important gaps for future research: while primarily tested against Lepidoptera, pesticidal proteins increasingly show activity against other orders, including Hemiptera. This database, integrated with recent nomenclature updates, provides a dynamic resource for researchers and regulators, facilitating advancements in understanding bacterial pesticidal proteins and their application for sustainable pest management.

1. Introduction

Many bacteria produce proteins that induce mortality in invertebrate targets. These proteins can exhibit a high degree of target specificity and high potency. These proteins are of great interest and importance on account of these attributes as potential biocontrol agents for the sustainable control of invertebrate pests of agriculture and human health. Control methods can include the use of native bacteria as pesticide sprays (a method that has been in use for over 60 years) or the incorporation of genes encoding the proteins into bioengineered plants (which has been implemented since the mid 1990s). These methods have been highly-successful for pest management in the field and have an excellent safety record (Raymond and Federici, 2017).

The best studied of these pesticidal proteins are those produced by gram positive bacteria such as *Bacillus thuringiensis* (Bt) and *Lysinibacillus sphaericus* or gram negative symbionts of invertebrate-pathogenic nematodes such as *Photorhabdus* and *Xenorhabdus* species. However, in addition to the ongoing discovery of new pesticidal protein variants from these bacteria, an increasing number of new invertebrate-active proteins are being discovered from a wide range of bacterial sources, including *Brevibacillus laterosporus*, *Pseudomonas entomophila* and *Yersinia entomophaga* (Dieppois et al., 2015; Glare et al., 2020; Marche et al., 2018; Waterfield et al., 2007). Recently, the nomenclature of such pesticidal proteins was revised to reflect the different structural classes of proteins that are able to kill invertebrates (Crickmore et al., 2021). This revision has been supported by the establishment of the Bacterial Pesticidal Protein Resource Center (BPPRC) that provides information on some source organisms, links to useful web pages and a set of tools and databases (Panneerselvam et al., 2022). As part of this ongoing project, we collect data from the literature (including peer-reviewed papers and patent applications), that give insight into the specificity of individual proteins. Two excellent historic reviews of the specificity of Bt pesticidal proteins were published in 2009 and 2013 by van Frankenhuyzen (van Frankenhuyzen, 2009; van Frankenhuyzen, 2013) and

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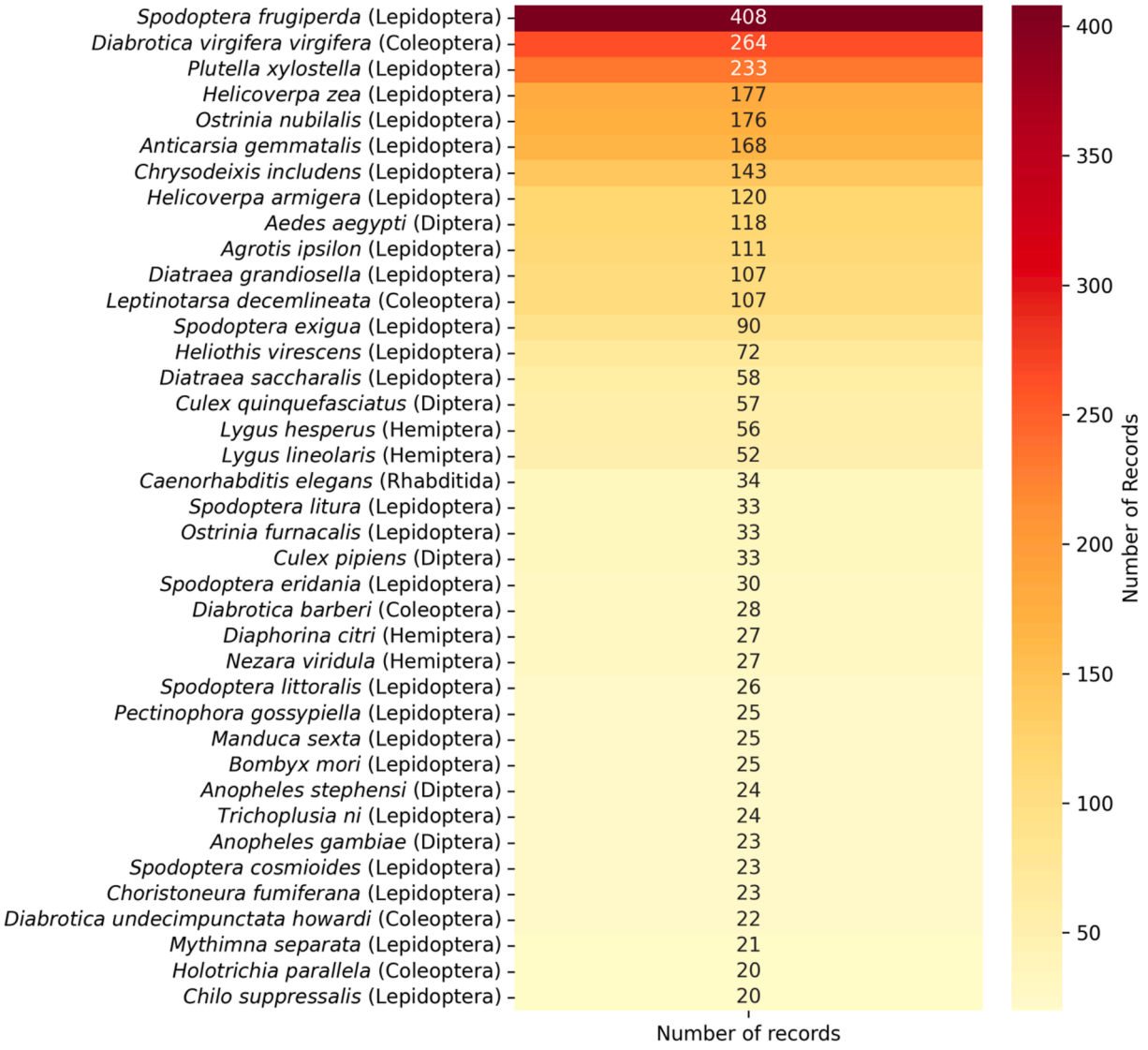

Fig. 1. Heat map showing species with more than 20 records.

served as useful resources for those working in the field to give an overview of what was known of specificity. Here, we present an overview of the current iteration of the specificity database, which can be used by individuals (e.g., researchers and regulators) to understand what is currently known of the activity and specificity of pesticidal proteins from bacteria.

2. Dataset description

2.1. Available data

The information provided by the specificity database encompasses reports of proteins that have been tested individually against invertebrates (whole organisms or, occasionally, cells in culture). Activity against targets may be defined by reported mortality or significant effects such as stunting. Users should refer to the source publication and the comments included with database entries for further details. Data are searchable by protein name, target species (by name or taxon id) and target order. In addition, the entries detail whether the proteins act alone or as a complex (with partners listed where they are necessary for activity), the material assayed, the assay method, the life stage tested and the citation (patent or journal publication) from which the data were derived are also listed. While the database contains descriptions for multi-part pesticidal proteins where more than one component is essential for activity, we have not included information on potential synergies between individual proteins where the effect may be enhancement of toxicity that is already innate in one or more of the proteins used (such effects have been reviewed previously (Baranek et al., 2020)).

Currently, the dataset comprises 3963 individual entries that derive data from 466 research papers and 174 patents. Information on toxicity to 253 different species in 5 taxonomic phyla, covering 25 invertebrate orders have been incorporated. Data are principally related to insects (Blattodea, Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Neuroptera, Orthoptera, Thysanoptera, Trichoptera) but also include orders in 9 other taxonomic classes, covering spiders (Araneae), mites/ticks (Mesostigmata, Sarcoptiformes, Trombidiformes), collembola (Entomobryomorpha, Poduromorpha), crustaceans (Amphipoda, Cyclopoida, Decapoda, Diplostraca, Isopoda), molluscs (Lepetellida), nematodes (Rhabditida), trematodes (Plagiorchiida) and segmented worms (Crassiclitellata). Fig. 1 shows all species for which there are currently 20 or more records in the database. Crucially, the database contains not only reports of individual proteins showing toxicity but also documents cases where individual proteins are demonstrated to be non-toxic to invertebrate targets (an important feature that will support both researchers and regulators). In addition, any potential future generation

Table 1
Cry3 protein activity and invertebrate species.

Target order	Target species	Protein name
Cry3: Reported toxicity		
Coleoptera	*Acanthoscelides obtectus*	Cry3Aa1
Coleoptera	*Alphitobius diaperinus*	Cry3Aa
Coleoptera	*Alphitobius diaperinus*	Cry3Bb
Coleoptera	*Cyclocephala borealis*	Cry3Aa1
Coleoptera	*Cyclocephala pasadenae*	Cry3Ba1
Coleoptera	*Cylas brunneus*	Cry3Aa3
Coleoptera	*Cylas brunneus*	Cry3Ba2
Coleoptera	*Cylas brunneus*	Cry3Bb3
Coleoptera	*Cylas brunneus*	Cry3Ca1
Coleoptera	*Cylas puncticollis*	Cry3Aa3
Coleoptera	*Cylas puncticollis*	Cry3Ba2
Coleoptera	*Cylas puncticollis*	Cry3Bb3
Coleoptera	*Cylas puncticollis*	Cry3Ca1
Coleoptera	*Diabrotica undecimpunctata*	Cry3Bb
Coleoptera	*Diabrotica undecimpunctata*	Cry3Bb.60**
Coleoptera	*Diabrotica virgifera virgifera*	Cry3Aa1
Coleoptera	*Diabrotica virgifera virgifera*	Cry3Bb
Coleoptera	*Leptinotarsa decemlineata**	Cry3Aa
Coleoptera	*Leptinotarsa decemlineata**	Cry3Bb
Coleoptera	*Monochamus alternatus*	Cry3Aa
Coleoptera	*Monochamus alternatus*	Cry3Aa-C**
Coleoptera	*Monochamus alternatus*	Cry3Aa-FKMW**
Coleoptera	*Monochamus alternatus*	Cry3Aa-FMRP**
Coleoptera	*Monochamus alternatus*	Cry3Aa-T**
Coleoptera	*Monochamus alternatus*	Cry3Aa-T-C**
Coleoptera	*Rhyzopertha dominica*	Cry3Aa
Coleoptera	*Tenebrio molitor*	Cry3Aa
Coleoptera	*Xylotrechus arvicola*	Cry3Aa1
Hemiptera	*Acyrthosiphon pisum**	Cry3Aa
Hemiptera	*Macrosiphum euphorbiae*	Cry3A
Cry3: Reported lack of toxicity		
Coleoptera	*Adalia bipunctata*	Cry3Aa
Coleoptera	*Atheta coriaria*	Cry3Aa
Coleoptera	*Cryptolaemus montrouzieri*	Cry3Aa
Coleoptera	*Monochamus alternatus*	Cry3Aa-FCKY**
Coleoptera	*Monochamus alternatus*	Cry3Aa-FMR**
Coleoptera	*Rhynchophorus ferrugineus*	Cry3Aa
Coleoptera	*Tribolium castaneum*	Cry3Aa
Crassiclitellata	*Lumbricus terrestris*	Cry3Bb1
Entomobryomorpha	*Folsomia candida**	Cry3A
Hemiptera	*Diaphorina citri*	Cry3Aa
Lepidoptera	*Manduca sexta*	Cry3Aa3
Lepidoptera	*Pieris brassicae*	Cry3Aa3
Poduromorpha	*Xenylla grisea*	Cry3A
Sarcoptiformes	*Oppia nitens*	Cry3A
Trombidiformes	*Tetranychus urticae*	Cry3Bb1

* The dataset has more than one record for this protein name/target pair.
** Modified Cry3 sequences.

of predictions of activity (based on machine learning/artificial intelligence) will require examples both of toxicity and lack of toxicity as training sets. It is very important that users of the database carefully check whether entries in the database show toxicity or non-toxicity. Users should not assume that the presence of an entry indicates activity.

The data also encompass a large range of bacterial proteins (not limited to Bt-derived proteins). In line with the BPPRC general inclusion criteria, toxin-complex (Tc) proteins have been excluded from the specificity data collection (and Tc protein research is supported by a separate database: https://www.mgc.ac.cn/dbTC/ (Song et al., 2021)). The proteins included in our data encompass many examples that are listed within the BPPRC nomenclature but also include numerous others, mainly derived from patents, that are yet to be incorporated into the official nomenclature. The nature of the information presented in the literature means that, in many cases, toxicity data can be associated with precise sequences, named to quaternary rank within the BPPRC nomenclature (and also specified mutants of these proteins). Overall, the current data cover 1141 protein names, however, in many cases, proteins listed in the publications are not named to quaternary rank (i.e., they may be listed as Cry1, Cry1A, or Cry1Aa rather than Cry1Aa1 for example) so that they cannot be associated with precise sequences. We have included these data but care needs to be taken when drawing conclusions from these entries as it is well established that very minor changes in protein sequence can affect target specificity (e.g., (Abdullah et al., 2003)). In future publications, we strongly encourage authors to provide full quaternary rank names for the proteins they work with, if necessary by requesting an official name assignment through the BPPRC web pages. The naming process is designed to be straightforward and efficient, enabling researchers to obtain an accurate and standardised designation for their proteins quickly. This practice will facilitate better understanding of sequence/activity relationships and improve consistency across studies.

2.2. Cross-sectional views of the data

Clearly, with an extensive dataset, it is not possible to present all findings. However, we present some cross-sectional analyses of the data to highlight key aspects.

As an example, we can overview reported activity for a protein family within the Cry structural class. For Cry3 proteins, for instance, the current database has 50 different entries, 34 of which demonstrate toxicity, all against species within the orders Coleoptera and/or Hemiptera. The remaining entries cover reports that Cry3 proteins are not active against the targets used, listing non-target Coleoptera and Hemiptera as well as other non-target insects, collembola, segmented worms, and mites/ticks (Table 1).

Data can also be probed by target species, for example, the data currently contain the most entries (408 entries) for assays against the fall armyworm, *Spodoptera frugiperda*, a major threat to agricultural production, reflecting the considerable effort undertaken to target this insect. Of the 379 reports of toxicity, many belong to the BPPRC structural classes Cry, Vip and Txp (either as wild-type or modified sequences). However, the majority of sequences are drawn from patent applications and have yet to be incorporated into the BPPRC nomenclature, reflecting the importance of this species to industrial partners. The remaining 29 entries for *S. frugiperda* in the database are reports of proteins with no effect against this target. These entries include individual proteins from the BPPRC classes Cry, Cyt, Mpf, Mpp, Tpp, Vip and Vpb, along with the BPPRC holding group Xpp and other sequences not yet incorporated into the BPPRC nomenclature.

A similar analysis of data for proteins tested against the mosquito, *Aedes aegypti*, a major vector of viral diseases of importance for human health, reveals 87 entries for protein activity encompassing BPPRC classes Cry, Cyt, Mpp, Mtx, Pra, Prb, Tpp, Txp and Vip (and modified variants) in addition to one Xpp protein and one artificial fusion protein (TIC6880: a fusion of proteins in the Pra1 and Prb1 families), which, as a non-natural protein, cannot be included in the nomenclature. Thirty-one proteins are reported to have no activity against this species and include proteins from the Cry, Cyt and Tpp classes.

Overall, the data confirm some general trends noted by van Frankenhuyzen (van Frankenhuyzen, 2009; van Frankenhuyzen, 2013), for example that Cry1 proteins tend to show activity against a subset of species within the Lepidoptera. However, the dataset also highlights that this is not an absolute, with some Cry1 proteins showing activity against species within the orders Coleoptera, Diptera, Hemiptera and Amphipoda. The current data also extend the target ranges of some pesticidal protein classes compared to those reported in these previous reviews e.g., Cry1Ca proteins were not reported to be active against Hemiptera in 2013 but more recently, activity against *Diaphorina citri* has been demonstrated (Tavares et al., 2024). As more data on the activity of pesticidal proteins are continuously being collected, data trends may change over time. Figs. 2 and 3 depict BPPRC database proteins that have been tested against different invertebrate orders with reports of toxicity and non-toxicity indicated (see also Supplementary Table 1). The data highlight that specificity must be assessed at the level of

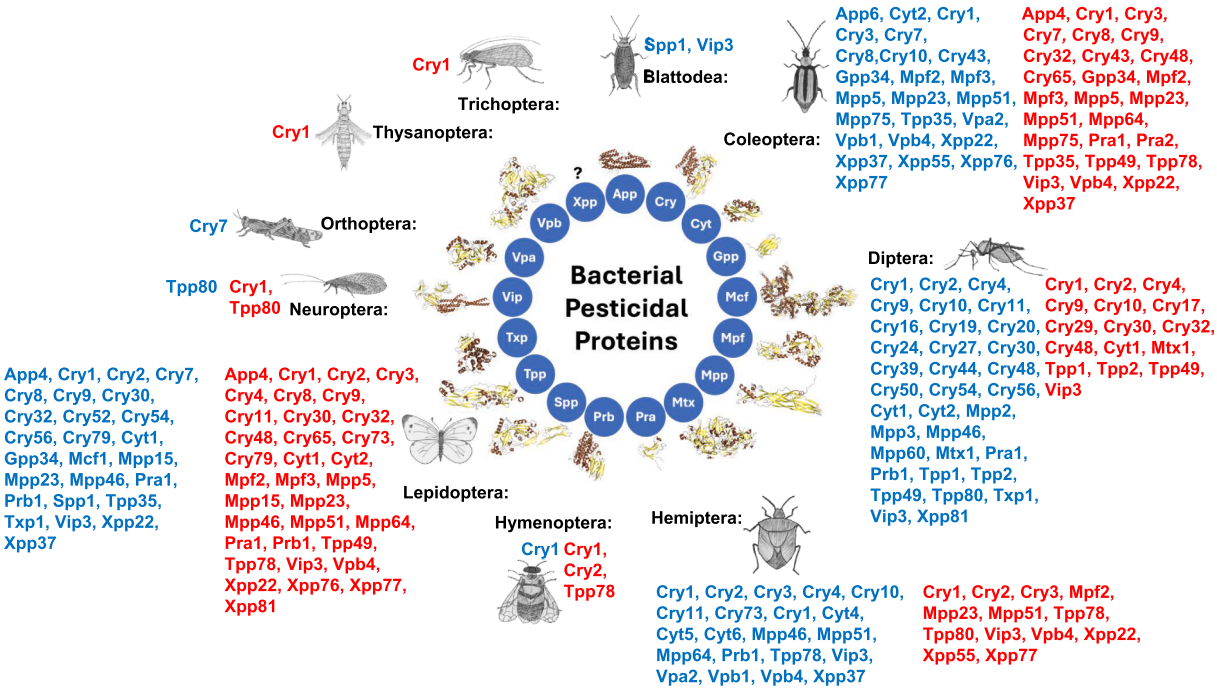

Fig. 2. BPPRC proteins tested against insects in different orders. Pesticidal protein classes in blue have been shown to contain members active against insect(s) in this order; classes in red have family members that have tested negative against insect(s) in this order. Data are shown for Blattodea (cockroaches), Coleoptera (beetles); Diptera, (flies, including e.g., mosquitoes); Hemiptera (true bugs); Hymenoptera (ants, bees and wasps); Lepidoptera (butterflies and moths); Neuroptera (lacewings); Orthoptera (locusts, crickets, grasshoppers), Thysanoptera (thrips); Tricoptera (caddis flies).

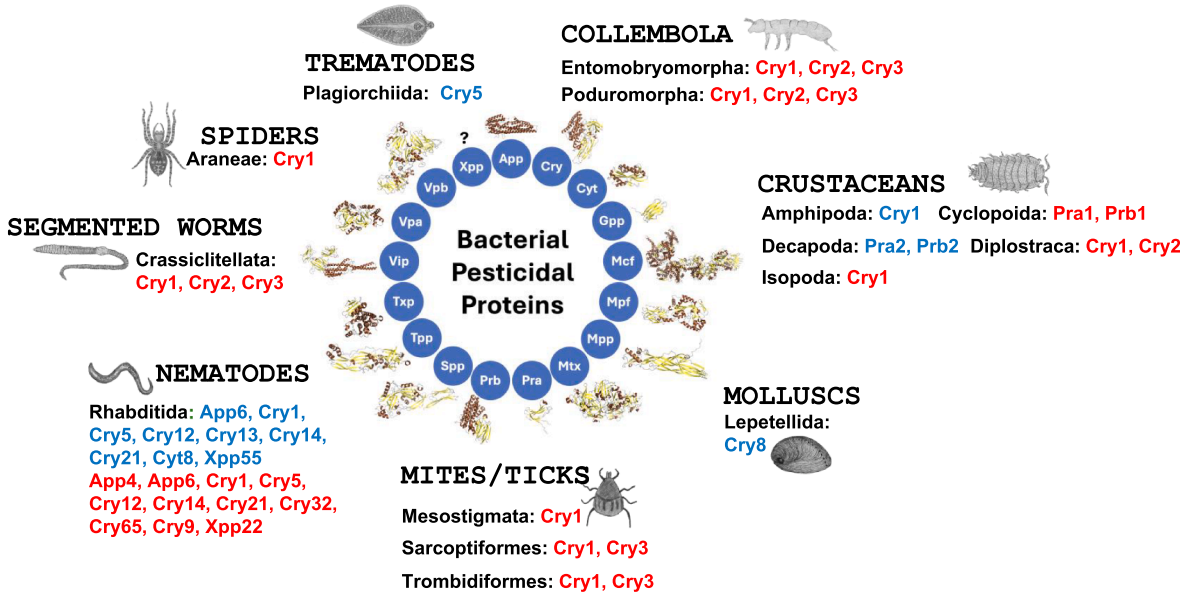

Fig. 3. BPPRC proteins tested against invertebrates of non-insect orders. Pesticidal protein classes in blue have been shown to contain members active against some invertebrate(s) in this order; classes in red have family members that have tested negative against some invertebrate(s) in this order.

individual species and for each individual pesticidal protein and that generalisations cannot be made. The profile of results illustrated in Figs. 2 and 3 also indicate areas where further testing may be required.

2.3. Limitations of the data

We continue to collect data on bacterial pesticidal proteins and to update the specificity database but clearly, given the amount of literature in this field, production of a comprehensive database is challenging. In addition, we can only work from publicly available data and do not have access to results held by companies undertaking large scale screening of proteins against target insects. Many reports in the literature give information on the toxicity of bacterial strains and list some of the candidate proteins that they may produce. However, without evidence that these are the agents responsible for activity, we have not included data from these reports in the database. Instead, we focus on activity of purified proteins or recombinant organisms producing single pesticidal proteins for inclusion in the database. It is also possible, due to human error, that mistakes are present in the data entered. Users encountering any errors are asked to notify the BPPRC via the feedback

Table 2
Number of database entries by target order.

Taxonomic order	Number of entries
Amphipoda	1
Araneae	1
Blattodea	3
Coleoptera	630
Crassiclitellata	6
Cyclopoida	2
Decapoda	2
Diplostraca	4
Diptera	326
Entomobryomorpha	12
Hemiptera	245
Hymenoptera	10
Isopoda	3
Lepetellida	1
Lepidoptera	2582
Mesostigmata	3
Neuroptera	4
Orthoptera	2
Plagiorchiida	1
Poduromorpha	4
Rhabditida	110
Sarcoptiformes	4
Thysanoptera	1
Trichoptera	4
Trombidiformes	2

form available on the bpprc-db.org webpage.

Information shown in the database, unavoidably uses a variety of measures of dose levels, as found in the source publications. The most informative bioassays use weights of the control agent (eg spore weight, or, preferably, purified protein weight) per unit volume or per surface area rather than spore or cell numbers. This approach has long been recommended for generating data that allow more reliable comparisons between agents and across studies (Dulmage, 1973).

Within the published data there are also unavoidable biases. As noted in previous reviews (van Frankenhuyzen, 2009; van Frankenhuyzen, 2013), any given protein is only ever tested against a very narrow cross section of invertebrate species. This testing tends to be limited by the species available in individual research laboratories or, where tests are conducted in the environment, species that are of interest and relevance to the ecosystems under study. Most testing is focused on agricultural pests with a significant but lower amount of screening against pests of interest to public health and nuisance insects (mainly Diptera). As a result, the current dataset is heavily biased towards testing on Lepidoptera (~65 % of entries) followed by Coleoptera (~16 %) and Diptera (~8%), (Table 2). Within these orders, we can also see a tendency to test against certain insects. As shown in Fig. 4, 86.7 % of the 326 tests against insects in the order Diptera involve mosquito species while other species in the taxonomic suborder Nematocera account for another 5.2 % of test data collected. Some elements of testing bias for individual proteins may also arise from the fact that bacterial strains (predominantly Bt) are often the first agents tested for activity. Clearly, if strains are inactive, this will act to limit the assay of individual proteins that they may encode.

Data in the database may appear contradictory in some instances with the same protein being shown as both toxic and non-toxic to the same target species. These discrepancies may result from differences in protein preparation, use of different bioassay protocols, tests against different life-cycle stages or differences in the genetic backgrounds of the insects tested. For example, many insects reared in laboratories have been in culture for many years and may have passed through bottlenecks that restrict their diversity and change their susceptibility to individual proteins. In addition, it is well known that there is natural variation in the sensitivity of different, non-selected field populations of some insects to pesticidal proteins (e.g., (Monnerat et al., 2006)). Further discrepancies may arise according to cut-offs used by different research groups to define activity, particularly when sublethal effects such as stunting and developmental arrest are used rather than more absolute measures such as mortality. In addition, for some proteins and targets there may be multiple entries because the same protein may be assayed against the target in different publications. We feel that it is important to include these data in the database.

Our data collection does not list the susceptibilities of colonies that have been the subject of selection for resistance in the laboratory or in the field (although susceptibilities of wild-type, non-selected invertebrates in the same publications may be reported in our data). In addition, there are a number of reports in the literature of BPPRC proteins that are active against human cancer cells in culture (e.g. Cry and Mpp family proteins often referred to as parasporins) (Akiba and Okumura, 2016) or potential antibacterial effects (e.g. (Revina et al., 2005)). These activities are not recorded in our database, which is restricted to invertebrate targets.

3. Concluding remarks

The extensive dataset, compiled in this study, highlights the wide pesticidal potential of bacterial proteins against invertebrate pests. By

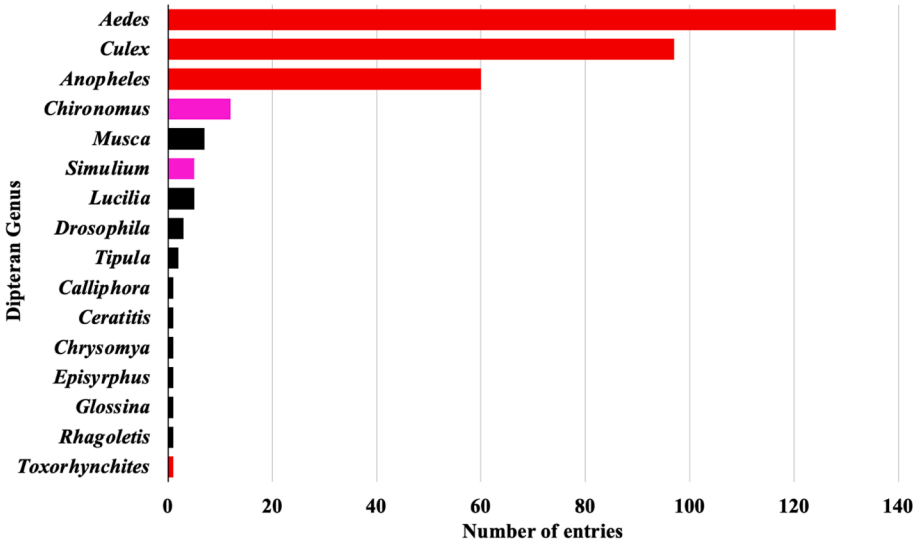

Fig. 4. Data entries for dipteran genera. Red bars: mosquito genera; magenta, other Nematocera; black bars, other Diptera.

integrating data from 466 research articles and 174 patents (to date), the database serves as a valuable resource for researchers and regulatory authorities, providing insights into protein activity and specificity, for sustainable pest management applications. While Cry proteins remain a key component of bacterial pesticides, the discovery of new protein classes underscores the highly-dynamic nature of this field. As biotechnology and data analysis tools advance and evolve, this database offers a critical foundation for developing innovative pest control strategies, optimising protein specificity, and addressing knowledge gaps. Continued updates to the dataset, coupled with refined testing methodologies, will further enhance its utility, supporting a transition towards more sustainable and effective biocontrol solutions.

Data access statement

Datasets for the specificity information presented here are available from the bpprc-db.org webpages from which they can be downloaded and are derived from original, publicly-available journal articles and patents.

CRediT authorship contribution statement

Colin Berry: Writing – review & editing, Writing – original draft, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Victoria Valby:** Investigation, Data curation. **Ruchir Mishra:** Writing – review & editing, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Bryony Bonning:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Leopoldo Palma:** Writing – review & editing, Investigation, Data curation. **Neil Crickmore:** Writing – review & editing, Supervision, Project administration, Investigation, Funding acquisition, 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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jip.2025.108319.

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