Available for millions of years but discovered through the last decade: Insects as a source of nutrients and energy in animal diets

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A B S T R A C T
The aim of this review is to present and discuss the most recent literature about the processing of insect biomass and its impact on nutritive value, further implementation of meals and fats derived from invertebrates to livestock (poultry and swine), aquaculture (salmonids), and companion animal diets and their impact on growth performance, metabolic response, and gastrointestinal microbiota shifts. Additionally, the most important barriers to obtaining unified products in terms of their nutritive value are considered, i.e., to define insects’ nutrient requirements, including various technological groups and further biomass processing (slaughtering, drying, and storage). Due to the current limitation in the insect production process consisting of the lack of infrastructure, there is stress on the relatively small amount of insect products added to the animal diets as a functional feed additive. Currently, only in the case of pet nutrition may insects be considered a full replacement for commonly used environmentally harmful and allergenic products. Simultaneously, the least information has been published on this topic. Thus, more scientific data are needed, particularly when the pet food branch and insect-based diets are rapidly growing.

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1. Introduction

Insect biomass is stated as a new alternative source of nutrients for various animal species. However, we should post the question of whether this is a real alternative or rather a natural choice for modern birds or fish present on earth for over 60 million years, which in wild conditions do not have access to soybean meal, fish meal, or other raw materials that have been developed in recent decades of animal production and nutrition. Furthermore, the production of these commonly used feed materials often causes environmental degradation (deforestation, ocean overharvesting, etc.) or are not accepted by consumers due to their genetic modification. Nonetheless, insect usage as the main protein source has been frequently published in the available literature (Allegretti et al., 2018; El-Hack et al., 2020; Józefiak et al., 2016; Kim et al., 2019). Thus, in the present review, the continuation of invertebrate administration as a substituent for commonly used and environmentally harmful ingredients such as soybean meal or fish meal was not deliberated. Based on the PubMed database (pubmed.ncbi.nlm.nih.gov), there is clearly shown that the last decade was the most intensive period for exploring the field of insect usage as a meal (Fig. 1A). Furthermore, in the scope of 2 insect species that are the most economically justified from the practical point of view, i.e.,
Fig. 1. Frequency of the scientific articles publishing based on PubMed database using the following keywords: (A) “insect meal”, or (B) the name of species considered as livestock by the EU Commission. The bolded lines were used to emphasize the 2 most profitable insect species (*Hermetia illucens* and *Tenebrio molitor*).
Hermetia illucens and Tenebrio molitor, the largest growth in the number of articles published in scientific journals is observed in the last 5 years (Fig. 1B). The abovementioned trend is connected to the recent development of the insect meal producer market, not only in Asia or North America but also in Europe, where in general the usage of invertebrates in the animal and human diet was forgotten. However, it should be emphasized that the limitation of invertebrate biomass production and application under field conditions is currently caused by 1) developing technology for invertebrate production; 2) processing of the invertebrate biomass for animal nutrition; 3) limited infrastructure availability; 4) the lack of systemic solutions for the distribution and collection of food wastes; 5) no nutrient requirements for invertebrates; and finally, 6) high variability in biomass nutritive value. Nonetheless, the infrastructure (production scaling up) seems to be the most important bottleneck of the insect farming industry, and consequently, there is no possibility of commonly administered invertebrate protein in animal diets, e.g., poultry at the suggested level, i.e., up to 20% (de Souza Villela et al., 2021). Additionally, the price per tonne of insect product is not acceptable in intensive rearing conditions of livestock, where 70% of all production costs are connected with nutrition. Based on the latest statistics by the European Feed Manufacturers Federation (FEFAC), compound feed only for poultry was produced by the EU-28 in 2019 at the level of approximately 56 million tonnes and was 9% higher than its production in 2013 (EU-28) (FEFAC.eu). Hence, 1% replacement of feed using insect meals needs to be produced, e.g., 1.68 million tonnes live black soldier fly larvae (BSFL; H. illucens). In contrast, insect market production by 2030 is estimated to be 250 thousand tonnes of invertebrate products, including whole dry insects and incorporated ingredients (IPIForg).

The introduction of novel feedstuffs requires many optimizations in terms of quality, availability, and supply chains. Therefore, the mass production of insects for livestock or companion animal nutrition should be at a consistent level and quality, which enforces different actions during insect rearing and processing. In this respect, one of the most important impediments of insect biomass implementation to animal nutrition is enormous nutritive value variability (Table 1). It is well documented that the chemical composition of insects is species (Janssen et al., 2017), development stage and sex (Liu et al., 2017), diet composition (Adebayo et al., 2021), and processing technique dependent (Huang et al., 2019). Nonetheless, the nutrition of larvae seems to be the most crucial to modulate the nutritive value of the final biomass. Therefore, the aim of this review is to focus not only on the application of insect-based raw materials in animal nutrition but also on an overview of various factors that affect their further nutritive value.

2. Insect nutrition

In the available literature, the usage of manure, sludge, slaughterhouse wastes, or catering waste as a rearing substrate has been frequently studied (Gold et al., 2020; Lalande et al., 2019; Rehman et al., 2019). However, in the European Union, due to the definition of the selected insect species, i.e., H. illucens (black soldier fly), T. molitor (yellow mealworm), Musca domestica (common housefly), Alphitobius diaperinus (lesser mealworm), Acheta domesticus (house cricket), Gryllodes sigillatus (banded cricket), and Gryllus assimilis (field cricket), as livestock by the European Parliament and the Council, does currently not allow to feed invertebrates using the abovementioned materials (EC No 178/2002; 852/2004; 183/2005), and it will not be presented in this review. Furthermore, the vast majority of the scientific literature has focused on compound diets such as chicken feed or vegetable wastes, which is not sufficiently informative and may make an illusory sense of progress in the field of insect nutrition. This is probably due to the high insects’ ability to adapt via flexibility of the midgut to wide spectra of various organic materials, particularly H. illucens, which is classified as a saprophagous species (Bonelli et al., 2020). It must be emphasized that insects should be fed specific nutrients, not specific feed materials, because they have a specific nutrient requirement. Thus, a permanent evaluation of the nutritive value of feed materials (byproducts of the agri-food industry) during insect rearing is needed. To date, there is scarce information about the impact of dietary macronutrients (crude protein or nitrogen-free extract) on the chemical composition of invertebrates. Some studies have been carried out on the protein-to-carbohydrate ratio (P:C) in the Lepidoptera, Orthoptera, Coleoptera, and Blattodea orders (Behmer, 2009; Raubenheimer and Simpson, 2003; Roeder and Behmer, 2014; Simpson et al., 1988; Waldhauer and Bhattacharya, 1973). Instead, from the authors’ point of view, the most stress of further research investigations should be put on recognizing and systemizing the nutrient requirements for economically justified insect species, such as H. illucens and T. molitor. Cammack and Tomberlin (2017) emphasized that an equal P:C ratio causes the fastest development of H. illucens and a beneficial survival rate when the substrate has 30% dry matter (DM), contrary to 5:1 or 1:5 ratios. Furthermore, not only the ratio between nutrients but also their distribution should be taken into consideration. Barragan-Fonseca et al. (2019) noted that development duration, as well as larval and pupal mass, is mostly dependent on protein and carbohydrate levels, >50% and 80%, respectively. The P:C interaction is responsible for approximately 20% of the effect on larval development. This finding is in line with the results of Le Gall and Behmer (2014), who reported that carbohydrates are responsible mainly for the increased biomass of larvae. Nevertheless, in the scope of the chemical composition, the crude protein (CP) content of the obtained H. illucens biomass is negatively related to increased concentration in the rearing medium (Barragan-Fonseca et al., 2018, 2019; Beniers and Graham, 2019; Tschirner and Simon, 2015). Simultaneously, the reports of Meneguz et al. (2018) indicated that not only the level but also the quality of protein (fruit wastes vs. brewery byproducts) has a crucial impact on its content in the larvae. Moreover, Barragan-Fonseca et al. (2021) estimated that both the protein and carbohydrate levels equally affected the protein content in the H. illucens biomass, while the variation between larval CP concentrations was modulated at the narrow spectrum, i.e., approximately between 41% and 45%. In contrast, the crude fat content varies over a considerable range (approximately 6% to above 30%), and increasing concentrations of protein and carbohydrates in the diet result in high fat levels (Barragan-Fonseca et al., 2019). This result is in agreement with Spranghers et al. (2019), who noted a high correlation ($R^2 = 0.94$) between the sum of carbohydrate and protein levels and larval growth. Furthermore, the results of Beniers and Graham (2019) exclude the hypothesis that carbohydrates may enlarge fat accumulation. It should be highlighted that the above-mentioned results stated only the beginning of the construction of the detailed nutrient requirements for selected insect species. Further research is needed to divide the specific nutritional needs for species, developmental stages, parental stocks, and intended biomass usage. Therefore, similar to other animals, insect rearing requires the nutritive value of feedstuffs and the nutrient composition of the diets. The impact of the substrates used in insect rearing is important, but today, it is not clear how their modification can influence final product quality and their usage in animal nutrition. Thus, it is highly recommended to expand the evaluation of the transfer chain of nutrients from rearing substrate to insect biomass in the future as a milestone to create a nutrient requirement for insect biomass production.
Table 1
The nutritive value variability of the selected insect species.1

| Item                        | Hermetia illucens | Tenebrio molitor | Musca domestica |
|-----------------------------|-------------------|------------------|-----------------|
| Crude matter, %             | 31.4 ± 5.2        | 54.0 ± 12.8      | 24.3 ± 0        |
| Crude protein, % DM         | 43.3 ± 7.1        | 53.3 ± 7.4       | 54.1 ± 10.7     |
| Crude fat, % DM             | 26.3 ± 11.2       | 29.8 ± 8.7       | 21.2 ± 6.3      |
| Crude ash, % DM             | 12.3 ± 7.9        | 4.2 ± 1.2        | 10.2 ± 6.8      |
| Chitin, % DM                | 4.6 ± 1.5         | 5.9 ± 1.4        | ND ± ND         |
| AMEn for poultry, MJ/kg     | 17.6 ± 3.6        | 21.7 ± 0         | 17.3 ± 0        |
| Gross Energy, MJ/kg         | 24.9 ± 2.9        | 24.5 ± 2.3       | 23.1 ± 4.4      |
| Minerals, g/kg DM           |                   |                  |                 |
| Calcium                     | 27.2 ± 13.7       | 0.9 ± 0.7        | 9.8 ± 8.9       |
| Phosphorus                  | 8.9 ± 2.1         | 7.9 ± 1.5        | 10.5 ± 2.6      |
| Magnesium                   | 3.6 ± 1.2         | 2.2 ± 0.6        | 2.3 ± 0         |
| Potassium                   | 14.7 ± 5.3        | 9.1 ± 1.0        | 12.7 ± 0        |
| Sodium                      | 4.1 ± 3.7         | 1.2 ± 0.5        | 6 ± 0.9         |
| Chlorine                    | 2.0 ± 0.6         | 5.7 ± 0          | ND ± ND         |
| Sulphur                     | 3.4 ± 1.3         | 3.5 ± 0          | ND ± ND         |
| Manganese, mg/kg DM         | 214.3 ± 78.5      | 11.6 ± 3.1       | 165.0 ± 154.2   |
| Zinc, mg/kg DM              | 104.2 ± 32.7      | 110.8 ± 11.2     | 638.0 ± 567.1   |
| Copper, mg/kg DM            | 9.4 ± 2.1         | 16.3 ± 2.9       | 33.2 ± 1.1      |
| Iron, mg/kg DM              | 263.1 ± 106.5     | 70.5 ± 16.9      | 539.3 ± 91.2    |
| Cobalt, mg/kg DM            | 0.3 ± 0.3         | ND ± ND          | ND ± ND         |
| Molybdenum, mg/kg DM        | 0.9 ± 0.3         | ND ± ND          | ND ± ND         |
| Amino acids, g/100 g of protein |                   |                  |                 |
| Lysine                      | 6.2 ± 0.9         | 4.6 ± 1.9        | 6.9 ± 1.5       |
| Threonine                   | 3.9 ± 0.5         | 3.6 ± 0.9        | 4.9 ± 1.3       |
| Methionine                  | 1.8 ± 0.4         | 1.2 ± 0.5        | 3.3 ± 1.6       |
| Cystine                     | 0.7 ± 0.2         | 1.4 ± 0.6        | 1.0 ± 0.3       |
| Tryptophan                  | 1.5 ± 0.4         | 1.2 ± 0.5        | 1.4 ± 0.2       |
| Isoleucine                  | 4.3 ± 0.5         | 4.0 ± 1.3        | 3.7 ± 1.3       |
| Valine                      | 5.9 ± 0.4         | 5.3 ± 1.9        | 4.7 ± 1.8       |
| Leucine                     | 6.9 ± 0.6         | 6.6 ± 2.3        | 6.3 ± 0.6       |
| Phenylalanine               | 4.1 ± 0.9         | 3.4 ± 1.0        | 7.1 ± 1.5       |
| Tyrosine                    | 5.9 ± 1.4         | 5.9 ± 1.5        | 5.6 ± 1.8       |
| Histidine                   | 3.1 ± 0.8         | 2.9 ± 1.1        | 4.0 ± 1.0       |
| Arginine                    | 5.3 ± 1.2         | 4.5 ± 1.4        | 6.0 ± 1.6       |
| Aspartic acid               | 8.9 ± 0.8         | 7.3 ± 2.2        | 8.3 ± 2.6       |
| Glutamic acid               | 11.1 ± 1.2        | 10.9 ± 3.1       | 11.8 ± 3.7      |
| Glycine                     | 5.0 ± 0.7         | 4.8 ± 1.7        | 3.3 ± 1.6       |
| Serine                      | 4.1 ± 0.3         | 4.3 ± 1.6        | 3.9 ± 0.2       |
| Proline                     | 5.4 ± 0.5         | 5.8 ± 1.87       | 4.6 ± 0.7       |
| Alanine                     | 6.3 ± 0.8         | 7.1 ± 2.19       | 5.0 ± 0.7       |

**AMEn** = apparent metabolizable energy corrected to zero nitrogen balance; **ND** — not detected.

1 The presented values are based on the literature listed separately in Supplementary material.

Finally, different agroindustry wastes are rich in structural fibers and/or soluble polysaccharides, which may need processing before they are used as substrates for insects. Feed structure, particle size, viscosity, dry matter content, etc., also play an important role in terms of feed distribution and its availability and need further investigation, while not only feed chemical composition but also its physical affect insect performance.

### 3. Larval biomass processing

In addition to the modulation of insect chemical composition by rearing substrate, there is also a possibility of negatively affecting larval nutritive value through the selection of inadequate biomass processing conditions, i.e., slaughter method, drying process, and storage. The most popular slaughtering methods include heating (desiccation, blanching), freezing, asphyxiation, and usage of mechanical techniques (grinding, high hydrostatic pressures). Among those listed, the blanching technique seems to be favorable because of its positive effect on the limitation of lipid oxidation and reduction of Maillard reaction occurrence (color stability; inactivate phenol oxidase) (Larouche et al., 2019). However, the usage of large quantities of water in field-intensive production, i.e., approximately 300 L per tonne of larvae, makes this technique environmentally harmful. Surprisingly, slow slaughtering methods such as freezing did not prevent protein and lipid degradation (Caligiani et al., 2019; Leni et al., 2019). Furthermore, Nyangena et al. (2020) have shown that various processing techniques, i.e., toasting, boiling, solar, and oven drying, can affect the chemical composition of insects. It should be highlighted that most authors observe an adverse effect of CP dilution during the boiling water process (Egan et al., 2014; Manditsera et al., 2019). It is well known that temperature can disrupt the quality of protein and further its availability (Ibañez et al., 2020). Thus, subsequent performance results of farm animals fed insect-based diets can be negatively affected by a reduction in the digestibility coefficients of crude protein and amino acid availability. The protein dispersibility index (PDI) of *H. illucens* larvae meals varied significantly and was characterized in the range from approximately 15% to 60% (Table 2). Low PDI values indicate the occurrence of the Maillard reaction and binding of lysine to carbohydrates, which makes indigestible complexes. Additionally, temperature treatment may result in the oxidation, aggregation, and formation of Schiff bases (Bax et al., 2012). This result is in line with Huang et al. (2019), where conventionally dried (60 °C in a drying oven to constant weight) *H. illucens* larvae were characterized by a better digestible indispensible amino acid score and digestibility than the microwave (500 W for 15 min) method, which may polymerize the protein and impede its digestion. It was confirmed for *T. molitor* and *A. domestica* that oven drying (150 °C
for 30 min and 200 °C for 10 min) and autoclaving significantly decreased in vitro CP disappearance during enzymatic hydrolysis (Poeaert et al., 2016). Finally, the storage of insect-derived products can also negatively affect their nutritive value. Independent of the packages, i.e., made of plastic, polyethylene, or polypropylene, the ambient or refrigerated storage temperature conditions significantly reduced house cricket meal mono- and polyunsaturated fatty acids in the period from 45 to 90 d (Kamau et al., 2017).

The diverse microbiota of the insects’ gastrointestinal tract (GT) (Daniele et al., 2022; Zhineng et al., 2021) may play an important role in the contamination of the final products. Because insects are processed with the gastrointestinal tract, evisceration is not possible. Therefore, all of the abovementioned technological issues should also relate to microbiological safety and quality. In conclusion, the development of optimal processing techniques is the key to ensuring that the nutritional value of feed materials made from insects is not destroyed; moreover, a balance between microbiological safety and biological value of the nutrients is important. It is therefore advisable to continue work on identifying effective methods of slaughter, drying, and storage.

### Table 2
Comparison of the protein dispersibility index (PDI) values of the selected feed materials.

| Item                        | Process             | Parameters | PDI, % | Reference                  |
|-----------------------------|---------------------|------------|--------|-----------------------------|
| Whole soybeans              | —                   | —          | 88.6   | Bruce et al. (2006)         |
| Soybeans                    | Roasted             | 143 °C     | 18.6   |                            |
| Raw maize-based food        | —                   | —          | 69.3   | Lasekan et al. (1996)       |
| Maize-based food            | Extrusion           | 100 °C     | 46.6   |                            |
| Maize-based food            | Extrusion           | 120 °C     | 29.6   |                            |
| Maize-based food            | Extrusion           | 135 °C     | 18.9   |                            |
| Animal byproducts           | Raw                 | —          | 18.9   | Pérez-Calvo et al. (2010)   |
| Animal byproducts           | Rendered            | 141.8 °C, 23.8 min; 2.3 bars | 11.02 to 15.42 | Authors data (unpublished) |
| Hermetia illucens larvae defatted meal | Drying | 100 °C, 24 h | 22.60 |                            |
| H. illucens larvae full-fat meal | Drying            | 100 °C, 24 h | 19.38 |                            |
| H. illucens                  | Drying              | —          | 29.05  | Authors data (unpublished)  |
| H. illucens                  | Freezing            | —80 °C, 24 h freeze-dried | 52.86 |                            |
| H. illucens                  | Microwave drying    | 450 W, 20 min | 31.15 |                            |
| H. illucens                  | Scalding            | Boiling water 5 min; freezing at 18 °C and freeze-dried | 34.35 |                            |
| H. illucens                  | Blanching           | Steam 5 min; freezing at 18 °C and freeze-dried | 33.70 |                            |
| H. illucens                  | Microwave drying    | 900 W at 120 °C, 5 bars pressure | 42.45 |                            |
| H. illucens                  | Fat extraction      | n-hexane   | 29.09  | Authors data (unpublished)  |
| H. illucens                  | Fat extraction      | 2-methyloxolane | 31.55 | Authors data (unpublished)  |
| Average PDI value of soybean by origin | —                   | —          | —      |                             |
| Argentina                    | 10.3 to 23.9        | —          | —      |                             |
| Brasil                      | 8.9 to 17.6         | —          | —      |                             |
| USA                         | 8.8 to 45.7         | —          | —      |                             |
| India                       | 9.6 to 33.6         | —          | —      |                             |

1 bar = 100 kPa.

4. Insects in petfood

The possible implementation of insect-derived products, mainly protein meals, in companion animals’ nutrition allows to expand the branch of hypoallergenic diets (Böhm et al., 2017, 2018). The constantly increased availability of invertebrate biomass on the market has resulted in an enlarged number of commercial foods. It should be highlighted that the ancestors of domestic dogs and cats ingest invertebrates as a part of their natural diets (Behrendorff et al., 2016; Tiralla et al., 2021; Woolley et al., 2020). Thus, the implementation of “novel” insect ingredients is in fact back to nature. Moreover, in the case of the petfood industry where “fresh meat” application is becoming more important, the question of whether insect biomass should be implemented as a direct replacement of vertebrate meat and its byproducts arises. In this case, drying and/or fat separation is avoided; however, appropriate devitalization of the larvae and further product stability are still important considerations.

4.1. Insect meals in petfood

The usage of various species, mainly T. molitor, as well as H. illucens larvae as the main source of protein in the diets of pets has not only a nutritional effect but also a beneficial environmental impact. It should be emphasized that the production of commercial pet food generates up to 30% of the environmental impact (including the use of land, water, fossil fuel, phosphate, and bicarbonates) from animal production and emits 64 million tonnes of CO2-equivalent methane and N2O (Okin, 2017). This is caused by the significant amounts of pets kept in households, i.e., 703.3 million globally (Hughes and Macdonald, 2013). Additionally, the global warming potential (GWP) of insects, particularly T. molitor and H. illucens, is smaller, from four to twenty-eight times, than chicken, pork, and beef protein production (Beynen, 2020). Thus, the CO2 equivalent per kg of product is stated at the level of 12 to 13 GWP/kg protein for insects, contrary to 50 or 335 GWP/kg of protein for chickens or beef production, respectively. Consequently, the provision of insect biomass into pet foods positively affects not only the diversification of hypoallergenic products but also stays in line with the idea of HORIZON2020, including the European Green Deal (ec.europa.eu). In addition to the abovementioned information, the most important from a practical point of view seems to be the palatability of insect biomass. Kieronczyk et al. (2018b) showed that insects may be used in dog diets as an additional attractant; however, differences between sexes were observed. Accordingly, females preferred more insect ingredients, while males favored T. molitor larvae. Based on Beynen (2020), the distinction between dog's and cats' preferences was also noted. H. illucens larvae meal was more suitable for dogs when the cats preferred the T. molitor larvae product.
Nonetheless, in the case of cat acceptance, *H. illucens* meal was also tolerated by most animal use in the PaBlack and Zentek (2018) study. Importantly, the high inclusion level of *G. sigillatus* meal, i.e., up to 24% (Kilburn et al., 2020), as well as 20% of *H. illucens* larvae meal (Frel et al., 2021) did not trigger feed intake in dogs. Additionally, the total replacement of chicken fat used as an energy source in beagle dog diets by *H. illucens* larvae fat (5% inclusion) did not influence palatability.

The in vitro DM digestibility measurements indicate no obstacles to the use of *H. illucens*, *M. domestica*, and *T. molitor* larvae meals in dog nutrition, which are characterized by 81.4%, 88.6%, and 92.3%, respectively (Bosch et al., 2016). Furthermore, the essential amino acid availability was above 91%. The results of in vivo studies confirmed the possibility of insect meal usage in pet nutrition. Lisenko et al. (2018) suggested the possibility of *Nauphoeta cinerea*, *Gromphadorhina portentosa*, and *Zophobas morio* larvae meal usage in beagle diets up to 15% without a negative effect on nutrient digestibility, fecal metabolites, or the excreta microbiota. Furthermore, Russo et al. (2019) concluded that DM digestibility was higher in the *H. illucens* meal diet than in the control feed with deer byproducts used as a main source of protein. Additionally, Frel et al. (2021) indicated that the administration of up to 20% *H. illucens* meal, as well as of the partial (5%) or total replacement of chicken fat by *H. illucens* larvae fat in the Beagle dog diet, resulted in no adverse effect on nutrient and energy availability.

### 4.2. Insect functional properties in petfood

However, in the available literature, there are scarce data in terms of experimentation carried out on dogs or cats to evaluate the potential effect of insect-based diets on pet organisms. The application of maggots at the level of 5% also did not influence dog growth, feed intake, blood hematology, biochemistry, or immune traits or reduce oxidative stress (Hong et al., 2020). Interestingly, the addition of a relatively small amount of *H. illucens* larvae meals, i.e., 1% or 2%, linearly improved the apparent total tract digestibility of DM (72% vs. 75%) and CP (73% vs 78.5%) and had a favorable impact on immune (tumor necrosis factor-a [TNF-a]) and anti-oxidative status (glutathione peroxidase) (Lei et al., 2019). Surprisingly, after 24% *Gryllodes sigillatus* was added to the beagle dogs’ diets, the alpha and beta microbial diversity was not affected, while only a few genera/families, i.e., *Catenibacterium*, *Lachnospiraceae*, *Faecalibacterium*, *Bacteroides*, *Faecalibacterium*, and *Lachnospiraceae* were influenced; however, their abundance comprised less or near 1% of the total microbial community (Jarett et al., 2019). However, *G. sigillatus* meals at each inclusion level, i.e., 8%, 16%, and 24%, negatively affected the nutrient digestibility of crude protein, ether extract, and gross energy and increased the daily fecal output (Kilburn et al., 2020). This could be a result of low acidic chitinase gene expression in dogs and a consequence of decreased chitin digestibility, which is the lowest in comparison to mouse, chicken, pig, and bovine, even if the insect products are well tolerated (intake) by the animal (Tabata et al., 2018). However, some doubts still occur in the scope of disease transmission or heavy metal accumulation (Ibitoye et al., 2019). Due to the limitations of available studies, there is a need to significantly expand knowledge in terms of various insect species or chitin incorporation into pet diets and evaluation of their effects on the nutrient digestibility coefficients (in vivo), physiological and immunological response, and the GIT microecosystem, particularly during long-term studies.

Currently, the pet food market frequently offers diets based on the insect as a sole protein source. This process excludes the most allergenic products from the dogs’ food, such as soy or chicken meat. There are limited data about the hypoallergenic properties of insects in terms of their inclusion in companion animal diets. According to Lee et al. (2021), the defatted *T. molitor* meal-based diet offered to dogs for 12 weeks has the potential to diminish cutaneous lesions and skin barrier dysfunction. Furthermore, a positive effect on the improvement of lesion scores and coat quality in atopic dermatitis dogs was observed after 2 weeks of insect-based diet administration (Böhme et al., 2018). However, it should be emphasized that each protein above 20 kDa may cause an allergy (Lee et al., 2021). Furthermore, the history of food allergy shows that protein availability is a significant factor in its occurrence, i.e., the geographical access to specific ingredients and frequency of protein ingested (Prélaud, 1999). Thus, there is still a possibility of invertebrate-origin allergies appearing in the future. Nevertheless, there is a priority to improve our knowledge about the effect of tropomyosin, arginine kinase, and other allergens present in insect biomass on companion animal health.

Eventually, dog owners have a positive attitude in terms of the future usage of insect products as an alternative to meat in dog food, particularly due to the benefits of reducing environmental pressure, and additionally claim that invertebrate biomass is nutrition’s sufficient substitute or replacement for current products (Ibitoye et al., 2019).

### 5. Insects in poultry nutrition

#### 5.1. Insect meals as a functional feed additive for poultry

According to the abovementioned challenges in terms of insect biomass production limitations, the current application of insect meals should be considered a potential functional feed additive according to their health-promoting properties (Gasco et al., 2018). It is well documented that chitin, as well as antimicrobial peptides (AMPs), occurring in invertebrates can positively affect the growth performance, GIT microbiota, and immune response of birds (Gasco et al., 2020; Józefiak and Engberg, 2017). It is indicated that feeding broiler chickens with meals as a source of chitin resulted in a decrease in the intestinal population of bacteria such as *Escherichia coli* and *Salmonella*; in contrast, the effect has not been confirmed in birds fed purified chitin. Insects also have been investigated as promising sources of antimicrobial peptides. According to the Antimicrobial Database (aps.unmc.edu), to date, 326 AMPs have been identified from insects. Research performed in vitro investigating the antimicrobial activities of fractionated extracts and AMPs purified from insects identified 16 peptides in samples of *H. illucens* and 16 in *T. molitor* (Tables 3 and 4). The inhibition activities of peptides extracted from *H. illucens* have been proven against gram-negative bacteria, *E. coli*, *E. coli* serotype O157:H7, *Salmonella pullorum*, *S. typhimurium*, *S. enteritidis*, *Enterobacter aerogenes*, and *Pseudomonas aeruginosa*; gram-positive bacteria, *Staphylococcus aureus*, methicillin-resistant *S. aureus* (MRSA), *S. epidermidis*, *Streptococcus suis*, *Listeria ivanovii*, *Bacillus subtilis*, and *Micrococcus luteus*; and fungi, *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, and *Candida albicans* (Table 3). To investigate the pharmacological activities of novel antibacterial peptides extracted from *T. molitor* against gram-positive bacteria, such as *B. subtilis*, *S. aureus*, *S. epidermidis*, *S. pyrogen*, *M. luteus*, and *Corynebacterium diphtheriae*, as well as gram-negative bacteria, such as *E. coli*, *Shigella flexneri*, *P. aeruginosa*, and *Proteus vulgaris*, and yeasts, such as *S. cerevisiae* and *C. albicans*. Research performed in vivo indicated the beneficial effects of synthetic AMP-A3 and AMP-P5 on the growth parameters of broiler chickens (Choi et al., 2013a, 2013b; Wang et al., 2016). Moreover, the addition of synthetic cecropins to broiler diets decreased pathogenic bacteria and enhanced intestinal villus height in the duodenum (Wen and He, 2012). Therefore, it is suggested that cecropin can be a possible alternative to some antibiotics used in poultry production.
| AMP name                  | Source/samples                                                                 | Amino acid sequence                        | Techniques                                      | Inhibited microorganisms                  | MIC            | AMP gene expression | Ref.                  |
|--------------------------|--------------------------------------------------------------------------------|--------------------------------------------|------------------------------------------------|-------------------------------------------|---------------|---------------------|----------------------|
| Cecropin-like peptide 1  | Hemolymph of immunized *H. illucens* larvae                                    | MNFTKLFVVFA                                | Fast protein liquid chromatography (FLPC), high-performance liquid chromatography (HPLC), matrix-assisted laser desorption/ionization-time-of-flight (MALDI-TOF) mass spectrometry (MS), RT–PCR | *E. coli* KCCM 11234                          | 0.52 to 1.03 μmol/L | AMP gene expression was increased in the muscle and trachea. | Sultana et al. (2021), Park and Yoe (2017a) |
|                          | *S. aureus* KCCM 40881                                                         | VVIVAFQASEGWRK                              |                                               | *Enterobacter aerogenes* KCCM 12177          | 1.03 to 2.07 μmol/L | --                  | --                   |
|                          |                                                                                 | RFVRQVEQGRQVRIDAGVQ                        |                                               | *Pseudomonas aeruginosa* KCCM 11328          | 1.03 to 2.07 μmol/L | --                  | --                   |
|                          |                                                                                 | GIAAQGQANLYATAGFCPPQQQ                     |                                               | *MRSA* KCCM 40881                           | ND            | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *Staphylococcus aureus* KCCM 12256          | ND            | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *S. epidermidis*                             | ND            | --                  | --                   |
| Cecropin-like peptide 2  | Hemolymph of immunized *H. illucens* larvae                                    | MNFAKLPYVAALVAFSGQ                        | Fast protein liquid chromatography (FLPC), high-performance liquid chromatography (HPLC), matrix-assisted laser desorption/ionization-time-of-flight (MALDI-TOF) mass spectrometry (MS), RT–PCR | *S. aureus* KCCM 40881, *S. aureus* ATCC25923 | 0.06 to 1.17 μmol/L | --                  | --                   |
|                          | *E. coli* KCCM 11234                                                           | SEAGWWKVFVPERGLQGRDAGV                   |                                               | *E. coli* ATCC43300                          | 0.12 μmol/L   | --                  | --                   |
|                          |                                                                                 | IQQLEAQQGAQLNYATAGFCPPQQQ                 |                                               | *S. aureus* ATCC538                          | 0.12 μmol/L   | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *S. aureus* CICC546                           | 0.23 μmol/L   | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *Listeria ivanovii ATCC19119*                | 0.93 μmol/L   | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *E. coli* CICC1515                           | 0.12 μmol/L   | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *E. coli* CICC21530 serotype O157:H7         | >29.97 μmol/L | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *Salmonella typhimurium* ATCC14028           | 0.59 to 1.17 μmol/L | --                  | --                   |
|                          |                                                                                 |                                             |                                               | *Salmonella enteritidis* CMCC50336           | --            | --                  | --                   |
|                         |                                                                                                  |                                             |                                               | *Staphylococcus epidermidis* KCCM 35494      | --            | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | not observed antimicrobial activity          |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | against *G. avium* clinical isolated, multidrug resistant |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *S. aureus* KCCM 408810                      | 0.5 to 1.17 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | MRSA clinical isolated, multidrug resistant  | 0.5 to 1.17 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *E. coli* KCCM 11234, *Enterobacter aerogenes* KCCM 12177 | 0.06 to 1.17 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *P. aeruginosa KCCM 11328*                  | 0.17 to 2.34 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *MRSA* KCCM 40881                           | 0.02 to 0.04 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *Staphylococcus epidermidis* KCCM 11316      | 0.59 to 1.17 μmol/L | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *Bacillus subtilis KCCM*                     |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *Salmonella enteritidis* CMCC50336           |               | --                  | --                   |
|                         |                                                                                                  |                                             |                                               | *Staphylococcus aureus* KCCM 12256          |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *Staphylococcus epidermidis* KCCM 35494      |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | not observed antimicrobial activity          |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | against *G. avium* clinical isolated, multidrug resistant |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *S. aureus* KCCM 408810                      |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | MRSA clinical isolated, multidrug resistant  |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *E. coli* KCCM 11234, *Enterobacter aerogenes* KCCM 12177 |               | --                  | --                   |
|                          |                                                                                                  |                                             |                                               | *P. aeruginosa KCCM 11328*                  |               | --                  | --                   |
|                         |                                                                                                  |                                             |                                               | *S. aureus* KCCM 40881                      |               | --                  | --                   |

Table 3: Antimicrobial peptides (AMPs) from *Hermetia illucens* inhibited microorganisms.
| Defensin 1 (hde1) | Hemolymph of *H. illucens* larvae immunized with *Lactobacillus* species | Sequence available in Antimicrobial Peptides Database (AP03308): ATCDLLSAT KVSTACAAH CLEKGRKGGYCNKSKLVCVR MASKFLQNPYNHINNNNCVFAA GNRTSINTPSLNFACNLKNKDSLGVSHITQCVSFTQSNARLINL KTPDHVRVANFIWHSFRLNGCF DIFKGRGSLDHTFHRAEXTSLGA SHPRGCCTAELGKANLWRRISPG LSITFKTGASRTGCGPMAIRNNGF GAGLGFHRF | Antimicrobial activities, analysis of AMPs transcription | E. coli KCCM 11234 Salmonella pullorum KVCC-BA0702509 S. typhimurium KCCM 40406 S. enteritidis KCCM 12021 | Range 100 to 200 µg/100 µl for all analyzed microorganism |
| H. illucens attacin (Hi-attacin) | Immunized *H. illucens* larvae with *E. coli*; fat body, muscle, fore-gut, mid-gut, hind-gut, Malpighian tubule, and trachea samples | ATCDLLSAT KVKSTACAAH CLLKGHKGGYCNKSKLVCVR | E. coli KCCM 11234 S. aureus KCCM 40881 MRSA | – |
| | | | Hi-attacin transcripts levels a 27.5-fold increase in the fat body, a 4-fold increase in fore-gut, a 10.2-fold increase in muscle, and a 3.7-fold increase in the trachea comparing to control | Shin and Park (2019) |
| Sarcotoxin 1, 2a, 2b, and 3 | Crushed *H. illucens* larvae immunized with *S. aureus*, and *E. coli* | Sarcotoxin 1: GWUKRRKIGMKFIL GTTLAIVVAIFGQCQAATWSYNP GCATVTWATANVATAR | Analysis of gene and 3D structures | S. aureus, and *E. coli*; Four isoforms were detected for sarcotoxin: sarcotoxin 1, sarcotoxin (2a), sarcotoxin (2b), and sarcotoxin 3 |
| | | Sarcotoxin 2a: GWUKRRKIGKKFILGTTLAIVVAIFGQCQAAT WSYNPGATYVTWATANVATAR Sarcotoxin 2b: GWUKRR KIGKKFILGTLAIVVAIFGQCQAAT WSYNPGATYVTWATANVATAR Sarcotoxin 3: GWUKRRKIGMMC MKNSIPSTEEREAARKRNKRKYVP | – | – |
| | | | Sultana et al. (2021) Elhag et al. (2017) |
| StomoxynnZH1 | Crushed *H. illucens* larvae immunized with *S. aureus*, and *E. coli* | RGFRKHFNPNNLPICVEGLAGD IG5ILIGVG | 3D structures of the AMP genes; protein expression, antimicrobial activity assay | E. coli S. aureus Rhizoctonia solani Sclerotinia sclerotiorum | 15 to 30 µg/mL 27 to 54 µg/mL >98 µg/mL |
| | | | – | Sultana et al. (2021) Elhag et al. (2017) Huang et al. (2020) Park et al. (2014) |
| Fractionated extract of *H. illucens* larvae | Lyophilized *H. illucens* larvae immunized with *S. aureus* | The water-soluble extract was applied to Sep-Pak C18, elution with 80% acetonitrile (ACN) | MRSA Candida albicans Kocuria rhizophila Micrococcus luteus E. aerogenes B. subtilis E. coli P. aeruginosa S. epidermidis | 25 mg/mL |
| | | | – | 12.5 mg/mL 50 mg/mL |

AMP – antimicrobial peptide; MIC – minimal inhibitory concentration; MRSA – methicillin-resistant *Staphylococcus aureus.*
| AMP name                      | Source/samples                                      | Amino acid sequence                                                                 | Techniques                                                                                           | Inhibited microorganisms                                                                 | MIC  | AMP gene expression | Ref.                          |
|-------------------------------|------------------------------------------------------|--------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------|---------------------------------------------------------------------------------------------|------|---------------------|--------------------------------|
| Teneclin 1                    | Hemolymph immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220, hemolymph of immunized larvae T. molitor with β-1,3-glucan | Sequence available in Antimicrobial Peptides Database [API00354]: VTCDLIS VEHGKGKLLAVSDACNCVLHCGRGSGVCNY GYRVCVCMGGYNGGRVRCYCR | Reversed-phase (C18) open column chromatography, reversed-phase high-performance liquid chromatography (HPLC), teneclin gene expression analysis | B. subtilis ATCC 17668<br>B. subtilis ATCC 6633<br>P. pyrogerm 77A<br>M. luteus ATCC 1024<br>S. aureus ATCC 6538<br>S. pyogenes 3060<br>S. epidermidis ATCC 12228<br>Micrococcus luteus ATCC 9341 | 1.6  | –                  | Moon et al. (1994) Keshavarz et al. (2019) Roh et al. (2009) |
| Teneclin 2                    | Hemolymph of immunized larvae of T. molitor with β-1,3-glucan | Full sequence not presented in references | Reversed-phase (C18) open column chromatography, HPLC, qRT–PCR and bactericidal activity analysis | 2.0  | Antimicrobial activities against E. coli and S. pyogenes 3060 | –    | –                  | Roh et al. (2009) Keshavarz et al. (2019) Jung et al. (1996) Lee et al. (1995) Keshavarz et al. (2019) Lee et al. (1995) |
| Teneclin 3                    | Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220; construction of plasmids for producing MBP-teneclin 3 fusion proteins | GenBank: [AAA97578.1]: 4DHDQHGLGGHQT GQHGQCGGQLHGQGCGQCGFG HLGQGQGQGQTGQGQHGCGHY GCYTHGH | Reversed-phase (C18) open column chromatography, HPLC; qRT–PCR; and bactericidal activity analysis | 3.7  | Antifungal activity C. albicans KFC1940 did not inhibit the growth of Aspergillus nidulans FG504, S. cerevisiae DBY747, E. coli, and S. aureus | –    | –                  | Chae et al. (2012) Keshavarz et al. (2019) |
| Teneclin 4                    | Injection of polymeric dianisomeric acid (DAP)-type peptidoglycan (PG); immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220 | GenBank: [BAD04117.1]: MLAQVQSACTELS SADFTASSXTRWDRP OQPIXQIHS GTFING GHRNLGKEVGKGLVSLQVHBRWPWWGGKLYNHN GSGLVSVQXHKGHRCTVQGKVEGNLYNRGYC FMDVSGKDYRTGYGASSNP59THLTDVF | The antibacterial activities of AMPs with radial diffusion assays; analysis of teneclin-4 gene expression (qRT–PCR) | E. coli ATCC K12<br>S. aureus Cowan 1<br>No bactericidal activity against B. subtilis ATCC 6633, and C. albicans TIMM 1768 | 0.5  | Observed changes of AMP gene expression | Chae et al. (2012) Keshavarz et al. (2019) |
| Attacin 1a                    | Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220 and SGSSLSVSAQHKEHRGTRVGVEGKYNLYRNGP DPLTARVYKLYTDLGSLVQAIQNRISFGT VLSXAEATNLYKRRSSLDVCVNYCTFSPV REEPFPRGFRHRGF | GenBank: [AXG21618.1]: MQQQLVSLIFAPA SLAPATINDKIPKPFPEGQTKEVXVEPIDF IHNJQHRKIEYGPHRFQDATATYKRNVDVDM DPARTARVYKLYTDLGSLVQAIQNRISFGT | Analysis of AMP gene expression (qRT–PCR), and antimicrobial activity | E. coli ATCC K12<br>E. coli ATCC RN4220, and C. albicans ATCC | 5.0  | –                  | Keshavarz et al. (2019) |
| Attacin 1b                    | Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220 and SGSSLSVSAQHKEHRGTRVGVEGKYNLYRNGP DPLTARVYKLYTDLGSLVQAIQNRISFGT VLSXAEATNLYKRRSSLDVCVNYCTFSPV REEPFPRGFRHRGF | GenBank: [AXG21619.1]: MNNQMQYTVLALCC LSAALAPIGNKTPIDGQXTKXVCRDGSXVNLVE HHCNYLVKNSNHRFGTASTVSNFLVNSVDKPLL VGGYRVDVWHPILPSNALSALVAAQFQCTQXYDVEA SRTIFLDRS5QEDCACSYSGPCQGNCSEPVCGGFRGRGF | Analysis of coleoptericins gene expression (qRT–PCR), and antimicrobial activity | E. coli ATCC K12<br>S. aureus ATCC RN4220; observed no effect on C. albicans AUMC 13529 | –    | AMP gene expression observed in young larvae in fat body, hemocytes, and gut | Keshavarz et al. (2019) |
| Coleoptericin 1               | Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220, SGSSLSVSAQHKEHRGTRVGVEGKYNLYRNGP DPLTARVYKLYTDLGSLVQAIQNRISFGT VLSXAEATNLYKRRSSLDVCVNYCTFSPV REEPFPRGFRHRGF | Full sequences not presented in references | Analysis of coleoptericins gene expression (qRT–PCR), and antimicrobial activity | E. coli ATCC K12<br>S. aureus ATCC RN4220; observed no effect on C. albicans AUMC 13529 | –    | AMP gene expression observed in young larvae in fat body, hemocytes, and gut | Keshavarz et al. (2019) |
| Coleoptericin 2               | Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220, SGSSLSVSAQHKEHRGTRVGVEGKYNLYRNGP DPLTARVYKLYTDLGSLVQAIQNRISFGT VLSXAEATNLYKRRSSLDVCVNYCTFSPV REEPFPRGFRHRGF | Full sequences not presented in references | Analysis of coleoptericins gene expression (qRT–PCR), and antimicrobial activity | E. coli ATCC K12<br>S. aureus ATCC RN4220; observed no effect on C. albicans AUMC 13529 | –    | AMP gene expression observed in young larvae in fat body, hemocytes, and gut | Keshavarz et al. (2019) |
Coleoptericins A
GenBank (A216033.1): MVYGFCSLAFVIAAAVAPFVQEDPVEIVEDASIPVYQLRSHSLQGAPWPCIQ
Analysis of coleoptericins gene expression (qRT-PCR) –
–
The distribution of mRNA was highly pronounced in the gut, hemocytes, and integument tissues of late-instar larvae, and only gut and hemocytes in the adult T. molitor.
Jang et al. (2020a)

Coleoptericins B
GenBank (A216033.1): MRLHAFYAVAVAVAALEQYQVYEFDPVEVEDEPPAWMVYVYRLSHSLQGAPWPCIQ
Analysis of coleoptericins gene expression (qRT-PCR) –
–
The AMP gene expression was greater during late larva, pupal day 2, pupal day 5, and adult day 1 stage, and declined in the late adult stages.
Jang et al. (2020a)

Coleoptericins C
GenBank (A216033.1): MNLQSFVIVAVAAAAASANRYDPEEVYEMYSPVEEVSEHQRLRRSLQPGAPSFPGAPQNGGWSVNPSVGRDERGNTRTEVQHKGQDNAGWGRVVDGN
Analysis of coleoptericins gene expression (qRT-PCR) –
–
The highest transcripts level observed in the gut, hemocytes, and the integument tissue comparing to Malpighian tubules, and fat body in late-instar larvae.
Jang et al. (2020a)

Defensin 1
Authors indicated defensins region: MPHEDVEVFEEAVHRVERGFFCNPGLCHRQCKQGHRRASCGEDVCLG
In silico methods, identification, and expression analyses of defensin genes; and antimicrobial activity
E. coli ATCC K12, S. aureus ATCC RN4220, C. albicans ATCC
The highest AMP gene expression observed after E. coli immunization of larvae; the AMP expression observed in fat body, gut, and Malpighian tubules of young larvae.
Keshavarz et al. (2019)

Defensin 2
Full sequences not presented in references, Authors indicated defensins region: MPHEDVEVFEEAVHRVERGFFCNPGLCHRQCKQGHRRASCGEDVCLG
In silico methods, identification, and expression analyses of defensin genes; and antimicrobial activity
E. coli ATCC K12, S. aureus ATCC RN4220, C. albicans ATCC
The highest expression after E. coli immunization of larvae; the AMP gene expression observed in fat body, gut, and Malpighian tubules of young larvae.
Keshavarz et al. (2019)

Thaumatin-like proteins 1 and 2
Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220, C. albicans ATCC
Analysis of thaumatin-like-proteins 1 and 2 gene expression (qRT-PCR) and antimicrobial activity
Antifungal activity, C. albicans
The highest expression was observed in larvae infected with C. albicans.
Keshavarz et al. (2019)

Cecropin-2
Immunized larvae of T. molitor with E. coli ATCC K12, S. aureus ATCC RN4220, C. albicans AUMC 13529
Analysis of antimicrobial Peptides database (AP00135):
Antimicrobial Peptides Database (AP00135): GLLIKKQKIERVQYHTFDRATIQTVQAQIAANVAAATIK
In silico characterization, analysis gene expression (qRT-PCR), analysis of antimicrobial activity
In young larvae AMP gene expression observed in fat body, and gut; no expression observed in hemocytes, and Malpighian tubules
Keshavarz et al. (2019)

AMP = antimicrobial peptide; MIC = minimal inhibitory concentration.
According to Benzertiha et al. (2020a), even a relatively small amount of *T. molitor* and *Z. morio* full-fat meals (2 or 3 kg per tonne of diet) supplemented on top can significantly improve the growth performance results, including body weight gain (BWG) and feed intake (FI), without a negative effect on the feed conversion ratio (FCR). This finding is in line with Islam et al. (2016), who reported improvement in BWG after 0.4% *T. molitor* or *Z. morio* addition to the broiler diet. Furthermore, 1% *T. molitor* full-fat meal supplementation positively affected the growth performance results (Ballitioc and Sun, 2013). No detrimental effect of relatively small amounts of insect inclusion on the apparent nutrient digestibility coefficients and pancreatic enzyme activities was noticed (Benzertiha et al., 2019a). The observed positive production effects are connected to beneficial microbial shifts, particularly in the ceca, where *Z. morio* meal (0.2% supplementation) enhanced the abundance of Actinobacteria, including the Bifidobacteriaceae family, and *Lactobacillus agilis* number, while *T. molitor* meal increased the Clostridia class level, especially Ruminococcaceae (Józefiak et al., 2020).

Moreover, the inhibition activity against the bacillus agilis *Z. morio* clusters in the ileum, was observed even when 0.05% rectale class level, especially Ruminococcaceae (Józefiak et al., 2020). The observed positive production effects are connected to beneficial microbial shifts, particularly in the ceca, where *Z. morio* meal (0.2% supplementation) enhanced the abundance of Actinobacteria, including the Bifidobacteriaceae family, and *Lactobacillus agilis* number, while *T. molitor* meal increased the Clostridia class level, especially Ruminococcaceae (Józefiak et al., 2020). Moreover, the inhibition activity against the Bac teroides-Prevotella cluster and *Clostridium perfringens* at this segment was noticed mainly after *T. molitor* (0.3%) and *Z. morio* (0.2%) addition. Bird GIT microbiota modulation, i.e., an increase in the number of butyrate-producing bacteria in the crop and *Lactobacillus* spp./*Eubacterium rectale* clusters in the ileum, was observed even when 0.05% *S. lateralis* was implemented (Józefiak et al., 2018). Moreover, due to the wide spectrum of potential bird responses, i.e., in terms of productivity, and GIT microbiota modulations after insect biomass implementation in poultry diets, further investigation should be stressed on the administration of a relatively small amount of these products. In particular, Benzertiha et al. (2020b) suggested a positive effect on the decrease in the bursa of Fabricius relative weight, as well as immunoglobulin M concentration. Furthermore, the application of 0.3% *H. illucens* full-fat meals in young turkey diets resulted in more efficient anti-inflammatory, immune stimulatory, and antioxidative impacts than commonly used monensin (Koztowski et al., 2021).

### 5.2. Insect fat as an energy source for poultry

Most of the research on the application of the insect in animal nutrition focuses on protein usage; however, fat is also an important nutrient present in insect biomass, sometimes in ranges comparable to CP (Benzertiha et al., 2020b). Moreover, fat derived from insects can fully replace environmentally unfriendly and commonly used feed materials such as palm or soybean oils used in poultry nutrition (Table 5). It should be emphasized that the quantity of crude fat as the second main nutrient in the invertebrate body varies from 1.3% (as is) for *Carebara* sp. to 61.1% (in DM) for termites (*Bessa* et al., 2020; Bukkens, 1997) and is highly dependent on the rearing substrate (Kierończyk et al., 2020). To

| Fat source | Species | Replaced oil | Inclusion level | Result | Reference |
|------------|---------|--------------|----------------|--------|-----------|
| *Hermetia illucens* | Broiler chickens | Soybean oil | 50%; 100% | The fatty acid profile was adversely affected. | Schiavone et al. (2016) |
| *H. illucens* | Broiler chickens | Soybean oil | 50%; 100% | No detrimental effects. | Schiavone et al. (2018) |
| *H. illucens* | Broiler chickens | Soybean oil | 25%; 50%; 75%; 100% | The positive impact on FCR in the first 2 weeks of age. | Kierończyk et al. (2020) |
| *H. illucens* | Broiler chickens | Soybean oil | 50%; 100% | Beneficial reduction of jejunum and ileum weight. | B. Kim et al. (2020a) |
| *H. illucens* | Broiler chickens | Soybean oil | 50%; 100% | Partial replacement induced elongation of the villi. The effect on lipase activity limitation. Acetate was reduced and butyrate enhanced in both *H. illucens* fat inclusions. | B. Kim et al. (2020b) |
| *H. illucens* | Broiler chickens | Soybean oil | 50%; 100% | Reduction of the gizzard relative mass. Increasing of saturated, monounsaturated fatty acids, and limitation of polyunsaturated fatty acids, and the unsaturated and saturated fatty acids ratio. | Cullere et al. (2019) |
| *H. illucens* | Broiler chickens | Soybean oil | 50%; 100% | The fatty acid profile was negatively enriched in saturated fatty acids. | Kierończyk et al. (2021) |
| *H. illucens* | Broiler chickens | Corn oil, coconut oil | 100% | The negative microbiota shift in the birds’ crop resulted from deficient releasing of lauric acid; the beneficial impact on the hindgut microecosystem. | Y.B. Kim et al. (2020) |
| *H. illucens* | Turkeys | Soybean oil | 50%; 100% | Decreasing of feed conversion ratio (1 to 30 d) contrary to corn oil. Limitation of cholesterol and high-density lipoproteins (HDL) in the serum. Increasing the breast meat yellowness and enrich the abdominal fat in medium-chain fatty acid. | Sypniewski et al. (2020) |
| *H. illucens* | Laying hens | Soybean oil | 100% | The limitation of trypsin activity, and immune status trait concentrations (interleukin-6, tumor necrosis factor-α); the reduction of the crop digesta pH, and inhibition of Enterobacteriaceae populations in the jejunal content. Increase of total cholesterol, HDL, and low-density lipoproteins (LDL) concentration in the plasma. | Heuel et al. (2021) |
| *Tenebrio molitor* | Broiler chickens | Palm oil, poultry fat | 100% | The positive impact on the limitation of fat, triglycerides, and total cholesterol in the liver. Improvement of fatty acid profile in the liver and breast meat. | Benzertiha et al. (2019b) |
| *T. molitor* | Broiler chickens | Soybean oil | 100% | The growth performance parameters improvement till 21 d of age and digestibility through the entire rearing period or exhibit a similar effect to soybean oil. The beneficial effect on the meat quality was noticed. | Kierończyk et al. (2018a) |

Zophobas morio

*Z. morio* fat generally performed comparably to soybean oil.
date, only three insect species have been considered an alternative energy source in poultry diets, i.e., *T. molitor*, *Z. morio*, and *H. illucens*. Nevertheless, significantly more insects, particularly Hymenoptera, Coleoptera, Lepidoptera, Homoptera, Hemiptera, and Orthoptera orders, are evaluated in human nutrition as an energy source (Ramos-Elorduy, 2008).

In general, no detrimental effect of the partial or total inclusion of insect fat on the growth performance and productivity parameters was observed. These results suggest that the metabolizable energy values of insect fat for broilers (Kierończyk et al., 2018a), laying hens (Heuel et al., 2021), and turkey (Sypniewski et al., 2020) are comparable to soybean oil. Nevertheless, the most important challenge in the case of insect fat provision to poultry diets seems to be the fatty acids profile of the final products, i.e., breast and leg meat, which are highly dependent on the quality of the feed material. Thus, there is a need to improve not only the quantity of the dietary fat of insect biomass through the diet composition and technique of extraction but also its quality, particularly in terms of economically justified species such as *H. illucens*. In the available literature, the authors mainly focus on the lauric acid (C12:0) concentration to enhance the functional properties of the *H. illucens* larvae fat (Borrelli et al., 2021; Dabbou et al., 2020; Sypniewski et al., 2020). However, the results of these studies indicate a need to improve the fatty acid composition of the *H. illucens* larvae fat by increasing the n-3 level and the polyunsaturated fatty acids (PUFAs) concentration which may result in enhanced broiler meat quality preferred by the consumer. To date, the most suitable and beneficial product from the final product’s quality point of view is *T. molitor* larvae fat inclusion in broiler diets. Mealworm fat improves the fatty acids profile by lowering the level of saturated fatty acids (SFAs) and increasing unsaturated fatty acids (UFAs) in comparison to soybean oil. Furthermore, the meat from broilers fed *T. molitor* fat characterizes atherogenic and thrombogenic indexes similar to soybean oil (Kierończyk et al., 2018a).

Eventually, in addition to the growth performance results and the possibility of applying insect fat in poultry nutrition, the consumer palatability of the final products should be evaluated as a crucial factor determining the economic success of this sustainable and novel feed material. To date, only a few scientific reports have been published: however, none of those have emphasized the adverse effect on consumer preferences. Additionally, it should be highlighted that there is a shortage of data about the poultry product preference test. Broiler chickens’ meat sensory traits were not affected by even the total replacement of soybean oil by *H. illucens* larvae fat (Cullere et al., 2019). Additionally, partial (50%) or total inclusion of *T. molitor*, as well as *H. illucens* as an energy source in rabbit diets, exhibit similar consumer acceptance in terms of meat palatability as in the control group (soybean oil) (Gasco et al., 2019). No changes in overall food liking or experience of selected bakery products, which include up to 50% butter derived from *H. illucens* larvae fat, were noted (Delicato et al., 2020). Thus, it could be concluded that there is no risk of insect fat administration as an energy source in poultry diets from bird production, as well as the consumer point of view; however, a continuation of UFA enrichment evaluation is needed to improve the quality of the final product.

5.3. Functional properties of insect fat in poultry nutrition

Furthermore, the intestinal microbiota composition is not adversely affected by insect fat inclusion, particularly in terms of *H. illucens* larvae fat, which is characterized by the highest medium-chain fatty acid (MCFa) content with the dominant lauric acid (C12:0) concentration, in contrast to other invertebrate species. Lauric acid exhibits significant inhibitory activity against gram-positive and gram-negative bacteria, including bird or poultry product pathobiota such as *Pasteurella multocida*, *Yersinia enterocolitica*, and *Listeria monocytogenes* (Dabbou et al., 2020). Furthermore, the results of Zeitz et al. (2015) underline the positive effect of lauric acid against Enterobacteriaceae, *Campylobacter jejuni*, and *E. coli*. Finally, lauric acid, characterized by strong inhibitory activity in the case of *C. perfringens* (Timbermont et al., 2010), which is an etiologic factor of necrotic enteritis, causes 6 billion USD costs in poultry flocks worldwide (profit lost per bird is estimated at US$ 0.062) (Wade and Keyburn, 2015). Thus, there are premises to define *H. illucens* larvae fat as a functional feed material. The antimicrobial and antiparasitic modes of action were also observed. Nevertheless, a negative microbiota population shift in the bird crop was noted, which is explained as insufficient lauric acid release at this segment (Kierończyk et al., 2021).

6. Insects in swine nutrition

Although boar (Sus scrofa) in wild conditions mainly ingest plant-origin material, invertebrates, particularly the wide spectrum of insect species in various stages of development, are constantly present in their diets. The most frequently consumed insects are in the following orders: Anoplura, Coleoptera, Diptera, Hymenoptera, Lepidoptera, Orthoptera, and Trichoptera (Herrero et al., 2006). They play the main role as compensation for protein deficiencies when the source of this nutrient is scarce (Schley and Roper, 2003). Additionally, insects, as a rich source of iron (Fe), may be an important basis of this microelement supplementation in wild piglet diets. Furthermore, Tabata et al. (2018) showed that pigs are well adopted to take material rich in chitin via the high activity of acidic chitinase (Chia mRNA) gene expression. Kawasaki et al. (2021) noticed that even 14-day-old piglets can synthesize chitin-degradable enzymes, and acidic mammalian chitinase gene expression rises in the whole stomach weight parallel to the animal’s age. Thus, it is not surprising that in the available literature, the usage of insect-derived feed materials is efficiently implemented at each pig rearing phase, i.e., nursing (Driemeyer, 2016), weaning piglets (Spranghers et al., 2018), growing (Chia et al., 2019), and finishing pigs (Yu et al., 2019a). In general, no detrimental effects in terms of growth performance results were noticed during *H. illucens* larvae meal or dietary fat, as well as *T. molitor* larvae meal, as the most commonly used protein and energy source in swine nutrition, i.e., fishmeal, soybean meal, corn and soybean oils (Ao and Kim, 2019; Biasato et al., 2019; Heugten et al., 2019; Ko et al., 2020; Meyer et al., 2020).

6.1. Insect meals in pig nutrition

It should be emphasized that in the experimental conditions, the insects’ meals were administered up to 18.5% or 19.06% (Chia et al., 2019; Håkenásen et al., 2020), while usually up to 10% inclusion is used (Biasato et al., 2019; Dankwa et al., 2000; Meyer et al., 2020). Due to the high nutritive value variability between insects, the obtained results between authors differ; however, some improvement effects on the BWG, FI, and FCR were observed (Jin et al., 2016; Yu et al., 2019a, 2020a). This result is in agreement with the linear increase in DM and CP digestibility coefficients, as well as N retention in weanling piglets fed 1%, 2%, or 4% *T. molitor* larvae meal (Jin et al., 2016). It should be highlighted that the digested lysine in the *H. illucens* larvae meals (full-fat and defatted) is comparable to soybean meal, blood meal, and fishmeal (Crossbie et al., 2020). Some differences between full-fat and defatted meals in the scope of standardized ileal digestibility of arginine, valine, alanine, and proline were noticed, while N...
retention, as well as N digestibility, was not affected. Furthermore, no influence in terms of fecal DM or the fecal score was observed in weaned piglets fed diets containing up to 19.06% \textit{H. illucens} meal (Häkenäs et al., 2020). Similarly, Yu et al. (2020a) did not show any changes in the diarrhea rate (from 4% to 7%) when full-fat \textit{H. illucens} larvae meal was administered up to 4%. Even live \textit{H. illucens} larvae administration did not affect the DM of piglet feces (Ipema et al., 2021). Additionally, no enhanced fecal gas emissions, i.e., ammonia, hydrogen sulfide, and total mercaptans, were noticed after \textit{H. illucens} incorporation into weaned pig diets (Ao et al., 2020). It needs to be highlighted that \textit{H. illucens} meal seems to be more suitable for piglets (25 kg), as well as growing pigs (60 kg), than \textit{Spirulina platensis} meal as a total substituent of \textit{H. illucens} larvae meal was administered up to 4%. Even live \textit{H. illucens} larvae meal was administered up to 4%. Additionally, Jin et al. (2016) confirmed the linear improvement of digestibility of DM, CP, and the tendency in terms of crude ash during \textit{T. molitor} larvae addition (1.5%, 3%, 4.5%, 6%) to weaning piglet diets. Simultaneously, nitrogen excretion was linearly reduced, while the control group (soybean meal) was characterized by the highest nitrogen footprint. Contrary to the abovementioned results, Yu et al. (2020a) showed that the 1%, 2%, and 4% inclusion of full-fat \textit{H. illucens} meal negatively affects CP and crude fat digestibility in a dose-dependent manner. Additionally, Ao and Kim (2019) observed decreased digestibility coefficients of DM and nitrogen in weaning pigs fed \textit{Pectescus tenebriifer}; however, the adverse effect was noted only during 50% replacement of fish meal. Similar to the results of Ao et al. (2020), only partial replacement of fishmeal was negatively affected by \textit{T. molitor} larvae meal. Despite the above, the results of Altmann et al. (2019) suggest that the inclusion of \textit{H. illucens} larvae meal improved the quality of pork meat by increasing PUFAs and reducing SFAs and monounsaturated fatty acids (MUFA’s), and the overall odor and juiciness were improved. Simultaneously, no adverse effect on carcass yield was found. Additionally, Chia et al. (2021) highlighted that the usage of \textit{H. illucens} meal as a total substituent of fishmeal significantly improved fasted and carcass weight, as well as increased fat content in loin muscle. Moreover, finishing pig tissues (heart, kidney, liver, lungs, loin muscle, and spleen) are characterized by increased macroelement concentrations, i.e., K and P, as well as microelements, i.e., Fe or Zn. Yu et al. (2019a) suggests that the inclusion of 4% or 8% \textit{H. illucens} meal to finishing pig diets resulted in increased loin eye area, marbling scores, and inosine monophosphate concentration, while 4% addition increased intramuscular fat content in the longissimus dorsi muscle.

Even if it is only possible to add insect biomass to swine nutrition in relatively small amounts (up to 3%) under practical conditions, some advantages can be observed. It should be highlighted that the results of Choi et al. (2019) demonstrated that the 1%, 2%, and 3% inclusion of \textit{H. illucens} meal used as a replacement of soybean meal in pigs’ diets may constitute similar economic efficiency (feed cost per kilogram weight gain) and simultaneously improve the average daily gain and DM digestibility. Chia et al. (2019) supported the abovementioned statement, where even higher inclusion, i.e., from 9% to 18.5% did not negatively affect the profit indexes. It is crucial from a practical point of view, where the price of insect meals cannot compete with the commonly used feed materials. However, the unification of prices allows emphasizing the additional properties of insect products in terms of, e.g., the possibility of significantly reducing global warming potential and land use through the implementation of waste-fed larvae in pig diets (van Zanten et al., 2018).

6.2. Functional properties of insects in pig nutrition

Further benefits related to invertebrate usage in swine diets have a positive impact on the immune response. Yu et al. (2020a) showed that the 2% inclusion of \textit{H. illucens} full-fat meals by 28 d of the trial decreased proinflammatory (interferon-γ, IFN-γ) and enhanced the concentration of anti-inflammatory (interleukin-10, IL-10) factors in weanling piglets. This is in agreement with the results of Yu et al. (2020b), who found downregulated mRNA expression of TNF-α and upregulated IL-10 (2% \textit{H. illucens} addition by 28 d), as well as Yu et al. (2019b), where supplementation of 4% \textit{H. illucens} larvae meal (48-d trial) reduced toll-like receptor 4 (TLR-4) and IFN-γ gene expression and enhanced IL-10. Furthermore, the addition of 4% \textit{H. illucens} to the finishing pig diets resulted in the upregulation of intestinal barrier genes, i.e., mucin-1, ZO-1, and occludin (Yu et al., 2019b). Nonetheless, Choi et al. (2020) and Ao et al. (2020) did not observe any immune response of weaning piglets (TNF-α, interleukin-1β [IL-1β], IL-6, immunoglobulin G [IgG]) during \textit{H. illucens} meal administration up to 3% by 14 d of the trial or IgG and lymphocyte concentrations after 1% or 2% \textit{T. molitor} application during 35-d experiment. This is supported by Ko et al. (2020), who did not notice any changes (during the 28-d test) in terms of IL-1β, TNF-α, or IL-6 concentrations after partial or total replacement of fishmeal by \textit{T. molitor} larvae meal (phase 1: up to 5%; phase 2: up to 3%) in weaning pig diets. Moreover, it is well known that the immunological response relates to GIT microbiota homeostasis, and frequently, the GIT is defined as the largest “immune organ” in the animal body. Thus, it is no surprise that the administration of \textit{H. illucens} larvae meal (5% by 61 d of the experiment) as a product rich in chitin, lauric acid, and AMPs to swine enhanced beta diversity in the ceca (Biasato et al., 2020). Furthermore, the proliferation of microbial populations engaged in polysaccharide fermentation, as well as short-chain fatty acids and consequently supporting epithelial cell metabolism production, i.e., \textit{Blautilia}, \textit{Coprocoecus}, \textit{Eubacterium}, \textit{Prevotella}, \textit{Roseburia}, and \textit{Ruminococaceae}, was enhanced in weaning piglets (Biasato et al., 2020). Additionally, after \textit{H. illucens} larvae meal inclusion, increased neutral mucin production was found in the small intestine to prevent intestinal pathobiota access to the epithelium. This is supported by Yu et al. (2019b), who reported a positive increase in butyrate-producing bacteria in the colon, as well as the limitation of pathogenic colon bacteria occurrence, i.e., \textit{Streptococcus}. Moreover, the main effect of \textit{H. illucens} inclusion on the weaning piglet GIT microbiota was observed in the colon, while the ileal microbiota was particularly changed in terms of enhanced \textit{Lactobacillus} and \textit{Bifidobacterium} populations. In contrast to the colon, Firmicutes, \textit{Ruminococcus}, \textit{Clostridium} cluster IV, and \textit{Prevotella} were significantly increased (Yu et al., 2020b). It should be highlighted that the studies conducted on the dietary supplementation of AMPs have indicated that synthetic analogs of hybrid cecropin-magainin (90 mg/kg AMP-A3 and 40 to 60 mg/kg AMP-P5) have a positive effect on the growth performance, fecal microbiota, and intestinal morphology of weanling piglets during 28-d long experiments (Yoon et al., 2012, 2013, 2014). Furthermore, the results of Crobie et al. (2021) clearly showed that the substitution of animal origin protein up to 50% by full-fat \textit{H. illucens} larvae meal (throughout the 42-d trial) can be as efficient as the addition of antibiotic growth promoter, i.e., 220 mg of aureomycin per kg of complete feed, in the scope of growth performance results, immune response, and gut health in nursery pigs. Moreover, a study performed in vivo indicated that an AMP complex provided as a mixture of lactoferrin, cecropin, defensin and plecetacin (2 g and
ponents, and most of them are not environmentally sustainable. Aquaculture production concerns feed composition, and large-scale pesticide use should be emphasized. In turn, their impact on biodiversity loss, tropical forest destruction, and FAO predictions and scientific literature, fish meat will play a crucial role in meeting the growing needs for livestock protein (FAO, 2020; FAO/WHO, 2018; Vianna et al., 2020). However, consumers’ criticism of aquaculture production concerns feed components, and most of them are not environmentally sustainable. Currently, the dominant protein and fat sources in fish feed are fish meals and oils, soybean meals and oils, and protein isolates. In the case of fishmeal and fish oil, the main disadvantage is the overfishing of seas and oceans. Up to 30% of the caught fish are used for animal feed production, while 90% of this value could be used for human consumption (Olsen and Hasan, 2012). Additionally, this situation leads to competition between the food market and animal production, and the erosion of natural sources of fish also affects rapidly increasing fish meal prices. While discussing plant sources of protein and fats in fish nutrition, mainly various soybean derivatives, their impact on biodiversity loss, tropical forest destruction, and large-scale pesticide use should be emphasized. In addition, progressively, many customers seem to be opposite to the usage of genetically modified products such as soybean meal (Costa-Pierce, 2010).

In the case of aquaculture production, the main interests in Europe are focused on salmonid fish. According to the Publications Office of the European Union report (EUMOFA, 2020), the 2 leading species produced in the EU are Atlantic salmon (Salmo salar) and rainbow trout (Oncorhynchus mykiss), whose total EU farmed production value is almost 40%. Due to the developing problem of using fishmeal as the main protein source in salmonid feed, scientific teams are looking for alternatives. Some of them are focused mainly on plant-derived compounds and proteins and their impact on the growth performance, feed utilization, and physiological response of fish (Bruce et al., 2017; Clarkson et al., 2017; Greiling et al., 2018). However, the substitution of fishmeal by plant ingredients in salmonid diets can lead to a reduction in feed utilization, which results in poor growth performance (Wacyk et al., 2012). Moreover, the effect of soybean addition to feeding on the occurrence of distal enteritis and deterioration of reproductive parameters has already been reported (Lazzarotto et al., 2015).

7. Insects in aquaculture

Aquaculture is one of the fastest-growing branches of animal products intended for food market purposes. According to WHO and FAO predictions and scientific literature, fish meat will play a crucial role in meeting the growing needs for livestock protein (FAO, 2020; FAO/WHO, 2018; Vianna et al., 2020). However, consumers’ criticism of aquaculture production concerns feed components, and most of them are not environmentally sustainable. Currently, the dominant protein and fat sources in fish feed are fish meals and oils, soybean meals and oils, and protein isolates. In the case of fishmeal and fish oil, the main disadvantage is the overfishing of seas and oceans. Up to 30% of the caught fish are used for animal feed production, while 90% of this value could be used for human consumption (Olsen and Hasan, 2012). Additionally, this situation leads to competition between the food market and animal production, and the erosion of natural sources of fish also affects rapidly increasing fish meal prices. While discussing plant sources of protein and fats in fish nutrition, mainly various soybean derivatives, their impact on biodiversity loss, tropical forest destruction, and large-scale pesticide use should be emphasized. In addition, progressively, many customers seem to be opposite to the usage of genetically modified products such as soybean meal (Costa-Pierce, 2010).

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7.1. Insect meals in salmonid nutrition

Carnivorous fish salmonids already count insects as a part of their diets in the natural environment (Henry et al., 2015). Depending on the salmonid species, fishmeal substitution can reach different levels, with or without various effects on growth performance and feed utilization (Table 6). According to Belghit et al. (2019), even 100% replacement of fishmeal with partially defatted H. illucens meal is possible without any adverse effect on growth performance or feed utilization of Atlantic salmon. The partially defatted meal did not cause any adverse effects on most physiological parameters related to the functioning of the GIT, such as apparent digestibility coefficients (ADCs) of nutrients, digestive enzyme activity, or total bile acid levels. Divergent results were reported by Wethasisinghe et al. (2021), where the 25% substitution of fishmeal with H. illucens meal resulted in a lower final body weight (FBW), specific growth rate (SGR), protein efficiency ratio (PER), and higher FCR. It is important to emphasize that this experiment was conducted using full-fat meals. While the ADC of CP was not affected by insect inclusion in salmonid diets, decreases in crude fat and tyrosine digestibility were observed in the 12.5% and 25% substitution groups. A decrease in the lipid efficiency ratio (LER) was observed in all groups fed insect meals. Experiments conducted on rainbow trout presented different possible substitution levels in the case of growth performance and feed utilization. Some of the literature pointed to no adverse effect on those parameters in substitution fishmeal level by H. illucens up to 30% (Józefiak et al., 2019; Terova et al., 2019), while others reported several negative effects on digestibility of nutrients and feed utilization (Melenchón et al., 2021; Renna et al., 2017; Stadtlander et al., 2017); however, the growth performance was still not disturbed. This effect is observed further with the usage of different insect species (Józefiak et al., 2019; Melenchón et al., 2021) but also in experiments conducted on sea trout (Salmo trutta m. trutta) fed diets containing full-fat and hydrolyzed full-fat meals obtained from Tenebriionidae family insects (Hoffmann et al., 2020; Mikołajczak et al., 2020). In most of the scientific literature, any disturbance in the digestibility of nutrients that occurs in fish fed insect meals is explained by the presence of chitin in the exoskeleton of insects. Even in the healthy GIT characterized by good homeostasis and chitinase activity, chitin digestibility will not be effective (Renna et al., 2017), and the presence of chitin can be correlated with lower protein digestion (Marono et al., 2015). Furthermore, it can be considered a low-energy filler (Karlson et al., 2017), and both of these observations can be crucial limiting factors due to the ultimate effect on poor growth performance.

7.2. Insect fat in salmonid nutrition

From the production point of view and the interests of future customers, the effect of insect inclusion in salmonid diets on fillet chemical composition and quality is crucial, especially since fish are considered healthy meat due to their valuable fatty acids composition that prevents coronary heart diseases. In the current literature, this impact has been investigated. Renna et al. (2017) reported that the effect of the addition of H. illucens in rainbow trout diets on the composition of fish meat is indeed present; however, this impact is still within the normal ranges and does not cause any deviations that could be potentially harmful to humans. However, Melenchón et al. (2021) proved that the inclusion of T. molitor in rainbow trout diets can affect meat quality due to an increase in MUFAAs and n-6 fatty acids, together with a decrease in n-3. The possibility of negative effects of insect usage in livestock nutrition on meat quality leads to new scientific area exploration — to examine the effect of different diets on insects’ fatty acids composition. Ewald et al. (2020) reported that modification of the fatty acid composition of H. illucens through its diet is possible; however, it seems to have some limitations, especially in SFA and MUFA content. Notwithstanding, Omolncx et al. (2020) proved that the substitution of flaxseed oil in edible insect diets can improve their nutritional quality, especially in n-3 content.
Table 6
Effect of various invertebrate meals used as an alternative to commonly used feed materials in salmonid nutrition on their productivity and physiological traits.

| Insect species | Replaced compounds | Processing form | Species | Substitution level | Main results | Reference |
|----------------|--------------------|----------------|---------|--------------------|--------------|-----------|
| Hermetia illucens | Fishmeal | Partially defatted | Atlantic salmon (Salmo salar) | 33%; 66%; 100% | The effect on whole fish fatty acids composition. Increase in glucose concentration in blood plasma in the group with 66% of substitution. | Belghit et al. (2019) |
| H. illucens | Protein compounds: Fishmeal, soy protein concentrate, corn gluten, faba bean | Full-fat meal | Atlantic salmon (S. salar) | 6.25%; 12.5%; 25% | The decrease in final body weight and specific growth rate, while an increase in FCR in the 25% replacement group. A decrease in 12.5 and 25% groups in the case of crude fat and tyrosine apparent digestibility coefficient (ADC) was observed. An increase in starch digestibility in the 25% group. The lower protein efficiency ratio, apparent lipid, and energy retention in the 25% group. The decrease in lipid efficiency ratio in all groups fed with insects. | Weththasinghe et al. (2021) |
| H. illucens | Fishmeal | Full-fat paste | Rainbow trout (Oncorhynchus mykiss) | 3.7%; 6.7% 46% | A decrease in protein efficiency ratio (PER) and protein productive value. | Stadtlander et al. (2017) |
| H. illucens | Fishmeal | Partially defatted | Rainbow trout (O. mykiss) | 10%; 20%; 30% | Modulation of gastrointestinal tract microbiota. | Terova et al. (2019) |
| H. illucens | Fishmeal | Partially defatted | Rainbow trout (O. mykiss) | 25%; 50% | The decrease in ADC of dry matter and crude protein in the 50% group. Strong impact on fatty acids composition of fish fillets. | Renna et al. (2017) |
| H. illucens | Fishmeal | Full-fat | Rainbow trout (O. mykiss) | 15%; 30% | The decrease in FCR values in both substitution groups. The modulation of digestive enzymes and hepatic enzymes activity. The effect on immune parameters in plasma. The impact on fatty acids composition of fish fillets. Lower ADC of protein in 30% substitution group. Higher value of viscerosomatic index (VSI) in 30% substitution group. The modulation of digestive enzymes and hepatic enzymes activity. The effect on immune parameters in plasma. The impact on fatty acids composition of fish fillets. | Melenchon et al. (2021) |
| Tenebrio molitor | Fishmeal | Full-fat meal | Rainbow trout (O. mykiss) | 30% | Impact on intestinal microbiota—lower concentration of Clostridium coccoides, and Lactobacillus/Enterococcus sp. | Józefiak et al. (2019) |
| Gryllodes sigillatus | Fishmeal | Full-fat meal | Rainbow trout (O. mykiss) | 41% | The decrease in villus height. Impact on intestinal microbiota—increase in concentration in all analyzed bacteria. A decrease in SGR and an increase in FCR. The decrease in villus height and mucosa thickness. Impact on intestinal microbiota—increase in concentration in most analyzed bacteria populations. | |
| Blatta lateralis | Fishmeal | Impact | Rainbow trout (O. mykiss) | 48% | Higher results of body weight gain. The increase in villus height and mucosa thickness. Impact on intestinal microbiota—increase in concentration in most analyzed bacteria. | |
7.3. Functional properties of insects in fish nutrition

Considering insects as a component in salmonid feeds, the effect on the microbiota of the GIT should be discussed. Several studies proved the positive effect of insect meal inclusion in salmonid fish diets due to the reduced concentration of pathogenic bacteria and an increasing number of health-promoting bacterial species (Józefiak et al., 2019; Mikolajczak et al., 2020; Terova et al., 2019). This impact should be explained by three main insect features, i.e., C12:0 antimicrobial properties (mentioned above), the presence of chitin, and AMPs. Despite the probable negative effect of chitin on nutrient digestion, chitin can be further considered a factor modulating the microbiome of the GIT. According to Askarian et al. (2012), chitin inclusion in the Atlantic salmon diet at the level of 5% led to decreases in the concentrations of Bacillus spp., Lactobacillus spp., Pseudomonas spp., and Staphylococcus spp. Therefore, chitin and its derivatives have potential as prebiotics and immunostimulants, and as their source, insect meals can also provide this effect. Second, AMPs additionally stimulate these effects. It is well documented that AMPs present in insects are characterized by activity against a wide spectrum of pathogenic bacteria, such as S. aureus, L. monocytogenes, and S. typhimurium (Yi et al., 2014).

8. Conclusion

In the available literature, invertebrate-derived products are presented as a natural and sustainable source of protein and energy for various animal species. The latest data confirm the possibility of their implementation in animal diets with mostly positive effects on growth performance and organism response. However, due to the low uniformity of insect products globally, i.e., 1) the usage of various technologies, which induces a need for different feeding system applications; 2) the usage of food waste in invertebrate production, which differs in the case of nutritive value; 3) the lack of nutrient requirement recommendations for commonly reared larval species; 4) and, last but not least, the divergent processing techniques of larvae, play a crucial role in terms of the quality of the final feed material and consequently cause different productivity and health effects in insect-fed animals. Consequently, to increase the efficiency of the insect larvae, as well as further livestock, aquaculture production, and pet conditions, the detailed nutrient requirements and biomass process technique parameters for economically justified species should be evaluated in the future.

Author contributions

Bartosz Kieronczyk: Conceptualization, Investigation, Writing - Original Draft; Mateusz Rawski: Conceptualization, Investigation, Writing - Original Draft; Zuzanna Mikolajczak: Investigation, Writing - Original Draft; Natalia Homska: Investigation, Writing - Original Draft; Jan Jankowski: Writing - Review & Editing, Supervision; Katarzyna Oginski: Writing - Review & Editing, Supervision; Agata Józefiak: Investigation, Writing - Review & Editing, Visualization; Jan Mazurkiewicz: Writing - Review & Editing, Supervision; Damian Józefiak: Conceptualization, Writing - Review & Editing, Supervision.

Declaration of competing interest

We declare that we have no financial and personal relationships with other people or organizations that can inappropriately influence our work, and there is no professional or other personal interest of any nature or kind in any product, service and/or company that could be construed as influencing the content of this paper.

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Appendix. supplementary data

Supplementary data to this article can be found at https://doi.org/10.1021.acs.jnini.2b00615.

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