



Edible insects and their potential anti-obesity effects: a review

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Abstract: Available evidence suggests that the consumption of edible insects may not only contribute protein and other valuable nutrients to the human diet but may also provide health benefits through various insect-derived peptides and bioactive compounds. Most studies of potential anti-obesity effects of edible insects have been conducted *in vitro*. The available *in vivo* evidence stems mainly from rodent models. Anti-obesity effects of various edible insect species, such as *Tenebrio molitor*, *Hermetia illucens*, and *Acheta domesticus*, have been suggested, and the findings of studies in mice models suggest the presence of bioactive compounds in edible insect swith a potential efficacy in weight control. The mechanisms suggested to underlie the lipid-lowering and anti-obesity effects of edible insect extracts include the inhibition of pathways related to lipid metabolism, downregulation of genes involved in the metabolism of adipose tissue, effects of insect-derived compounds need to be sufficiently established, and trials in humans are a prerequisite. With respect to anti-obesity (and other health) effects, no such compound identified in insects has thus far been tested in humans. Further studies of the effects of bioactive compounds contained in edible insects on human health are therefore needed in order to validate the potential of edible insects as a novel measure in combatting obesity and promoting health in general.

Keywords: edible insects; bioactives; obesity; overweight; antilipidemic effect

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1 Introduction

The global prevalence of overweight and obesity is rising and has been forecasted to continue to increase in the coming years. Global obesity has almost tripled since 1975, with most of the world's population living in countries where overweight and obesity are responsible for the death of more people than underweight [1]. More than 1.9 billion adults worldwide were reported in 2016 to be overweight, with 650 million of these being obese [1]. It has been predicted that one in two adults in the United States will be obese by 2030, with approximately one in four suffering from severe obesity [2]. The problem of obesity is not exclusive to high-income countries but increasing rates of obesity alongside undernutrition have also been found in low-income and middle-income countries. Obesity, caused by energy input exceeding energy output over a prolonged period of time, can lead to various health problems. Excessive body weight is causally associated with diabetes, cardiovascular diseases and cancer [3]. Disability-adjusted life-years attributable to obesity may have more than doubled since 1990 [4]. Obesity has been reported in an observational study to be associated with a wide range of medical conditions, including 21 cardiometabolic, respiratory, digestive, musculoskeletal, neurological and infectious diseases [5]. Furthermore, the risk for complex multimorbidity was found to be accentuated by obesity among adults younger than 50 years [5]. The increase in the prevalence of obesity in childhood and young adulthood has accelerated in most high-income countries [6]. Obesity in children has been a cause for concern for several decades and has now become a crisis of public health worldwide [7]. In addition, obesity and related non-communicable conditions have also been shown to be associated with worse outcomes in people with COVID-19 [8–10].

Overweight and obesity are major preventable causes of death worldwide. The mainstay of therapeutic intervention in individuals with obesity is a multicomponent lifestyle change [11,12]. The relevant components in this context are lifestyle or behavioral training, diet control to decrease energy intake and an increase in physical activity [13]. In addition to dietary and other lifestyle changes, pharmacotherapy may contribute to weight loss efforts. The pharmacological agents used can support body weight reduction through different physiological modes of action [14], including the suppression of dietary fat absorption by gastric and pancreatic lipase inhibition or a decrease in appetite [15]. Several medications for this indication have been approved in the European Union and the United States [16]. However, pharmacotherapy for obesity must be demonstrated in individual patients to result in clinically meaningful and sustained weight loss. Adverse effects, such as diarrhea, oily stools, flatulence and a reduced absorption of fat-soluble vitamins may occur [17]. Dietary supplements and appetite suppressants known to reduce body weight may also have side-effects [18]. Finally, surgical procedures to treat obesity, such as gastric bypass, gastric banding or sleeve gastrectomy, have been shown to improve health significantly and to reduce mortality in people who are severely obese [19,20].

In food science, there is growing interest in decreasing body weight through functional foods with anti-obesity efficacy and no side-effects. For example, bioactive ingredients contained in a wide range of plants have been suggested to have weight-loss effects [21,22]. Furthermore, edible insects have been suggested to

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have anti-obesity effects, and the findings of studies in mice models suggest the presence of bioactive compounds in edible insects with potential efficacy in weight control. For example, cricket extracts appear to have beneficial effects on lipid metabolism and body fat content in rats fed a high-fat diet [23]. The isonitrogenous replacement of casein by a protein-rich insect meal, produced from large-scale mass-rearing of edible insects, has been demonstrated in a rat model of hyperlipidemia (obese Zucker rats) to have beneficial effects on metabolic health, in particular by inducing substantial lipid-lowering effects in liver and plasma [24]. Furthermore, regular intake by obese mice of powder from the larvae of yellow mealworm (Tenebrio molitor) has been shown to attenuate the gaining of body weight through a decrease in lipid accumulation and triglyceride content in adipocytes [25], which are highly specialized cells playing a critical role in the regulation of lipid metabolism and energy balance [26].

Edible insects may offer a plethora of potential health benefits that require further investigation. For example, insect-derived bioactive agents with antioxidant or other properties and dietary fiber seem to promise beneficial effects on health [27,28]. Insects may prevent micronutrient deficiencies and play a role in the management of chronic diseases. The high concentrations of iron and zinc contained in crickets and termites are of particular interest, since deficiencies in these minerals are common in low-income countries. Twenty-five percent and 17% of the world's population have been shown to be at risk of iron and zinc deficiency, respectively. This has led to the use of edible insects in fortification programs [28]. Based on the findings of *in vitro* and *in vivo* animal studies, potential health-promoting effects of insect consumption have been suggested for the cardiovascular system, the gastrointestinal tract, immune functions, carcinogenesis and metabolic problems, such as obesity and type-2 diabetes [28]. However, there is a significant dearth of studies evaluating health outcomes in humans following the intake of insects. The findings of a small number of well-designed randomized trials in humans suggest that consumption of certain insects may enhance health by compensating for deficiencies in micronutrients or promoting gut health [28].

Insects are one of numerous food sources that have been consumed throughout the history of human development [29,30]. Today, the eating of insects remains popular in many regions worldwide, with regular consumption of edible insects estimated to form part of traditional diets of more than two billion people [31]. Edible insects are a promising source of macronutrients and micronutrients. The available evidence suggests a high nutritional value of insects, since they are rich in protein, fat, vitamins, minerals and fiber [32]. In many respects, the nutritional value of edible insects has been found to be equivalent or even superior to that of other animal-based foods. Furthermore, the production of edible insects may have environmental benefits, which are related to the relatively high feed-to-meat conversion rate, with insects converting plant proteins to insect proteins far more efficiently than other animals [33]. Furthermore, edible insects appear to be more climate-friendly than cattle, pigs or chickens, since they require less space and water to grow and develop and cause fewer greenhouse gas emissions [31]. Large-scale production of insect-based foods may help solve the looming global food insecurity problem and contribute to accomplishing the sustainable development goals set by the United Nations [34]. Whole insects and their parts have been approved as novel foods by the European Food Safety Authority, thus enabling the regulated and safe introduction of edible insects in the European Union. Insect species with a strong potential to be used as food and feed in the European Union include the following: *Tenebrio molitor* (yellow mealworm beetle), *Hermetia illucens* (black soldier fly), *Acheta domesticus* (house cricket), *Musca domestica* (housefly), *Gryllodes sigillatus* (tropical house cricket), *Alphitobius diaperinus* (lesser mealworm or litter beetle), *Zophobas atratus* (giant mealworm beetle), *Achroia grisella* (lesser wax moth), *Bombyx mori* (domestic silk moth), *Locusta migratoria migratorioides* (African migratory locust), *Galleria mellonella* (greater wax moth or honeycomb moth), and *Schistocerca americana* (American grasshopper) [35].

In addition to their nutritional value, edible insects appear to be a source of food bioactives with potential utility in medicine. Bioactivities evaluated in edible insects include antioxidant, anti-inflammatory, antihypertensive, anti-obesity, antimicrobial and immunomodulatory activities [27,28]. Most research on bioactivity of edible insects has been conducted in yellow mealworms (*Tenebrio molitor*) and house crickets (*Acheta domesticus*), since these species are very promising with respect to large-scale commercial production [36].

2 Antilipidemic and anti-obesity effects of different edible insect species

2.1 Tenebrio molitor (yellow mealworm beetle)

Tenebrio molitor, one of the most popular insects consumed by humans, is reared on an industrial scale. Some insect species, including Tenebrio molitor, have been suggested to show bioactivity regarding lipid metabolism, with beneficial effects on obesity and metabolic syndrome. A potential mechanism proposed to underlie these effects is the inhibition of lipid absorption during digestion, in particular due to the inhibition of the enzyme pancreatic lipase, which is involved in the digestion of lipids. Non-protein extracts obtained using aqueous ethanol have been shown to inhibit the pancreatic lipase in vitro [37]. Another study of mealworms as feed confirmed in vivo the reduction in lipase activity, with an increase of Tenebrio molitor larvae in the feed being associated with a progressive inhibition of intestinal lipase in juvenile meagre (Argyrosomus regius) [38]. An ethanol extract from Tenebrio molitor larvae was found to inhibit the differentiation of 3T3-L1 adipocytes by decreasing lipid droplet formation and triglyceride content [25]. Lipid accumulation and triglyceride content in mature adipocytes were decreased significantly (up to 90%), without a reduction in cell viability [25]. Tenebrio molitor extract was also shown to reduce the expression levels of lipogenesis-specific genes, such as sterol regulatory element binding transcription factor 1c (SREBP-1c), lipoprotein lipase (LPL), stearoyl-CoA desaturase 1 (SCD1) and fatty acid synthase (FAS). These genes have central functions in determining the phenotype of mature adipocytes. Furthermore, a reduction was found in the expression of adipogenic differentiation factors (peroxisome proliferator-activated receptor y (PPARy) and CCAAT/enhancer-binding protein a (C/EBPa)) together with elevated phosphorylation of AMPactivated protein kinase (AMPK), suggesting an inhibition of the differentiation through the AMPK pathway [25].

In addition, daily oral administration of *Tenebrio molitor* larvae powder to obese mice fed a high-fat diet attenuated the gain in body weight and reduced visceral fat mass [25]. The powder also

reduced hepatic steatosis, the process of the abnormal lipid retention, as well as plasma levels of hepatic enzymes related to liver damage, such as alanine transaminase and aspartate transaminase [25]. The anti-obesity effects of a diet containing *Tenebrio molitor* larvae powder in a high-fat diet-induced obese mouse model were confirmed by another report [39]. The mice fed this diet showed reductions in body weight, subcutaneous and visceral fat volumes, adipocyte accumulation in the liver, adipocyte size, leptin concentration, adipogenesis-related gene levels as well as plasma concentrations of total cholesterol, triglyceride and glucose [39]. In another *in vivo* study, spontaneously hypertensive rats fed *Tenebrio molitor*-based diets showed a slight decrease in fat mass [40]. This decrease in visceral fat improved hepatic insulin action and reduced the expression of inflammatory cytokines [25].

While the anti-obesity effects both in vitro and in vivo of Tenebrio molitor larvae could be demonstrated, the mechanism through which appetite regulation in mice with diet-induced obesity was mediated by the larvae remains unknown. The hypothesis of an involvement of the regulation of neuropeptide expression was tested by investigating the effects of Tenebrio molitor extract on anorexigenesis and endoplasmic reticulum stressinduced orexigenic neuropeptide expression in the hypothalami of mouse models of obesity [41]. The intracerebroventricular administration of Tenebrio molitor extract to mice fed a high-fat diet was found to suppress feeding by downregulating the expression of the orexigenic neuropeptides neuropeptide Y and agouti-related protein via hypothalamic mammalian target of rapamycin (mTOR) and mitogen-activated protein kinase (MAPK) signaling pathways. Central mTOR signaling has been shown to play an important role in the hypothalamic modulation of feeding behavior [42,43]. The attenuated food intake and body weight and the related downregulation of orexigenic neuropeptides suggest an appetite-suppressing effect of mealworm extract. Tenebrio molitor extract also significantly reduced the expression of endoplasmic reticulum stress response genes. These findings suggest a potential therapeutic efficacy of Tenebrio molitor extract in obesity and endoplasmatic reticulum stress-driven disease conditions. In addition, the protective effect against endoplasmic reticulum stress is interesting in that this chronic stress is involved in pathological processes related to metabolic syndrome.

In summary, the above findings suggest an anti-obesity effect of *Tenebrio molitor* extracts when administered as a food supplement.

2.2 *Hermetia illucens* (black soldier fly)

Hermetia illucens is one of the most popular edible insects. The available evidence regarding the use of Hermetia illucens as animal feed suggests that it may have a potential value in respect to aspects of lipid metabolism related to obesity and metabolic syndrome. For example, a reduced intraperitoneal fat index was reported in juvenile mirror carp (Cyprinus carpio var. specularis) fed Hermetia illucens oil rich in omega-3 fatty acids [44]. This was associated with a significant upregulation of PPARa and CPT-1 in intraperitoneal fat tissue as well as a reduced lipid content of the hepatopancreas, with either a higher β-oxidation of lipids or an elevated transport of lipids to other tissues [44]. Furthermore, Hermetia illucens-derived chitin has been related to a reduction in fatty acid synthesis and an increase in the hydrolysis of lipoproteins and triglycerides in the liver of juvenile Jian carp (Cyprinus carpio var. Jian) [45]. These findings were also linked to the presence of lauric acid, which causes a decrease in lipid storage. In addition, triglycerides and low-density lipoproteins were reduced following feeding with Hermetia illucens. However, the latter effects may have been mainly the result of the enrichment of the feed with omega-3 fatty acids. A decrease in lipid content in fish hepatopancreas following Hermetia illucens feeding has also been demonstrated in other studies [46,47]. Another potential mechanism underlying the reduction in plasma lipids or lipid tissue content could be a reduced activity of intestinal lipases, which has been observed in juvenile grass carp (Ctenopharyngodon idella) fed defatted Hermetia illucens [48]. Reduced plasma triglyceride levels were also found after the feeding of piglets with Hermetia illucens [49]. A decrease in the digestibility of fat was related to the negative effect of chitin on nutrient digestibility [49]. In regard to cholesterol, reduced concentrations of total cholesterol in blood plasma have been observed in white shrimp (Litopenaeus vannamei) fed diets containing defatted Hermetia illucens larvae [50]. Reduced plasma total cholesterol and/or triglyceride levels following Hermetia illucens feeding have also been found in juvenile Jian carp and laying hens [45,51]. This effect has been related to the potential interference of chitin in the absorption of cholesterol and to its ability to attract negatively charged bile acids and free fatty acids [51].

2.3 Musca domestica (housefly)

With respect to antilipidemic activity, a protein-enriched extract from housefly maggots has been shown to decrease the plasma concentrations of triglycerides, total cholesterol and low-density lipoproteins and to increase the levels of high-density lipoproteins in mice [52]. The same extract was found in another study to decrease the plasma concentrations of oxidized low-density lipoprotein, low-density lipoprotein and malondialdehyde, and to increase levels of high-density lipoproteins [53]. The feeding of Sprague-Dawley rats with a meal containing different amounts of housefly pupae was found to reduce visceral fat when the diet contained 20% pupae and to decrease total cholesterol and lowdensity lipoprotein concentrations when the meal contained as little as 5% pupae [54]. It was suggested that the housefly pupae promoted the efflux of excess cholesterol and inhibited the absorption of cholesterol from the intestine. These effects were probably promoted by chitin and monounsaturated fatty acids as well as bioactive compounds contained within housefly pupae that have not as yet been identified [54]. Moreover, a protein-enriched fraction from housefly larvae decreased plasma total cholesterol and triglyceride concentrations, and increased high-density lipoprotein cholesterol, lactoperoxidase and reduced-glutathione in mice with hyperlipidemia induced by Triton WR-1339 [55].

2.4 Acheta domesticus (house cricket)

The *in vitro* pancreatic lipase inhibitory activity of extracts obtained with ethanol or aqueous ethanol from *Acheta domesticus* has recently been assessed. It could be shown that pressurized-liquid extraction and aqueous ethanol were most suitable for producing bioactive extracts capable of inhibiting pancreatic lipase. The compounds responsible for such activity have not as yet been identified.

Chitin, a polysaccharide naturally occurring in insects, is insoluble in water and organic solvents and can be converted to chitosan [56]. Chitosan isolated from *Acheta domesticus* has been shown to trap lipids, with a lipid-binding capacity comparable to shrimp chitosan [57], which was demonstrated to exert anti-obesity effects by controlling body weight in a pig model [58].

2.5 Allomyrina dichotoma (Korean horn beetle)

Allomyrina dichotoma larvae ethanol extract has been reported to suppress adipogenesis and lipogenesis in an *in vitro* model, with the formation of lipid droplets and triglyceride content in differentiated 3T3-L1 adipocytes being markedly reduced. The extract could therefore have anti-obesity activity as a food supplement [59]. A further study was able to demonstrate that *Allomyrina dichotoma* larvae decreased, in a dose-dependent manner, body weight gain, organ weight and adipose tissue volume of mice fed a high-fat diet [60]. Moreover, the gene expression levels of transcription factors PPAR γ and C/EBP α as well as of lipoprotein lipase in the epididymal fat tissue of mice fed a high fat diet were reduced significantly following daily administration for six weeks of *Allomyrina dichotoma* powder [60].

In addition, the anorexigenic and endoplasmic reticulum stressreducing effects of ethanol extract of *Allomyrina dichotoma* larvae have been studied in the hypothalamus of diet-induced obese mice. The intracerebroventricular administration of *Allomyrina dichotoma* ethanol extract was found to have an antagonizing effect on ghrelin-induced feeding behavior through mTOR and MAPK signaling pathways [61]. The finding that *Allomyrina dichotoma* extract greatly decreased endoplasmic reticulum stress both *in vitro* and *in vivo* suggests that bioactive constituents of *Allomyrina dichotoma* may be of therapeutic use in diseases driven by prolonged endoplasmic reticulum stress [61].

2.6 Gryllus bimaculatus (two-spotted cricket)

Gryllus bimaculatus ethanolic extracts have been observed to display anti-obesity properties in a high fat-treated rat model [62]. Rats receiving the extract for two months were found to have decreased fat weight, particularly abdominal fat [62]. Rats administered different amounts of isolated glycosaminoglycan from *Gryllus bimaculatus* for one month showed a decrease in adipose tissue weight, abdominal fat and epididymal fat [63]. Another study showed that ethanolic cricket extract reduced body weight, intestinal adipose tissue and total cholesterol in mice provided high-fat food for 14 weeks [64]. An effect of *Gryllus bimaculatus* extract on obesity was also found in genes involved in lipogenesis and lipid accumulation, including leptin, adiponectin, acetyl-CoA carboxylase, fat-specific protein 27 and PPARy, which were downregulated [64].

A summary of the available evidence of antilipidemic and anti-obesity effects of various edible insects is presented in Table 1.

 Table 1
 Edible insect species and their antilipidemic and anti-obesity effects

Insect species	Antilipidemic effects	Anti-obesity effects
<i>Tenebrio molitor</i> (yellow mealworm beetle)	Inhibition of lipid absorption <i>in vitro</i> through inhibition of pancreatic lipase by non-protein aqueous ethanol extract from insect [37]; Decrease in intestinal lipase activity <i>in vivo</i> by insect larvae in juvenile meagre [38]; Inhibition of 3T3-L1 adipocyte differentiation <i>in vitro</i> through reduction of lipid droplet formation and triglyceride content by ethanol extract from insect [25]; Reduction of expression of lipogenesis-specific genes determining mature adipocyte phenotype and reduction of expression of adipogenic differentiation factors by insect extract [25]; Reduction of plasma levels of total cholesterol, triglyceride and glucose by larvae powder in obese mice fed high-fat diet [39]	Reduced body weight gain and visceral fat mass by oral administration of larvae powder in obese mice fed high-fat diet [25]; Reductions in body weight, subcutaneous and visceral fat volumes, hepatic adipocyte accumulation and adipocyte size by larvae powder in obese mice fed high-fat diet [39]; Slight reduction of fat mass by insect-based diet in spontaneously hypertensive rats [40]; Suppression of feeding by intracerebroventricular administration of insect extract in mice fed high-fat diet [41]
<i>Hermetia illucens</i> (black soldier fly)	Reduction of plasma triglycerides by feeding insects in piglets [49]; Reduction of plasma total cholesterol by defatted insect larvae in white shrimp [50]; Reduction of plasma total cholesterol and/or triglycerides levels by insect feeding in juvenile Jian carp [45] and laying hens [51]; Chitin-related reduction of fatty acid synthesis and increased hydrolysis of lipoproteins and triglycerides in the liver by defatted insect larvae in juvenile Jian carp [45]; Reduction of intestinal lipases by defatted insect in juvenile grass carp [48]; Reduction of intraperitoneal fat index and lipid content of the hepatopancreas by insect pulp [46] or insect oil rich in omega-3 fatty acids [44] in juvenile mirror carp	
<i>Musca domestica</i> (housefly)	Reduction of plasma triglycerides, total cholesterol and low-density lipoproteins and increase in high-density lipoproteins by protein-enriched extract from insect maggots in mice [52]; Reduction of plasma oxidized low-density lipoprotein, low-density lipoprotein and malondialdehyde and increase in high-density lipoproteins by protein-enriched extract from insect maggots in mice [53]; Reduction of total cholesterol and low-density lipoprotein by insect pupae in rats [54]; Reduction of plasma total cholesterol and triglycerides and increase in high-density lipoprotein cholesterol, lactoperoxidase and reduced-glutathione by protein-enriched insect larvae in mice with hyperlipidemia [55]	Reduction of visceral fat by insect pupae in rats [54]
Acheta domesticus (house cricket)	Inhibition of pancreatic lipase activity <i>in vitro</i> by ethanol or aqueous ethanol extracts from insect [37]	Lipid binding of insect-derived chitosan similar to shrimp chitosan [57] with anti-obesity effects through control of body weight in pigs [58]

Table 1 (Continued)				
Insect species	Antilipidemic effects	Anti-obesity effects		
<i>Allomyrina dichotoma</i> (Korean horn beetle)	Reduction of lipid droplet formation and triglyceride content in differentiated 3T3-L1 adipocytes <i>in vitro</i> by insect larvae ethanol extract [59]; Reduction of lipoprotein lipase <i>in vivo</i> by insect powder in mice fed high-fat diet [60]	Dose-dependent reduction of body weight gain, organ weight and adipose tissue volume by insect larvae powder in mice fed high-fat diet [60]; Antagonistic effect of intracerebroventricular administration of insect ethanol extract on food intake and body weight [61]		
<i>Gryllus bimaculatus</i> (two-spotted cricket)	Downregulation of genes involved in lipogenesis and lipid accumulation by insect extract [64]	Reduction of abdominal fat by insect ethanol extract in rats fed high-fat diet [62]; Reduction of adipose tissue weight, abdominal fat and epididymal fat by insect-derived isolated glycosaminoglycan in rats [63]; Reduction of body weight, intestinal adipose tissue and total cholesterol by insect ethanol extract in mice fed high-fat diet [64]		

3 Discussion

Of the edible insect species described in the present review, *Tenebrio molitor, Hermetia illucens* and *Musca domestica* are those that have been investigated most thoroughly in respect to their potential antilipidemic and anti-obesity efficacy. The potential of other insects requires further research. In addition, the nutritional and bioactivity profile of edible insects can be highly variable and depends on the species, the food consumed, the developmental stage when harvested as well as the methods of sacrificing and technological processing [35]. Other environmental factors affecting the nutritional profile of edible insects include day length, light intensity, humidity and temperature [65].

With regard to the mechanisms underlying the lipid-lowering effect found following the feeding of obese rats a protein-rich insect meal obtained from industrial mass-rearing of Tenebrio molitor, convincing evidence suggests a coordinated inhibition of pathways involved in cholesterol and fatty acid or triglyceride synthesis in the liver [24]. Further evidence of an inhibitory effect of the insect meal on hepatic lipid synthesis stems from lipidomic analysis of important plasma phospholipid species, which reflect the hepatic phospholipid fatty acid profile and are therefore suitable indicators of changes in liver lipid metabolism [24]. However, the compounds contained in the protein-rich insect meal that are responsible for the lipid-lowering effect remain unidentified. It seems unlikely that specific fatty acids in the insect meal caused the effects, since, as a result of the adjustment of the fatty acid composition through the adding of individual amounts of different fats in the diet, both fat content and fatty acid composition of the insect meal and the casein control diet were very similar. Compared to casein, lipid-lowering effects in both animals and humans have also been shown for legume proteins, such as lupine and soy [66-68]. Causative factors proposed to explain the effects include differences in the amino acid composition and the presence of bioactive peptides and accompanying compounds [69-72]. Bioactive peptides that are resistant to hydrolysis in the intestinal tract and are thus able to enter the organism in intact form have been described in different legume proteins. These peptides have been shown to stimulate lipid-lowering mechanisms [70]. However, such peptides have so far not been found in insect protein. There are marked differences in the amino acid composition between casein and the protein from Tenebrio molitor used in the above insect meal study. Both insect proteins and legume proteins contain relatively little methionine in comparison with casein [73]. The lower methionine content of insect protein and the subsequent reduction in available methionine for homocysteine formation may be causally involved in the lipidlowering effects of insect meal. However, any other component of the insect meal could also be responsible for its effects on lipid metabolism.

The finding of a decrease in the gene expression levels of various transcription factors following administration of *Allomyrina dichotoma* larvae to high fat diet-fed mice [60] suggests that the larvae inhibit the development of high fat diet-induced obesity through downregulation of genes involved in the metabolism of adipose tissue. Visceral adiposity is considered a central factor for obesity-associated diseases [74,75]. Surgical removal of visceral fat has been shown to improve hepatic insulin action [76–78] and to decrease excessive inflammatory cytokines [78,79]. The effect of *Allomyrina dichotoma* larvae on the reduction of visceral fat therefore suggests a role in preventing and treating visceral obesity-related diseases.

In recent years, the role of the gut microbiome in human health has attracted increasing interest, with gut microbiota being associated with the pathogenesis of various diseases [80]. In this context, some available evidence suggests the gut microbiota as a mechanism involved in anti-obesity effects of edible insects. In a randomized, double-blind dietary intervention study, the consumption of whole cricket powder by healthy adults for 14 days was shown to support the growth of the probiotic bacterium, *Bifidobacterium animalis*, which increased 5.7-fold [81]. *Bifidobacterium animalis* has been found to have potential in the management of obesity by improving anthropometric adiposity biomarkers, particularly in abdominally obese women [82].

The satiating effect of food is an important factor contributing to the control of body weight. The satiating potential of food products based on edible insects has been explored in humans [83]. In a recent study, varying proportions of wheat flour in pancakes were substituted with flour from insects (Tenebrio molitor, Alphitobius diaperinus or Acheta domesticus). In order to assess the satiating potential of the pancakes, 71 healthy volunteers were required to rate levels of hunger and satiety prior to and following the ingestion of the pancakes at 30-minute intervals over the subsequent three hours [83]. The satiety values after pancake consumption depended on the proportion of insect flour substituted and on the insect species. The average satiety levels reported were highest for pancakes with an addition of 30% Alphitobius diaperinus flour and of 20% or 30% Acheta domesticus flour. The least satiating pancakes were those containing Tenebrio molitor flour. The largest addition of an insect flour (30%) for each type of pancake showed a marked increase in the satiating effect compared to the control sample [83]. Furthermore, satiety was found to be affected the most by the protein content of the insect flour pancakes. These findings in humans support the potential value of using insect-based food products in the management of obesity. Further research into the satiety provided by edible insects may be warranted.

The mechanisms proposed to underlie the antilipidemic and anti-obesity effects of edible insects are summarized in Table 2.

Table 2 Mechanisms proposed to underlie the antilipidemic and anti-obesi	y effects of edible insects.
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No.	Mechanisms
1	Inhibition of lipid absorption during digestion (inhibition of pancreatic lipase) [37,38,48]
2	Inhibition of pathways involved in hepatic synthesis of cholesterol, fatty acids and triglycerides [24]
3	Reduction of plasma levels of triglycerides [39,45,49,51,52,55], total cholesterol [39,50-52,54,55,64] or low-density lipoproteins [45,53,54] and elevated plasma levels of high-density lipoproteins [52,53,55]
4	Inhibition of differentiation of 3T3-L1 adipocytes by reducing lipid droplet formation and triglyceride content [25,59]
5	Reduction of expression of genes involved in lipogenesis and lipid accumulation (e.g. LEP, ADIPOQ, ACACA, Fsp27 and PPARy) [64]
6	Reduction of expression of lipogenesis-specific genes (SREBP-1c, LPL, SCD1, FAS) determining the phenotype of mature adipocytes [25]
7	Reduction of gene expression of transcription factors PPARG, CEBPA and lipoprotein lipase [60]
8	Reduction of expression of adipogenic differentiation factors together with elevated AMPK phosphorylation [25]
9	Lipid-binding capacity of chitin-derived chitosan [57] and interference of chitin in the absorption of cholesterol and free fatty acids [49,51]
10	Chitin-related reduction of fatty acid synthesis and increased hepatic hydrolysis of lipoproteins and triglycerides [45]
11	Support of gut microbiota growth (e.g. Bifidobacterium animalis) [81]
12	Antagonistic effect on ghrelin-induced feeding behavior via mTOR and MAPK signaling pathways [61]
13	Suppression of appetite and food intake by downregulation of expression of orexigenic neuropeptides (neuropeptide Y, agouti-related protein) via hypothalamic mTOR and MAPK signaling pathways [41-43]
14	Increased satiety in humans [83]

4 Conclusion

Edible insects may be able to provide a wide range of food supplements and functional food ingredients for specific purposes, including the management of obesity. However, in view of the very large number of edible insect species and the many factors affecting their bioactive content, generalizable conclusions concerning their potential anti-obesity properties cannot be drawn. It is important to note that the findings regarding potential anti-obesity effects of edible insects are based mainly on studies conducted *in vitro*. The available *in vivo* evidence stems mainly from rodent models. There is currently a significant lack of relevant studies assessing health outcomes in humans.

Research performed with insects as feed for livestock may provide important results concerning the *in vivo* biological activities of edible insects. As with bioactive constituents of other foods, any claims of health benefits of insect-derived compounds need to be clearly established, necessitating trials in humans. With respect to anti-obesity (and other health) effects, no lipid-lowering compound identified in insects has thus far been tested in humans. Further studies of the effects of bioactive compounds contained in edible insects on human health are therefore needed in order to validate the potential of edible insects as a novel approach in addressing the growing worldwide problem of obesity and for promoting health in general.

Conflict of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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