

Annual Review of Entomology

Taxonomy, Biology, Symbionts,
Omics, and Management of
Rhynchophorus Palm Weevils
(Coleoptera: Curculionidae:
Dryophthorinae)

Mark S. Hoddle,^{1,*} Binu Antony,²
Hamadttu A.F. El-Shafie,³ M. Lourdes Chamorro,⁴
Ivan Milosavljević,¹ Bernhard Löhr,⁵
and J. Romeno Faleiro⁶

¹Department of Entomology, University of California, Riverside, California, USA;
email: mark.hoddle@ucr.edu, ivanm@ucr.edu

²Chair of Date Palm Research, Department of Plant Protection, College of Food and
Agricultural Sciences, King Saud University, Riyadh, Saudi Arabia; email: bantony@ksu.edu.sa

³Sustainable Date Palm Pest Management Research Program, Date Palm Research Center of
Excellence, King Faisal University, Hofuf-Al-Ahsa, Saudi Arabia; email: elshafie62@yahoo.com

⁴Systematic Entomology Laboratory, Agricultural Research Service, US Department of
Agriculture, c/o National Museum of Natural History, Smithsonian Institution, Washington,
DC, USA; email: lourdes.chamorro@usda.gov

⁵Biocontrol Entomologist, Annweiler, Germany; email: blohr55@gmail.com

⁶Red Palm Weevil Specialist, Goa, India; email: jrfaleiro@yahoo.co.in

**ANNUAL
REVIEWS CONNECT**

www.annualreviews.org

- Download figures
- Navigate cited references
- Keyword search
- Explore related articles
- Share via email or social media

Annu. Rev. Entomol. 2024. 69:455–79

The *Annual Review of Entomology* is online at
ento.annualreviews.org

<https://doi.org/10.1146/annurev-ento-013023-121139>

This work is licensed under a Creative Commons Attribution 4.0 International License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited. See credit lines of images or other third-party material in this article for license information.

*Corresponding author

Keywords

biological control, dispersal, eradication, invasive species, integrated pest management, phylogeny

Abstract

Palm weevils, *Rhynchophorus* spp., are destructive pests of native, ornamental, and agricultural palm species. Of the 10 recognized species, two of the most injurious species, *Rhynchophorus ferrugineus* and *Rhynchophorus palmatus*, both of which have spread beyond their native range, are the best studied. Due to its greater global spread and damage to edible date industries in the Middle East, *R. ferrugineus* has received more research interest. Integrated pest management programs utilize traps baited with aggregation

pheromone, removal of infested palms, and insecticides. However, weevil control is costly, development of resistance to insecticides is problematic, and program efficacy can be impaired because early detection of infestations is difficult. The genome of *R. ferrugineus* has been sequenced, and omics research is providing insight into pheromone communication and changes in volatile and metabolism profiles of weevil-infested palms. We outline how such developments could lead to new control strategies and early detection tools.

IMPORTANCE, NATIVE DISTRIBUTION, AND INVASION HISTORY OF PALM WEEVILS

Species of *Rhynchophorus* Herbst (100) (Coleoptera: Curculionidae: Dryophthorinae), commonly known as palm weevils, are pests of native, ornamental, and agriculturally important palm species (Arecales: Arecaceae) because of highly destructive feeding by larvae in meristematic regions of infested palms. Extensive larval feeding damage to meristem in offshoots or the palm crown frequently results in palm death, and damage permits entry of pathogens and other pest insects that may also be lethal (63, 79, 142). *Rhynchophorus* spp. all have native distributions confined to the tropics and subtropics (200). Palm weevils are naturally occurring in parts of Asia, Sub-Saharan Africa, Mexico, Central and South America, the Caribbean, and the southeastern United States (79, 200). In some of these native ranges, weevil larvae, collected from infested palms or commercially farmed, are consumed by humans (101, 150, 181) or used as a protein source in animal feed (17).

Three species, *Rhynchophorus ferrugineus* (Olivier), *Rhynchophorus vulneratus* (Panzer), and *Rhynchophorus palmarum* (L.), have successfully colonized areas outside of their native ranges (73, 104, 105). The most successful invader, the red palm weevil, *R. ferrugineus*, first officially recorded outside of its native Asian range in the Middle East in 1985 (5, 73), was unintentionally moved via imports of weevil-infested palms (10, 79). Continued export of live palms infested with *R. ferrugineus* facilitated an extensive range expansion throughout the Middle East, the Mediterranean, the Canary Islands, the Maghreb region of North Africa, Japan, China, and the Caribbean (79). In 2022, populations of *R. ferrugineus* were confirmed from Uruguay. Invasive *R. ferrugineus* populations may threaten conservation of some native palm species (33), UNESCO World Heritage Sites (203), and ornamental landscape palms (142). Native and invasive *R. ferrugineus* populations can destabilize food and income security derived from economies based on edible dates (*Phoenix dactylifera* L.) (10, 79), oil palms (*Elaeis* spp.) (159), and coconuts (*Cocos nucifera* L.) (63). More than 50% of edible date-producing countries are infested with *R. ferrugineus*, in contrast with just 15% of coconut-producing countries (63). The first record of *R. vulneratus* outside of its native range, Indonesia, was made in 2010 in California, and it was later eradicated (105). Range expansion of *R. palmarum* in Mexico commenced around 2000, when established populations were detected in Baja California Sur for the first time (77). By 2014, *R. palmarum* had likely established in southern California. Prior to 2014, populations of *R. palmarum* had not been recorded elsewhere in the United States (104), despite collection records of dubious quality purporting collections in what was termed Lower California and in Texas (200).

Invasive *R. ferrugineus* and *R. palmarum* populations have established permanent populations in areas with desert, semiarid, and Mediterranean climates, which suggests that some tropical palm weevil species have broad ecological amplitudes, possibly due to cold tolerance (121) rather than desiccation resistance (201), and can thrive in climatically diverse habitats where palms grow. Conversely, *Rhynchophorus cruentatus* (F.), a subtropical species with a natural range spanning from Florida through to the coastal regions of South Carolina and Texas (110), has not expanded its

range despite extensive movement of plant material from its home range to other parts of the United States.

SYSTEMATICS OF *RHYNCHOPHORUS* SPECIES

Taxonomy

Due to extensive variability in size and color, the taxonomy of *Rhynchophorus* species has been confused. In 1795, Herbst (100) established the genus *Rhynchophorus* for 22 species of weevil. Of these, three species remain valid: *R. palmarum*, *R. ferrugineus*, and *R. cruentatus*. The type species, *R. palmarum*, designated by Schönherr (184), was originally described by Linnaeus in *Curculio* in 1758 (123). The most comprehensive and detailed taxonomic study of *Rhynchophorus* was undertaken by Wattanapongsiri (200), who recognized 10 valid species, including two new species and eight junior synonyms. Of the 10 species of *Rhynchophorus* currently recognized, two (*Rhynchophorus distinctus* Wattanapongsiri from West Sumatra and *Rhynchophorus lobatus* Ritsema from Borneo) are each known from single specimens and are suspected to be variants of *R. vulneratus* (157). *Rhynchophorus lobatus* was not studied by Wattanapongsiri (200), and based on the original description, he was unable to determine if it was a synonym of *R. ferrugineus* or *R. vulneratus*. Based on the geographical occurrence of the species (173), *R. lobatus* is probably a junior synonym of *R. vulneratus* (157). However, whether unique morphological features, including the distinctive male genitalia (200) of *R. distinctus*, represent intraspecific variation of an aberrant male *R. vulneratus* (157) or a separate species altogether, as determined by Wattanapongsiri (200), remains to be confirmed. The remaining eight *Rhynchophorus* species include three from Australasia, *Rhynchophorus bilineatus* (Montrouzier), *R. ferrugineus*, and *R. vulneratus*; three from the New World, *R. cruentatus*, *R. palmarum*, and *Rhynchophorus ritcheri* Wattanapongsiri; and two from the Afrotropical region, *Rhynchophorus phoenicis* (F.) and *Rhynchophorus quadrangulus* Quedenfeldt. A map showing the distributions of *Rhynchophorus* species in both native and invaded ranges is shown in **Supplemental Figure 1**.

Supplemental Material >

Morphology and Identification

The probable nonmonophyly of *Rhynchophorus* is apparent from efforts to determine diagnostic characteristics for adult specimens. Many features, such as the dorsal surface and the shape of the rostrum, the shape of mandibles and the scutellum, and the relative length of the dorsal margin of the metepimeron, are shared among *Dynamis* Chevrolat, *Omotemnus* Chevrolat, *Paratasis* Chevrolat, *Protocerus* Schoenherr, *Rhynchodynamis* Heller, *Rhynchophorinus* Günther, and *Rhynchophorus*. However, the following characteristics may serve to distinguish *Rhynchophorus* from similar-looking genera: The rostrum is usually cylindrical (except in *R. quadrangulus*), dorsally densely setose (except in *R. cruentatus*), and granulate or toothed in the male; the scutellum is long and broad at the base; the pronotum has a complete basal submarginal sulcus and is usually without a basal lobe (19, 120, 157); and the spermatheca is distally truncate (200).

In addition to adult *Rhynchophorus* (176, 200), the egg (11, 200), larva (20, 34, 37, 137, 195, 200), pupa (200), and fibrous cocoon (200) are well documented. Eggs of *Rhynchophorus* spp. are indistinguishable among species (200). Differences among the six species for which the larvae have been described lie mainly in the number, shape, and relative placement of setae on the labrum and sensory pores on the epipharynx; the location of medial epipharyngeal setae; and the morphology of dorsal malar setae on the maxillae (94, 195, 200). For the six species of exarate *Rhynchophorus* pupae studied, the presence or absence and relative placement of the tuberculate setae on the epicranium, rostrum, thorax, and abdominal tergites are diagnostic (200).

Identification of *Rhynchophorus* species is challenging, particularly for sympatric species of the Australasian region, which may exhibit high variation in body color and patterns, as well as morphology. Adults of allopatric *Rhynchophorus* species can be distinguished morphologically with examination of the armature of the endophallus (157). However, this characteristic is not consistently different between the Australasian *R. ferrugineus* and *R. vulneratus*, yet it differentiates *R. bilineatus* (157). Additional morphological features used to distinguish adults are primarily on the head: morphological variability of the shape of the apex of the submentum, subgenal sutures, and indentation of the mandibles (94, 157). *Rhynchophorus* males and females are subequal in size, color, and markings (200). Males have setose profemora and curved rostra with dorsal setae, as opposed to the straight and glabrous rostra in females, and male *R. ferrugineus* and *R. vulneratus* have a shorter rostrum and less pointed pygidia than females (200).

Morphometrics has been used with limited success to distinguish species (173, 182, 183); molecular-based methods may be more reliable when used correctly (51, 53, 128, 173, 178). Species-level identifications can be made using DNA sequences of the mitochondrial cytochrome c oxidase subunit I (COI) gene and regions of the nuclear ribosomal genes (e.g., the D2 domain of 28S rRNA and the internal transcribed spacers, e.g., ITS2) (52–54, 173). However, molecular identification tools must be rigorously validated, and users should proceed with care and an awareness of potential pitfalls. Simple errors, like failure to trim primers or errors in checking the direction of sequence reads, or issues related to sampling small geographic populations (51–53, 94, 173) may result in incorrect species identifications, the outcomes of which could have significant negative implications for research findings and trade and quarantine decision makers.

Phylogeny

Higher-level phylogenetic studies necessary to understand the evolution and natural limits of *Rhynchophorus* and relatives are limited (35, 160). Phylogenetic studies of Curculionoidea, including *Rhynchophorus*, which originated 15–35 million years ago (35), have firmly placed the subfamily Dryophthorinae within Curculionidae and corroborated its monophyly (91, 120, 133–136, 141, 151, 185). Although the subtribe Rhynchophorina is monophyletic, the genus *Rhynchophorus* may be paraphyletic with respect to *Dynamis* and *Cyrtotrachelus* Schoenherr (35, 160).

Phylogeographic studies have focused mainly on understanding the species limits of Australasian *Rhynchophorus* (51–53, 94, 173, 174). Importantly, Rugman-Jones et al. (173) recognized three species in the region, *R. ferrugineus*, *R. bilineatus*, and *R. vulneratus*, the last of which was elevated from synonymy with *R. ferrugineus* (173). Each species has a distinct geographic distribution (173) (see **Supplemental Figure 1** for a species distribution map).

Supplemental Material >

DEVELOPMENTAL BIOLOGY, REARING, AND POPULATION DYNAMICS

Egg-to-adult development of palm weevils most commonly occurs in palm hosts, and the subset of genera and species that successfully support development is extensive. At least 40 palm species in at least 19 genera are known reproductive hosts for *R. ferrugineus* (79). Similarly, *R. palmarum* and *R. cruentatus* can develop in a diversity of palm species (93, 109, 110). Interestingly, *Phoenix canariensis* Chabaud is a highly preferred host for *R. ferrugineus* (85), *R. palmarum* (109), *R. cruentatus* (110), and *R. vulneratus* (105), none of which has a natural association with this species.

Oligophagy extends to nonpalm hosts such as sugarcane, which supports the development of *R. ferrugineus*, *R. palmarum*, and *R. cruentatus* (80, 93, 122). Additionally, mango, papaya, and breadfruit are recorded as reproductive host plants for *R. palmarum* (93), and *R. cruentatus* can be reared on pineapple fruit (80). Artificial, semiartificial, palm, and nonpalm plant diets can be used to rear

palm weevils (7, 13, 58, 76, 115, 177). Food type may have significant impacts on larval development times and survivorship rates; the number of larval instars; and subsequent adult female reproductive parameters, which affect demographic rates and drive population growth (7, 12, 41, 114, 177).

Females oviposit eggs into holes that are excavated into suitable host material with mandibles located at the distal end of the rostrum, and eggs are covered with a rapidly drying secretion (79, 93). Gravid females can lay multiple eggs per day, which can amount to hundreds of eggs laid over the course of a several-months-long lifetime (93, 114). Daily egg laying and hatching rates decline as females age (93, 114). Weevil larvae build cocoons from palm fibers within which they pupate (200). Adult mating is frequent and promiscuous (64, 111, 194). Survivorship and development rates and population growth parameters are strongly influenced by temperature (41, 45, 122).

Degree-day models constructed from temperature-driven developmental rate data can be used to estimate the number of weevil generations under varying temperature scenarios (41, 42, 122), which can enable interpretation of phenology data (45) and development of ecological niche models to predict spread (73, 78). Use of ecological niche modeling to examine the effects of climate change on the distribution of *R. ferrugineus* in China, part of the invaded range, suggests that the overall distribution of this weevil will not change greatly. However, the suitability of different geographic regions within occupied areas could change, resulting in favorable areas becoming less suitable for *R. ferrugineus*, while marginal areas may increase in favorability (78). However, predicted changes in distribution resulting from climate change may be tempered by the cryptic lifestyles of immature and mature *Rhynchophorus* species, which protect weevils from extreme climatic conditions, possibly enabling persistence of populations across a wide range of climates (73).

Population dynamics of *Rhynchophorus* species can be tracked over time using baited pheromone traps, which can be used to assess effects of climate, location, host palm species, trap-type efficacy, and time of year on weevil densities (2, 38, 131, 161, 180, 202). Weevil density time series data derived from trap capture data can be correlated with palm mortality rates (110) and used to determine impacts of multiyear management programs (102) and to evaluate spatiotemporal factors influencing range expansion patterns following invasions into new areas (85) or infestation patterns in commercial palm plantations (49).

FLIGHT DISPERSAL CAPABILITIES

In the laboratory, flight mill studies indicate that individual weevils are capable of sustained flight over a 12–24 h period (28, 103, 106, 107) and that multiple flights over the course of a lifetime are possible (32, 108). Flight mill assays, regardless of *Rhynchophorus* species tested, indicate that test weevils exhibit a range of flight distances (zero to tens of kilometers flown), with a small proportion (<5%) of weevils, so-called superdispersers, being capable of flying >100 km in a 24 h period (103, 107). Cumulative lifetime distances flown by *R. ferrugineus* and *R. palmarum* can exceed 300 and 750 km, respectively (32, 108). Flight distances are not significantly correlated with weevil size, weight, sex, or mating status for *R. ferrugineus* (28, 106) or *R. palmarum* (107), and flight distances tend to decrease with increasing weevil age and number of repeat flights (32, 108). Flight data can be analyzed to determine the underlying probability distribution of distances flown. The tails of probability distributions (i.e., kurtosis) have important implications for dispersion models investigating rates and patterns of spread and for the development of monitoring and management plans (103, 106, 108). Flight mill data are generated under highly artificial conditions and should be viewed with caution, as it is unknown if *Rhynchophorus* spp. exhibit these types of flight activities outside of the laboratory.

Field studies in the invaded and native ranges of *R. ferrugineus*, *R. vulneratus*, *R. palmarum*, and *R. cruentatus* indicate that flight is predominantly diurnal (68, 93, 202), and flight activity is influenced by temperature, humidity, solar radiation, and wind speed (27, 68, 201). Mark-release-recapture studies indicate that *R. ferrugineus* can be recaptured up to 0.5–7 km from release sites after 3–7 days (2, 27). Mark-release-recapture data need to be interpreted carefully, as flights from release points to traps where weevils are collected are probably not linear, and distances flown are likely underestimated. Additionally, traps close to release points tend to catch more released weevils, and individuals that may have been capable of longer dispersal distances are inadvertently trapped. In addition, as distances from release points increase, the number of traps deployed per unit area decreases, which reduces the likelihood of capturing weevils, potentially resulting in underestimation of dispersal capabilities (204).

SYMBIONTS

Microbiome and Endosymbionts

Palm weevils host a diverse assemblage of protozoan, fungal, viral, and bacterial species, the majority of which have been documented in *R. ferrugineus* (18, 29, 113, 145, 152, 191). A γ -proteobacterial endosymbiont lineage, *Nardonella*, an intracellular obligate specialist, is found in symbiotic organs called bacteriomes in *R. ferrugineus*. *Nardonella* provisions tyrosine, a key component for cuticle formation and hardening in weevils (18). Interestingly, *Wolbachia*, a sex-ratio-distorting rickettsia-like organism commonly associated with weevils (147), has not been isolated from *Rhynchophorus* spp. (15, 29). Gut microbiome studies of larval *R. ferrugineus* are dominated by metagenomes of proteobacteria. At least seven bacterial species have been identified from *R. ferrugineus* gut microbiome studies, of which two dominate and, together with one yeast isolate, exhibit cellulolytic and probiotic functions (23, 113, 145, 152, 153, 191). These endosymbionts may contribute to the digestion of palm material or have immune-related functions for maintaining homeostasis by mediating the production of antimicrobial peptides targeting pathogens (92, 145, 152, 154).

A complete understanding of the contribution of microbial endosymbionts to weevil physiology, reproduction, and detoxification of plant secondary metabolites in palm weevils, and *R. ferrugineus* in particular, remains elusive. Improved understanding of the identities and functions of microbial endosymbionts may provide insights into coevolutionary relationships with palm weevils and processes affecting weevil interactions with palm hosts.

Macrosymbionts

Phoretic mite associations with dryophthorine weevils are at least 19 million years old (39). In native and invaded ranges, phoretic mites have been recorded in association with adults of all known species of *Rhynchophorus* (200), and they tend to be primarily species belonging to the infraorder Uropodina (Acari: Mesostigmata) (86).

At least 30 mite species representing at least 23 genera in approximately 14 families have been recorded from *R. ferrugineus*, *R. palmarum*, and *R. phoenicis* pupae and adults in 12 countries (Supplemental Table 1). Limited mite surveys have been conducted in weevil native ranges (48, 118, 129, 172). The majority of mite faunistic studies have examined invasive *R. ferrugineus* populations, primarily in the Middle East and the Mediterranean Basin (3, 9, 60, 71, 98, 117, 163, 186). A commonly encountered phoretic mite, *Centrouropoda almerodai* Hiramatsu and Hirschmann, lays eggs on rotting palm fibers. Deutonymphs associate themselves with prepupal larvae and are enclosed within cocoons made by weevil larvae. Prior to adult weevil emergence, deutonymphs cluster onto teneral adults and attach themselves, most commonly under the elytra, with an anal

pedicel, which remains under the elytra after the deutonymphs abandon their hosts (163). Dispersing weevils introduce mites into new palms. In contrast to *C. almerodai*, *Fuscuropoda marginata* (Koch) (often listed as *Uroobovella marginata*) preferentially attaches to exposed surfaces of the sternum, pygidium, head, and legs (86); thus, attachment site may be a good indicator of mite species (163). Adult Uropodina are primarily saprophytic and seldom form phoretic associations with weevils (4).

Centrouropoda almerodai and *Centrouropoda rhynchophorus* (El-Bishlawy and Allam) have deleterious impacts on the fitness (e.g., reduced life span) of adult weevils, possibly due to feeding on pupae, indicating that these mites may function as facultative parasites (4, 138). Invasive *Rhynchophorus* spp. can introduce new mite species into areas where they did not previously exist. Consequently, phoretic mites may act as biomarkers that provide insight into invasion pathways, patterns of spread, and temporal changes in mite species compositions over the course of an invasion (86).

Numerous nematode species associated with *R. palmarum*, *R. cruentatus*, and *R. ferrugineus* have been identified. Individual weevils can simultaneously harbor more than one nematode genus, and the ecological niche occupied by weevils influences the nematode community (40). Generally, little is known about the biological (e.g., parasitic effects) and ecological (e.g., commensal saprobionts) relationships that nematodes have with palm weevils. Notable exceptions are the effects that entomopathogenic nematodes used as biological control agents have on weevil survivorship and the well-documented association of *R. palmarum* with the red ring nematode (RRN), *Bursaphelencus cocophilus* Baujard (Nematoda: Aphelenchoididae), the causative agent of a lethal palm malady, red ring disease (RRD). RRN, an obligate palm specialist, is restricted to parts of Mexico, Central and South America, and the Caribbean. Annual mortality rates of approximately 15% attributable to RRN in coconut and oil palm plantations cause significant economic impacts (81). RRN is acquired by weevil larvae feeding on infested palm material, and heavy nematode loads significantly reduce adult weevil size, fat body content, and fecundity (88). RRN cannot multiply within weevil hosts; approximately 16% of female *R. palmarum* vector RRN; and during oviposition, infective third-stage dauer juveniles move from the hemocoel via the ovipositor into oviposition wounds in palms (88, 116). As few as 10–50 infective dauer juveniles inoculated into oviposition wounds can cause RRD (87). Weevils are attracted to palms infested with RRN, further intensifying rates of attack, RRN acquisition and spread, and subsequent RRD incidence (82). It is possible that all *Rhynchophorus* spp. can vector RRN, and the potential destructiveness of RRD will be greatly enhanced if additional species of *Rhynchophorus* come into contact with infected palms and acquire RRN (81). This situation likely exists now in the Caribbean and Uruguay, where *R. ferrugineus*, *R. palmarum*, and *B. cocophilus* are sympatric; this possibility warrants research attention.

WEEVIL AND HOST PALM OMICS

Palm weevil and host palm omics (e.g., genomics, metabolomics, phenomics, proteomics, transcriptomics, and volatilities) are emerging new research areas with potential applications for management (Figure 1).

Transcriptomics

Palm weevil research on transcriptomics commenced in 2013 with the release of the first large-scale transcriptome data set for *R. ferrugineus* (199). Subsequently, the annotation of numerous genes involved in important biological functions, such as chemoreception, detoxification, digestion, reproduction, neurobiology, and immunity, has been achieved (21, 23, 25, 61, 168, 199, 205–207). Importantly, peripheral chemosensory gene families have been identified and coupled

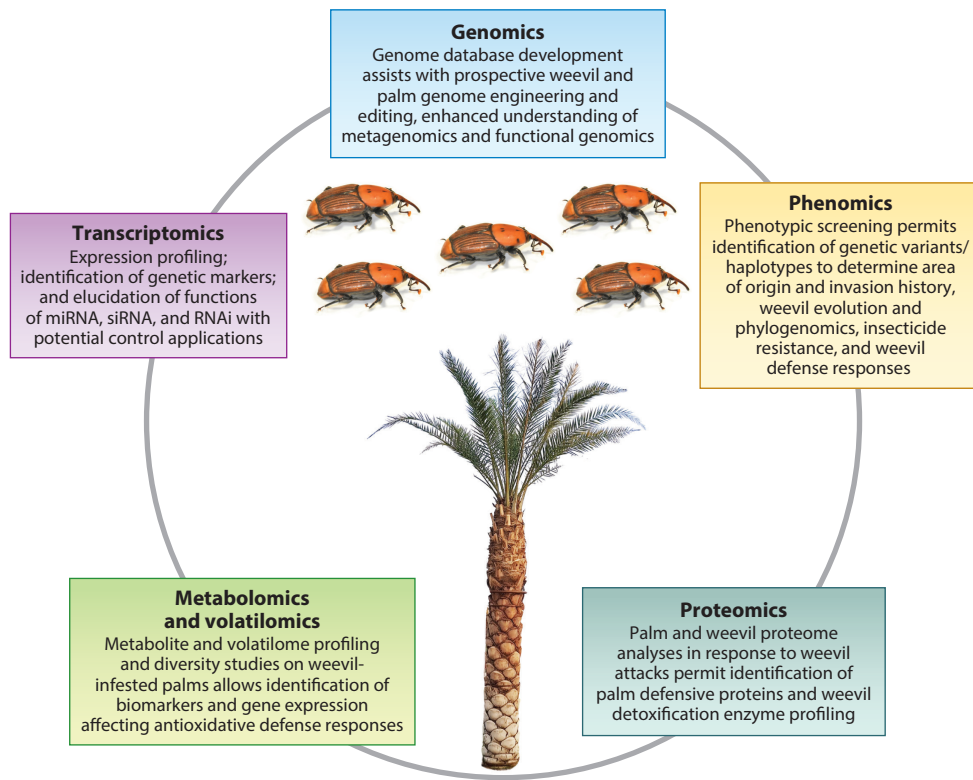
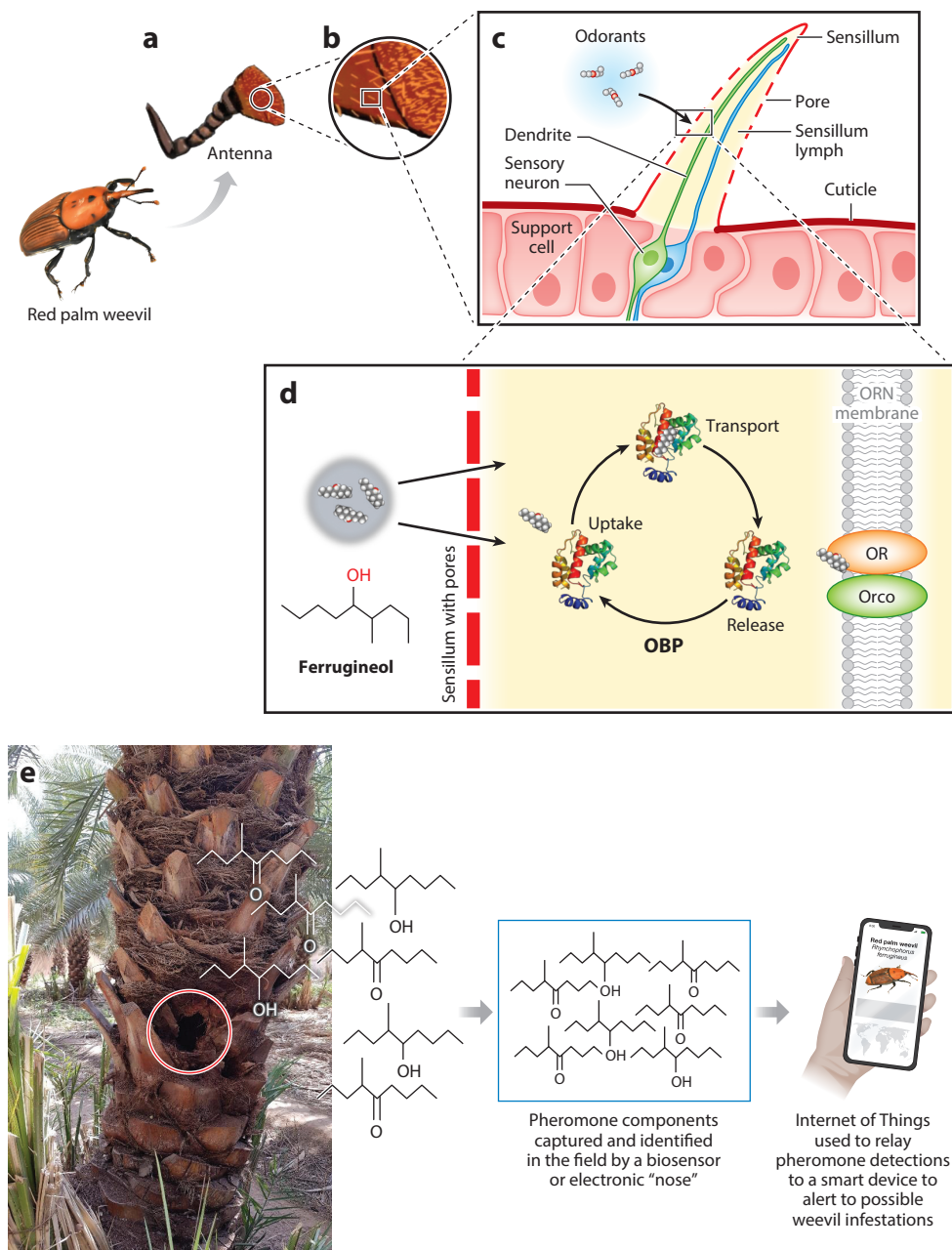


Figure 1

An overview of the potential integration of omics research for management of palm weevils. Data on weevil and palm genomics and transcriptomes may help with the development of gene editing of palms and potentially weevils and permits investigation of RNAi for the production of potential biopesticides targeting weevils. Metabolomics and volatiliomics research can identify biomarkers produced by palms in response to weevil attack that may be of use for early detection of weevil infestations. Proteomics provides insight into production of defensive secondary metabolites by palms that may have use in developing next-generation biopesticides. Phenomics exploits phenotypic and haplotype variations that are used to elucidate invasion histories and pathways and to identify insecticide-resistant populations and mechanisms underlying resistance development. When taken together, information from omics research may provide new avenues for detecting, monitoring, and managing palm weevils. Abbreviations: miRNA, microRNA; RNAi, RNA interference; siRNA, small interfering RNA.

with functional studies (22, 24, 112, 187). This has enabled the deciphering of the molecular basis of *R. ferrugineus* chemoreception, especially pheromone communication (22, 24, 25, 187). Functional genomics studies include loss-of-function experiments with RNA interference (RNAi), which can be used to induce disruption of pheromone communication (187) by impairing the function of odorant-binding proteins and odorant receptors in antennae (22, 24) (**Figure 2a–d**). Furthermore, work using the heterologous expression for functional characterization of odorant receptors identified a receptor of a nonhost volatile that repels palm weevils (112), as well as a pheromone receptor that responded selectively to ferrugineol and ferrugineone, the two components of the *R. ferrugineus* male-produced aggregation pheromone (24). Practical applications of this latter finding could result in the development of biosensors for the early detection of *R. ferrugineus* infestations (**Figure 2e**).



(Caption appears on following page)

(a,b) Graphical representation of the antennal sensilla and (c) peripheral odor detection of the red palm weevil, *Rhynchophorus ferrugineus*. (d) Based on results from functional genomics studies, the putative binding of the odorant binding protein (OBP) to one component of the aggregation pheromone, ferrugineol, results in transportation to receptors and subsequent interaction of ligands with the odorant receptor (OR) and the odorant coreceptor (Orco) proteins housed within the odorant receptor neuron (ORN) membrane. (e) Application of findings from panels a–d could result in the development of biosensors based on the function of the OBP and OR that respond to interaction with a ligand(s), ferrugineol and/or ferrugineone, the two components of the *R. ferrugineus* aggregation pheromone. Detection of palm weevil aggregation pheromone by the biosensor results in the transmission of an alert via cellular networks to an app on a smart device warning of a potential weevil infestation. This field detection method using palm weevil aggregation pheromones would be species specific and potentially highly sensitive and amenable to automation.

Transcriptome profiling and insecticide-induction analyses have identified a family of detoxifying enzymes, cytochrome P450-dependent monooxygenases (P450s), and identified two key P450s that might play a role in developing tolerance to neonicotinoid insecticides (21). This study demonstrated through RNAi that upregulation of P450 gene expression has evolved as an adaptation to insecticide stress arising from exposure to systemic insecticides like imidacloprid (21). Similarly, RNAi knockdown of the antioxidant enzyme catalase in *R. ferrugineus* larvae significantly increased larval mortality due to increased susceptibility to oxidative stress (6). These types of RNAi proof-of-principle studies demonstrating successful knockdown of target genes may guide development of novel methods for palm weevil management (6, 21, 22, 24, 169, 187).

Genomics

There are several online resources for the *R. ferrugineus* genome (see, e.g., <https://bipaa.genouest.org/is/coleoptera/>) (46, 99, 146). The two published *R. ferrugineus* genomes (i.e., the complete set of DNA) resulted in estimated genome sizes that differed: 590 Mb (46) and 720 Mb (99), respectively. This outcome is likely due to the number of individuals (single versus multiple males and females) and assembly method (nonhybrid versus hybrid) used to construct the genome sequences. The *R. ferrugineus* genome analysis revealed the duplication of gene families (i.e., genes with chemosensory, detoxification of secondary metabolites, insecticide resistance, digestion, and immunity functions) essential for weevil adaptation to palm trees (46, 99).

Volatilomics, Metabolomics, and Proteomics of Weevil-Infested Palms

Volatilomics, metabolomics, and proteomics have been used to generate information on palm responses to weevil infestations (83, 84, 126, 166, 167). The volatilome diversity of economically important palms such as date palm, coconut, and oil palm is well documented (47, 70, 74, 188) and provides insights into metabolic processes that can be indicative of internal physiological changes (e.g., defense responses) due to weevil infestations (30). Volatilomics identified airborne organic compounds (e.g., esters, acids, alcohols, and ketones) released by damaged palms (5), in contrast to the terpene hydrocarbons associated with healthy plant tissue (192).

Transcriptome analyses showed higher transcript abundances for fatty acid, tryptophan, and phenylpropanoid metabolism in weevil-infested palms (83). Weevil infestations induce a reprogramming of carbohydrate and organic acid metabolism and selective upregulation of genes involved in synthesis of secondary metabolites, especially terpenoids and alkaloids (84), which have larvicidal and growth-inhibiting activities (16).

Proteomics studies have identified 32 differentially expressed peptides related to plant stress, defense compounds, and protein degradation in association with *R. ferrugineus* infestations in date palm (166). Studies investigating *R. ferrugineus* infestation of coconut and date palm reported an

increase in enzymatic antioxidant activity and antioxidant production, suggesting induced activation of host antioxidative defense responses that increase weevil susceptibility to oxidative stresses (132). Proteomic analyses on oil palm artificially infested with *R. ferrugineus* showed abscisic acid hormone signaling to be the primary driver of responses to insect herbivory (97).

Signature compounds identified from volatilomics, transcriptomics, and proteomics research could enable early detection programs if rapid, accurate, and cost-effective technologies amenable to large-scale field use can be developed.

Phenomics and Invasion Pathways of *Rhynchophorus ferrugineus*

Analyses of the mitochondrial COI gene from *R. ferrugineus* populations throughout native and invaded ranges identified weevil lineages with strong geographically isolated and mixed haplotypes (54, 75, 173, 174, 190, 198). These studies suggest that the native range of *R. ferrugineus* is likely southeast Asia, from where it was introduced into Middle Eastern countries through Pakistan. A westward expansion out of India then followed (173). Invasive *R. ferrugineus* populations in the Mediterranean Basin, characterized by the H8 haplotype (54), may have been introduced from China, where this weevil is also invasive. COI analyses indicate that *R. ferrugineus* populations in the Mediterranean Basin are closely related to weevils that inhabit parts of the native range in Thailand and Malaysia and invaded regions in southern China (36, 173, 198). The invasive H8 haplotype is closely related to haplotypes (H17–H36) from Cambodia, Vietnam, and the Philippines (173). However, conclusive information on *R. ferrugineus* genetic variations in southeast Asian countries needed to confirm the origins of invasive populations remains elusive due to insufficient sampling in the native range.

PALM WEEVIL MANAGEMENT

Economic Impacts

Analyses of the economic impacts of *Rhynchophorus* spp. are limited. Weevil-induced mortality of palms results in economic losses due to yield reductions and costs to remove infested or dead palms and subsequent control expenditures associated with monitoring, trapping, and insecticide treatments. Additional expenses include replanting; decreased trade due to quarantine restrictions; adverse environmental impacts due to regular chemical treatments; and aesthetic damage and property value reductions in urban, recreational, and heritage landscapes due to mortality of ornamental palms, especially *P. canariensis* (142, 159; <https://gd.eppo.int/taxon/RHYCFE>).

Across the six nations that comprise the Gulf Region of the Middle East, annual losses due to removal of *R. ferrugineus*-infested date palms were estimated to range from US\$5.18 million to US\$25.92 million at 1% and 5% infestation levels, respectively (55). In Egypt, total losses due to *R. ferrugineus* infestations of date palms from 1992 to 2019 were estimated to be US\$400 million, with an estimated total annual management cost of approximately US\$20 million (1). Losses incurred by ornamental palm growers in Veracruz, Mexico due to *R. palmarum*-RRN infestations are estimated at US\$6,000 per hectare (162). Similarly, *R. palmarum*-RRN infestations can cost oil palm producers in Costa Rica millions of US dollars per year (159). Furthermore, replacement costs for transplanting mature *P. canariensis* to replace palms killed by *R. palmarum* in California may exceed US\$5,000 per palm (104).

Economic Thresholds

Economic threshold levels define the relationship between pest densities and impacts on yield, which drives economics-based decisions on whether control measures are warranted (189). Economic thresholds are not well established for palm weevils. Because palms are high-value

agricultural and ornamental crops, and palm weevil infestations are lethal to palms, pest tolerance levels are very low. An economic threshold of a 1% infestation rate for *R. ferrugineus* is used in commercial date gardens (63), and use of statistically derived sampling plans is recommended to assess infestation levels to determine if control is needed (65).

Early Detection

Early detection of infested palms, combined with monitoring of adult weevils using pheromone traps, is key to successful palm weevil management (69; <https://gd.eppo.int/taxon/RHYCFE>, <https://gd.eppo.int/taxon/RHYCPA>). Although visual inspection to detect palm weevil infestation is difficult, it is recommended (10). Technologies for use in early detection include sniffer dogs, visual inspection of palm crowns by cutting observation windows or use of drones with high-resolution optics, acoustic detection, detection of key volatile chemicals and metabolomics signatures, use of infrared cameras, and thermal and satellite imaging (26, 50, 130, 156, 165, 170).

Cultural Practices

Decreasing planting density, precision irrigation methods, and use of weevil-free planting materials are important practices that affect success of palm weevil management (69, 179). Build-up of humidity within palm plantations because of closely spaced palms that are flood irrigated is favorable for the development of *R. ferrugineus* populations. Increased planting distances and use of precision watering systems can reduce environmental suitability to *R. ferrugineus* (179). Injury to palm tissue due to frond and offshoot removal releases volatiles that attract gravid females. Pruning during winter when weevil activity is low can mitigate risks associated with frond removal (41). Sanitation of infested material, by rogueing and destruction of infested palm trunks and fronds via shredding, chipping, or burial, are important management tactics that kill larvae, pupae, and adult weevils (69; <https://gd.eppo.int/taxon/RHYCPA>). Destruction of infested trunk material via shredding is costly. An alternative approach is to cut infested trunk parts into logs and treat with insecticides to kill emerging weevils or adults attracted to cut material (72). Interestingly, diversity and density of palms in ornamental nurseries and frequency of fertilizer and insecticide use affect *R. palmarum* phenotypes, potentially increasing pestiferousness (162).

Biological Control

More than 50 species of natural enemy (viruses, fungi, bacteria, nematodes, predators, and parasitoids) are known to attack *Rhynchophorus* palm weevils; of these, the natural enemy species associated with *R. ferrugineus* in native and invaded ranges are best documented (139, 155). The parasitoids *Billaea menezesi* (Guimarães) and *Billaea rhynchophorae* (Blanchard) (Diptera: Tachinidae: Dexiini) (127, 148, 149) are potentially important natural enemies associated with *R. palmarum*. Parasitism rates of up to 72% have been recorded for *B. menezesi* (148), while year-round parasitism by *B. rhynchophorae* averages 40% (149). In Spain, use of commercially available entomopathogenic nematodes, *Steinernema* sp., alone and in combination with neonicotinoid insecticides (43) and entomopathogenic fungi (44, 90) has demonstrated efficacy against *R. ferrugineus*. However, economically feasible management with natural enemies has not been achieved at a significant scale in the field, and concealed life stages increase the difficulty associated with this approach (10, 139, 155).

Insecticides

Insecticides are widely used to control palm weevils and are applied as sprays or paints to stipes, frond bases, and trunks; as soil and trunk injections; or as soil or crown drenches (42, 63, 124,

142). Insecticides can be applied prophylactically to protect uninfested palms from weevils or used curatively to kill weevils during the early stages of infestation. These procedures need to be carried out with caution and by trained professionals or under technical supervision (69). Overuse of insecticides can result in resistance development and unacceptable residue levels in edible palm crops (56, 102, 197).

Male-Produced Aggregation Pheromones and Mass Trapping

Male-produced aggregation pheromones are known for seven *Rhynchophorus* spp. and are critical components of trapping programs used for detecting, monitoring, and controlling populations of pest weevils, especially *R. ferrugineus* and *R. palmarum* (95, 96, 158, 159, 171). Interestingly, the alcohol and ketone components of the aggregation pheromone are the same for *R. ferrugineus* and *R. vulneratus* (31, 159). However, a minor male-specific compound, 3-methyloctan-4-ol, is produced only by *R. vulneratus* and differentiates this species from *R. ferrugineus* (31).

Aggregation pheromones attract both males and females, but females are attracted at significantly higher rates (102). Traps loaded with pheromone and baited with fermenting fruit are widely used to mass trap adult weevils that threaten date, coconut, and oil palm plantations (63, 96, 159). Windowed bucket traps are commonly used, but retention efficacy is low, approximately 30% (144). In comparison, cone-shaped ground traps are more efficient and retain >90% of weevils attracted to them (144). Olfactometer studies indicate that only 35% of *R. ferrugineus* adults are attracted to the pheromone alone, and attraction declines with mating and increasing weevil age (57). Therefore, pheromones must be combined with other volatile stimuli, like fermenting fruit bait, to enhance attractiveness (82, 143, 159, 196). Esters of ethyl acetate, ethyl propionate blends, acetoin, and ethanol improve captures in food-baited pheromone traps (89, 175, 193).

Trap deployment rates in mass-trapping programs for population-level suppression of *R. ferrugineus* vary from 1 to 10 traps per hectare (66). However, regardless of program efficacy, maintaining trap densities greater than one trap per hectare in date gardens is not sustainable, as costs associated with biweekly servicing to replace food bait and record weevil capture data are not economical. In contrast, *R. palmarum*-RRN in oil palm plantations in Costa Rica can be managed effectively with 1 trap per 5 hectares (159). Smart traps, which exploit the Internet of Things (IoT), make it possible to automate monitoring, and wireless data transmission enables data visualization in near real time using smart devices (14, 164).

Sterile Insect Technique

Work on the sterile insect technique (SIT) for palm weevil control has focused on *R. ferrugineus*. Irradiation doses between 15 and 80 Gy cause a significant drop in sperm quality and egg hatch rates (8, 119, 140). Field application of the SIT against *R. ferrugineus* in India, where seven releases totaling >7,700 sterile *R. ferrugineus* males on an isolated island with a 2-ha coconut plantation, reportedly reduced population densities (119). An estimated ratio of 10 sterile males to 1 wild male was needed to reduce population densities. The expense of this approach dictates use only when weevil populations are low; thus, the SIT could be viable following effective trapping and insecticide treatment programs (119). Sterile *R. ferrugineus* males can be used to vector *Beauveria bassiana* (Balsamo-Crivelli), an entomopathogenic fungus, to weevil-infested palms (125).

Push-Pull and Attract and Kill

Semiochemicals that act as repellents (e.g., tumerone) have been identified that, in combination with attractants, such as aggregation pheromones, could be used to develop push-pull strategies in which repellents push weevils from areas of concern, and baited pheromone traps generate the

pull to lure weevils away from the area of concern. When used in combination, these chemicals provide control (67). Another way to exploit the chemical ecology of palm weevils is through attract and kill techniques, where an inert matrix infused with an aggregation pheromone attracts weevils, and upon interaction with the matrix, they obtain a lethal dose of a contact insecticide (59).

Population Eradication

Eradication of invasive palm weevil populations is possible if, at the time of program inception, populations are small and isolated; sensitive monitoring tools (i.e., pheromones) are available to detect very low-density populations; and there is sustained public, political, and regulatory support for the program. *Rhynchophorus vulneratus*, possibly originating from Bali, Indonesia (173), was detected in California in 2010 and declared eradicated in 2015 (105). Similarly, *R. ferrugineus* has been eradicated from the Canary Islands (62).

Combining Efficacious Management Tactics into Integrated Pest Management Programs

Combining different tactics, such as strict quarantine measures to prevent movement and propagation of infested planting material, good sanitation and orchard management practices, monitoring and early detection of infested palms, trapping, and judicious use of insecticides, forms the core of sustainable palm weevil management programs. Comprehensive management programs need to be applied area wide, and use of geographic information systems-based spatial and temporal maps and databases can assist with implementation, coordination among program participants, and long-term application of control methods (64). Various combinations of these tactics have been integrated to successfully manage *R. palmarum* and *R. ferrugineus* (62, 102, 158, 159, 196).

FUTURE CHALLENGES AND OPPORTUNITIES

Technologies that are accurate, simple to operate, and amenable to automation; have long field durability; and are cheap enough for massive field deployments are needed for early detection of weevil infestations of palms and for population monitoring. Advances in omics and electronic sensing may potentially lead to the development of new tools for early detection. One possibility could be the deployment of arrays of electronic noses or biosensors in the crowns of individual date palms in commercial date gardens that detect species-specific aggregation pheromones. Pheromone detections in GPS-tagged palms reported via IoT could provide expeditious and precise tree-specific information on possible new infestations that could then be managed rapidly. IoT is being similarly applied to weevil monitoring through the use of smart traps, which could be improved with the development of highly attractive dry or bait-less traps. Proactive surveillance programs using new technologies in areas vulnerable to invasion would enable rapid detection and containment, making eradication of incipient populations more likely and control in commercial production areas more efficacious. Identification of additional odorant ligands may help identify new attractants or repellents with potential use as behavioral disruptors.

Classical and “new association” biological control of invasive *Rhynchophorus* weevils with tachinid flies, *Billaea* spp., about which very little is known, deserves significant research attention. Foreign exploration in the hotter, drier interior regions of Bahia State in Brazil may result in the discovery of flies adapted to environmental conditions that typify regions (i.e., the Middle East, Mediterranean, and North Africa) invaded by *R. ferrugineus*, a potential new association host. Similarly, *Billaea* spp. could have use in a classical biological control program targeting *R. palmarum* in California. Phylogenomic analyses, focusing on comprehensive taxon sampling of all species

and relevant populations, are needed to bring a stable classification and natural limits to species and genera of Dryophthorinae. Findings from phylogenomics may result in improved predictions identifying future pest species and natural enemy associations with potential for use in biological control programs targeting pest *Rhynchophorus* species. Additional novel controls for palm weevils may result from ongoing research into the development of RNAi-based biopesticides. Gene editing of commercial and ornamental palm species could produce altered metabolomes and proteomes that increase resistance or tolerance to weevil and RRN infestations or altered volatilomes that make airborne semiochemicals produced by palms less attractive to adult weevils. As palm weevils continue to invade and potentially vector destructive palm pathogenic nematodes into new regions, demand for development and application of new management technologies will increase. Fortunately, significant innovative work, as outlined in this review, is already underway and may be utilized in the near future.

DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

We thank Emmanuelle Jacquin-Joly, Robert Anderson, Stefano Colazza, Óscar Dembilio, and two anonymous reviewers for constructive feedback on an earlier draft of this article. We are indebted to Paul Rugman-Jones for his thorough explanation following reanalysis of web-based molecular data as to why the two *R. ferrugineus* haplotypes, “H8” and “H17,” were misidentified as *R. bilineatus* in Saudi Arabia. Both of these haplotypes, “H8” and “H17,” have been detected previously in Saudi Arabia. We thank Robin Giblin-Davis for insight on the native distribution of *R. cruentatus*. The authors extend their appreciation to the Deanship of Scientific Research, King Saud University, for funding through the Vice Deanship of Scientific Research Chairs and the Chair of Date Palm Research. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the US Department of Agriculture (USDA). The USDA is an equal opportunity employer and provider.

LITERATURE CITED

1. Abbas MK. 2019. The economic impact of red palm weevil *Rhynchophorus ferrugineus* Olivier in Egypt. *Arab J. Plant Prot.* 37:205
2. Abbas MST, Hanounik SB, Shahdad AS, Al-Bagham SA. 2006. Aggregation pheromone traps, a major component of IPM strategy for the red palm weevil, *Rhynchophorus ferrugineus* in date palms (Coleoptera: Curculionidae). *J. Pest Sci.* 79:69–73
3. Abolafia J, Ruiz-Cuenca AN. 2020. Phoretic invertebrates associated with *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Canarian date palm from southern Spain. *J. Nat. Hist.* 54:2265–84
4. Abo-Shnaf RIA, Allam SFM. 2019. A new species of *Centrouropoda* (Acari: Uropodidae: Uropodina), with a key to the world species of the genus. *Zootaxa* 4706:501–16
5. Abraham V, Shuaibi M, Faleiro J, Abozuhaiah R, Vidyasagar PS. 1998. An integrated management approach for red palm weevil *Rhynchophorus ferrugineus* Oliv. a key pest of date palm in the Middle East. *J. Agric. Mar. Sci.* 3:77–83
6. Al-Ayedh H, Rizwan-ul-Haq M, Hussain A, Aljabr AM. 2016. Insecticidal potency of RNAi-based catalase knockdown in *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae). *Pest Manag. Sci.* 72:2118–27

7. Al-Ayedh HY. 2011. Evaluating a semisynthetic diet for rearing the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *Int. J. Trop. Insect Sci.* 31:20–28
8. Al-Ayedh HY, Rasool KG. 2010. Determination of the optimum sterilizing radiation dose for control of the red date palm weevil *Rhynchophorus ferrugineus* Oliv. (Coleoptera: Curculionidae). *Crop Prot.* 29:1377–80
9. Al-Deeb MA, bin Muzaffar S, Abuagla AM, Sharif EM. 2011. Distribution and abundance of phoretic mites (Astigmata, Mesostigmata) on *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *Fla. Entomol.* 94:748–55
10. Al-Dobai S, Elkahky M, Faleiro R, eds. 2019. *Proceedings of the Scientific Consultation and High-Level meeting on Red Palm Weevil Management, March 29–31*. Rome: FAO. <https://www.fao.org/publications/card/en/c/CA1541EN/>
11. Al-Dosary MM, Al-Bekairi AM, Moursy EB. 2010. Morphology of the egg shell and the developing embryo of the red palm weevil, *Rhynchophorus ferrugineus* (Olivier). *Saudi J. Biol. Sci.* 17:177–83
12. Al-Nujiban AA, Aldosari SA, Al Suhaiban AM, Abdel-Azim MM, Ibrahim SMM, et al. 2015. Effect of date palm cultivar on fecundity and development of *Rhynchophorus ferrugineus*. *Bull. Insectol.* 68:199–206
13. Aldawood AS, Rasool KG, Surkino S, Husain M, Sutanto KD, Alduailij MA. 2022. Semi-artificial diet developed for successful rearing of red palm weevil: *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) in the laboratory. *J. King Saud Univ. Sci.* 34:102272
14. Aldhryhim YN, Al-Ayedh HY. 2015. Diel flight activity patterns of the red palm weevil (Coleoptera: Curculionidae) as monitored by smart traps. *Fla. Entomol.* 98:1019–24
15. Ali H-M, Hou Y. 2018. Absence of *Wolbachia* in red palm weevil, *Rhynchophorus ferrugineus* Olivier (Coleoptera: Curculionidae): a PCR-based approach. *Appl. Ecol. Environ. Res.* 16:1819–33
16. AlJabr AM, Hussain A, Rizwan-ul-Haq M, Al-Ayedh H. 2017. Toxicity of plant secondary metabolites modulating detoxification genes expression for natural red palm weevil pesticide development. *Molecules* 22:169
17. Amobi MI, Ebenebe CI. 2018. Performance of broiler chicks fed on two insect based-diets in South East Nigeria. *J. Insect Food Feed* 4:263–68
18. Anbutso H, Moriyama M, Nikoh N, Hosokawa T, Futahashi R, et al. 2017. Small genome symbiont underlies cuticle hardness in beetles. *PNAS* 114:E8382–91
19. Anderson RS. 2002. The Dryophthoridae of Costa Rica and Panama: checklist with keys, new synonymy and descriptions of new species of *Cactophagus*, *Mesocordylus*, *Metamasius* and *Rhodobaenus* (Coleoptera; Curculionoidea). *Zootaxa* 80:1–94
20. Anderson WH. 1948. Larvae of some genera of Calendrinae (= Rhynchoporinae) and Stromboscerinae (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 51:413–37
21. Antony B, Johny J, Abdelazim MM, Jakše J, Al-Saleh MA, Pain A. 2019. Global transcriptome profiling and functional analysis reveal that tissue-specific constitutive overexpression of cytochrome P450s confers tolerance to imidacloprid in palm weevils in date palm fields. *BMC Genom.* 20:440
22. Antony B, Johny J, Aldosari SA. 2018. Silencing the odorant binding protein RferOBP1768 reduces the strong preference of palm weevil for the major aggregation pheromone compound ferrugineol. *Front. Physiol.* 9:252
23. Antony B, Johny J, Aldosari S, Abdelazim MM. 2017. Identification and expression profiling of novel plant cell wall degrading enzymes from a destructive pest of palm trees, *Rhynchophorus ferrugineus*. *Insect Mol. Biol.* 26:469–84
24. Antony B, Johny J, Montagné N, Jacquín-Joly E, Capoduro R, et al. 2021. Pheromone receptor of the globally invasive quarantine pest of the palm tree, the red palm weevil (*Rhynchophorus ferrugineus*). *Mol. Ecol.* 30:2025–39
25. Antony B, Soffan A, Jakše J, Abdelazim MM, Aldosar SA, et al. 2016. Identification of the genes involved in odorant reception and detection in the palm weevil *Rhynchophorus ferrugineus*, an important quarantine pest, by antennal transcriptome analysis. *BMC Genom.* 17:9
26. Ashry I, Mao Y, Al-Fehaid Y, Al-Shawaf A, Al-Bagshi M, et al. 2020. Early detection of red palm weevil using distributed optical sensor. *Sci. Rep.* 10:31–55

27. Ávalos JA, Balasch S, Soto A. 2016. Flight behavior and dispersal of *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) adults using mark-recapture-recapture method. *Bull. Entomol. Res.* 106:606–14
28. Ávalos JA, Martí-Campoy A, Soto A. 2014. Study of the flying ability of *Rhynchophorus ferrugineus* (Coleoptera: Dryophthoridae) adults using a computer-monitored flight mill. *Bull. Entomol. Res.* 104:462–70
29. Awad M, Sharaf A, Elrahman TA, El-Saadany HM, ElKraly OA, Elnagdy SM. 2021. The first report for the presence of *Spiroplasma* and *Rickettsia* in red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Egypt. *Acta Parasitol.* 66:593–604
30. Baldwin IT, Halitschke R, Paschold A, Von Dahl CC, Preston CA. 2006. Volatile signaling in plant-plant interactions: “talking trees” in the genomics era. *Science* 311:812–15
31. Bandeira PT, Fávaro CF, Francke W, Bergmann J, Zarbin PHG. 2021. Aggregation pheromones of weevils (Coleoptera: Curculionidae): advances in the identification and potential uses in semiochemical-based pest management strategies. *J. Chem. Ecol.* 47:968–86
32. Barkan S, Hoffman A, Hezroni A, Soroker V. 2018. Flight performance and dispersal potential of red palm weevil estimated by repeat flights on flight mill. *J. Insect Behav.* 31:66–82
33. Bombi P. 2020. Potential conflict extent between two invasive alien pests, *Rhynchophorus ferrugineus* and *Paysandisia archon*, and the native populations of the Mediterranean fan palm. *J. Nat. Conserv.* 58:125927
34. Chamorro ML. 2019. An illustrated synoptic key and comparative morphology of the larvae of Dryophthorinae (Coleoptera, Curculionidae) genera with emphasis on the mouthparts. *Diversity* 11:4
35. Chamorro ML, de Medeiros BAS, Farrell BD. 2021. First phylogenetic analysis of Dryophthorinae (Coleoptera, Curculionidae) based on structural alignment of ribosomal DNA reveals Cenozoic diversification. *Ecol. Evol.* 11:1984–98
36. Chong J, H'Ng T, Azmi WA, Amansuria NH. 2015. Genetic variation and invasion history of the invasive red palm weevil (*Rhynchophorus ferrugineus* (Olivier)) in Terengganu. *Int. J. Agric. For. Plant* 1:34–43
37. Cotton RT. 1924. A contribution toward the classification of the weevil larvae of the subfamily Calendrinae, occurring in North America. *Proc. U. S. Natl. Mus.* 66:1–11
38. Cysne AQ, Cruz BA, da Cunha RNV, da Rocha RNC. 2013. Flutuação populacional de *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae) em palmeiras oleíferas no Amazonas. *Acta Amaz.* 43:197–202
39. Davis SR, Engel MS. 2006. Dryophthorine weevils in Dominican amber (Coleoptera: Curculionidae). *Trans. Kans. Acad. Sci.* 109:191–98
40. De Luca F, Fanelli E, Oreste M, Scarcia G, Troccoli A, et al. 2019. Molecular profiling of nematode associates with *Rhynchophorus ferrugineus* in southern Italy. *Ecol. Evol.* 9:14286–94
41. Dembilio Ó, Jacas JA. 2011. Basic bioecological parameters of the invasive red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), in *Phoenix canariensis* under Mediterranean climate. *Bull. Entomol. Res.* 101:153–63
42. Dembilio Ó, Jacas JA. 2012. Bio-ecology and integrated management of the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), in the region of Valencia (Spain). *Hell. Plant Prot. J.* 5:1–12
43. Dembilio Ó, Llacer E, del Mar Martínez de Altube M, Jacas JA. 2009. Field efficacy of imidacloprid and *Steinernema carpocapsae* in a chitosan formulation against red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in *Phoenix canariensis*. *Pest Manag. Sci.* 66:365–70
44. Dembilio Ó, Quesada-Moraga E, Santiago-Alvarez C, Jacas JA. 2010. Biocontrol potential of an indigenous strain of the entomopathogenic fungus *Beauveria bassiana* (Ascomycota; Hypocreales) against the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *J. Invertebr. Pathol.* 104:214–21
45. Dembilio Ó, Tapia GV, Téllez MM, Jacas JA. 2012. Lower temperature thresholds for oviposition and egg hatching of the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), in a Mediterranean climate. *Bull. Entomol. Res.* 102:97–102
46. Dias GB, Altammami MA, El-Shafie HA, Alhoshan FM, Al-Fageeh MB, et al. 2021. Haplotype-resolved genome assembly enables gene discovery in the red palm weevil *Rhynchophorus ferrugineus*. *Sci. Rep.* 11:9987

47. Diboun I, Mathew S, Al-Rayyashi M, Elrayess M, Torres M, et al. 2015. Metabolomics of dates (*Phoenix dactylifera*) reveals a highly dynamic ripening process accounting for major variation in fruit composition. *BMC Plant Biol.* 15:291
48. Dilipkumar M, Ahadiyat A, Maşan P, Chuah TS. 2015. Mites (Acari) associated with *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Malaysia, with a revised list of mites found on this weevil. *J. Asia-Pac. Entomol.* 18:169–74
49. Dionisio LFS, Lima ACS, de Moraes EGF, Faria PRS, Correia RG, et al. 2020. Distribuição espacial de *Rhynchophorus palmarum* L. (Coleoptera: Curculionidae) em palma de óleo em Roraima, Brasil. *Rev. Bras. Cienc. Agrar.* 15:e5683
50. El-Faki MS, El-Shafie HAF, Al-Hajhoj MBR. 2016. Potentials for early detection of red palm weevil (Coleoptera: Curculionidae) infested date palm (Arecaceae) using temperature differentials. *Can. Entomol.* 148:239–45
51. El-Mergawy RAAM, Al Ajlan AM, Abdalla N, Nasr MI, Silvain J-F. 2011. Determination of different geographical populations of *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae) using RAPD-PCR. *Int. J. Agric. Biol.* 13:227–32
52. El-Mergawy RAAM, Al Ajlan AM, Abdalla N, Nasr MI, Silvain JF. 2011. Genetic comparison among *Rhynchophorus ferrugineus* and four *Rhynchophorus* species. *J. Agric. Sci. Technol. B1* 2011:610–15
53. El-Mergawy RAAM, Al Ajlan AM, Abdalla N, Vassiliou V, Capdevielle-Dulac C, et al. 2011. Preliminary study on geographical variation of cytochrome b gene and ITS2-rDNA among populations of *Rhynchophorus ferrugineus*. *J. Agric. Sci. Technol. B1* 2011:189–97
54. El-Mergawy RAAM, Faure N, Nasr MI, Avand-Faghieh A, Rochat D, et al. 2011. Mitochondrial genetic variation and invasion history of red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), in Middle-East and Mediterranean Basin. *Int. J. Agric. Biol.* 13:631–37
55. El-Sabea AMR, Faleiro JR, Abo-El-Saad MM. 2009. The threat of the red palm weevil *Rhynchophorus ferrugineus* to date plantations of the Gulf Region in the Middle-East: an economic perspective. *Outlooks Pest Manag.* 20:131–34
56. El-Saeid MH, Al-Dosari SA. 2010. Monitoring of pesticide residues in Riyadh dates by SFE, MSE, SFC, and GC techniques. *Arab. J. Chem.* 3:179–86
57. El-Shafie HAF, Faleiro JR. 2017. Optimizing components of pheromone-baited trap for the management of red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in date palm agroecosystem. *J. Plant Dis. Prot.* 124:279–87
58. El-Shafie HAF, Faleiro JR, Abo-El-Saad MM, Aleid SM. 2013. A meridic diet for laboratory rearing of red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *Sci. Res. Essays* 8:1924–32
59. El-Shafie HAF, Faleiro JR, Al-Abbad AH, Stoltman L, Mafra-Neto A. 2011. Bait-free attract and kill technology (Hook™ RPW) to suppress red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in date palm. *Fla. Entomol.* 94:774–78
60. El-Sharabasy HM. 2010. A survey of mite species associated with the red palm weevil, *Rhynchophorus ferrugineus*, in Egypt. *J. Biol. Pest Control* 20:67–70
61. Engsontia P, Satasook C. 2021. Genome-wide identification of the gustatory receptor gene family of the invasive pest, red palm weevil, *Rhynchophorus ferrugineus* (Olivier, 1790). *Insects* 12:611
62. Fajardo M. 2019. The Canary Island success story in eradicating red palm weevil. See Reference 10, pp. 116–25
63. Faleiro JR. 2006. A review of the issues and management of the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Rhynchophoridae) in coconut and date palm during the last one hundred years. *Int. J. Trop. Insect Sci.* 26:135–54
64. Faleiro JR. 2019. Advances in semiochemical mediated technologies against red palm weevil. See Reference 10, pp. 164–75
65. Faleiro JR, Ben Abdallah A, Ashok Kumar J, Shagagh A, Al-Abdan S. 2010. Sequential sampling plan for area-wide management of red palm weevil, *Rhynchophorus ferrugineus* (Olivier) in date plantations of Saudi Arabia. *Int. J. Trop. Insect Sci.* 30:145–53
66. Faleiro JR, El-Saad MA, Abdul Hadi AH. 2011. Pheromone trap density to mass trap *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae/Rhynchophoridae/Dryophthoridae) in date plantations of Saudi Arabia. *Int. J. Trop. Insect Sci.* 31:75–77

67. Faleiro JR, El-Shafie HAF, Oehlschlager AC, Aleid SMA, Mahajan GR. 2022. Field evaluation of repellents against red palm weevil *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae) through trap shutdown studies. *J. Plant Dis. Prot.* 129:791–804
68. Fanini L, Longo S, Cervo R, Roversi PF, Mazza G. 2014. Daily activity and non-random occurrence of captures in the Asian palm weevils. *Ethol. Ecol. Evol.* 26:195–203
69. FAO. 2020. *Red Palm Weevil: Guidelines on Management Practices*. Rome: FAO. <https://www.fao.org/documents/card/en/c/ca7703en>
70. Farag MA, Mohsen M, Heinke R, Wessjohann LA. 2014. Metabolomic fingerprints of 21 date palm fruit varieties from Egypt using UPLC/PDA/ESI-qTOF-MS and GC-MS analyzed by chemometrics. *Food Res. Int.* 64:218–26
71. Farahani VRF, Ahadiyat A, Mašan P, Dehvari MA. 2016. Phoretic uropodine mites (Acari: Mesostigmata) associated with the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Iran. *J. Entomol. Acarol. Res.* 48:5853
72. Ferry M. 2019. Recent advances in insecticide treatments against the red palm weevil. See Reference 10, pp. 127–41
73. Fiaboe KKM, Peterson AT, Kairo MTK, Roda AL. 2012. Predicting the potential worldwide distribution of the red palm weevil *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae) using ecological niche modeling. *Fla. Entomol.* 95:659–73
74. Flowers JM, Hazzouri KM, Lemansour A, Capote T, Gros-Balthazard M, et al. 2022. Patterns of volatile diversity yield insights into the genetics and biochemistry of the date palm fruit volatilome. *Front. Plant Sci.* 13:853651
75. Fouda M, Tufail M, Takeda M, Mahmoud SH. 2022. DNA barcoding and population genetic structure of the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) in Egypt based on mtDNA sequencing. *Biologia* 77:1017–25
76. Francardi V, Benvenuti C. 2010. Artificial diets for the rearing of *Rhynchophorus ferrugineus* Olivier. *Redia* 93:83–88
77. García-Hernández JL, Beltrán-Morales LF, Loya-Ramírez JG, Morales-Cota JR, Troyo-Diéguez E, Beltrán-Morales FA. 2003. Primer informe del *Rhynchophorus palmarum* (Coleoptera: Dryophthoridae) en Baja California Sur. *Fol. Entomol. Mex.* 42:415–17
78. Ge X, He S, Wang T, Yan W, Zong S. 2015. Potential distribution predicted for *Rhynchophorus ferrugineus* in China under different warming scenarios. *PLOS ONE* 10:e0141111
79. Giblin-Davis RM, Faleiro JR, Jacas JA, Peña JE, Vidyasagar PSPV. 2013. Biology and management of the red palm weevil, *Rhynchophorus ferrugineus*. In *Potential Invasive Pests of Agricultural Crops*, ed. JE Peña, pp. 1–34. Wallingford, UK: CAB Int.
80. Giblin-Davis RM, Gerber K, Griffith R. 1989. Laboratory rearing of *Rhynchophorus cruentatus* and *R. palmarum* (Coleoptera: Curculionidae). *Fla. Entomol.* 72:480–88
81. Giblin-Davis RM, Kanzaki N, Davies KA. 2013. Nematodes that ride insects: unforeseen consequences of arriving species. *Fla. Entomol.* 96:770–80
82. Giblin-Davis RM, Oehlschlager AC, Perez A, Gries G, Gries R, et al. 1996. Chemical and behavioral ecology of palm weevils (Curculionidae: Rhynchophorinae). *Fla. Entomol.* 79:153–67
83. Giovino A, Bertolini E, Fileccia V, Al Hassan M, Labra M, et al. 2015. Transcriptome analysis of *Phoenix canariensis* Chabaud in response to *Rhynchophorus ferrugineus* Olivier attacks. *Front. Plant Sci.* 6:817
84. Giovino A, Martinelli F, Saia S. 2016. *Rhynchophorus ferrugineus* attack affects a group of compounds rather than rearranging *Phoenix canariensis* metabolic pathways. *J. Integr. Plant Biol.* 58:388–96
85. Goldshtein E, Cohen Y, Hetzroni A, Cohen Y, Soroker V. 2020. The spatiotemporal dynamics and range expansion of the red palm weevil in Israel. *J. Pest Sci.* 93:691–702
86. Gómez-Marco F, Klompen H, Hoddle MS. 2021. Phoretic mite infestations associated with *Rhynchophorus palmarum* (Coleoptera: Curculionidae) in southern California. *Syst. Appl. Acarol.* 26:1913–26
87. Griffith R. 1968. The mechanism of transmission of the red ring nematode. *J. Agric. Soc. Trinidad Tobago* 67:436–57
88. Griffith R. 1987. Red ring disease of coconut palm. *Plant Dis.* 71:193–96

89. Guarino S, Peri E, Bue PL, Germanà MP, Colazza S, et al. 2013. Assessment of synthetic chemicals for disruption of *Rhynchophorus ferrugineus* response to attractant baited traps in an urban environment. *Phytoparasitica* 41:79–88
90. Güerri-Agulló B, López-Follana R, Asensio L, Barranco P, Lopez-Llorca LV. 2011. Use of a solid formulation of *Beauveria bassiana* for biocontrol of the red palm weevil (*Rhynchophorus ferrugineus*) (Coleoptera: Dryophthoridae) under field conditions in SE Spain. *Fla. Entomol.* 94:737–47
91. Gunter NL, Oberprieler RG, Cameron SL. 2016. Molecular phylogenetics of Australian weevils (Coleoptera: Curculionoidea): exploring relationships in a hyperdiverse lineage through comparison of independent analyses. *Austral Entomol.* 55:217–33
92. Habineza P, Muhammad A, Ji T, Xiao R, Yin X, et al. 2019. The promoting effect of gut microbiota on growth and development of red palm weevil, *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Dryophthoridae) by modulating its nutritional metabolism. *Front. Microbiol.* 10:1212
93. Hagley EAC. 1965. On the life history and habits of the palm weevil, *Rhynchophorus palmarum*. *Ann. Entomol. Soc. Am.* 58:22–28
94. Hallett RH, Crespi BJ, Borden JH. 2004. Synonymy of *Rhynchophorus ferrugineus* (Olivier), 1790 and *R. vulneratus* (Panzer), 1798 (Coleoptera, Curculionidae, Rhynchophorinae). *J. Nat. Hist.* 38:2863–82
95. Hallett RH, Gries G, Gries R, Borden JH, Czyzewska E, et al. 1993. Aggregation pheromones of two Asian palm weevils, *Rhynchophorus ferrugineus* and *R. vulneratus*. *Naturwissenschaften* 80:328–31
96. Hallett RH, Oehlschlager AC, Borden JH. 1999. Pheromone trapping protocols for the Asian palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *Int. J. Pest Manag.* 45:231–37
97. Harith-Fadzilah N, Lam SD, Haris-Hussain M, Ghani IA, Zainal Z, et al. 2021. Proteomics and interspecies interaction analysis revealed abscisic acid signaling to be the primary driver for oil palm's response against red palm weevil infestation. *Plants* 10:2574
98. Hassan MF, Nasr AK, Allam SF, Taha HA, Mahmoud RA. 2011. Biodiversity and seasonal fluctuation of mite families associated with the red palm weevil, *Rhynchophorus ferrugineus* Oliver (Coleoptera: Curculionidae) in Egypt. *Egypt. J. Biol. Pest Cont.* 21:317–23
99. Hazzouri KM, Sudalaimuthuasari N, Kundu B, Nelson D, Al-Deeb MA, et al. 2020. The genome of pest *Rhynchophorus ferrugineus* reveals gene families important at the plant-beetle interface. *Commun. Biol.* 3:323
100. Herbst JFW. 1795. *Natursystem aller bekannten in- und ausländischen Insekten, als eine Fortsetzung der von Buffonschen Naturgeschichte*. Berlin: J. Pauli
101. Hoddle MS. 2015. Red palm weevils—food or foe? *Palms* 59:21–30
102. Hoddle MS, Al-Abbad AH, El-Shafie HAF, Faleiro JR, Sallam AA, et al. 2013. Assessing the impact of area-wide pheromone trapping, pesticide applications, and eradication of infested date palms for *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) management in Al Ghowaybah, Saudi Arabia. *Crop Prot.* 53:152–60
103. Hoddle MS, Hoddle CD. 2016. How far can the palm weevil, *Rhynchophorus vulneratus* (Coleoptera: Curculionidae), fly? *J. Econ. Entomol.* 109:629–36
104. Hoddle MS, Hoddle CD. 2017. Palmageddon: The invasion of California by the South American palm weevil is underway. *CAPCA Advis.* 20:40–44
105. Hoddle MS, Hoddle CD, Alzubaidy M, Kabashima J, Nisson JN, et al. 2016. The palm weevil *Rhynchophorus vulneratus* is eradicated from Laguna Beach. *Cal. Agric.* 71:23–29
106. Hoddle MS, Hoddle CD, Faleiro JR, El-Shafie HAF, Jeske DR, Sallam AA. 2015. How far can the red palm weevil (Coleoptera: Curculionidae) fly? Computerized flight mill studies with field-captured weevils. *J. Econ. Entomol.* 108:2599–609
107. Hoddle MS, Hoddle CD, Milosavljević I. 2020. How far can *Rhynchophorus palmarum* (Coleoptera: Curculionidae) fly? *J. Econ. Entomol.* 113:1786–95
108. Hoddle MS, Hoddle CD, Milosavljević I. 2021. Quantification of the life time flight capabilities of the South American palm weevil, *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae). *Insects* 12:126
109. Hoddle MS, Johansen G, Kast E, Lopez AM, Shaw MM. 2021. Four new palm species records for *Rhynchophorus palmarum* (Coleoptera: Curculionidae) in California. *Fla. Entomol.* 104:143–44

110. Hunsberger AGB, Giblin-Davis RM, Weissling TJ. 2000. Symptoms and population dynamics of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae) in Canary Island date palms. *Fla. Entomol.* 83:290–303
111. Inghilesi AF, Mazza G, Cervo R, Cini A. 2015. A network of sex and competition: the promiscuous mating system of an invasive weevil. *Curr. Zool.* 61:85–97
112. Ji T, Xu Z, Jia Q, Wang G, Hou Y. 2021. Non-palm plant volatile alpha-pinene is detected by antenna-biased expressed odorant receptor 6 in the *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae). *Front. Physiol.* 12:701545
113. Jia S, Zhang X, Zhang G, Yin A, Zhang S, et al. 2013. Seasonally variable intestinal metagenomes of the red palm weevil (*Rhynchophorus ferrugineus*). *Environ. Microbiol.* 15:3020–29
114. Ju R-T, Wang F, Wan F-H, Li B. 2011. Effects of host plants on development and reproduction of *Rhynchophorus ferrugineus* (Olivier) (Coleoptera: Curculionidae). *J. Pest Sci.* 84:33–39
115. Kaakeh W. 2005. Longevity, fecundity, and fertility of the red palm weevil, *Rhynchophorus ferrugineus* Olivier (Coleoptera: Curculionidae) on natural and artificial diets. *Emir. J. Agric. Sci.* 17:23–33
116. Kanzaki N. 2016. Pine wilt and red ring, lethal plant diseases caused by insect-mediated *Bursaphelenchus* nematodes. In *Vector Mediated Transmission of Plant Pathogens*, ed. JK Brown, pp. 87–107. St. Paul, MN: Am. Phytopathol. Soc.
117. Kontschán J, Mazza G, Nannelli R, Roversi PF. 2014. The true identity of the red palm weevil associated Uropodina mite, *Centrouropoda almerodai* Hiramatsu and Hirschmann, 1992. *Redia* 97:83–88
118. Kontschán J, Tambe JT, Riolo P. 2012. *Uroobovella phoenicicola* sp. n. a new Uropodina mite (Acari: Megostigmata) associated with the African palm weevil (*Rhynchophorus phoenicis* Fabricius, 1801) from Cameroon. *Afr. Invertebr.* 53:593–600
119. Krishnakumar R, Maheshwari P. 2007. Assessment of the sterile insect technique to manage red palm weevil *Rhynchophorus ferrugineus* in coconut. In *Area-Wide Control of Insect Pests from Research to Field Implementation*, ed. MJB Vreysen, AS Robinson, J Hendrichs, pp. 475–85. Berlin: Springer
120. Kuschel G. 1995. A phylogenetic classification of the Curculionoidea to Families and Subfamilies. *Mem. Entomol. Soc. Wash.* 14:5–33
121. León-Qunito T, Serna A. 2022. Cryoprotective response as part of the adaptive strategy of the red palm weevil, *Rhynchophorus ferrugineus*, against low temperatures. *Insects* 13:134
122. Li L, Qin W-Q, Ma Z-L, Yan W, Huang S-C, et al. 2010. Effect of temperature on the population growth of *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) on sugarcane. *Environ. Entomol.* 39:999–1003
123. Linnaeus C. 1758. *Systema Naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis. Tomus I. Edition decima, reformata*. Stockholm: Laurentii Salvii
124. Llácer E, Dembilio Ó, Jacas JA. 2010. Evaluation of the efficacy of an insecticidal paint based on chlorpyrifos and pyriproxyfen in a micro encapsulated formulation against *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *J. Econ. Entomol.* 103:402–8
125. Llácer E, Santiago-Álvarez C, Jacas JA. 2013. Could sterile males be used to vector a microbiological control agent? The case of *Rhynchophorus ferrugineus* and *Beauveria bassiana*. *Bull. Entomol. Res.* 103:241–50
126. Lo Verde G, Fileccia V, Lo Bue P, Peri E, Colazza S, Martinelli F. 2019. Members of the WRKY gene family are upregulated in canary palms attacked by red palm weevil. *Arthropod-Plant Interact.* 13:109–16
127. Löhr B, Negrisoni A, Molina JP. 2019. *Billaea rhynchophorae*, a palm weevil parasitoid with global potential. *Arab. J. Plant Prot.* 37:101–8
128. Löhr B, Vásquez-Ordóñez AA, Becerra Lopez-Lavalle LA. 2015. *Rhynchophorus palmarum* in disguise: undescribed polymorphism in the “black” palm weevil. *PLOS ONE* 10:e0143210
129. Lokela JCM, Le Gof GJ, Kayisu K, Hance T. 2021. Phoretic mites associated with *Rhynchophorus phoenicis* Fabricius (1880) (Coleoptera: Curculionidae) in the Kisangani region, D.R. Congo. *Acarologia* 61:291–96
130. Mankin RW. 2011. Recent developments in the use of acoustic sensors and signal processing tools to target early infestations of red palm weevil in agricultural environments. *Fla. Entomol.* 94:761–65
131. Manzoor M, Ahmad JN, Ahmad SJN, Naqvi SA, ud-din Umar U, et al. 2020. Population dynamics, abundance, and infestation of the red palm weevil, *Rhynchophorus ferrugineus* (Olivier) in different geographical regions of date palm in Pakistan. *Pak. J. Agric. Sci.* 57:381–91

132. Manzoor M, Yang L, Wu S, El-Shafie H, Haider MS, et al. 2022. Feeding preference of *Rhynchophorus ferrugineus* (Oliver) (Coleoptera: Curculionidae) on different date palm cultivars and host biochemical responses to its infestation. *Bull. Entomol. Res.* 112:494–501
133. Marvaldi AE. 1997. Higher level phylogeny of Curculionidae (Coleoptera: Curculionoidea) based mainly on larval characters, with special reference to broad-nosed weevils. *Cladistics* 13:285–312
134. Marvaldi AE, Duckett CN, Kjer KM, Gillespie JJ. 2009. Structural alignment of 18S and 28S rDNA sequences provides insights into phylogeny of Phytophaga (Coleoptera: Curculionoidea and Chrysomeloidea). *Zool. Scr.* 38:63–77
135. Marvaldi AE, Morrone JJ. 2000. Phylogenetic systematics of weevils (Coleoptera: Curculionoidea): a reappraisal based on larval and adult morphology. *Insect Syst. Evol.* 31:43–58
136. Marvaldi AE, Sequeira AS, O'Brien CW, Farrell BD. 2002. Molecular and morphological phylogenetics of weevils (Coleoptera, Curculionoidea): Do niche shifts accompany diversification? *Syst. Biol.* 51:761–85
137. May BM. 1993. *Larvae of Curculionoidea (Insecta: Coleoptera): A Systematic Overview*. Fauna N. Z.—Ko te Aitanga Pepeke o Aotearoa 28. Lincoln/Canterbury, N. Z.: Manaaki Whenua
138. Mazza G, Cini A, Cervo R, Longo S. 2011. Just phoresy? Reduced lifespan in red palm weevils *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae) infested by the mite *Centrouropoda almerodai* (Uroactiniinae: Uropodina). *Ital. J. Zool.* 78:101–5
139. Mazza G, Francardi V, Simoni S, Benvenuti C, Cervo R, et al. 2014. An overview on the natural enemies of *Rhynchophorus* palm weevils, with focus on *R. ferrugineus*. *Biol. Control* 77:83–92
140. Mazza G, Inghilesi AF, Stasolla G, Cini A, Cervo R, et al. 2016. Sterile *Rhynchophorus ferrugineus* males efficiently impair reproduction while maintaining their sexual competitiveness in a social context. *J. Pest Sci.* 89:459–68
141. McKenna DD, Sequeira AS, Marvaldi AE, Farrell BD. 2009. Temporal lags and overlap in the diversification of weevils and flowering plants. *PNAS* 106:7083–88
142. Milosavljević I, El-Shafie HAF, Faleiro JR, Hoddle CD, Lewis M, Hoddle MS. 2018. Palmageddon: the wasting of ornamental palms by invasive palm weevils, *Rhynchophorus* spp. *J. Pest Sci.* 92:143–56
143. Milosavljević I, Hoddle CD, Mafra-Neto A, Gómez-Marco F, Hoddle MS. 2020. Effects of food bait and trap type on captures of *Rhynchophorus palmarum* (Coleoptera: Curculionidae) and trap bycatch in southern California. *J. Econ. Entomol.* 113:2407–17
144. Milosavljević I, Hoddle CD, Mafra-Neto A, Gómez-Marco F, Hoddle MS. 2020. Use of digital video cameras to determine the efficacy of two trap types for capturing *Rhynchophorus palmarum* (Coleoptera: Curculionidae). *J. Econ. Entomol.* 113:3028–31
145. Montagna M, Chouaia B, Mazza G, Prosdocimi EM, Crotti E, et al. 2015. Effects of the diet on the microbiota of the red palm weevil (Coleoptera: Dryophthoridae). *PLOS ONE* 10:e0117439
146. Montiel EE, Mora P, Rico-Porras JM, Palomeque T, Lorite P. 2022. Satellitome of the red palm weevil, *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae), the most diverse among insects. *Front. Ecol. Evol.* 10:826808
147. Morera-Margarit P, Pope TW, Mitchell C, Karley AJ. 2021. Could bacterial associations determine the success of weevil species? *Ann. Appl. Biol.* 178:51–61
148. Moura JIL, Mauriau D, Delabie JHC. 1993. Eficiência de *Paratheresia menezesi* Townsend (Diptera: Tachidae) no controle biológico natural de *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae). *Oléagineux* 48:219–23
149. Moura JIL, Toma R, Sgrillo RB, Delabie JHC. 2006. Natural efficiency of parasitism by *Billaea rhynchophorae* (Blanchard) (Diptera: Tachinidae) for the control of *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae). *Neotrop. Entomol.* 35:273–74
150. Muafor FJ, Gnetegha AA, Le Gall P, Levang P. 2015. *Exploitation, trade and farming of palm weevil grubs in Cameroon*. Work. Pap 178, Cent. Int. For. Res., Bogor, Indones. <http://www.jstor.org/stable/resrep02387.1>
151. Mugu S, Pistone D, Jordal BH. 2018. New molecular markers resolve the phylogenetic position of the enigmatic wood-boring weevils Platypodinae (Coleoptera: Curculionidae). *Arthropod Syst. Phylogeny* 76:45–58

152. Muhammad A, Fang Y, Hou Y, Shi Z. 2017. The gut entomotype of red palm weevil *Rhynchophorus ferrugineus* Olivier (Coleoptera: Dryophthoridae) and their effect on host nutrition metabolism. *Front. Microbiol.* 8:2291
153. Muhammad A, Habineza P, Ji T, Hou Y, Shi Z. 2019. Intestinal microbiota confer protection by priming the immune system of red palm weevil *Rhynchophorus ferrugineus* Olivier (Coleoptera: Dryophthoridae). *Front. Physiol.* 10:1303
154. Muhammad A, Habineza P, Wang X, Xiao R, Ji T, et al. 2020. Spätzle homolog-mediated toll-like pathway regulates innate immune responses to maintain the homeostasis of gut microbiota in the red palm weevil, *Rhynchophorus ferrugineus* Olivier (Coleoptera: Dryophthoridae). *Front. Microbiol.* 11:846
155. Murphy ST, Briscoe BR. 1999. The red palm weevil as an alien invasive: biology and prospects for biological control as a component of IPM. *Biocontrol News Inf.* 20:35N–46N
156. Nakash J, Osam Y, Kehat M. 2000. A suggestion to use dogs for detecting red palm weevil (*Rhynchophorus ferrugineus*) infestation in date palm in Israel. *Phytoparasitica* 28:153–54
157. Oberprieler RG, Jennings D. 2016. *Specialist diagnostic guide to pest weevils—Rhynchophorus palm weevils*. Rep., CSIRO Natl. Res. Coll. Aust., Canberra
158. Oehlschlager AC. 2005. Current status of trapping palm weevils and beetles. *Planter* 81:123–43
159. Oehlschlager AC. 2016. Palm weevil pheromones—discovery and use. *J. Chem. Ecol.* 42:617–30
160. O'Meara B. 2001. *Bacterial symbiosis and plant host use evolution in Dryophthorinae (Coleoptera, Curculionidae): a phylogenetic study using parsimony and Bayesian analysis*. Honors thesis, Harvard Univ., Cambridge, MA
161. Ovando-Cruz ME, Serrano-Altamirano V, Gálvez-Marroquin LA, Ariza-Flores R, Martínez-Bolaños M, et al. 2019. Evaluación de trampas para *Rhynchophorus palmarum* L. (Coleoptera: Curculionidae) en la costa de Oaxaca, México. *Agro Prod.* 12:3–8
162. Ponce-Méndez M, García-Martínez MA, Serna-Lagunes R, Lasa-Covarrubias R, Presa-Para E, et al. 2022. Local agricultural management filters morphological traits of the South American palm weevil (*Rhynchophorus palmarum* L.; Coleoptera: Curculionidae) in ornamental palm plantations. *Agronomy* 12:2371
163. Porcelli F, Ragusa E, D'Onghia AM, Mizzi S, Mifsud D. 2009. Occurrence of *Centrouropoda almerodai* and *Urobovella marginata* (Acari: Uropodina) phoretic on the red palm weevil in Malta. *Bull. Entomol. Soc. Malta* 2:61–66
164. Potamitis I, Eliopoulos P, Rigakis I. 2017. Automated remote insect surveillance at a global scale and the internet of things. *Robotics* 6:19
165. Pugliese M, Rettori AA, Martinis R, Al-Rohily K, Al-Maashi A. 2018. Devices to detect red palm weevil infestation on palm species. *Precis. Agric.* 19:1049–61
166. Rasool KG, Khan MA, Aldawood AS, Tufail M, Mukhtar M, et al. 2015. Identification of proteins modulated in the date palm stem infested with red palm weevil (*Rhynchophorus ferrugineus* Oliv.) using two dimensional differential gel electrophoresis and mass spectrometry. *Int. J. Mol. Sci.* 16:19326–46
167. Rasool KG, Khan MA, Tufail M, Husain M, Mehmood K, et al. 2018. Differential proteomic analysis of date palm leaves infested with the red palm weevil (Coleoptera: Curculionidae). *Fla. Entomol.* 101:290–98
168. Rasool KG, Mehmood K, Husain M, Tufail M, Alwaneen WS, et al. 2021. De novo transcriptome analysis and identification of reproduction control genes from the red palm weevil *Rhynchophorus ferrugineus*. *PLOS ONE* 16:e0251278
169. Rasool KG, Mehmood K, Tufail M, Husain M, Alwaneen WS, et al. 2021. Silencing of vitellogenin gene contributes to the promise of controlling red palm weevil, *Rhynchophorus ferrugineus* (Olivier). *Sci. Rep.* 11:21695
170. Rigakis I, Potamitis I, Tatlas N-A, Potirakis SM, Ntalampiras S. 2021. TreeVibes: modern tools for global monitoring of trees for borers. *Smart Cities* 4:271–85
171. Rochat D, Gonzalez AV, Mariau D, Villanueva AG, Zagatti P. 1991. Evidence for male-produced aggregation pheromone in American palm weevil, *Rhynchophorus palmarum* (L.) (Coleoptera: Curculionidae). *J. Chem. Ecol.* 17:1221–30
172. Rodríguez-Morell H, Quirós-Mc Intire EI, Domingo-Quirós AE, Chico-Morejón R, Porcelli F. 2012. Presencia de *Centrouropoda almerodai* y *Glyptobolaspis* sp. (Acari: Uropodina, Macrochelidae) sobre el

- picudo negro del cocotero (*Rhynchophorus palmarum*) (Coleoptera: Curculionidae) en Panamá. *Métod. Ecol. Sist.* 7:1–7
173. Rugman-Jones PF, Hoddle CD, Hoddle MS, Stouthamer R. 2013. The lesser of two weevils: Molecular-genetics of pest palm weevil populations confirm *Rhynchophorus vulneratus* (Panzer 1798) as a valid species distinct from *R. ferrugineus* (Olivier 1790), and reveal the global extent of both. *PLOS ONE* 8:e78379
 174. Sadder MT, Vidyasagar PSPV, Aldosari SA, Abde-Azim MM, Al-Doss A. 2015. Phylogeny of red palm weevil (*Rhynchophorus ferrugineus*) based on ITS1 and ITS2. *Orient. Insects* 49:198–211
 175. Saïd I, Renou M, Morin J-P, Ferreira JMS, Rochat D. 2005. Interactions between acetoin, a plant volatile and pheromone in *Rhynchophorus palmarum*: behavioral and olfactory neuron responses. *J. Chem. Ecol.* 31:1789–805
 176. Saïd I, Tauban D, Renou M, Mori K, Rochat D. 2003. Structure and function of the antennal sensilla of the palm weevil *Rhynchophorus palmarum* (Coleoptera, Curculionidae). *J. Insect Physiol.* 49:857–72
 177. Salama HS, Abdel-Razek AS. 2002. Development of the red palm weevil, *Rhynchophorus ferrugineus* (Olivier), (Coleoptera: Curculionidae) on natural and artificial diets. *J. Pest Sci.* 75:137–39
 178. Salama HS, Saker MM. 2002. DNA fingerprints of three different forms of the red palm weevil collected from Egyptian date palm orchards. *Arch. Phytopathol. Plant Prot.* 35:299–306
 179. Sallam AA, El-Shafie HAF, Al-Abdan S. 2012. Influence of farming practices on infestation by red palm weevil *Rhynchophorus ferrugineus* (Olivier) in date palm: a case study. *Int. Res. J. Agric. Sci. Soil Sci.* 2:370–76
 180. Salman TAA, Abbas MK, Mandour NSA, Osman MAM, El-Kady GA. 2020. Fluctuations in the population density of red palm weevil *Rhynchophorus ferrugineus* (Curculionidae: Coleoptera) in Ismailia Governorate, Egypt. *Egypt. J. Plant Prot. Res. Inst.* 3:977–85
 181. Sancho D, de Jesus Alvarez M, del Rocio L, Sánchez F. 2015. Insectos y alimentación. Larvas de *Rhynchophorus palmarum* L, un alimento de los pobladores de la Amazonía Ecuatoriana. *Entomotropica* 30:135–49
 182. Sazali SN, Hazmi IR, Abang F, Rahim F, Jemain AA. 2018. Morphometric study of the palm weevils, *Rhynchophorus vulneratus* and *R. ferrugineus* (Coleoptera: Curculionidae) in view of insular and mainland populations of Malaysia. *Trop. Agric. Sci.* 41:1329–40
 183. Sazali SN, Hazmi IR, Abang F, Rahim F, Jemain AA. 2019. Population variation of the red stripe weevils, *Rhynchophorus vulneratus* (Coleoptera: Curculionidae) isolated by geographical limit. *Raffles Bull. Zool.* 67:378–84
 184. Schönherr CJ. 1826. *Curculionidum dispositio methodica cum generum characteribus, descriptionibus atque observationibus variis, seu Prodromus ad Synonymiae Insectorum, partem IV.* Leipzig: Fridericum Fleischer
 185. Shin S, Clarke DJ, Lemmon AR, Lemmon EM, Aitken AL, et al. 2017. Phylogenomic data yield new and robust insights into the phylogeny and evolution of weevils. *Mol. Biol. Evol.* 35:823–36
 186. Slimane-Kharrat S, Ouali O. 2019. Mites associated with the red palm weevil (*Rhynchophorus ferrugineus*) in Tunisia. *Tunis. J. Plant Prot.* 14:29–38
 187. Soffan A, Antony B, Abdelazim M, Shukla P, Witjaksono W, et al. 2016. Silencing the olfactory co-receptor RferOrco reduces the response to pheromones in the red palm weevil, *Rhynchophorus ferrugineus*. *PLOS ONE* 11:e0162203
 188. Stephan N, Halama A, Mathew S, Hayat S, Bhagwat A, et al. 2018. A comprehensive metabolomic data set of date palm fruit. *Data Brief* 18:1313–21
 189. Stern VM. 1973. Economic thresholds. *Annu. Rev. Entomol.* 18:259–80
 190. Sukirno S, Tufail M, Rasool KG, Husain M, Aldawood AS. 2020. Diversity of red palm weevil, *Rhynchophorus ferrugineus* Oliv. (Coleoptera: Curculionidae) in the Kingdom of Saudi Arabia: studies on the phenotypic and DNA barcodes. *Int. J. Trop. Insect Sci.* 40:899–908
 191. Tagliavia M, Messina E, Manachini B, Cappello S, Quatrini P. 2014. The gut microbiota of larvae of *Rhynchophorus ferrugineus* Oliver (Coleoptera: Curculionidae). *BMC Microbiol.* 14:136
 192. Vacas S, Abad-Paya M, Primo J, Navarro-Llopis V. 2014. Identification of pheromone synergists for *Rhynchophorus ferrugineus* trapping systems from *Phoenix canariensis* palm volatiles. *J. Agric. Food Chem.* 62:6053–64
 193. Vacas S, Melita O, Michaelakis A, Milonas P, Minuz R, et al. 2017. Lures for red palm weevil trapping systems: aggregation pheromone and synthetic kairomone. *Pest Manag.* 73:223–31

194. Vanderbilt CF, Giblin-Davis RM, Weissling TJ. 1998. Mating behavior and sexual response to aggregation pheromone of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae). *Fla. Entomol.* 81:351–60
195. Vásquez-Ordoñez AA, Löhr BL, Marvaldi AE. 2020. Comparative morphology of the larvae of the palm weevils *Dynamis borassi* (Fabricius) and *Rhynchophorus palmarum* (Linnaeus) (Curculionidae: Dryophthorinae): two major pests of peach palms in the Neotropics. *Pap. Avulsos Zool.* 60:e202060(s.i.).27
196. Vidyasagar PSPV, Hagi M, Abozuhairah RA, Al-Mohanna OE, Al-Saihati AA. 2000. Impact of mass pheromone trapping on red palm weevil adult population and infestation level in date palm gardens of Saudi Arabia. *Planter* 76:347–55
197. Wakil W, Yasin M, Qayyum MA, Ghazanfar MU, Al-Sadi AM, et al. 2018. Resistance to commonly used insecticides and phosphine fumigant in red palm weevil, *Rhynchophorus ferrugineus* (Olivier) in Pakistan. *PLOS ONE* 13:e0192628
198. Wang G, Hou Y, Zhang X, Zhang J, Li J, et al. 2017. Strong population genetic structure of an invasive species, *Rhynchophorus ferrugineus* (Olivier), in southern China. *Ecol. Evol.* 7:10770–81
199. Wang L, Zhang X-W, Pan L-L, Liu W-F, Wang D-P, et al. 2013. A large-scale gene discovery for the red palm weevil *Rhynchophorus ferrugineus* (Coleoptera: Curculionidae). *Insect Sci.* 20:689–702
200. Wattanapongsiri A. 1966. *A revision of the genera Rhynchophorus and Dynamis (Coleoptera: Curculionidae)*. Bull., Dept. Agric. Sci., Bangkok, Thail.
201. Weissling TJ, Giblin-Davis RM. 1993. Water loss dynamics and humidity preferences of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae) adults. *Environ. Entomol.* 22:93–98
202. Weissling TJ, Giblin-Davis RM, Center BJ, Hiyakawa T. 1994. Flight behavior and seasonal trapping of *Rhynchophorus cruentatus* (Coleoptera: Curculionidae). *Ann. Entomol. Soc. Am.* 87:641–47
203. Witt A, Hula V, Suleiman AS, Van Damme K. 2020. First record of the red palm weevil *Rhynchophorus ferrugineus* (Olivier) on Socotra Island (Yemen), an exotic pest with high potential for adverse economic impacts. *Rend. Lincei Sci. Fis. Nat.* 31:645–54
204. Yamamura K, Kishita M, Arakaki N, Kawamura F, Sadoyama Y. 2003. Estimation of dispersal distance by mark-recapture experiments using traps: correction of bias caused by the artificial removal by traps. *Popul. Ecol.* 45:149–55
205. Yan W, Liu L, Qin W, Li C, Peng Z. 2015. Transcriptomic identification of chemoreceptor genes in the red palm weevil *Rhynchophorus ferrugineus*. *Genet. Mol. Res.* 14:7469–80
206. Yin A, Pan L, Zhang X, Wang L, Yin Y, et al. 2015. Transcriptomic study of the red palm weevil *Rhynchophorus ferrugineus* embryogenesis. *Insect Sci.* 22:65–82
207. Zhang H, Bai J, Huang S, Liu H, Lin J, et al. 2020. Neuropeptides and G-protein coupled receptors (GPCRs) in the red palm weevil *Rhynchophorus ferrugineus* Olivier (Coleoptera: Dryophthoridae). *Front. Physiol.* 11:159