Chapter 11

The Genus *Hypothenemus*, with Emphasis on *H. hampei*, the Coffee Berry Borer

Fernando E. Vega[1], Francisco Infante[2], and Andrew J. Johnson[3]

[1] *Sustainable Perennial Crops Laboratory, United States Department of Agriculture, Agricultural Research Service, Beltsville, MD, USA,* [2] *El Colegio de la Frontera Sur (ECOSUR), Carretera Antiguo Aeropuerto Km. 2.5, Tapachula, Chiapas, Mexico,* [3] *School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA*

1. INTRODUCTION

Hypothenemus is one of the most speciose genera of Scolytinae, common in all tropical and subtropical areas (Wood, 1986). Most *Hypothenemus* species are very small (<2 mm long), poorly described, and difficult to distinguish. Several species are globally distributed, undoubtedly aided by human activities. Although the vast majority of *Hypothenemus* species live innocuously in twigs, some have become important pests, most notably the coffee berry borer *Hypothenemus hampei* (Ferrari), which lives inside the coffee berry and consumes the seeds, and the tropical nut borer *Hypothenemus obscurus* (F.), which attacks a range of seeds and fruits. This chapter will introduce the reader to taxonomic characters useful in identifying members of the genus, followed by some of the most important species, and concluding with an in-depth review of the vast body of multilingual literature on the coffee berry borer.

2. THE GENUS *HYPOTHENEMUS*

2.1 Key Characters for Identification to Genus

The majority of the 181 described *Hypothenemus* species are poorly known (Wood and Bright, 1992; Bright and Skidmore, 1997, 2002; Bright, 2014) and most species are not distinguishable when using the original published descriptions. The book *The Bark and Ambrosia Beetles of South America* (Wood, 2007) is the most extensive work to date and includes the 46 species reported from South America, in addition to others recorded from Central and North America.

Species are distinguished by details of vestiture (often lost from abrasion), frontal sculpture, and surface texture. However, the combination of some characters described below and illustrated in Figures 11.1–11.4 can be used to distinguish *Hypothenemus* from all other bark beetles.

The antennae have three to five funicular segments. The antennal club has sutures marked with setae and a partial septum, visible as a dark line. The eye in the female is emarginate, although in the smaller species this might be as slight as a few facets missing. There are one to 10 marginal asperities on the anterior margin of the pronotum, and usually more than 10 asperities on the pronotal declivity. A raised line that partially extends forward along the lateral margins marks the posterior edge of the pronotum. The males are smaller than females, often appearing deformed, and although in most keys they are described as wingless, they actually have vestigial wings and are effectively flightless and have reduced compound eyes by comparison with females (Vega *et al.*, 2014). Most species have prominent setae, particularly the interstrial bristles, which are in rows and usually flattened. With a few exceptions, the elytra are rounded without distinctive sculpturing.

2.2 Taxonomy

Hypothenemus was first established with the description of the species *H. eruditus* Westwood (Westwood, 1836; Figures 11.1 and 11.2A). The genus name was derived from "υπο subtus, εν, and νεμω pasco" referring to the downward facing mouthparts (Westwood, 1836). The species contained within *Hypothenemus* have been described in and moved from 23 other genera (Wood and Bright, 1992).

The genus *Stephanoderes* was first described for a number of species by Eichhoff (1871). This later encompassed Westwood's *Hypothenemus* genus (Eichhoff and Schwarz, 1896), giving priority to *Stephanoderes*, and accounting for the erroneous generic description by Westwood in which *H. eruditus* was described as having three funicular segments, when the specimens had four

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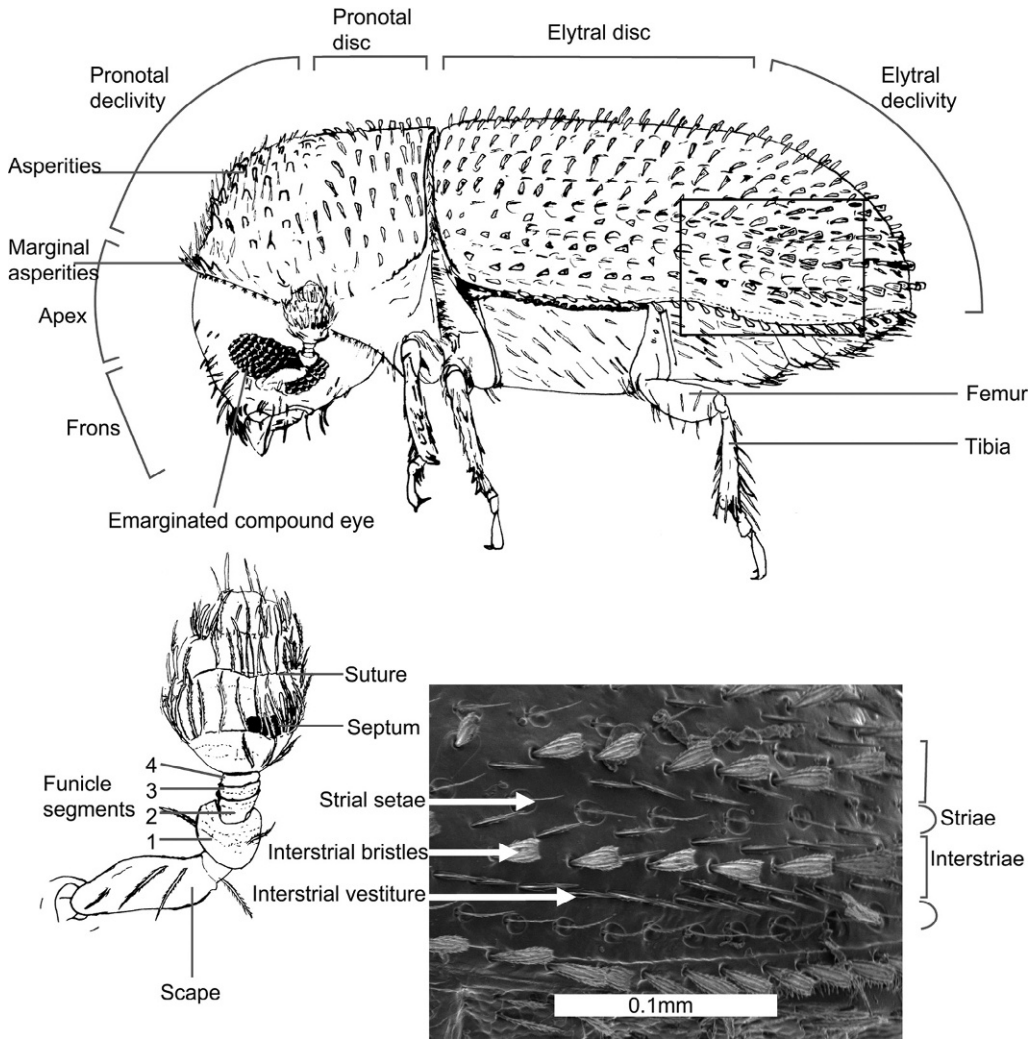

FIGURE 11.1 Top: Morphology of *Hypothenemus eruditus*, with terminology used in the chapter. Square box on lateral region of elytron is shown in detail in scanning electron microscopy photograph on bottom right. Bottom left: Enlarged diagram of an antenna of *H. eruditus*. In the text, "vestiture" is used to globally encompass all types of setae, and these can be divided into three types: strial setae, interstrial bristles, and interstrial vestiture.

(Figure 11.1). However, Swaine (1909) treated *Stephanoderes* as a redundant genus while Hopkins (1915a) listed both *Hypothenemus* and *Stephanoderes* as separate genera, with *Stephanoderes chapuisii* Eichhoff (current name: *H. dissimilis* (Zimmermann)) chosen as the generic type. Hopkins (1915b) also described the differences between the two genera, in that the antennal funicle of *Stephanoderes* is five segmented with the last segment widened, in contrast to only four segments for *Hypothenemus*. This distinction, however, is unreliable, especially with species such as *H. birmanus* (Eichhoff) having a range from three to five funicular segments. *Stephanoderes* was finally moved back into synonymy by Browne (1963). The genus has remained in occasional use since, especially for the coffee berry borer.

The genus *Trischidias* was also described by Hopkins (1915b). This genus of minute beetles shares many characters with *Hypothenemus* and differs only in lacking the septum of the antennal club, and a lack of emargination of the eye. Hopkins (1915b) also described several *Hypothenemus* species that have since been moved into *Trischidias*, highlighting the similarity or the two genera. Wood (1954) even comments that *Trischidias* "obviously were derived from" *Hypothenemus*. *Trischidias* has the unusual habit of breeding in wood infected with decaying fungi (Deyrup, 1987) and may just be a specialized group within *Hypothenemus*.

Other genera similar and likely to be phylogenetically close to *Hypothenemus* are *Cryptocarenus* and *Periocryphalus*, which share many morphological characters and mating systems. The antennal club, however, is distinctly different, lacking a septum and sutures. These genera are naturally distributed in the Americas (Wood, 2007).

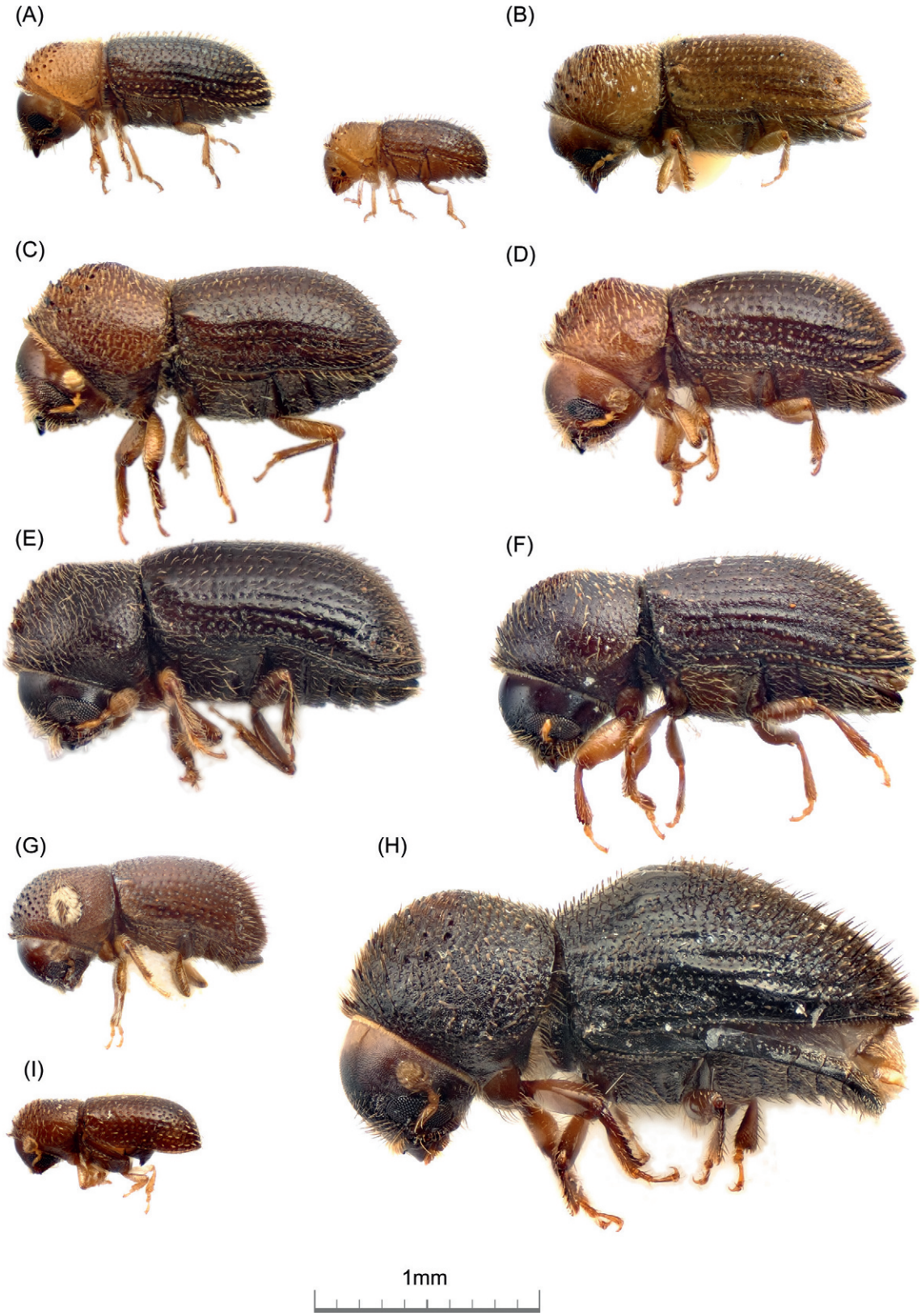

FIGURE 11.2 (A) *Hypothenemus eruditus* female and male. Females of (B) *H. areccae*; (C) *H. javanus*; (D) *H. birmanus*; (E) *H. dissimilis*; (F) *H. opacus*; (G) *H. curtipennis*; (H) *H. concolor*; and (I) *H. distinctus*. *All photos by A. J. Johnson.*

2.3 Typical *Hypothenemus* Life Cycle

A gallery is started by a single, mated female, referred to as the foundress, and in coffee berry borer literature as the colonizing female. The cues used to locate hosts are poorly known. Many species, however, are attracted to traps baited with ethanol, which is produced by plants under stress (Kimmerer and Kozlowski, 1982). The foundress initiates the gallery with a single entrance hole, usually located at stem or leaf nodes, or in a coffee berry for the coffee berry borer. A gallery may have just one hole, out of which frass and debris are pushed. Often, there are multiple galleries on the twig, which merge as they expand, becoming "inextricably intermingled" (Browne, 1961). Different species may be found together in the same gallery system after merging of original independent galleries (Wood, 1954). Galleries in twigs may also extend into leaf petioles or fruits.

The eggs are large relative to the size of the female, and the larvae are found within or very close to the parental gallery. Approximate development time in the field is 28 days (Browne, 1961). Males are produced at a much lower ratio, and for all *Hypothenemus* species, sex is believed to be determined by pseudo-arrhenotoky (see below). Adult females mate with their brothers (sibling mating), or perhaps non-sibling males if the gallery is merged with that of other families. The adult females remain in the galleries for some time, probably waiting for suitable weather conditions to disperse. When they disperse, the females may leave via the single entrance hole, or make new exit holes.

2.4 Host Plants

The diversity of plants any one *Hypothenemus* species can be found on is remarkable and many species are highly polyphagous (Wood, 1954; Wood and Bright, 1992). *Hypothenemus javanus* (Eggers) has been recorded from 32 families of plants (Atkinson, 2014). The most extreme, however, is *H. eruditus* (Figures 11.1 and 11.2A) which has been found breeding in innumerable hosts, in nearly any part of the plants, sometimes within the galleries of other insects including active and abandoned *Hypothenemus* galleries, fruiting bodies of fungi (Browne 1961; Deyrup, 1987), and manufactured products such as drawing boards (Browne, 1961) and books (Westwood, 1836). Some species, however, are much more restricted in their host range, such as *H. pubescens* Hopkins, which is only known from coastal grasses (Wood, 2007).

The plant host substrates for most *Hypothenemus* species, such as dead twigs, are nutritionally poor, and undoubtedly the microbial communities, inside or outside the beetle, play a role in allowing the beetles to thrive in such environments. These may also mediate the extreme polyphagy, especially since feeding on decomposed material may reduce plant species-specific defenses faced by insects that feed on live plant tissues. At least one species, *H. curtipennis* (Schedl), has adaptations associated with inoculation and cultivation of fungi (Beaver, 1986), which is known to permit a wide diversity of host plant substrates.

2.5 An Introduction to Some *Hypothenemus* Species

The diversity of *Hypothenemus* species is briefly described with figures depicting some of the most commonly encountered globally distributed species, morphological extremes, and economically significant species. The descriptions are focused on females since males are smaller, harder to find, and have fewer differentiating characters.

Hypothenemus areccae (Hornung) (Figure 11.2B) is found in all tropical regions, with origins in Southeast Asia. The body shape is slender, 1.2–1.4 mm long, and usually has eight marginal asperities and a distinctly concave frons. It is found on a broad range of plants, and is an occasional pest of transplants and seedlings.

Hypothenemus birmanus (Eichhoff) (Figure 11.2D) is another widely distributed, common species, found in every tropical region. Females can have three to five funicular segments. The marginal asperities are distinctive: they are narrowly separated, the median pair are large, and the outer pair are small. The flattened interstrial bristles are much denser on the elytral declivity than on the disc, and the interstrial vestiture on the declivity is made of rows of slightly flattened setae.

Hypothenemus concolor Hagedorn (Figure 11.2H) is one of the largest, most robust of all *Hypothenemus* species, with some specimens reaching 2.9 mm in length. The elytral disc is reduced, and there is an obvious summit between the elytral disc and declivity. It is likely that this species also has a fungus farming lifestyle, since the galleries are inside woody tissue and only extend to 20 mm (Schedl, 1961). Conversely, ***H. distinctus*** Wood (Figure 11.2I) is one of the smallest species, usually just 0.9 mm, seldom collected, and its biology is unknown.

Hypothenemus crudiae (Panzer) (Figures 11.3A and 11.4A) is widespread and common across much of the tropics, except Australia, with probable origins in the Americas (Wood, 2007). It is very similar and sometimes indistinct from *H. seriatus* (Eichhoff) (see below). The key character reported to distinguish *H. crudiae* from similar species is the presence of a frontal tubercle on the frons, often with a short central groove extending into the tubercle. However, the tubercle is sometimes reduced (Wood, 2007). There are usually six marginal asperities of a similar size and spacing, and the anterior margin is

FIGURE 11.3 Lateral and dorsal view of female (and lateral view of male, when available, in last column) for (A) *Hypothenemus crudiae*; (B) *H. seriatus*; (C) *H. interstitialis*; (D) *H. obscurus*; and (E) *H. hampei*. *All photos by A. J. Johnson.*

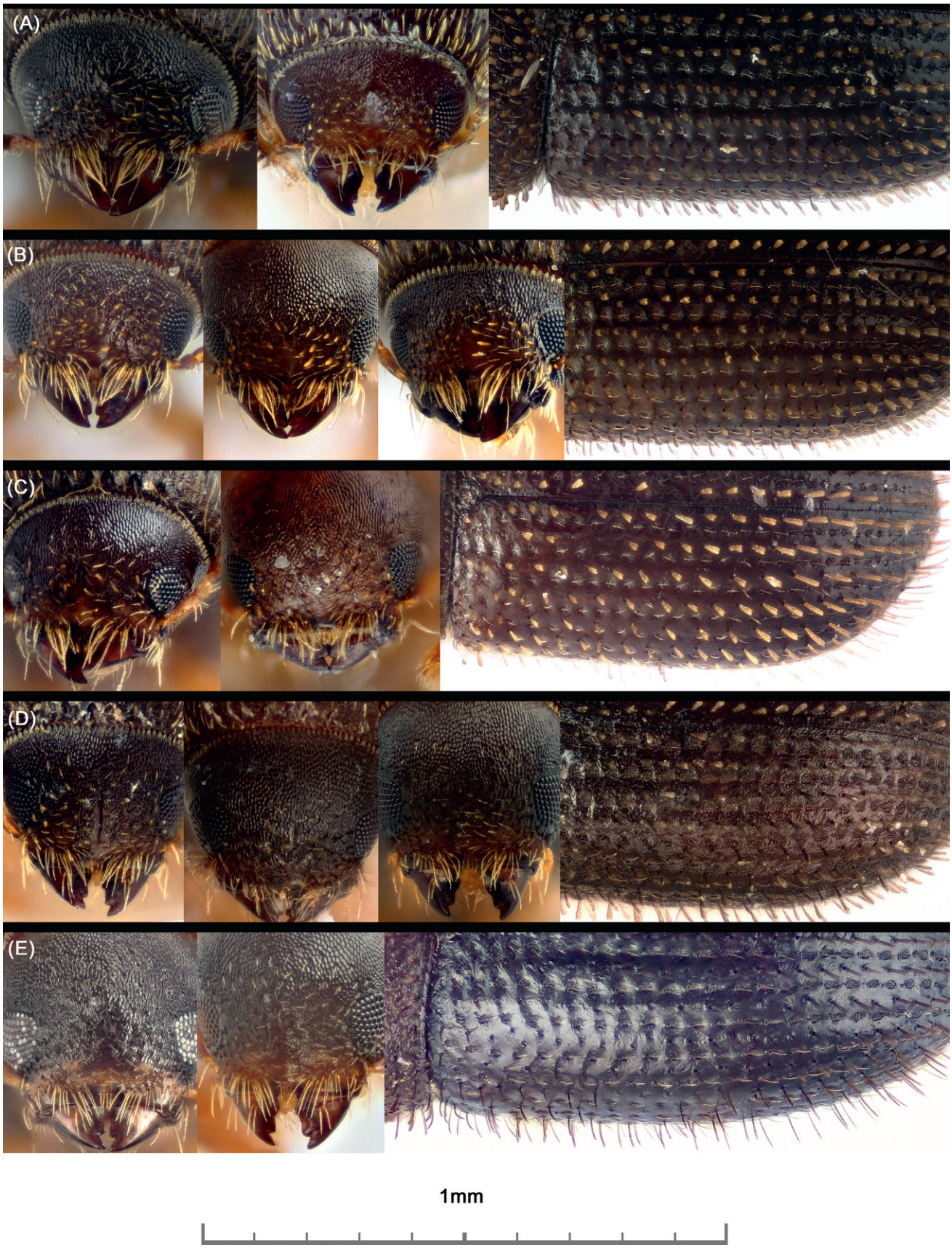

FIGURE 11.4 From left to right: Close-up of head of multiple individuals to show variation and enlarged dorsal view of eltyron showing vestiture and texture. (A) *H. crudiae*; (B) *H. seriatus*; (C) *H. interstitialis*; (D) *H. obscurus*; and (E) *H. hampei*. *All photos by A. J. Johnson.*

broadly rounded. The texture of the lateral regions of the pronotum is variable from smooth to rugose. The elytral declivity is rounded and quite steep, slightly steeper than *H. seriatus* (Wood, 2007). The interstrial bristles are strongly flattened, and usually have a square tip (sometimes curved along its length making the tip appear recurved). The interstrial bristles are only slightly longer on the declivity than on the elytral disc and the interstrial vestiture is usually completely absent, even on the lateral regions of the declivity. The hair-like strial setae arch over the strial punctures, which are prominent and distinct, rugose in the center. The interstrial areas are variable, from almost entirely smooth and shining (as in Figure 11.4A), to mostly rugose, but not with an irregular micropunctate surface as in *H. obscurus*. Usually at least some of the elytra in the discal region are smooth. The adult color is also variable, mostly monotonous, brown to black, sometimes red-brown at the elytral summit, and the setae are often light brown. This species inhabits twigs, fruits, and seeds of a wide range of plants and is rarely reported as a pest. García Martell (1980) illustrated this species breeding in the fruits of cocoa (*Theobroma cacao* L.).

Hypothenemus curtipennis (Schedl) (Figure 11.2G) has undoubtedly developed cuticular mycangia for an ambrosia fungus-farming lifestyle (Beaver, 1986). Mycangia (sing. mycangium) are pits or recesses on the cuticle or in the mandibles that serve to carry fungal spores (Batra, 1963; Crowson, 1981). In *H. curtipennis*, mycangia are evident as wide, abrupt pits on the sides of the pronotum (visible in Figure 11.2G), lined with plumose setae, which fill with fungal spores before the young beetles disperse. The behavior of this species is also modified for fungus cultivation. The foundress makes a gallery much shorter than those made by typical *Hypothenemus* species, which is followed by a period where the beetle waits, blocking the gallery entrance with the steep elytral declivity. The larvae develop in the gallery, sometimes extending it no more than 15 mm, and then wall themselves off for pupation (Beaver, 1986).

Hypothenemus dissimilis (Zimmermann) (Figure 11.2E) is a large, robust species from the Americas. This species has only two marginal asperities, and hair-like interstrial bristles among short, flattened interstrial vestiture. It has a typical habit of living in the pith or under the bark of a range of woody plants.

Hypothenemus eruditus Westwood (Figures 11.1 and 11.2A) is a widely distributed *Hypothenemus* species, present in every tropical and subtropical region. In the Americas, the range extends from Michigan (USA) to Argentina (Wood, 2007). This species is also remarkable for the extreme diversity of habits, recorded from hundreds of host plants and even fungal fruiting bodies, from all sorts of plant material including leaf petioles, twigs, seeds, fruits, and from manufactured products (Browne, 1961; Wood, 1982). The type specimen was found living in the bindings of a book (Westwood, 1836); therefore, the name *eruditus* (i.e., erudite). This species has also been reported killing seedlings of cocoa and transplants of trees (Browne, 1961).

Hypothenemus eruditus is 1.1–1.3 mm long, usually with six marginal asperities, the median pair usually narrowly separated. The vestiture is variable in the shape and size of the interstrial bristles (Wood, 1954), and in the abundance of interstrial vestiture. The coloration is variable; the female and male depicted in Figure 11.2A are distinctly bicolored, but many are entirely dark brown to black. It is common to find multiple, distinct variants at any one location, which may represent different species, yet when specimens are compared to the global diversity, the distinctions are unclear. The distribution, variation, profound polyphagy, and minute size may explain the array of junior synonyms, with 71 recognized (Wood and Bright, 1992). It is very likely that a species complex is involved.

Hypothenemus interstitialis (Hopkins) (Figures 11.3C and 11.4C) is a slightly larger species (1.4–1.7 mm long) that is similar to *H. seriatus and H. hampei*. It is restricted to the Americas. The frons is variable, often with a frontal groove. There are four to six marginal asperities and the lateral regions of the pronotum are micropunctate. There is often a difference between the color of the pronotum and elytra. The interstrial bristles are prominent and as in *H. seriatus*, they are short on the disc, but on the declivity, the interstrial bristles are long and narrow, with the length being eight times the width or more (Wood, 2007). The strial setae are hair-like and arch over the strial punctures. The interstrial vestiture is absent. The elongate interstrial bristles on the declivity could cause confusion with *H. hampei*, especially since this species has been found on twigs of *Coffea* sp. (Wood, 2007). However, the interstrial bristles are short and flattened on the disc, whereas for *H. hampei*, the interstrial bristles are similar in length over all the elytra.

Hypothenemus javanus (Eggers) (Figure 11.2C) is a species with pantropical distribution with likely origins in Africa (Wood, 1977). This species is larger (1.4–1.7 mm long) and much more robust than *H. areccae*, with four marginal asperities, a concave frons, and hair-like interstrial vestiture (Wood, 2007).

Hypothenemus obscurus (F.) (Figures 11.3D and 11.4D), the tropical nut borer, is the second most economically damaging species in the genus (after the coffee berry borer), attacking a range of seeds and fruits. Originally from the Americas, this species is now found across the tropical world, although not in Australia. It is frequently intercepted in Brazil nuts (*Bertholletia excelsa* Bonpl.; Wood, 1982). *Hypothenemus obscurus* was first described in the genus *Hylesinus* by Fabricius (1801), briefly and non-specifically, mentioning only the color, minute size, and shape of the pronotum. In some reviews (e.g., Wood, 1954), this species'

name has been used to describe specimens of *H. seriatus* and *H. crudiae*. *Hypothenemus obscurus* should not be confused with *Cryphalus obscurus* (current name: *H. eruditus*, synonymy by Wood, 1975), described by Ferrari (1867) alongside *Cryphalus hampei* (current name: *H. hampei*), or *Stephanoderes obscurus* as described by Eichhoff (1871) (current name: *H. setosus*, synonymy by Wood, 1975).

Hypothenemus obscurus usually has a narrow frontal groove although this is variable, sometimes just partial or absent, even within families in a gallery (Figure 11.4D). There are four to six marginal asperities. The pronotum and elytra is entirely very finely textured with irregular pits throughout (*H. seriatus* and *H. crudiae* usually have some smooth areas of interstriae). The interstrial bristles are flattened, about four to six times long as wide, and longer on the declivity. The apex of the interstrial bristles is usually rounded. There does not seem to be the amount of variation in setae between specimens as seen in *H. seriatus* and *H. crudiae*.

Hypothenemus obscurus has some interstrial vestiture on the declivity (Mitchell and Maddox, 2010), often overlooked, which contradicts many keys (e.g., Wood, 1982). This can be seen as a few coarse, pointed setae lying flat among the erect interstrial bristles, restricted to the lateral regions of the declivity. Such setae are absent or rare in *H. crudiae* and *H. seriatus*. The described size of female *H. obscurus* ranges from 1.2–1.4 mm (Wood, 1982) to 1.4–1.6 mm (Wood, 2007), and specimens in Hawaii were 1.5–1.8 mm (Mitchell and Maddox, 2010), while insects reared in artificial diet in Colombia were on average 1.75 mm (Constantino *et al*., 2011). The males are also variable; within one gallery in a tamarind seed (*Tamarindus indica* L.) collected in Florida, the males ranged from 0.8 to 1.2 mm (A. J. Johnson, unpubl.).

Hypothenemus obscurus feeds on a remarkably diverse array of seeds and fruits. Commercially important products include nutmeg (*Myristica fragrans* Houtt.), macadamia nuts (*Macadamia* sp.), cocoa, tamarind, longan (*Dimocarpus longan* Lour.), *Melicoccus bijugatus* Jacq., and jackfruit (*Artocarpus heterophyllus* Lam.) (Beardsley, 1990). It has also been collected in coffee berries, although it does not complete its development (Constantino *et al*., 2011). The worldwide cost to the industry is unknown. Between 1998 and 2012, *H. obscurus* caused from 0.8 to 4.6% of harvested macadamia nuts in Hawaii to be rejected, equivalent to $0.3–$1.8 million per year (calculated from NASS reports; NASS 1998–2012). This does not account for the costs associated with mitigating the damage though management strategies. In particular, regular harvesting of fallen nuts avoids high insect prevalence, which otherwise could result in infestations as high as 30% (Jones, 2002). Working in Hawaii, Jones *et al.* (1992) found that continuous harvest and processing within 3 weeks after *H. obscurus* infestation could result in decreased damage. At this time the insect was still in the husk and had not yet started consuming the kernel. Unfortunately, this recommendation is not practical among growers and processors. Unharvested nuts, including those that do not fall, could be a source for reinfestation, and reducing these through cultural practices and cultivar selection may reduce damage.

Hypothenemus opacus (Eichhoff) (Figure 11.2F) has been collected in Central and South America. This species, and a few others, has deep circular pits at the summit of the pronotum. These pits are often filled with debris, which led Wood (2007) to speculate that they could be mycangia.

Hypothenemus seriatus (Eichhoff) (Figures 11.3B and 11.4B) is widely distributed across the tropical regions. It is very similar to *H. crudiae*, usually distinguished by the absence of the tubercle. The frontal groove may be partial or absent, and in some specimens there is an area of shining cuticle in the place of the frontal tubercle. Beardsley (1990) and Mitchell and Maddox (2010) report than the frontal groove of *H. seriatus* in Hawaii is absent, whereas Beaver and Maddison (1990) report it is normally present in specimens from Niue (Polynesia). In Florida, the presence of the frontal groove is variable, even among specimens within a single gallery (A. J. Johnson, unpubl.).

There are usually six marginal asperities (sometimes five to eight), of approximately equal size, although the outermost pair may be reduced. The texture of the lateral regions of the pronotum is smooth to rugose or weakly micropunctate. Compared with *H. crudiae*, the overall shape of the pronotum and elytra tends to be narrower in *H. seriatus* than in *H. crudiae*. The declivity is usually less steep, and the strial rows are often more prominently impressed on the declivity.

The setae on the elytra are similar to *H. crudiae*, although the interstrial bristles are noticeably longer on the declivity than the elytral disc (typically with a length three times the width on the disc and six times the width on the declivity). The interstrial vestiture is absent or one or two setae near the apex of the elytra. The scultpturing of the elytra is similar to *H. crudiae*, but *H. seriatus* usually have less prominent strial punctures. Like *H. crudiae*, usually at least some areas of the interstriae are smooth, and if rugose, the cuticle is not covered by small irregular pits. Fonseca (1937) presented an illustration of *H. seriatus* galleries inside a coffee berry. This species is also known to damage cocoa seedlings (García Martell, 1980).

Hypothenemus crudiae, *H. interstitialis*, *H. obscurus*, and *H. seriatus* are very similar. The differentiating characters appear variable within each species to the point where there is a large overlap and many specimens in collections cannot be assigned to a particular species. Wood (1982) suggested that some of the intermediate forms could be from hybridization between different species. Both

H. crudiae and *H. seriatus* have a worldwide distribution, and are undoubtedly still being transported within and between continents. If they once were regionally distinct, it is possible that this has since been lost. They also have similar habits and biology, and neither are significant pests, so conclusive differentiation between the four species is not always necessary.

2.6 Molecular Phylogenetics of *Hypothenemus* Species

Despite the difficulties in identification, *Hypothenemus* species are yet to receive much attention using molecular techniques. Jordal and Cognato (2012) included two species (*Hypothenemus* sp. 1 and *H. birmanus*) in a molecular phylogeny of many bark and ambrosia beetles, placing *Hypothenemus* nearest to *Ptilopodius*.

Within-species variation of the mitochondrial DNA (mtDNA) cytochrome oxidase subunit I gene (*COI*), the typical insect "barcode" region, has been studied for several species, finding variation within *H. obscurus*, *H. seriatus*, and *H. hampei* as 2.9%, 1.9%, and 1.9%, respectively (Mitchell and Maddox, 2010). More detailed work on *H. hampei* found variation to be as high as 11.8% (Gauthier, 2010), and another study examining specimens identified as *H. eruditus* found a remarkable level of variation as high as 20.1% (Kambestad, 2011). Such deep divergence suggests the presence of many distinct, cryptic species units present within *Hypothenemus* species. With very few distinct morphological characters between species, molecular tools are invaluable for species identification. However, the effects of routine inbreeding on species boundaries may remain unclear, and linking genetically determined species to traditional classification will remain a challenge.

No phylogenetic analyses have yet been done with a focus on between-species relationships. Further study could result in a better understanding of some of the unusual traits that vary within the genus, including the evolution of seed feeding, as well as the ambrosial habit. Molecular phylogenetics also could resolve taxonomic issues such as the questionable monophily of *Hypothenemus* with respect to *Trischidias*.

3. COFFEE AND THE COFFEE BERRY BORER

The genus *Coffea* (Rubiaceae) comprises 123 species (Davis *et al.*, 2006), of which only two are commercially traded: *C. arabica* L. and *C. canephora* Pierre ex A. Froehner (commonly referred to as robusta) (Vega, 2008a). In their natural habitat, both species were inhabitants of the humid, evergreen forests of Africa (Davis *et al.*, 2006), with *C. arabica* being a high altitude species (900–2000 m) occurring in southwestern Ethiopia and surrounding regions, and *C. canephora* being a predominantly lowland plant (50–1500 m) found throughout much of tropical Africa, west of the Rift Valley (Davis *et al.*, 2006). Coffee is grown in more than 10 million hectares in ca. 80 countries (FAOSTAT, 2014), with ca. 20 million families dependent on this plant for their subsistence (Osorio, 2002; Gole *et al.*, 2002; Vega *et al.*, 2003a, 2008a; Lewin *et al.*, 2004). The theoretical yearly gross earnings in coffee producing countries for 2000–2012 was US$11.6 billion, while in 2012 the value of the entire coffee industry was estimated at US$173.4 billion (ICO, 2014).

Of all *Hypothenemus* species, the coffee berry borer *Hypothenemus hampei* (Ferrari) (Figures 11.3E, 11.4E, and 11.5) is without doubt the most studied as a result of the losses in yield and quality that it causes in coffee plantations worldwide. Nevertheless, a recent review of the literature published on the coffee berry borer from 1910 to 2013 (Infante *et al.*, 2014) revealed that of 1603 papers published on the insect, only ca. 602 were peer-reviewed, equivalent to ca. six papers per year. This figure was contrasted with a total of 75 peer-reviewed papers per year published on the Mediterranean fruit fly, *Ceratitis capitata* (Weidemann) from 1990 to 2012. These figures indicate that coffee berry borer research outputs are not what would be expected for such an economically important commodity as coffee.

3.1 Taxonomy and Synonymies

The coffee berry borer was described in Austria by Count Johann Angelo Ferrari as *Cryphalus hampei* from coffee seeds imported into France from an unknown origin, and named after Dr. Clemens Hampe, who provided the samples (Ferrari, 1867). The species was later moved to *Stephanoderes* with Eichhoff's (1871) description of the genus. Swaine (1909) treated *Stephanoderes* as a synonym of *Hypothenemus*, although *hampei* was not specifically listed, and the genus *Stephanoderes* continued to be used widely by others.

Hagedorn (1910) described what is now a synonym of *H. hampei*, *Stephanoderes coffeae*, arguing that it was not the same as *hampei*, based on some morphological differences. The same year, van der Weele (1910) described *Xyleborus coffeivorus* from coffee plantations in Java (Indonesia), recognizing the species' potential as a pest to coffee production, as well as the life history, and the difficulties controlling it. Strohmeyer (1910), however, quickly recognized *X. coffeivorus* to be a synonym of *S. hampei*, yet acknowledged *S. coffeae* as a related but distinct species. Meanwhile, Hopkins (1915a) relisted *Stephanoderes* as a genus separate from *Hypothenemus*, and soon after described it (Hopkins, 1915b), along with *Stephanoderes cooki* Hopkins, which also became a synonym of *S. hampei* (Schedl, 1959).

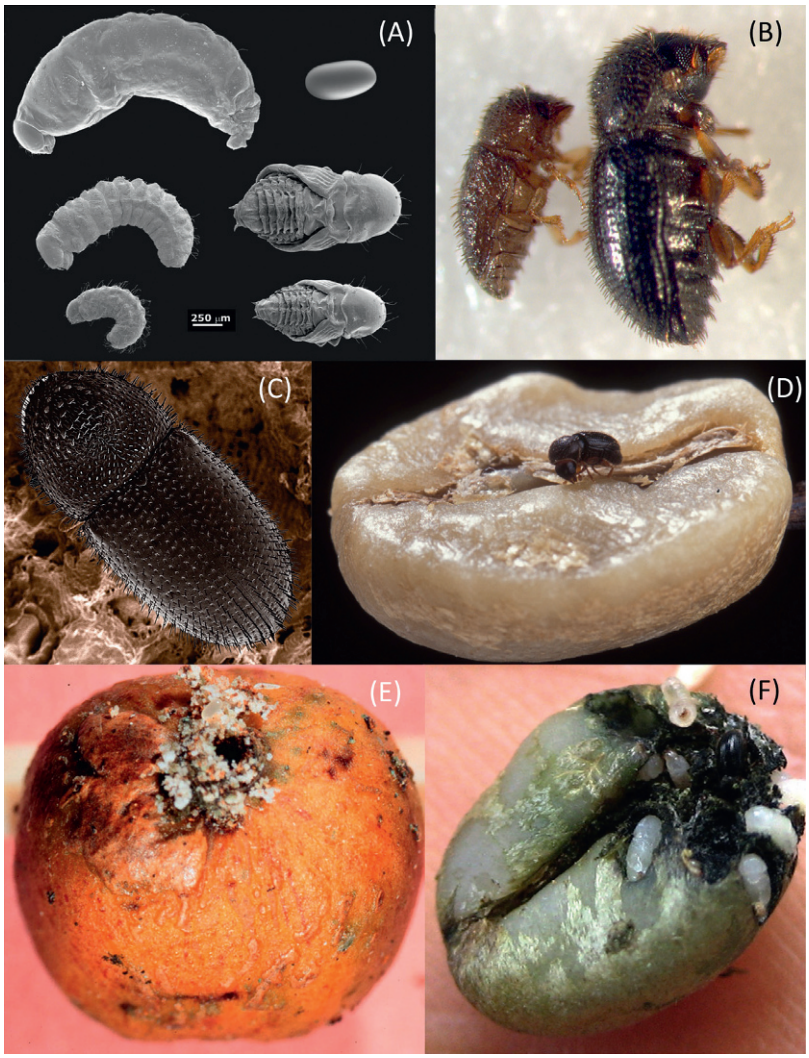

FIGURE 11.5 (A) Immature stages of the coffee berry borer. Clockwise starting in upper right: egg, female pupa, male pupa, first instar, second instar, and prepupa. There are two instars for females and only one for males; the first instar between sexes cannot be differentiated. (B) Male (left) and female (right) adults. (C) Dorsal view of an adult female. (D) Adult female on coffee seed. (E) Hole bored by colonizing female. (F) Damage caused to the seed. *Photos by: (A) Francisco Infante; (B) Ann Simpkins (USDA); (C) Eric Erbe (USDA); (D) Peggy Greb (USDA); (E) Guy Mercadier (USDA); and (F) Jaime Gómez (ECOSUR).*

Stephanoderes coffeae was synonymized with *S. hampei* by Roepke (1919). Eggers (1923) argued against the synonymy, suggesting that *hampei* had much broader interstrial bristles than *S. coffeae*. Sampson (1923), however, agreed with the synonymy, noting the specimens Eggers used for comparison were incorrectly identified as *S. hampei*, when instead they were *Stephanoderes cassiae* Eichhoff (current name: *Hypothenemus obscurus*).

Another synonym of *hampei* was described in a different genus as *Xyleborus cofeicola* (de Campos Novaes, 1922), synonymized 2 years later (Costa Lima, 1924a). Two further names, *Stephanoderes punctatus* Eggers (Eggers, 1924) and *Stephanoderes glabellus* Schedl (Schedl, 1952), were described and subsequently synonymized by Wood (1972 and 1989, respectively). The genus *Stephanoderes* was moved to *Hypothenemus* by Browne (1963), but the name *Stephanoderes hampei* continued to be used for some time.

Other *Hypothenemus* species have been recorded on coffee in Africa, including *H. areccae* (Ghesquière, 1933), *H. crudiae* (LePelley, 1968), *H. eruditus* (Schedl, 1960, 1961; Mayné and Donis, 1962), *H. grandis* Schedl (Schedl, 1961), *H. liberiensis* Hopkins (Schedl, 1961), *H. obscurus* (Le Pelley, 1968), *H. plumeriae* (Nordlinger) (Schedl, 1960), *H. seriatus* (Schedl, 1960; Le Pelley, 1968), and *H. solitarius* (Schedl) (Wood and Bright, 1992).

The term "falsa broca del café" or "false coffee berry borer" has been used to describe some of the *Hypothenemus* species that are similar in their appearance or habits to the coffee berry borer. It may be used in reference to a specific species such as *H. seriatus* (Fonseca, 1937; Decazy, 1987; Vega *et al.*, 2002b), *H. obscurus* (García Martell, 1980; Constantino *et al.*, 2011), or *H. crudiae* and *H. eruditus* (García Martell, 1980). Fonseca (1937) reported that *H. seriatus* never bores into green berries but that it bores into drier berries, where it consumes the pulp and reproduces,

although it never attacks the seeds. In Mexico, *H. crudiae*, *H. eruditus*, and *H. obscurus* have been reported attacking coffee berries, but they never consume the seed, although all the life stages of *H. crudiae* and *H. eruditus* have been found inside the berry (García Martell, 1980).

In laboratory experiments, Constantino *et al.* (2011) found that *H. obscurus* will bore into coffee berries but only a small percentage causes superficial damage of the seed; the insect can complete its life cycle after larvae feeds on the pulp. *Hypothenemus obscurus* has been artificially reared in a coffee seed-based diet, with a reduced fecundity when compared to a macadamia-based artificial diet (Constantino *et al.*, 2011). In Hawaii, Greco and Wright (2012) noted that *H. obscurus* were usually only found in coffee berries when macadamia plantations are nearby, which suggests that they are unlikely to be, or become, a problem for coffee production.

3.2 Taxonomic Characters (Figures 11.3E and 11.4E)

The frons of *H. hampei* may have a broad, indistinct frontal groove, or no groove at all. There are usually four marginal asperities. The setae on the pronotum are mixed, with some slightly flattened. The shape of the pronotum, viewed from above, is slightly more narrowly rounded (i.e., more triangular) than the similar *Hypothenemus* species.

The elytral declivity of *H. hampei* is much more broadly rounded than in the similar species, without a distinct transition from the elytral disc. When viewed laterally, the declivity takes up more than half of the length of the elytra, whereas in the similar species, the elytral disc takes up more than half of the length.

As with most *Hypothenemus*, the interstrial bristles are prominent and in almost perfectly uniseriate rows. The shape of the interstrial bristles, however, is distinctive, and differentiates the coffee berry borer from most other *Hypothenemus* species. The bristles are long, narrow, and slightly flattened. The tip of each bristle is square, and not much wider than the rest of its length. The bristles on the elytral disc are not much shorter than those on the declivity. Males are smaller with reduced eyes (Vega *et al.*, 2014). The interstrial bristles are relatively long, and often not in distinct rows.

3.3 Distribution

The coffee berry borer is endemic to Africa (Vega *et al.*, 2009; Gauthier, 2010) and has disseminated to most of the coffee producing world (Table 11.1). It was first collected in the field in 1897 in Mount Coffee, Liberia, and reported as *S. cooki* (Hopkins, 1915b). In 1901 the insect was reported as a pest of *C. canephora* in the Republic of Congo (Fleutiaux, 1901). The insect was found in Indonesia in 1908 (Hagedorn, 1910) and in 1913 was accidentally taken to Brazil (Table 11.1) in seeds imported from the Democratic Republic of the Congo (Berthet, 1913). Ihering (1924) proposed, to no avail, pruning to the ground all 900 million coffee plants in the state of São Paulo to completely eliminate all possibilities for survival of the insect.

Molecular methods have been used to elucidate the dissemination of the coffee berry borer throughout coffee-producing countries (Breilid *et al.*, 1997; Andreev *et al.*, 1998; Benavides *et al.*, 2005, 2006, 2007; Gauthier, 2010). Use of the mtDNA COI gene to track possible dispersal routes led to the identification of three clades: (1) Colombia, Honduras, and Mexico; (2) Fiji, Indonesia, Ivory Coast, Jamaica, New Caledonia, the Philippines, and Thailand; and (3) Kenya (Breilid *et al.*, 1997; Andreev *et al.*, 1998). Clades 1 and 2 imply introduction of two separate inbreeding lines, none of which is related to Kenyan specimens. It is noteworthy that specimens from Jamaica, where the insect was first reported in 1978 (Table 11.1), were more closely related to distant countries (clade 2, above) than to specimens from close-by countries, i.e., Honduras, Mexico, or Colombia, where the insect was first reported in 1977, 1978, and 1988, respectively (Table 11.1). This finding was also supported by Gauthier (2010), but not by Benavides *et al.* (2005).

Based on amplified length fragment polymorphism (AFLP) fingerprinting, Benavides *et al.* (2005, 2006, 2007) concluded that there were multiple coffee berry borer introductions into Colombia, with Brazil, Ecuador, and Peru being likely sources, and that introduction of the insect into Costa Rica most likely originated from Colombian insects. Benavides *et al.* (2005, 2007) also used AFLP fingerprinting to analyze genetic variability and biogeography in specimens originating in 17 countries. Results suggest the possibility of three separate introductions to the Americas and that West Africa was the origin of introductions into America and Asia. Genetic variability was low among specimens, as is to be expected for a species with extreme inbreeding (Andreev *et al.*, 1998), although using microsatellite markers developed by Gauthier and Rasplus (2004) as well as mtDNA, Gauthier (2010) reported low genetic variability within countries, but "considerable variation among groups of *H. hampei* specimens," which was presented as evidence for a species complex within *H. hampei*.

3.4 Damage and Losses

Damage caused by the coffee berry borer commences after adult females bore a hole in the coffee berry (Figure 11.5E) and lay their eggs in galleries built in the endosperm (i.e., the coffee seed, which is the marketable product), followed by larval feeding within the galleries (Figure 11.5F). Consequences of infestation include abscision of berries, loss in

TABLE 11.1 Reports for First Detection of the Coffee Berry Borer in Various Countries, in Chronological Order

Country and Year	Reference
Liberia 1897	Hopkins, 1915b
Gabon 1901	Beille, 1925
Republic of Congo 1901	Fleutiaux, 1901
Central African Republic and Republic of Chad 1902–1904	Chevalier, 1947
Democratic Republic of the Congo 1903	Leplae, 1928
Uganda 1908	Gowdey, 1911
Indonesia—Java 1908	Hagedorn, 1910
Angola 1912	Morstatt, 1912
Brazil 1913	Berthet, 1913; Neiva, 1928
Indonesia—Borneo and Sumatra 1919	Corporaal, 1921; Corbett, 1933
Côte d'Ivoire 1922	Beille, 1925
Cameroon 1924	Mbondji, 1988
United Republic of Tanzania 1924–1925	Ritchie, 1925
Benin 1925	Hesse, 1925
Kenya 1928	Wilkinson, 1928, 1929
Malaysia 1928	Corbett, 1933
Democratic Republic of São Tomé and Príncipe, 1929	Kaden, 1930
Togo 1930	Wegbe, 2012
Sri Lanka 1935	Hutson, 1936
Mariana Islands (Micronesia) 1945	Wood, 1960
New Caledonia 1948	Bugnicourt, 1950
Surinam 1951	van Dinther, 1960
Pohnpei (Micronesia) 1953	Wood, 1960
Peru 1962	de Ingunza, 1964
Tahiti 1963	Johnston, 1963
Philippines 1963	Gandia and Boncato, 1964
Ethiopia 1967	Davidson, 1967
Guatemala 1971	Hernández Paz, 1972
Honduras 1977	Muñoz, 1985
Jamaica 1978	McPherson, 1978; Reid 1983
Bolivia 1978	Rogg, 1997
Mexico 1978	Baker, 1984
Fiji 1979	Anonymous, 1979
Ecuador 1981	Klein-Koch, 1990
El Salvador 1981	Vega Rosales and Romero, 1985
Colombia 1988	Cárdenas M. and Bustillo, 1991
Nicaragua 1988	Monterrey, 1991
India 1990[1]	Kumar *et al.*, 1990
Cuba 1994	Hernández, 2002
Dominican Republic 1994	Serra, 2006
Bolivarian Republic of Venezuela 1995	Rosales Mondragón et al., 1998
Costa Rica 2000	Staver *et al.*, 2001
Lao People's Democratic Republic 2004	CABI, 2008
Panama 2005	Inwood, 2005
Vietnam 2007	Beaver and Liu, 2010
Puerto Rico (USA) 2007[2]	Osorio, 2007; NAPPO, 2007
Hawaii (USA) 2010	Burbano *et al.*, 2011
Martinique 2012	Dufour, 2013

[1]*A 1930 report on the presence of the coffee berry borer in India (Anonymous, 1930) became a matter of proper identification (Coleman, 1931; Kannan, 1931) and turned out to be a misidentification (Coleman, 1931; Thomas, 1949).*
[2]*Earlier reports on the presence of H. hampei in Puerto Rico are incorrect and were based on a misidentification (Vega et al., 2002b).*

seed weight, and loss in quality (Duque O., 2000; Duque-Orrego *et al.*, 2002; Duque O. and Baker, 2003). To the best of our knowledge, of more than 3000 insect and mite species associated with coffee (Waller *et al.* 2007), the coffee berry borer is the only insect that completes its development after consuming the seeds inside coffee berries in the field, even though other insects have been reported to feed on the berry or as seed feeders in storage conditions (Bigger, 2008).

Yearly losses caused by the coffee berry borer have been estimated at US$500 million (Vega *et al.* 2002b), although a recent paper by Oliveira *et al.* (2013), which estimates losses for Brazil at US$215–358 million, indicates that the US$500 million is very conservative. In Colombia, more than 715,000 ha had been infested by 1998, equivalent

to ca. 82% of the total coffee-growing area, and associated losses were estimated at ca. US$100 million in 2002 (Duque O., 2000). By 2002, over 800,000 ha were infested, equivalent to 90% of the total coffee-growing area (Duque-Orrego *et al*., 2002). Costs associated with managing the insect in Colombia have been estimated at 5.5–11% of total production costs (Duque-Orrego *et al*., 2002). To illustrate the magnitude of the problem in Brazil, in 1924 ca. 8,000,000 trees were infested in Campinas, out of a total of ca. 24,700,000 trees. To educate growers, a coffee berry borer film describing the biology of the insect, the damage it causes, how to differentiate it from other insects, and available control methods was produced in 1925 and seen by 104,634 people after being shown in cinemas 232 times (Pamplona, 1927).

3.5 Biology

Several extraordinary papers on the basic biology of the coffee berry borer and possible control methods were published in the early 1900s by scientists in Africa (Mayné, 1914; Beille, 1925; Hargreaves, 1926, 1935; Ghesquière, 1933), Brazil (Costa Lima, 1924a, b; Neiva *et al*., 1924a, b; Neiva, 1928; Oliveira Filho, 1927; Fonseca, 1937, 1939; Fonseca and Araujo, 1939; Bergamin, 1943a), and Asia (Hagedorn, 1910; Roepke, 1919; Leefmans, 1920, 1923, 1924; Friederichs, 1922a, b, 1923, 1924a, b; Friederichs and Bally, 1922, 1923; Corbett, 1933). A common theme in these papers, mostly published in French, Portuguese, or Dutch, is that like many other Scolytinae, the coffee berry borer has female colonizers, males are smaller than females, sibling and pre-dispersal mating occurs, females are preponderant, and males cannot fly. These topics are discussed in detail below.

3.5.1 Boring into the Berry

Even though the term "berry" is commonly used when referring to the coffee fruit (and will be used throughout the chapter), the correct botanical name is drupe (Wrigley, 1988). Females usually bore the coffee berry through the disc, originally the floral disc of the flower, located on the upper part of the berry; at the other end of the fruit is the pedicel, which is the part attaching the fruit to the stem, via the inflorescence (called the "infructescence" when the plant is in fruit) (Figures 11.5E and 11.8A, B). The style passes through the floral disc in the flower stage; during fruit development the hole closes up as the style dies back (Wrigley, 1988). It has been assumed that the disc is the preferred area for boring, as it provides a non-smooth surface for the insect to hold on while initiating the boring process (Costa and Faria, 2001; Cárdenas Murillo and Posada Flórez, 2001). The rough surface area on the disc presents a contrast to the smooth surfaces elsewhere on the berry.

The first step in the infestation process is the entrance of a colonizing female into the berry (Figure 11.5E). The entrance hole is circular, 0.6–0.8 mm (Varón *et al*., 2004) to 1 mm in diameter (Wilkinson, 1928), which is very close to the width of a female insect (0.7 mm; Roepke, 1919; Bergamin, 1943a). In a laboratory study, Penagos Dardón and Flores (1974) placed female coffee berry borers on each one of eight green berries within four different branches removed from plants in the field and determined boring time until the insect "disappeared" inside the berry. The experiment was repeated several times and a total of 146 females were evaluated. The minimum time to enter the berry was 2 h, with a maximum time of 7 h 20 min. The average time to enter the berry was 4 h 16 min.

In a laboratory study in Ethiopia, the boring process until the insect is partially inside the berry took 8 h in green berries, 5.5 h in ripe berries, and 4 h in dry berries (Mendesil *et al*., 2004). Wrigley (1988) stated that (1) it takes 2.5–4 h for the insect to enter the berry; (2) after 24 h the insect can no longer be seen through the entrance hole; and (3) it takes a minimum of 2 days before the insect starts building galleries in the seed. In a field study in Guatemala, Campos Almengor (1982) observed insects boring into berries for a 12-h period (6:00 AM–6:00 PM) and reported that highest boring activity occurred between 12:00 and 5:00 PM.

Boring in the field usually commences when berries are in the green stage and the determining factor for the progress of the penetration is the dry content of the berry, which has to be 20% or higher (Baker, 1984, 1999; Bustillo *et al*., 1998). The 20% dry weight stage is reached ca. 120–150 days after flowering (Baker, 1999; Ruiz-Cárdenas and Baker, 2010; Arcila Moreno, 2011), with harvesting occurring 200–250 days after flowering (Baker *et al*., 1992a). In a laboratory study, Ticheler (1961, 1963) found that there was no insect development in berries with moisture content of 75% or higher.

In some studies, four different positions for the colonizing female are described using letters: (A) female searching for a berry or initiating perforation; (B) female boring into berry, with part of the abdomen visible on the external part of the berry; (C) female inside the berry, boring into the seed; and (D) female and progeny inside seeds (Bustillo P. *et al*., 1998). Camilo *et al*. (2003) assessed the position of colonizing females in berries starting at 77 days after flowering. Between 70 and 86% of females were observed to initiate the boring process and remained in position B until 112 days after flowering; at 161 days after flowering less than 10% remained in position B, having therefore completely entered the berry.

There is usually one hole per berry, unless infestations are high (Neiva *et al*., 1924a; Hargreaves, 1940; Mendesil *et al*., 2004; Vega *et al*., 2011). As stated by Wrigley (1988), "during periods of intense infestation more

than one female may bore into a single berry, each with its own entrance."

When suitable berries are absent, the insect could bore into the peduncles of young berries (Friederichs, 1922a) and after severe pruning, insects can bore into branches as well as older wood (Friederichs, 1923). Reproduction was not observed in any of these sites.

3.5.2 Oviposition

Females build galleries within the seed, where they oviposit. The number of eggs per female and oviposition period varies greatly. Friederichs (1924a) reported an average of 56 eggs per female and an oviposition period extending to 40 days. At 27°C in the laboratory, Bergamin (1943a) reported 24–63 eggs per female (with a maximum 119 eggs) and an oviposition period of 11–15 days. Leefmans (1923) obtained 164 insects from one coffee berry and Jaramillo *et al.* (2009a) recorded up to 288 eggs by an individual female in a berry.

Corbett (1933) found that after removing a female from a coffee berry it would not stop ovipositing, indicating they only need to be fertilized once. This also implies that "as in most female insects" (Chapman, 2003), coffee berry borer females must have a spermatheca, which by definition is "used for the storage of sperm from the time the female is inseminated until the eggs are fertilized" (Chapman, 2003). Rubio-Gómez *et al.* (2007) and Rubio G. *et al.* (2008) present details on the reproductive system of male and female coffee berry borers, including the spermatheca.

3.5.3 Larval Instars, Life Cycle, Adult Size, and Mating

Upon hatching, female coffee berry borers exhibit two larval instars in contrast to males, which only have one (Bergamin, 1943a; Figure 11.5A). The average time to complete the life cycle (egg to adult), as well as longevity, will depend on temperature and on how the assessment is made, i.e., natural conditions in the field, insects reared on berries in the lab, artificial diet, etc. Several papers have reported on these two parameters and only a few will be mentioned for illustrative purposes.

At constant temperatures of 19.2, 24.6, and 27°C, it takes 63, 27.5, and 21 days, respectively, to complete the life cycle (Bergamin, 1943a). In the field in Java, the life cycle takes about 1 month (Roepke, 1919) or 20–36 days, with an average of 25 days (Leefmans, 1923). In the Ivory Coast, Ticheler (1961, 1963) reported completion of the life cycle in 40.5 days at an average field temperature of 26°C, while in the Democratic Republic of the Congo, Steyaert (1935) reported completion of the life cycle in 36 days. In the laboratory, Muñoz (1989) reported completion of the life cycle in 35.8 days at 23°C, while in Ethiopia, completion of the life cycle took 24–43 days at 25°C and 60% relative humidity (RH) (Mendesil *et al.*, 2004). In artificial diet it takes 5–6 weeks (López-Pazos *et al.*, 2009).

Adult females are larger (1.6–1.9 mm) than males (0.99–1.3 mm) (Roepke, 1919; Hargreaves, 1926; Corbett, 1933; Bergamin, 1943a) (Figures 11.3E and 11.5B–D). The width of males and females is ca. 0.6 and 0.7 mm, respectively (Roepke, 1919). Sibling mating occurs inside the berry (Leefmans, 1923; Sladden, 1934; Bergamin, 1943a) and males never leave the berry (Friederichs, 1922a, 1924a; Wilkinson, 1928; Corbett, 1933; Mathieu *et al.*, 1997a). According to Bergamin (1943a), males hatch first and also reach the adult stage first in order to be sexually active once females become sexually active, ca. 3–4 days after molting into adults. Borsa and Kjellberg (1996a) also found that there is a tendency for earlier maturity in males than in females. In contrast, Dias Silva *et al.* (2012) reported that in the laboratory, both males and females take less than 2 days to reach sexual maturity. Similarly, Baker *et al.* (1992a) found that male and female offspring appear at the same time. Because there is a skewed sex ratio favoring females (discussed below; Table 11.2), males mate with multiple females (Brun *et al.*, 1995a). Leefmans (1923) reported one male could mate with 12 females while Giordanengo (1992) recorded one male inseminating 128 females and four others individually inseminating 70–121 females. Multiple matings by females were observed by Dias Silva *et al.* (2012) in the laboratory, although it remains unknown whether this occurs in natural conditions in the field.

According to Roepke (1919), "The mother-beetle does not appear to leave the infested berry until the larvae are full grown; it then leaves with them, probably through the entrance hole." Various papers contradict this finding. Ticheler (1961, 1963) and López-Guillén *et al.* (2011) found that once females enter the berry and start ovipositing, their muscles degenerate; therefore, it is not clear why the colonizing female would leave the berry, as stated by Roepke (1919), if it cannot fly. Baker *et al.* (1992a) reported that the colonizing female remains with the developing progeny.

3.5.4 Generations per Year

Using seeds in the laboratory and not controlling for temperatures, Bergamin (1943a) was able to rear seven generations in 1 year. Ticheler (1961, 1963) reported that depending upon mean temperatures, there is an average of nine generations in Ivory Coast, a maximum of 13, and a minimum of five to six. In New Caledonia, Giordanengo (1992) reported four to five generations per year. Using degree-days, Jaramillo *et al.* (2009c) estimated the possible number of coffee berry borer generations in

TABLE 11.2 Sex Ratios Reported for the Coffee Berry Borer

Sex ratio (♀:♂)	Reference
56:1[1]	Leefmans, 1920
14.5:1[2]	Corporaal, 1921
40:1	Leefmans, 1923
8:1	von Ihering,1924
10:1	Hargreaves, 1926
21.5:1	Wilkinson, 1928
8.5:1.5 to 8.3:1.7[3]	Bemelmans, 1930
56:1; 9.8:1; 13:1; 15.5:1[4]	Corbett, 1933
9.2:0.8[5]	Leroy, 1936
9.75:1	Bergamin, 1943a
11.4:1; 11.6:1; 15.9:1; 8.2:1	Ticheler 1961, 1963
10.3:1; 5.9:1; 10.3:1[6]	Ticheler 1961, 1963
5:1 to 20:1	Morallo-Rejesus and Baldos, 1980
231:1; 257:1; 494:1	Bautista Martínez and Atkinson Martín, 1988
10:1	Baker et al., 1992a
5.8:1; 113:1; 33.9:1; 11:1	Baker and Barrera, 1993
5.2:1 (artificial diet)	Pérez López *et al.*, 1995
11.2:1; 6.8:1; 5:1 (artificial diet)[7]	Borsa and Kjellberg, 1996b
20:1 to 30:1	Mendesil *et al.*, 2004
7.4:1 (artificial diet)	Portilla R. and Street, 2006
6.7:1[8]	Portilla R. and Street, 2006
5.7:1 (artificial diet)	López- Pazos et al., 2009
8.8:1.2	Jaramillo *et al.*, 2009a
8.4:1.6; 8.5:1.5; 9:1	Jaramillo *et al.*, 2009c

[1]*The percentage males was reported as 0.23 to 5%, with an average of 1.7% (427 males out of 23,842 females).*
[2]*The percentage males was reported as 0 to 50%, with an average of 6.87% (192 males out of 2793 females).*
[3]*Reported as 15 to 17% males.*
[4]*Ratios for insect collected from ripe berries, black berries from the ground, pupae from ripe and black berries, and from one black berry from the ground, respectively.*
[5]*Reported as 92% females.*
[6]*Sex ratio for 1, 2, and 4 females per berry.*
[7]*Sex ratios for 1, 2 or 3 females, respectively, in artificial diet.*
[8]*Sex ratio for progeny of females from the F_{48} to F_{64} generation in artificial diet after transferring to parchment coffee.*

four locations as follows: 2.4–4.7 in Tanzania; 2.9–4.3 in Colombia; 2–3.1 in Kenya; and 0–2 in Ethiopia. According to Baker (1999), there could be up to three generations within a berry.

3.5.5 Sex Ratio

The coffee berry borer is spanandrous, i.e., "females greatly preponderate" (see Hamilton, 1967). Even though most of the recent literature gives a 10:1 sex ratio for the coffee berry borer, in actuality a wide range of sex ratios favoring females (5.1:1 to 494:1) have been reported (Table 11.2). This range was recognized by Corbett (1933) 80 years ago: "The variation in the proportion of the sexes is significant."

The skewed sex ratio favoring females might be due to the presence of *Wolbachia* (Vega *et al.*, 2002a), a maternally inherited cytoplasmic α-proteobacterium that infects gonads and somatic tissues and which is quite common in insects (Jeyaprakash and Hoy, 2000; Hilgenboecker *et al.*, 2008). *Wolbachia* manipulates host reproduction via various mechanisms, including feminization (sex conversion), parthenogenesis, cytoplasmic incompatibility, and male killing (O'Neill *et al.*, 1998; Vega *et al.*, 2002a; Kageyama *et al.*, 2012).

The four studies reporting sex ratios for insects reared in artificial diet (Table 11.2) show a lower proportion of females than in all other studies, which report sex ratios in berries. A possible explanation is that among the ingredients included in the artificial diets are antimicrobial agents (e.g., sorbic acid, tetracycline, methyl paraben, benzoic acid, formol), some of which might be having an inhibitory effect on *Wolbachia*.

Borsa and Kjellberg (1996a) determined that competition among female coffee berry borers in artificial diet influenced the brood sex ratio, with the number of males significantly increasing as the number of competing females increased from one to two or three (Table 11.2). The experiment also revealed that competition among females led to fighting and occasional mutilation. Removal of dead immature stages from berries by the colonizing female, referred to as brood hygiene, has been reported by Baker *et al.* (1992a, 1994).

3.5.6 Longevity

Reports for female longevity vary widely, e.g., 55 days (Friederichs, 1924a); 96 days (Corbett, 1933); 102 days (Leefmans 1923); 81–282 days with an average of 156 (Bergamin 1943a); and 131 days (Muñoz, 1989). Brun *et al.* (1993) reported one female living 380 days in artificial diet. Longevity of males in the laboratory ranges from 21–43 days (Oliveira Filho, 1927) to 24–52 days (Giordanengo, 1992). Bergamin (1943a) reports that overall, males do not live more than 40 days, although three males he separately assessed lived to 78, 80, and 103 days. For insects reared in berries in the laboratory, Bautista Martínez and Atkinson Martín (1988) noted that adults could survive 6 months.

According to Corbett (1933), females can live without food for 81 days. This is in contrast to Mathieu *et al.*'s (1997a)

finding that once females emerge from dry berries they can live for up to 11 days without food. Baker (1999) reported survival of more than 3, and even up to 8 months on dried or overripe berries.

3.5.7 Parthenogenesis

The production of fertile offspring from unfertilized eggs is known as parthenogenesis. Even though various papers have reported that the coffee berry borer does not reproduce parthenogenetically (Leefmans, 1923; Hargreaves, 1926; Bergamin, 1943a; Browne, 1961; Entwistle, 1964), Muñoz (1989) and Trejo *et al.* (2000) reported parthenogenetic reproduction in the coffee berry borer. Subsequent experiments have not been able to confirm parthenogenetic reproduction (Barrera *et al.*, 1995; Alvarez Sandoval and Cortina Guerrero, 2004; Berrio E. and Benavides M., 2008; Constantino *et al.*, 2011). Thus, virgin coffee berry borers can lay eggs, but they are not fertile (Bergamin, 1943a).

3.5.8 Functional Haplodiploidy

The coffee berry borer exhibits functional haplodiploidy (see Chapter 3). The concept is best understood by first presenting individual definitions for various terms. Haplodiploidy means that reproduction is arrhenotokous, i.e., males are only produced from unfertilized eggs and females are produced from fertilized eggs, resulting in haploid males and diploid females. The use of "functional" to define haplodiploidy in the coffee berry borer means that reproduction is pseudoarrhenotokous, i.e., male eggs are fertilized and even though the male is a diploid, it is functionally a haploid because the paternal set of chromosomes condenses into a mass of chromatin, resulting in (1) failure to be incorporated into semen during spermatogenesis or (2) inactivation in the somatic cells (Brun *et al.*, 1995a, b; Borsa and Kjellberg, 1996b). It is possible that *Wolbachia* is involved in this process of chromosome condensation (see Vega *et al.*, 2002a).

The fact that the eggs of unfertilized females do not hatch (Bergamin, 1943a) also serves as evidence for functional haplodiploidy (Brun *et al.*, 1995b; Borsa and Kjellberg, 1996b), i.e., males would hatch from unfertilized eggs if the insect were truly haplodiploid. Further evidence for diploid males was presented by Borsa and Coustau (1996) after finding heterozigozyty in a cyclodiene resistance locus (*Rdl*) in male and female coffee berry borers. Cytogenetic evidence for diploid coffee berry borer males has been published by Bergamin and Kerr (1951), Brun *et al.* (1995a, b), and Constantino *et al.* (2011).

As mentioned above, once a colonizing female lays eggs within galleries in the berry the progeny has a skewed sex ratio favoring females and there is sibling mating, which by definition implies inbreeding. High inbreeding and low genetic variability has been demonstrated in various coffee berry borer studies (Borsa and Gingerich, 1995; Gingerich *et al.*, 1996; Borsa and Coustau, 1996; Andreev *et al.*, 1998; Gauthier and Rasplus, 2004). When infestation levels are high, it is not unusual to find a berry attacked by more than one colonizing female as evidenced by several entrance holes (Leefmans, 1923; Neiva *et al.*, 1924b; Wilkinson, 1928; Sladden, 1934; Leroy, 1936). Leefmans (1923) found that 83% of the black berries remaining on the plants and 8% of ripe berries were infested with more than one colonizing female. This situation could serve as a mechanism for outbreeding, although in such situations fecundity is hindered (Friederichs, 1924a; see Vega *et al.* (2011) for similar results in artificial diet). Based on a laboratory experiment, Mathieu *et al.* (1997a) proposed that females emerging from dry berries in the field during the interseason (i.e., between harvests) might enter dry berries again as a result of not finding suitable berries on trees. Such situations could theoretically result in outbreeding. The genetic relatedness among progenies where more than one colonizing female is present (as described above) has not been experimentally determined.

3.5.9 Pheromones

No sexual pheromones have been reported for the coffee berry borer. The biology of the female, which is inseminated by its sibling inside the berry, makes the production of a sex pheromone unlikely (de Kraker, 1988). According to Wood (1982) pheromones "apparently have not been reported from any species with the habit of consanguineous polygyny."

3.5.10 Vision

An important feature in the basic biology of an insect is the responses to movement and color. These responses will depend on visual acuity, and in the case of the coffee berry borer there is a marked sexual dimorphism in terms of the development of the compound eyes. Wood (2007) reported that males in 14 of 51 *Hypothenemus* species from South America have reduced eyes when compared to females. Using an optomotor response apparatus, Vega *et al.* (2014) demonstrated that in contrast to females, male coffee berry borers do not respond to movement, most likely as a result of the biology of males, whereby they are born inside the coffee berry and never leave it, thus not having need for vision. Male coffee berry borers have rudimentary eyes, with a significantly lower number of facets in males (19.1 ± 4.10) than in females ($127.5 \pm v3.88$) (Vega *et al.*, 2014).

Color preferences by females have been examined using both artificial and field-collected berries. Ticheler (1961, 1963) compared female preference for black, red, yellow, and green artificial berries (painted cotton balls imbibed with paraffin and shaped like a coffee berry) and found

preference for black berries, followed by red. Mathieu *et al.* (2001) tested visual responses to red and green artificial berries made with paraffin wax and found that red berries were more attractive to females. Mendoza *et al.* (2000) determined female preference for green, yellow, red, and black berries, as well as berries made with polystyrene. Females preferred red and black, both in real berries and polystyrene berries. The studies involving artificial berries eliminate olfactory cues associated with real berries and demonstrate that females can detect color.

In a choice test laboratory study using field-collected red, green, and dry berries placed in Petri dishes, females showed preference for red berries over mature green berries, for red berries over dry berries, and for dry berries over immature green berries (Giordanengo *et al.*, 1993). It is important to note that even though females can colonize red berries in the field, it is likely that development of the progeny into adults will not be completed before harvest (Baker, 1999).

3.5.11 Microbiota and its Role in Caffeine Detoxification

Caffeine (1,3,7-trimethylxanthine) is a purine alkaloid present in many plants, including coffee. The seeds of *C. arabica*, on which the coffee berry borer feeds, contain ca. 1.0% caffeine on a dry weight basis, while *C. canephora* contains ca. 1.7% (Lean *et al.*, 2012). The presence of caffeine and other alkaloids in plants have been proposed to have anti-herbivore roles (Levinson, 1976; Nathanson, 1984), and several studies have shown the negative effects of caffeine on insects (Vega *et al.*, 2003b and references therein).

Guerreiro Filho and Mazzafera (2003) tested adult female coffee berry borer feeding responses to seeds from 12 *Coffea* species containing different caffeine contents. The authors could not detect a significant negative correlation between caffeine content and damage caused by the insect. The same occurred when seeds were imbibed in aqueous solutions of caffeine to increase caffeine content. There was also no significant correlation in attraction to mature berries with different caffeine content. Guerreiro Filho and Mazzafera (2003) conclude that caffeine levels are not involved in resistance and that the insect "has evolved an adaptation to avoid the toxic effects of caffeine."

The adaptation required to survive caffeine consumption must involve a caffeine metabolizing mechanism. Based on the role of yeasts in detoxifying allelochemicals in insects (Vega and Dowd, 2005), Vega *et al.* (2003b) tested a yeast present in the coffee berry borer for caffeine breakdown properties, with negative results. Subsequent work has focused on the role of the gut microbiota. The terms microbiota and microbiome have been used to describe the "organisms that live inside and on humans" and "the genomes of these microbial symbionts," respectively (Turnbaugh *et al.*, 2007). The terms are no longer used just for humans and are applicable to all types of organisms.

The first step in elucidating the role of gut microbes in caffeine breakdown was to develop a technique to dissect the ca. 3.5-mm-long alimentary canal of live female coffee berry borers, in order to subsequently isolate and identify the associated microbiota (Ceja-Navarro *et al.*, 2012). Ceja-Navarro *et al.* (submitted) isolated and identified 13 bacterial species (*Pseudomonas fulva*, *P. fluorescens*, *Pantoea vagans*, *P. septica*, *P. eucalypti*, *Ocrobactrum* sp., *Enterobacter* sp., *Kosakonia cowanii*, *Brachybacterium rhamnosum*, Jonesiae, *Microbacterium binotii*, *Novosphigobium* sp., and *Stenotrophomonas maltophilia*) that subsist on caffeine as the sole source of carbon and nitrogen. Addition of antibiotics to the coffee berry borer artificial diet eliminated caffeine degradation, thus demonstrating the involvement of the microbes in the process. The caffeine demethylase gene (*ndmA*) was expressed *in vivo* in field specimens as well as in *P. fulva* isolated from the alimentary canal. Diet inoculation with *P. fulva* restored the ability to degrade caffeine. Elucidating the mechanism for caffeine detoxification in the coffee berry borer presents new research options, as well as challenges, for managing the insect. For example, the use of bacteriophages might result in interference with the microbes involved in caffeine detoxification, although their introduction and survival in the field might not be feasible due to the biology of the insect, i.e., the introduced trait, and by definition would cause death of the insect and would not be able to compete with wild populations.

3.5.12 Association with Fungi

The mycobiota associated with the coffee berry borer has been shown to be quite extensive. Pérez *et al.* (2003) isolated 38 fungal species in 21 genera from the insect cuticle (29 species), alimentary canal (18 species), and feces (10 species), and four genera from galleries (five species). Carrión and Bonet (2004) identified 12 fungal species associated with the insect and seven with the galleries, while Gama *et al.* (2005, 2006) identified 10 fungal genera associated with the insect and five with the galleries.

Rojas *et al.* (1999) isolated *Fusarium solani* (Mart.) Sacc. (current name: *Haematonectria haematococca* (Berk. and Broom) Samuels and Rossman; Hypocreales: Nectriaceae) from adult female coffee berry borers reared in artificial diet as well as from insects collected in the field in Mexico and Benin. This association led them to propose this as a "close association." In a subsequent study (Morales-Ramos *et al.*, 2000) concluded that this was a symbiotic association, and that insects reared in beans

infected with *F. solani* had significantly higher fecundity than insects reared in sterile beans. This was ascribed to higher ergosterol levels in beans infected with the fungus. Such symbiotic association would require the presence of mycangia. Even though Morales-Ramos *et al.* (2000) were unable to find mycangia, they proposed that the asperities and setae on the pronotum might serve a similar function. One issue with this proposal is that the exposed asperities would have to be selective for *H. haematococca* spores, and it is not clear how this could happen. Another issue is that based on size, the photograph included in Morales-Ramos *et al.* (2000) depicts bacteria and not *H. haematococca* conidia, whose size is 6–24 × 2.5–5 μm (Rossman *et al.*, 1999). Pérez *et al.* (2005) pursued the topic of mutualistic fungi using three different fungi (including *H. haematococca*) and did not find any evidence for beneficial effects on the insect. To our knowledge, *H. curtipennis* (Figure 11.2G) remains the first and only cryphaline ambrosia beetle and the only *Hypothenemus* species for which mycangia have been identified (Beaver, 1986).

3.5.13 Genome

Very little is known about the coffee berry borer genome. Nuñez *et al.* (2012) reported an estimated genome size of 170–180 Mb with 20,653 unigenes while Benavides *et al.* (2014) reported a 194 Mb genome, with ≈20,500 unigenes. A gene of bacterial origin encoding for mannanase (discussed in Section 3.12), has been identified in the coffee berry borer genome (Acuña *et al.*, 2012).

3.6 Ecology

3.6.1 Host Plants

Vega *et al.* (2012a) presented evidence for the possible polyphagous nature of the coffee berry borer, based on a study by Schedl (1960), who collected the insect in 20 genera other than *Coffea* in forests in the Democratic Republic of Congo. Schedl (1960) suggested that the coffee berry borer might be polyphagous: "...there exists inside the rainforest a series of natural hosts for the parasite that give it the possibility to develop independently from coffee plantations" (translated from the French original). The paper by Schedl (1960) as well as two additional papers (Beille, 1925; Ghesquière, 1933) bring to the forefront the possibility that the insect originates in the humid, evergreen forests and that it feeds on various plants, perhaps including wild *Coffea* species. This scenario would make the insect movement to cultivated coffee more plausible as coffee cultivation increased in deforested areas.

Ghesquière (1933) unequivocally stated that he obtained different life stages of the coffee berry borer from the legume *Dialium lacourtianum* Vermoesen (current name: *D. englerianum* Henriq.; Leguminosae). Based on these results, he proposed that the plant could be used as a trap. Gumier-Costa (2009) reported the insect breeding in Brazil nuts (Lecythidaceae) collected in the field.

Even though several papers have reported the coffee berry borer in many different plants, none has shown that the insect completes its life cycle in these plants (Eggers, 1922; Oliveira Filho, 1927; Hargreaves, 1935, 1940; Baguena Corella, 1941; Viana, 1965; Morallo-Rejesus and Baldos, 1980; Campos Almengor, 1981; Quezada and Urbina, 1987; Vijayalakshmi *et al.*, 1994; Messing, 2012). The presence of the insect in these plants is either temporary, perhaps as a result of seeking shelter, or possibly a misidentification of the insect (Oliveira Filho, 1927; Le Pelley, 1968; Wrigley, 1988).

3.6.2 Host Finding

Insect attraction to plants can be influenced by kairomones, as well as by plant shape and color, among others factors (Vinson, 1976; Prokopy and Owens, 1983; Miller and Strickler, 1984; Vet and Dicke, 1992; Vet, 1999). A kairomone is a chemical signal produced by one organism, in this case the coffee plant, which "evokes in the receiver" (the coffee berry borer), "a behavioral or physiological reaction which is adaptively favorable to the receiver, but not to the emitter" (Price *et al.*, 2011). Thus, a search for signals produced by coffee plants that end up attracting the coffee berry borer has been an area of research interest for many years.

The pioneer studies on coffee plant kairomones were based on extracts from coffee berries, without focusing on the identification of the particular components in the extract. For example, Prates (1969) conducted a laboratory experiment in which extracts of coffee berries (the solvent is not mentioned) were tested for their attraction to the coffee berry borer. Pure extracts and 50% diluted extracts were significantly more attractive to the insect than water or extracts diluted at 25%. In Mexico, Velasco Pascual *et al.* (1997a, b) collected berries from two varieties of *C. arabica* and from *C. canephora* and homogenized them in 80 ml of methanol and 120 ml of ethanol, followed by placement of traps with the extracts in a *C. canephora* plantation. There were significant differences in insect capture based on the coffee variety used for preparing the extracts, and traps containing methanol, ethanol, or a methanol: ethanol mixture were also shown to capture insects, in some cases at levels not significantly different than those in the traps with the extracts. The results indicate there might be one or more components in the berry extract that increases attraction.

In similar studies, Gutiérrez-Martínez *et al.* (1990) and Gutiérrez-Martínez and Ondarza (1996) used six different solvents to extract different *C. canephora* parts (flower, leaves, berries, branches, roots, etc.). The extracts were

tested in the field and the laboratory for their attraction to the coffee berry borer. The highest insect capture in the field resulted from a methylene chloride/ethanol extract of ripe coffee berries. Giordanengo *et al.* (1993) used a Y-shaped olfactometer and reported significantly higher female attraction towards red berry volatiles than towards green berry volatiles. Females also responded to unidentified volatiles obtained from green berry acetone extracts, but not to hexane or ethanol extracts.

An ingenious experiment conducted by Ticheler (1961, 1963) used groups of green or red berries, each placed inside one half of a divided Petri dish. Females were allowed to walk on a mesh placed over the dish, and preferred walking over the area enclosing the green berries at a significantly higher rate than over red berries. The results suggest that volatiles emanating from green berries are more attractive to the insect than volatiles from red berries. Other experiments by Ticheler (1961, 1963) showed that females were significantly more attracted towards areas in Petri dishes where red or green berries were not covered with cellophane. Thus, the entire arena over which the insects were walking was the same color (red or green), and the only difference was the presumed volatiles emanating from the area not covered with cellophane (in separate experiments, cellophane had been shown not to influence selection). In an interesting twist, Ticheler (1961, 1963) removed the antennas and repeated the experiment using red berries and covered one half of the dish with cellophane. Females preferred the area over the red berries without cellophane at a significantly higher rate. He concluded that the antennae are not the only sensory organs involved in volatile detection in the coffee berry borer.

In a laboratory experiment in which red berries were placed on one half of a platform over which the insect release arena was located, Mathieu *et al.* (2001) found that colonizing females (those that emerged from berries or artificial diet) were significantly more attracted to the area above the berries than to the other half of the platform, under which no berries were present. In contrast, non-colonizing females, defined as virgin and mated nulliparous females still within the artificial diet, avoided the area above the berries, and the negative response became stronger with age. The results are noteworthy because it separates visual from olfactory cues and demonstrates that olfactory responses are influenced by the physiological state of the female.

Starting in the early 1990s, various studies focused on the identification of volatiles emanating from coffee berries with the goal of eventually identifying candidates that might be serving as coffee berry borer attractants (Mathieu *et al.* 1991, 1996, 1998; Ortiz *et al.*, 2004). Ortiz *et al.* (2004) identified 27, 34, 41, and 68 compounds in green, half-ripe, ripe, and overripe berries, respectively. Mendesil *et al.* (2009) ran olfactometer bioassays using green, ripe, and dry berries and found positive responses to volatiles emanating from ripe and dry berries, but not to volatiles from green berries. They chose to examine the volatile profile from dry berries. Using gas chromatography-mass spectrometry (GC-MS), six compounds with positive electroantennogram responses were identified: ethylbenzene, limonene, methylcyclohexane, nonane, 1-octen-3-ol, and 3-ethyl-4-methylpentanol. Only one of these, methycyclohexane, was present in the volatile profile of green berries. All six were present in ripe berries but at lower concentrations than in dry berries. Three of the six compounds (nonane, 3-ethyl-4-methylpentanol, and 1-octen-3-ol) were also identified by Ortiz *et al.* (2004) as volatiles from coffee berries. Four of the electroantennogram-positive compounds elicited attraction in the olfactometer bioassay: 3-ethyl-4-methylpentanol, nonane, methylcyclohexane, and ethylbenzene. A blend of these four compounds also elicited attraction. Because these compounds are not specific to *C. arabica*, Mendesil *et al.* (2009) presume that as single compounds, they are not used for host recognition by the coffee berry borer, but that a blend might be more likely for host recognition.

Jaramillo *et al.* (2013) identified 49 volatile compounds in ripe berries (defined as having a yellow-orange exocarp) and 26 in green berries. Four compounds in ripe berries (conophthorin, chalcogran, frontalin, and sulcatone) serve as pheromones for some conifer bark beetles (e.g., *Dendroctonus*, *Pityogenes*, *Gnathotrichus*). Only one of these compounds (conophthorin) was present in green berries. In Y-tube olfactometer bioassays, female coffee berry borers were attracted to conophthorin and chalcogran.

3.6.3 Dispersal

Females are the dispersal unit in the coffee berry borer. Females living inside berries left on trees after harvest or in berries that have fallen on the ground serve as a source for subsequent dispersal and infestation of newly formed berries. For example, Corbett (1933) counted 93 females and six male coffee berry borers in one robusta berry collected from the ground. Leefmans (1924) calculated that ca. nine million coffee berry borers could be present in fallen berries in 875 acres, equivalent to 10,285 insects/acre. He also found that covering the infested berries in the soil with 8, 12, or 20 inches of loose soil would not prevent the insects from emerging, a finding also supported by Friederichs (1922a). Baker (1984) estimated that over 500,000 insects/ha could remain in berries that have fallen on the ground. Bustillo *et al.* (1999) and Vera *et al.* (2011) have reported on the use of fungal entomopathogen conidial suspension sprays on berries on the ground to reduce numbers of females emerging from these berries.

Another source of insects are the pruned branches left on the ground in the process of rejuvenation of plantations (Baker, 1999). In Colombia, insects emerging from berries on branches left on the ground after pruning plantations have been estimated at 1.5–2 million/ha (Baker, 1999) and 2–3.5 million flying females/ha from an estimated seven to nine million total number of insects (Benavides M., 2010).

Various factors influence female emergence from the native berry, such as high light intensity, and the presence of green berries nearby (Mathieu *et al*., 1997a), although Steyaert (1935) found beetles were more active in cloudy weather than on bright days. Low (<60%) and high (>90%) RH occurring after rains also induces emergence from the berry (de Kraker, 1988; Baker *et al*., 1992b; Baker and Barrera, 1993), as well as increases in temperature (Baker *et al*., 1992b; Jaramillo *et al*., 2010a). Baker *et al*. (1994) showed that the insect is very sensitive to RH, with survival time at 93.5% RH being twice that at 84%.

Acevedo-Bedoya *et al*. (2009) examined the use of a DayGlo® fluorescent pigment to mark coffee berry borers for dispersal studies. The pigment could only be detected for 5 days and examinations had to be conducted in the dark using a black light and a stereoscope. Therefore, the use of these pigments is of limited value for dispersal studies. On the other hand, a molecular marker developed by the same authors showed more potential for dispersal studies.

3.6.4 *Flight*

Seven different types of flight muscles have been identified in female coffee berry borers (López-Guillén *et al*., 2011), and the flight muscle surface area in flying females is larger than that in ovipositing females, indicating (as mentioned above) that the muscles degenerate after oviposition commences (Ticheler, 1961, 1963; López-Guillén *et al*., 2011).

In Java, Roepke (1919) observed females emerging from the berry and attempting to fly at sunset. Also in Java, Leefmans (1923) noted that flight was common between 4:00 and 6:00 PM and that females could cover distances extending up to 348 m. In Uganda, Hargreaves (1926) observed females flying late in the afternoon. Highest flight activity in Nicaragua was between 1:30 and 3:30 PM (Borbón-Martínez *et al*., 2000). In the Democratic Republic of the Congo, Leroy (1936) observed that females exit the berry from 4:00 to 5:00 PM, flying at 4–5 m in elevation and covering up to 300–400 m. Bemelmans (1930) reported that females fly up to 5 m and more than that when pushed by the wind. In Mexico, Baker (1984) reported 22 min as the longest free flight observed in the laboratory and when tethered the longest continuous flight lasted 100 min. In New Caledonia, Giordanengo (1992) reported that colonizing female activity in lab and field peaks at 2:00 PM and noted that unmated females will not fly and therefore disperse. According to Cárdenas Murillo and Posada Flórez (2001) insects can fly in a spiral pattern for 1–2 h, which allows for wide dispersal if winds are prevalent.

The wing length of females is ca. 2.2 mm in contrast to 0.34 mm in males (Corbett, 1933). According to Leefmans (1923), "the wings in the male sex are so much reduced that the males certainly cannot fly." Corbett (1933) reached a similar conclusion when he stated, "the wings in the male do not appear to be sufficiently large for sustained flight." Hargreaves (1926) noted, "males seem incapable of flight" and Bemelmans (1930) stated, "The male cannot fly, being devoid of useful wings" (translated from the French original). Similarly, Leroy (1936) wrote, "The wings seem stunted and consist of small membranous appendages that do not allow the insect to fly" (translated from the French original).

3.7 Shade

As discussed above, in their natural habitat the two commercial coffee species were inhabitants of the humid, evergreen forests in Africa (Davis *et al*., 2006). One of the first reports on the effects of deforestation on an insect is a 1925 paper by the French botanist Lucien Beille (1862–1946), in which he relates how the coffee berry borer became a pest of coffee (Beille, 1925): "The onset of the trouble coincided with the destruction of the forest; it appears that *Stephanoderes*,[1] lacking the plants that it frequents, has found in the new coffee plantations, conditions that are favorable to his evolution" (translated from the French original). Thus, from its natural habitat as an understory plant in forests, coffee plantations can now be found under a wide range of conditions, from full-sun (i.e., no shade trees) to variable shade levels provided by different types of plants (e.g., *Inga*, *Gliricidia*, avocados, bananas, etc.; Figure 11.6).

Shade trees and the ensuing shade levels provide several benefits to coffee plantations: (1) prevent soil erosion; (2) serve as windbreakers; (3) promote biodiversity; (4) increase nutrient recycling and organic matter from fallen leaves; (5) buffer temperatures (see below); (6) maintain higher RH; and (7) provide additional sources of food as well as income for the grower, e.g., wood for burning or for sale, or if shade is provided by bananas, avocados, etc., availability of fruits for family consumption or for sale (Muschler, 2004; Somarriba *et al*., 2004; Albertin and Nair, 2004; Rice, 2011; Tscharntke *et al*., 2011). On the other hand, yields in shaded plantations can be lower than in plantations at full sun (Brun *et al*., 1989a; Gobbi, 2000; Soto-Pinto *et al*., 2000; Muschler, 2004; Haggar *et al*., 2011) while coffee berry borer

1. Old genus for the coffee berry borer.

FIGURE 11.6 Coffee grown at full sun (left) and under shade (right) in Puerto Rico. *Photos by Fernando E. Vega.*

infestation levels have been reported to be higher in shaded plantations (discussed below). These two issues (yields and infestation levels) have been used as justification for eliminating shade in coffee plantations.

Two main reasons have been proposed to explain why shaded plantations have higher coffee berry borer population levels than non-shaded plantations: (1) since the insect evolved in the shade of forests, it is better adapted to that environment and not to the lower RH of sun-exposed plantations, and (2) shade has a negative effect on parasitoids (discussed below). Adult coffee berry borers are very sensitive to RH with an optimum range for survival and development of 90–95% RH at 25°C (Baker *et al*., 1994). These high humidity conditions would be more likely to be encountered in shaded plantations.

The first papers reporting on the effects of shade on the coffee berry borer were conducted by Hargreaves (1926, 1935, 1940) in Uganda and by Jervis (1939) in present-day Tanzania. We have chosen to include relevant quotes from these and other papers to accurately reflect the understanding of the situation at various points in time (Table 11.3). Hargreaves (1926, 1935, 1940) ascribed the reduced damage in the plantations growing at full sun to what he calls parasite preferences for this habitat, although no evidence for this was presented. Hargreaves (1935) further expanded on this topic and stated that shade "is distinctly favourable to the berry-borer" and explains that coffee berry borer damage is higher in unpruned trees and when large trees provide dense shade to the coffee plant (Table 11.3). Similarly, Jervis (1939) reported (Table 11.3) on the sanctuary provided to the insect by a dense plant canopy in Bukoba (Tanzania), where the insect had caused a 73% reduction in value in 1931, and presents branch thinning as a solution to the problem. Jervis (1939) also mentions that the heaviest insect infestations occurred in areas of extreme humidity. It is important to point out that the papers by Hargreaves and by Jarvis (cited above) are based on observations and not on actual experiments, i.e., no data are presented.

From 1939 to 1945, 11 papers dealing with shade and the coffee berry borer were published in Brazil (Mendes, 1938; Fonseca, 1939; Mendes, 1939, 1940a, b; Bergamin, 1943b, 1944b, c, 1945a, b; Rocha Lima, 1945). The goal was to reach a recommendation for the state of São Paulo on whether plantations should be shaded or not. Mendes (1938) presents information from two farms that had shade-grown coffee in which coffee berry borer infestation levels were much higher than in sun-grown coffee, and two farms in which problems with the insect became so severe that the owners in one farm decided to abandon the crop while the owners in the other decided to cut down the entire plantation. Fonseca (1939) notes that during a trip to Uganda he observed higher infestation levels in shaded coffee and that in Brazil, dry and well-aired coffee plantations do not provide favorable conditions to the insect, when compared to more humid and wind-protected shaded plantations. Mendes (1939) presents data showing higher infestation levels in shade-grown coffee and observes that when shade is used, coffee takes longer to mature, which is favorable for development of the coffee berry borer. He concludes by stating that, based on the knowledge available at the time, shade cannot be recommended for growers in São Paulo. In a second study, Mendes (1940a) found higher

TABLE 11.3 Statements in the Literature Related to the Effects of Shade on the Coffee Berry Borer

	Reference
"We have noticed that shaded Coffee is more susceptible to attack than unshaded. In fact, we have seen unshaded Coffee entirely escape, whilst a few yards away, shaded trees were badly infested. It would be of great interest to learn if the beetle is a shade-loving insect."	Brown and Hunter, 1913
"Observations indicate that damage to coffee growing under shade is more extensive than is the case with unshaded coffee. It is the writer's opinion that this is due to preference by the parasites[1] for a sunny habitat, and not, as might be inferred, to any preference by the beetle for shaded conditions."	Hargreaves, 1926
"Damage in Uganda appears to be greatest to coffee under shade."	McDonald, 1930
"The shading of coffee berries, either by overhead shade or by dense foliage of the coffee tree themselves, is distinctly favourable to the berry-borer. In this case, however, it appears that the influence is indirect, by making the habitat less suitable for the parasites. Instances have occurred where estates or parts of estates under heavy shade have suffered intense borer damage continuously, and thinning or complete removal of shade has greatly reduced the incidence of the pest." "Again, large natural trees, providing dense shade, left growing in coffee have been proved to be centres of infestation; the further away from such trees the coffee, the less intense the infestation, until at 50 yards distance the borer could scarcely be found."	Hargreaves, 1935
"Under the methods of cultivation practised by the natives these trees become enormous botanical candelabra with their branches spreading to the ground and from which sprang innumerable shoots, forming a dense canopy and affording complete sanctuary to the coffee berry borer (*Stephanoderes hampei*)..."	Jervis, 1939
"Shade for coffee was, and still remains, the subject of much controversy in Uganda. In the past excessive shade was provided and this depressed yields and encouraged insect pests, especially *Stephanoderes*; later there was a movement for removal of all shade, but recently the consensus of opinion among planters has been more in favour of controlled shade. *Robusta* is essentially a forest plant and is more susceptible to lack of shade than is *arabica*."	Thomas, 1940
"The beetle is capable of causing very serious losses of crop during intense infestation, which occur normally under conditions of dense shade..." "A second factor of great importance[2] is that of shade, both overhead and that provided by the foliage of the coffee itself in closely planted or unpruned trees. Many examples of intense attack, due primarily to forest-like conditions, have been observed by the writer..." "In one instance, where spacing of plants was normal, an almost immediate reduction of the infestation followed thinning of the shade trees, and further removal of shade reduced the borer incidence to almost negligible proportions. In another instance, a reduction in density of the unusually close stand of coffee was necessary in addition to shade-thinning. A striking example of the influence of shade was observed on one plantation where a very large natural tree with immense spread was left among the coffee (otherwise unshaded): near the trunk of this shade tree the berries were intensely infested, and the infestation gradually became less intense in berries more and more distant, until at 50 yards from the trunk the borer could scarcely be found." "The effect of shade appears to be double: direct, as shown above; and indirect, because the parasites prefer better-lighted conditions, or because dense coffee growth makes the search for hosts by the parasites more difficult and more hazardous." "The fruits of wild coffee plants growing in dense forest are almost invariably intensely infested by *S. hampei*."	Hargreaves, 1940
"It is recommended to maintain the shade on the plantations to foster the development of fungal entomopathogens..."[3]	Chevalier, 1947
"Several authorities state that the pest is usually more troublesome in dense shade." "Heavy shade and close planting appear to favour the insect, possibly because of a moisture complex, since there would be too great a competition for the moisture in the soil. Wider spacing and the reduction of shade has immediately reduced an infestation. Dense shade may possibly reduce the population of the controlling parasites."	Haarer, 1962
"Heavy shade, from either shaded trees or inadequately pruned coffee causes conditions unsuitable for the natural enemies of the borer and should be removed."	Crowe and Gebremedhin, 1984
"It is worth remembering that originally coffee was an understory plant in tropical forest and that therefore the broca might find strong direct sunlight in dry season conditions inimical to survival."	Baker, 1984
"*Hypothenumus hampeii* [*sic*] prefers shaded coffee, and removal of shade trees is beneficial."	Bardner, 1985
"Attacks are also more severe where the coffee is grown under heavy shade or is closely planted and unpruned. A single, very large, dense shade tree can cause a serious local infestation. The fruits of wild coffee growing in the	Wrigley, 1988

TABLE 11.3 Statements in the Literature Related to the Effects of Shade on the Coffee Berry Borer—cont'd

	Reference
dense forest are frequently heavily infested. In Brazil the infestation is greater in damp, shaded plantations than in dry, open areas (da Fonseca 1939)."	
"The following cultural measures, if conscientiously applied, do much to reduce the infestation: 1) Reduce heavy shade. 2) Prune the coffee to keep the bush as open as possible. . ." "Heavy shading brought by inefficient pruning favors the survival of CBB, and is unfavorable to natural enemies. Proper pruning is, therefore, necessary for direct or indirect control of CBB."	Crowe, 2004
"At altitudes where berry borer is a problem, the incidence of damage caused by the pest can be reduced by thinning of shade trees and pruning the coffee bushes to open the canopy."	Waller *et al.*, 2007

[1]*What Hargreaves (1926, 1935) calls parasites are nowadays referred to as parasitoids, i.e., insects that oviposit on the coffee berry borer, causing its eventual death.*
[2]*In addition to altitude.*
[3]*Translated from the French: "On recommande de maintenir l'ombrage des plantations pour favoriser le développement des champignons entomophages. . ."*

infestation levels in shaded plots, while in a third set of experiments, Mendes (1940b) found lower infestation levels than in previous years, but these were still higher in shaded plantations. Bergamin (1943b) stated that it is impossible to mimic the shade conditions occurring in the natural habitat of coffee plants, and that berries produced in such conditions are slender with almost no body, and therefore production is null. He also states that depending upon the trees used to provide shade, leaves falling on the ground might decompose slowly, providing a hiding place for berries that have fallen from the plant and which can harbor the insect. Bergamin (1944b) reports infestation levels in shaded coffee in 1943 were 44% vs. 5% in coffee grown at full sun; in 1944, infestation levels were 89.5% and 13.9%, respectively. Bergamin (1944c) discusses that even though there are ideal goals for shading plantations (e.g., providing organic matter, reducing cold winds, reducing thermal variations, etc.), these theoretical observations do not account for the positive biological responses of the insect to shade conditions. Bergamin (1945a, b) and Rocha Lima (1945) conclude that after years of field research it is evident that the coffee berry borer prefers shaded plantations because they provide better conditions for their development, and that shading should not be recommended for coffee plantations in São Paulo.

Another series of experiments in Brazil, starting in 1953 and ending in 1971, in which one of the parameters assessed was coffee berry borer infestation levels in shade and no shade, revealed that in all instances infestations were higher in shaded plantations (Graner and Godoy Junior, 1959, 1962, 1971; Godoy Junior and Graner, 1961, 1967). In Honduras, Muñoz *et al.* (1987) reported higher infestation levels in "half shaded" plantations with shade provided by pruned *Erythrina* (Leguminosae), followed by unshaded plantations, and finally, plantations growing at "full shade" under *Erythrina*. Unfortunately, statistical analyses were not conducted.

In Brazil, Passos *et al.* (2005) sampled coffee berry borers in volatile-containing traps installed at different distances (3, 6, 12, 15, 24, and 36 m) from *Grevillea robusta* A. Cunn. ex R. Br. (Proteaceae), a tree used to provide shade in coffee plantations. The mean number of insects collected 3 m from the tree was 24 times higher (1506 insects) than the number collected at 36 m (63 insects), a statistically significant difference. They recommend placing emphasis—in terms of pest management strategies against the coffee berry borer—in areas that are proximate to trees that provide shade in order to reduce the number of insects that could infest the next crop.

Féliz Matos (2003) and Féliz Matos *et al.* (2004) examined coffee berry borer infestation levels under three shade levels in Nicaragua: no shade, medium shade (40–50%) using *Gliricidia sepium* (Jacq.) Walp. (Leguminosae), and dense shade (60–70%) using *Eugenia jambos* L. (current name: *Syzygium jambos* (L.) Alston; Myrtaceae). Percent infestation was significantly higher (17–25%) in dense shade compared to <2% under no shade and medium shade. Infestation levels for no shade and medium shade were not significantly different. Wegbe *et al.* (2007) in Togo have also reported significantly higher coffee berry borer infestation levels in densely shaded coffee plantations. In Colombia, Bosselmann *et al.* (2009) reported a trend towards higher infestation levels under shade.

In contrast to all the papers cited above, Baker *et al.* (1989) found no significant differences in coffee berry borer infestation levels at two different elevations in Mexico based on four different shade levels (no shade, light, medium, and high shade). Also working in Mexico, Soto-Pinto *et al.* (2002) found no correlation between shade cover and coffee berry borer levels. In Kenya, Jaramillo *et al.* (2013) reported lower infestation levels in shaded plantations.

In terms of abundance of parasitoids, Mendes (1940a) found lower *Prorops nasuta* population levels in shaded

plots, while de Toledo (1948) found that shade and the parasitoid *P. nasuta* were perfectly compatible. Ticheler (1961, 1963) was able to find *Cephalonomia stephanoderis* in full sun plantations but not in shaded plantations. Parasitoids are discussed in detail below.

Shade has been shown to buffer temperatures in coffee plantations. For example, Vaast *et al.* (2006) found that coffee shading in Costa Rica reduced temperatures by 2°C and 4°C in outer and inner leaves, respectively, when compared to unshaded plantations. In New Caledonia, Brun and Suckling (1992) measured differences of 3°C between sun grown and shaded plantations. Using *Inga densiflora* Benth. (Leguminosae) to shade plantations, Siles *et al.* (2010) reported a reduction of up to 5°C in shaded coffee leaves vs. leaves in monocultures. Average maximum temperatures in non-shaded plantations in Mexico were 5.4°C higher that in shaded plantations (Barradas and Fanjul, 1986). In Kenya, Kirkpatrick (1935) found that between 11:00 AM and 1:00 PM, the temperatures in non-shaded coffee were up to 5–6°C higher than in shaded coffee. Also in Kenya, Jaramillo *et al.* (2013) reported that mean temperatures in shaded plantations were 2°C lower than in coffee growing at full sun. It has not been determined how these temperature differences translate to temperatures inside the berry, and consequently, on the coffee berry borer life history parameters.

3.7.1 Shade and Fungal Entomopathogens

One of the impediments towards the success of fungal entomopathogens is exposure to ultraviolet light and low humidity levels (Vega *et al.*, 2012b). Therefore, it is to be expected that under shade, fungal entomopathogens would have a higher chance of success than in unshaded plantations. Experimental results on this topic vary. For example, Chevalier (1947) recommended maintaining shade over coffee plantations in order to favor the development of fungal entomopathogens, a recommendation based on work by Friederichs and Bally (1923) in Java. Pascalet (1939) states that insect infection with *B. bassiana* will be much easier in shaded than in non-shaded plantations. Similarly, Féliz Matos (2003) recommended maintaining shade levels of 40–50% to encourage *B. bassiana* sporulation, although infection was almost non-existent in his study and not significantly different from levels encountered in dense shade or no shade. Vélez Arango (1997) reported no significant differences in *B. bassiana* recovery percentages (based in colony forming units) up to 14 days after spraying unshaded and shaded coffee plantations in Colombia. One interesting aspect of the study is that self-shading, due to dense foliage within individual plants, is mentioned as a factor that could have contributed to fungal survival due to a decrease in solar radiation reaching the fungal propagule.

3.7.2 Effects of Shade on the Effectiveness of Insecticides

Brun *et al.* (1990) found that resistance to endosulfan was significantly lower in shaded plantations, possibly due to (1) the lower temperatures (average of 3°C—see Brun and Suckling, 1992), which reduce the effectiveness of the insecticide and consequently the selective pressure for resistance, and (2) interruption of insecticidal sprays penetration by plant canopy in shaded plantations. Related to the last point, Parkin *et al.* (1992) reported more even deposition of insecticidal sprays in shaded plantations, possibly due to factors related to laminar flow whereby in non-shaded plantations the insecticidal mist can drift outside of the field due to unimpeded wind patterns.

3.7.3 Shade and Ants

Several papers have reported on the effects of shade on different ant species. For example, Armbrecht and Perfecto (2003) reported significantly different levels of litter and twig-nesting ants (e.g., *Pheidole*, *Solenopsis*, *Hypoponera*, *Wasmannia*, etc.) in Mexico when distance from the forest was compared for shaded monocultures (i.e., coffee under *Inga*) and shaded polycultures (coffee shaded with various tree species). For the shaded monoculture, ant species decreased with increased distance from the forest, while an increase in ant species was reported for the shaded polyculture with increased distance from the forest. Thus, even within one system (i.e., shaded coffee), various levels of different ant species can be found. This has important implications for the coffee berry borer because one particular shaded habitat may be more favorable towards ant species that might potentially prey on the insect when compared to a different habitat. Perfecto and Vandermeer (1996), Roberts *et al.* (2000), and Philpott and Armbrecht (2006) have also reported increased ant diversity in shaded coffee habitats.

In Colombia, Gallego Ropero and Armbrecht (2005) examined ant predation using coffee berry borer-infested parchment seeds placed under no shade or shade provided by different species (e.g., *Cedrela odorata* L., *Cordia alliodora* (Ruiz and Pavon) Oken, *Erythrina rubrinervia* Kunth, *Inga edulis* Mart., *Persea americana* Miller, etc.). Seven ant species in four genera (*Solenopsis*, *Tetramorium*, *Pheidole*, and *Myrmelachista*) were found inside the parchment seeds and a lower number of adult *H. hampei* were found when ants had access to infested seeds, and the number of adults was even lower in plantations under diverse shade. In a subsequent study in the same locations, Armbrecht and Gallego (2007) reported higher adult coffee berry borer predation in shaded coffee farms when a glass spiral trap was used. Ant predation is discussed in further detail below.

3.8 Rearing

Rearing large numbers of coffee berry borers is essential for obtaining large numbers of healthy insects of known age and developmental stage that can be used in controlled experiments, both in the field and in the laboratory. The use of coffee berries for coffee berry borer rearing presents many problems, including availability of berries and possible presence and development of fungi that could cause insect mortality (Villacorta, 1985; Pérez López *et al*., 1995). To avoid these problems, artificial diets have been developed to rear insects in the laboratory.

The first to develop an artificial diet for the coffee berry borer was Amador Villacorta (1985), a scientist at the Instituto Agronõmico do Paraná (IAPAR) in Brazil. Even though the main component in the 19-ingredient diet was cotton and not a single component included coffee, the diet was successful in rearing 30,000 insects per month and 15 generations of coffee berry borers. In contrast to Villacorta's (1985) diet, Bautista Martínez and Atkinson Martín (1988) used a diet consisting only of three components (ground coffee, distilled water, sorbic acid or methyl paraben) and observed insect burrowing into galleries, oviposition and hatching, but no pupae were formed.

The Villacorta (1985) diet was modified by Villacorta and Barrera (1993) and by Brun *et al*. (1993) to include ground coffee among its many ingredients. Subsequently, diet modifications and/or evaluations have been reported by Pérez López *et al*. (1995), Villacorta and Barrera (1996), Ruiz S. *et al*. (1996), Portilla-Reina (1999), Villacorta *et al*. (2000), Cirerol *et al*. (2002), Portilla R. and Streett (2006), and López-Pazos *et al*. (2009). Portilla R. and Streett (2006) developed an automated rearing system with the goal of rearing massive amounts of coffee berry borers and were able to rear ca. 900,000 females and males in 20 liters of diet.

The use of artificial diets for rearing coffee berry borers has also been instrumental for mass rearing parasitoids (Villacorta and Barrera, 1996; Portilla, 1999; Villacorta and Torrecillas, 2000). In lieu of using an artificial diet, Bautista Martínez and Atkinson Martín (1988), Benavides-G. and Portilla-R. (1990), Hirose and Neves (2002), and Jaramillo *et al*. (2009a) have developed rearing methodologies based on the use of coffee berries in the laboratory. Green coffee seeds and parchment coffee (i.e., coffee seeds removed from the berry and dried) have also been used for rearing the coffee berry borer (Benavides-G. and Portilla-R., 1990; Bustillo-Pardey *et al*., 1996; Portilla-Reina, 1999; Priyono *et al*., 2004). Finally, Friederichs (1924a) observed insects biting each other's legs off when crowded in a glass tube. This has occasionally been observed in artificial diet (Vega, unpubl.).

3.9 Sampling

Numerous sampling methods have been developed for estimating coffee berry borer population levels in the field (de Toledo, 1945; Decazy *et al*., 1989; Barrera *et al*., 1993a, 2004; Bustillo *et al*., 1998; Baker, 1999; Ruiz *et al*., 2000; Segura *et al*., 2004; Trujillo E. *et al*., 2006), including methods that account for losses due to infested berries that fall off the plant (Wegbe *et al*., 2003), as well as methods that correlate ethanol:methanol trap captures with infestation levels in the field (Pereira *et al*., 2012).

In a sampling method developed in Mexico (Barrera *et al*., 1993a), a plantation is divided into plots of approximately 4 ha/each (if the plot is <4 ha, then it does not need to be divided further). In each plot, 20 sampling sites representative of areas throughout the entire plot sites are selected. In each site, five coffee plants in a row are selected and from each plant a branch in the central part of the plant is selected. On this branch, all the berries are examined and the numbers that are infested and non-infested are counted. This method allows to sample different plots without bias, and to determine infestation levels in each plot. Another sampling method involves selecting 20 sites in a 1–5 ha plantation and in each site five plants in a row are selected and 20 berries per plant examined for infestation (Barrera, 2008).

According to Leefmans (1923), "Experiments with light traps did not give appreciable results; the beetles are practically not attracted to light." Subsequent studies have shed more light on this topic. Giordanengo (1992) found that 1, 7, and 14-day-old virgin females are negatively phototropic, although the level of negative photrotropism diminishes as the insect becomes older. For mated colonizing females, phototropic responses ranged from 62% at 1 h, to 40% at 3 h, and 53% at 24 h. Giordanengo *et al*. (1993) also used the phototropic response to collect females as they emerge from berries. Infested berries were placed inside a black container to which an empty plastic tube was connected and into which the females would walk, attracted by the light.

More detailed light-related experiments were conducted by Chong *et al*. (2006), who tested 14 wavelengths ranging form 340 to 670 nm. Six wavelengths, between 400 and 540 nm, resulted in the highest attraction percentage for females. In addition, at 460, 490 and 520 nm, 90-day-old females had a stronger response than 45-day-old females. Therefore, mating status and age influence female coffee berry borer responses to light. We could not find any papers on the use of light traps to attract coffee berry borers in the field.

3.10 Traps and Attractants

Several different coffee berry borer traps have been developed and tested in various coffee producing countries,

e.g., the IAPAR trap in Brazil (Villacorta *et al*., 2001; Pereira *et al*., 2012); the Ecobroca, ECOIAPAR and ETOTRAP in Mexico (Velasco Pascual *et al*., 1997a; Barrera *et al*., 2008); the tip CENICAFE trap in Colombia (Cárdenas M., 2000); and the Fiesta trap in Costa Rica (Borbón-Martínez *et al*., 2000; Barrera *et al*., 2006), among others (Figure 11.7). Most of these traps are made by hand (and referred to as artisanal traps) using empty 2-liter plastic soda bottles (IAPAR, ECOIAPAR, ETOTRAP, tip CENICAFE) or with plastic cups (Fiesta). One trap, designed by scientists at PROCAFE (El Salvador) and CIRAD (France) (González and Dufour, 2000; Dufour *et al*., 2002), is commercially available under the name BROCAP® and has been used in many countries throughout Latin America.

Many factors will influence the efficacy of coffee berry borer trapping devices, including trap color, shape, placement in the field, and attractant used (Dufour, 2002; da Silva *et al*., 2006; Barrera *et al*., 2006). The literature dealing with these topics is quite extensive, and because there are so many different trapping devices it is necessary to cover some topics briefly. For example, in terms of trap color, Mathieu *et al*. (1997b), Saravanan and Chozhan (2003), and Dufour and Frérot (2008) reported that red traps result in higher insect capture than the other colors tested in contrast to Borbón-Martínez *et al*. (2000) finding higher captures in white traps. As for vertical placement of the traps in the field, Fernández and Cordero (2005) found no significant differences in trap captures when traps were placed at 0.2 and 1 m in height, while Uemura-Lima *et al*. (2010) obtained significantly higher captures in traps placed at 0.5 m in height, when compared to 1 and 1.5 m. Dufour and Frérot (2008) captured three times as many insects when the traps were 1.2 m high, than when they were placed at ground level.

Ethanol, which is produced by plants under stress (Kimmerer and Kozlowski, 1982), has been shown to serve as an attractant for bark beetles in general (Cade *et al*., 1970; Moeck, 1970; Montgomery and Wargo, 1983; Klimetzek *et al*., 1986; Chénier and Philogène, 1989; Byers, 1992; Miller and Rabaglia, 2009; Gandhi *et al*., 2010; Kelsey *et al*., 2013). For the most part, all coffee berry borer traps use a mixture of methanol and ethanol as the attractant (Brun and Mathieu, 1997; Mathieu *et al*., 1997b, 1999; Cárdenas M., 2000; Borbón-Martínez *et al*., 2000; Saravanan and Chozhan, 2003; Fernández and Cordero, 2005; Dufour and Frérot, 2008; Barrera *et al*., 2008; Agramont *et al*., 2010; Fernandes *et al*., 2011; Pereira *et al*., 2012; Messing, 2012; Suárez *et al*., 2013). Mendoza-Mora (1991) was the first to demonstrate the synergistic effect of a 3:1 mixture of methanol to ethanol in attracting the coffee berry borer.

As mentioned in Section 3.6.3, coffee berry borer levels per hectare can reach the millions. The main problem with the coffee berry borer traps is that they only capture a low percentage of the population. For example, insect captures per trap in various countries using methanol:ethanol mixtures follow: (1) in Mexico, weekly captures ranged from 83 to 1484 (Barrera *et al*., 2008); (2) in Brazil, captures

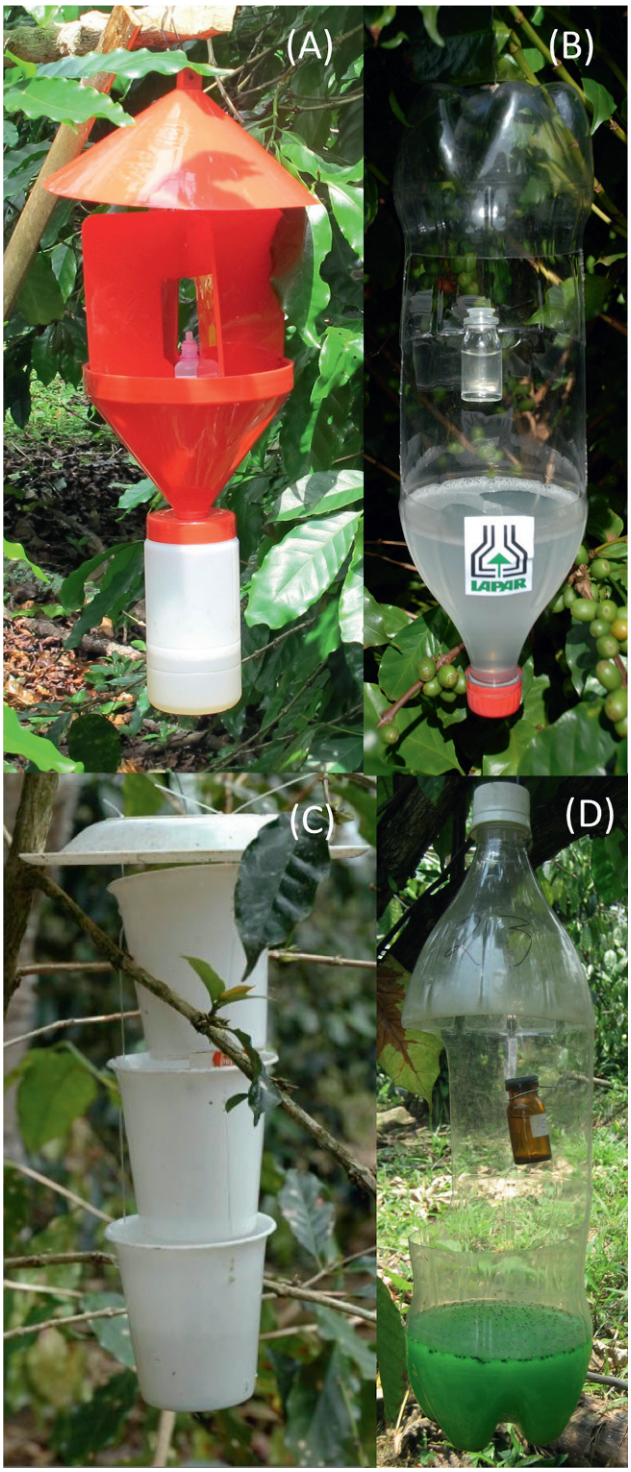

FIGURE 11.7 Coffee berry borer traps. (A) BROCAP® trap; (B) IAPAR trap (Brazil); (C) Fiesta trap (Costa Rica); and (D) Trampa Brocap casera (Mexico). *Photos by: (A) Bernard Dufour (CIRAD); (B) E. F. da Silva (IAPAR); (C) Fernando E. Vega; (D) Jaime Gómez (ECOSUR).*

ranged from 11 to 87 insects per day, depending on trap height (Uemura-Lima *et al*., 2010); (3) in Bolivia, 10 day insect captures averaged 3414 insects (Agramont *et al*., 2010); (4) in Venezuela, weekly captures averaged 432 insects (Fernández and Cordero, 2005); (5) in Cuba, weekly captures averaged 205 insects (Moreno Rodríguez *et al*., 2010); (6) in India, 2 week captures ranged from 18 to 303 insects (Saravanan and Chozhan, 2003); (7) in Costa Rica, daily captures ranged from ca. 18–33 insects (Borbón-Martínez *et al*., 2000); and (8) in El Salvador, daily BROCAP® trap captures for different concentrations and composition of attractants tested ranged from 6 to 111 insects (González and Dufour, 2000). In contrast, Dufour (2002) states that when infestations are high and during periods of high migration, the BROCAP® trap can capture more than 10,000 coffee berry borers per trap per day. Barrera *et al*. (2006) compared the BROCAP® trap to the ECOIAPAR and Fiesta traps, with the BROCAP® trap capturing 2653 insects per trap per week, corresponding to 2.4 and 3.2 the captures obtained in the ECOIAPAR and Fiesta traps, respectively.

In addition to low captures, a more significant issue is that with few exceptions (Mathieu *et al*., 1999; Fernandes *et al*., 2011; Pereira *et al*., 2012) trap captures are not correlated to actual coffee berry borer infestation levels in the field. Therefore, growers do not have any idea as to how effective trap captures are in reducing insect numbers and in increasing yields. It is clear that traps could be useful for monitoring the presence and dispersal of the coffee berry borer, especially when it is first reported in an area. Traps can also help monitor movement and increase in numbers of colonizing females throughout the season (as described by Pereira *et al*., 2012), but at present trapping devices are not a practical pest management strategy against the coffee berry borer.

Another issue to consider is that, as mentioned before, alcohol-based traps are not specific to the coffee berry borer and, therefore, other bark beetles will also be trapped. Pereira *et al*. (2012) reported from 2850 to 9048 non-coffee berry borers collected in traps placed in four different fields. Consequently, insects will need to be manually sorted and identified, a tedious process that increases labor costs (Messing, 2012). Another cost involves servicing the traps to replenish the attractant. Messing (2012) obtained higher captures when the attractant was placed in a plastic pouch that required less servicing, but the plastic pouch on its own involves additional costs.

Based on finding various coffee berry borer life stages in *D. lacourtianum* (discussed above), Ghesquière (1933) suggested the use of this plant as a trap crop in the field, an experiment that has not been conducted in the 80 years that have passed since the publication of the paper.

There is an urgent need to identify and deploy attractants specific to the coffee berry borer. These should have a reasonable cost, be easy to use, and must result in dramatically higher captures than the currently used trapping methods.

3.11 Repellents

Some papers have provided field and laboratory evidence suggesting that coffee berry borers infesting berries might produce a female deterrent chemical. Wilkinson (1928) was the first to observe reduced offspring when a high number of coffee berry borers were infesting a limited number of berries. In Ivory Coast, Ticheler (1961, 1963) found that increasing the number of females per berry in the laboratory from one, to two, and to four, greatly reduced fecundity per female, with an average progeny number, 32 days post-infestation, of 44, 12, and 6, respectively. A decline in per capita fecundity with increased female density per berry in the laboratory was also reported by Moore *et al*. (1990). In a field experiment in Mexico, de Kraker (1988) obtained data that "suggests that already infested berries repel attacking borers." The possible repellency was further expanded upon by Gutiérrez-Martínez and Ondarza (1996), who hypothesized that a "chemical signal" deposited on the berry by a colonizing female might function as a deterrent for subsequent colonization by other females. Such a "chemical signal" could be a marking pheromone, as proposed by Vega *et al*. (2009). Marking pheromones can affect fecundity, as has been shown for many insects, including bark beetles (see Vega *et al*., 2011).

A laboratory study using coffee berry borers in artificial diet revealed a reduction in fecundity as the number of females increased (Vega *et al*., 2011), confirming the findings of Ticheler (1961, 1963) and Moore *et al*. (1990). The artificial diet study was expanded to include infested berries, leading to the identification of a sesquiterpene, which acts as a female deterrent in the laboratory (Vega and Cossé, unpubl.). This latter finding provides support to the repellency hypotheses presented by de Kraker (1988) and Gutiérrez-Martínez and Ondarza (1996).

Borbón-Martínez *et al*. (2000) reported various levels of repellency towards the coffee berry borer by verbenone (4,6,6-trimethylbicyclo [3.1.1]hept-3-en-2-one), (Z)-3-hexenol, and methylcyclohexenone (3-methylcyclohex-2-en-1-one). These compounds have been identified as anti-aggregation pheromones in other bark beetles (Byers, 1995; Zhang and Schlyter, 2004; Reddy and Guerrero, 2010; Strand *et al*., 2012; Fettig *et al*., 2012). Jaramillo *et al*. (2013) reported coffee berry borer avoidance of verbenone and α-pinene and recommended "cultivating coffee intercropped with plants producing conifer monoterpenes compounds that are repellent to *H. hampei*."

Góngora *et al*. (2012) identified high overexpression of the isoprene synthase gene in *Coffea liberica* Hiern berries exposed to the coffee berry borer, but not in *C. arabica* berries. Addition of isoprene to artificial diet had negative

effects on survival and development of the coffee berry borer and the authors suggest that isoprene might have repellent properties against the insect. A concern with this concept is that isoprene is highly reactive and is produced and emitted by many species of trees in large amounts (Monson and Fall, 1989; Hewitt *et al*., 2011). Therefore, with so much isoprene in the atmosphere it is unlikely that it could be used as a repellent against the coffee berry borer. Finally, isoprene is very volatile, highly flammable, and, consequently, not easy to handle.

The identification and field deployment of highly repellent volatile compounds could become another useful tool in the arsenal of strategies used to manage the coffee berry borer.

3.12 Plant Resistance

No resistance to the coffee berry borer has been reported in commercially traded coffee varieties (Friederichs, 1924b; Vuillet, 1925; Romero and Cortina-Guerrero, 2004a; Sera *et al*., 2010). Two studies have reported some level of resistance in laboratory experiments using parchment coffee as the experimental unit, but it is not clear how the results translate to the field when insects have to select a berry (Romero and Cortina-Guerrero, 2004b; Romero and Cortina G., 2007).

In an attempt to elucidate differences in plant responses to coffee berry borer infestation, Idárraga *et al*. (2012) identified metabolic pathways induced in *C. arabica* var. Caturra and *C. liberica* after plants had been artificially infested with the insect for 24 h. *Coffea arabica* responded with an increased expression of stress-related proteins while *C. liberica* had increased expression of proteins related to insect defense. This information is useful for developing possible resistance strategies.

One area related to plant resistance to the coffee berry borer involves the digestive enzymes used by the insect and developing transgenic coffee plants with genes coding for inhibitors of these enzymes. About 50% of the dry weight in green coffee seeds is constituted by polysaccharides, including mannan, arabinogalactan (arabinose and galactose), and cellulose (a linear chain of glucose units) (Bradbury and Halliday, 1990; Redgwell *et al*., 2003; Redgwell and Fischer, 2006). In order to metabolize these polymers as they move through the alimentary canal, the coffee berry borer needs to use enzymes such as amylases, mannanases, and galactosidases, among others. For a detailed description of the coffee berry borer alimentary canal see Rubio G. *et al*. (2008) and Ceja-Navarro *et al*. (2012).

The α-amylases are a family of carbohydrate-metabolizing enzymes common in plants, microorganisms, and animals (Grossi-de-Sá and Chrispeels, 1997). Extensive research has been published on α-amylase inhibitors in insects (Grossi-de-Sá and Chrispeels, 1997; Carlini and Grossi-de-Sá, 2002; Strobl *et al*., 1998; Zeng *et al*., 2013; and references therein) and various papers have elucidated basic aspects of amylase presence in the midgut of the coffee berry borer (Valencia-Jiménez *et al*., 1994; Martínez D. *et al*., 2000; Martínez Díaz *et al*., 2000; Valencia *et al*., 2000; Valencia-Jiménez, 2000). A common bean (*Phaseolus vulgaris* L.) seed protein crude extract was shown to have amylase inhibitory properties when it reduced the α-amylase activity in whole coffee berry borer extracts by ca. 80% (Valencia *et al*., 2000). An α-amylase inhibitory gene from *Phaseolus coccineus* L. expressed in tobacco plants inhibited α-amylase activity in whole coffee berry borer insect extracts by 65% (de Azevedo Pereira *et al*., 2006).

Acuña *et al*. (2012) presented evidence for a horizontally transferred bacterial gene encoding mannanase (*HhMAN1*) in the genome of the coffee berry borer. The gene, which presumably allows the coffee berry borer to use seed galactomannans (a type of mannan, consisting of galactose and mannose), apparently originated from bacteria inhabiting the alimentary canal and could be detected in specimens originating in 16 countries. The horizontal transfer of this gene serves as an example of the biological complexity of the coffee berry borer, including the importance of the microbiota. Aguilera-Gálvez *et al*. (2013) cloned and characterized the mannanase gene (*HhMAN1*) from the midgut of the coffee berry borer, while Padilla-Hurtado *et al*. (2012) identified a xylanase gene (*HhXyl*) in the alimentary canal of the coffee berry borer; xylanases metabolize arabinoxylans (a copolymer of arabinose and xylose) present in the coffee seed.

In addition to polysaccharides, green coffee beans contain approximately 8.5–12% crude protein content (Rawel *et al*., 2005). Proteases, also referred to as proteinases, are essential in order for the coffee berry borer to metabolize coffee seed proteins as they move through the alimentary canal. Proteases, including serine, cysteine, and aspartic, can be inhibited with plant protease inhibitors, which can be a valuable source of resistance against insect pests (Grossi-de-Sá and Chrispeels, 1997; Carlini and Grossi-de-sá, 2002; Bode *et al*., 2013; da Silva *et al*., 2014; and references therein). The first paper focused on understanding the role of proteases in the digestive system of the coffee berry borer was published by Valencia-Jiménez *et al*. (1994), who reported a high activity of trypsin and chymotrypsin (two serine proteases) in coffee berry borer larvae, and only a small amount of trypsin activity in adults. Ruiz Serna *et al*. (1995) ran bioassays with various commercial trypsins, chitinases, and trypsin-chymotrypsin inhibitors incorporated into coffee berry borer artificial diet and found significant differences in mortality levels when compared to the control, but not in

the time from egg hatch to adult emergence. Preciado-Rodríguez *et al.* (2000) identified an aspartic protease in the coffee berry borer midgut. An aspartic protease inhibitor from *Lupinus bogotensis* Benth. was "highly effective" in inhibiting coffee berry borer midgut aspartic proteases in *in vitro* experiments (Molina *et al.*, 2014). In addition, two concentrations of the inhibitor separately mixed into artificial diet resulted in significant differences in larval mortality when compared to the control, depending on the concentration. Similarly, *in vitro* studies showed that a serine protease inhibitor from *P. coccineus* inhibited trypsin-like enzymes in the coffee berry borer (Azevedo Pereira *et al.*, 2007).

What this type of enzyme-related research is aiming for is transgenic coffee plants expressing genes codifying for amylase or protease inhibitors (Valencia-Jiménez *et al.*, 1994; Valencia *et al.*, 2000; Martínez D. *et al.*, 2000; de Azevedo Pereira *et al.*, 2006; Barbosa *et al.*, 2010). One such example is transgenic *C. arabica* with an α-amylase inhibitor-1 gene from *P. vulgaris* (Barbosa *et al.*, 2010). Use of transgenic seed extracts fed to the coffee berry borer resulted in up to 88% inhibition of α-amylase enzymatic activity. Even though the idea of using amylase inhibitors is straightforward, transfer of this type of technology to the field remains a challenge.

3.13 Endosulfan Resistance

Endosulfan ($C_9H_6Cl_6O_3S$), a broad-spectrum chlorinated cyclodiene insecticide, first entered the market in the mid-1950s. It has been used in many countries under the trade name Thiodan® as an insecticide against the coffee berry borer. Due to human and environmental hazards related to its use, including bioaccumulation, endosulfan has now been banned in at least 70 countries (Lubick, 2010; Janssen, 2011).

Ingram (1968) experimented with endosulfan in Uganda and found that it could have fumigant effects, i.e., contact toxicity did not appear to be essential. After 10 years of biannual applications, coffee berry borer resistance to endosulfan was reported in New Caledonia (Brun *et al.*, 1989a), with up to 1000-fold resistance detected in five localities. The development of resistance could have been due to a higher selective pressure, based on the higher levels of active ingredient used when compared to other countries (Brun *et al.*, 1989a). Another possibility the authors discuss is that fumigant action could have enhanced the development of resistance in all life stages of the insect inside the coffee berry. Finally, Brun *et al.* (1989a) hypothesized that selective pressure for resistance would be higher in sun grown plantations in contrast to shaded plantations, due to better spray coverage and higher temperatures, which would increase the fumigant action. In a subsequent paper, Brun *et al.* (1990) reported a significantly higher percentage of resistant insects in sun grown plantations vs. shade plantations.

In order to assess and subsequently manage resistance in the field, Brun *et al.* (1989b) developed three methods for detecting endosulfan resistance, of which a method based on vapor action was the most convenient due to its low cost, reproducibility, and ease of use. This method was further developed by exposing coffee berry borers to endosulfan vapors at five different temperatures (Brun *et al.*, 1991). Another method involves the molecular detection of the cyclodiene resistance gene *Rdl*, which is present in coffee berry borers from New Caledonia (ffrench-Constant *et al.*, 1994; Borsa and Kjellberg, 1996b; Andreev *et al.*, 1998) and Colombia (Góngora *et al.*, 2001; Navarro *et al.*, 2010).

With resistance management in mind, Brun and Suckling (1992) conducted a study involving the traditional endosulfan application method in New Caledonia, which is based on roadside applications using sprayers mounted on vehicles. The findings showed reduced resistance frequency away from the road in both sun grown and shaded coffee. Two applications of endosulfan in a sun grown field resulted in a 61% increase in the frequency of resistance, implying it would be unwise to apply endosulfan in areas where resistance frequency is low (Brun and Suckling, 1992). The roadside vehicle-mounted sprayer results in most of the spray being deposited within 20 m of the point of application (Parkin *et al.*, 1992), thus confirming a higher selective pressure close to the road.

In Nicaragua, Pérez *et al.* (2000) used the bioassay method developed by Brun *et al.* (1991) and could not find evidence for endosulfan resistance in the coffee berry borer. Specimens from the Philippines, Guatemala, Brazil, and Cameroon also tested negative for endosulfan resistance (Kern *et al.*, 1991).

Endosulfan resistance has been used to study the segregation of resistance phenotypes, functional haplodiploidy, pseudoarrhenotoky, and extreme inbreeding (Brun *et al.*, 1995b; Borsa and Kjellberg, 1996b, Borsa and Coustau, 1996; Gingerich *et al.*, 1996; Andreev *et al.*, 1998).

3.14 Biological Control

3.14.1 Bacteria

A well-known entomopathogen is *Bacillus thuringiensis* (Bt), a Gram-positive bacterium that during sporulation produces crystal proteins known as delta endotoxins (δ-endotoxins; also referred to as Cry toxins; Jurat-Fuentes and Jackson, 2012). The toxin becomes activated in the midgut and disrupts the midgut epithelial cells, causing death of the insect.

After the coffee berry borer was first reported in Costa Rica in 2002, Arrieta *et al.* (2004) reported 202 Bt isolates in environmental samples (soil, leaf litter, leaves, coffee

berries, coffee berry borers) collected in coffee berry borer-infested coffee plantations. Even though no laboratory bioassays were conducted with any of the isolates, the study reveals the widespread presence of a potential biological control agent in coffee agroecosystems.

Most laboratory bioassays examining toxicity of Bt to the coffee berry borer have used first instar larvae feeding on artificial diet surface contaminated with spore-crystal suspensions. Using Bt isolates from a Mexican collection, Méndez-López *et al*. (2003) found that out of 170 isolates, only the mosquitocidal strains, especially Bt serovar *israelensis*, exhibited significant toxicity. They also reported high toxicity when using four out of nine mosquitocidal strains from the Institut Pasteur collection. De la Rosa *et al*. (2005) used 61 Mexican Bt isolates from the same collection used by Méndez-López *et al*. (2003) and found toxicity levels ranging from 8 to 83%. López-Pazos *et al*. (2009) reported moderate levels of toxicity of recombinant Cry1Ba (from Bt serovar *aizawai*) and Cry3Aa (from Bt serovar *san diego*) proteins. López-Pazos *et al*. (2010) reported no toxicity of a hybrid Cry protein in contrast to the parental toxins Cry1B and Cry1I, which caused 60% and 52% mortality, respectively. In contrast to results published by Méndez- López *et al*. (2003), Naidu *et al*. (2001) reported Bt serovar *sumiyoshiensis* was toxic to larvae of the coffee berry borer.

The main issue with using Bt as a biological control strategy against the coffee berry borer is that the insect needs to ingest the bacterium or toxin for an effect to occur, and, furthermore, epidemics would need to be induced to result in significant reductions in population levels. Thus, the use of Bt in the field presents a formidable challenge, i.e., reaching the insects feeding inside the berry. It is also important to consider that use of commercial formulations of Bt would require spraying, a non-feasible option in most of the coffee-producing world due to cost and storage of the product, difficulty in properly spraying the entire plantation (e.g., steep hills), and easy access to water.

One obvious alternative strategy to spraying is the use of transgenic coffee plants expressing the Bt toxin protein, but whether this is a viable option for the coffee industry, in terms of grower and consumer acceptance, remains a debatable question. For example, a French team had developed transgenic *C. canephora* plants expressing the Bt toxin protein (Leroy *et al*., 1997) and planted them in French Guiana to test their effectiveness against the coffee leaf miner (*Leucoptera coffeella* Guérin-Mèneville and Perrottet) (Perthuis *et al*., 2005). Even though resistance to the coffee leaf miner was demonstrated in the field (Perthuis *et al*., 2005), the plantation was vandalized in 2004, bringing the project to an early demise (Coghlan, 2005).

As for other bacteria, Cárdenas (1995) mentions *Serratia marcescens* as an "antagonist" (i.e., opportunistic or potential pathogen) of coffee berry borer larvae and pupae. Bustillo *et al*. (1998) includes *Serratia* sp. and *Bacillus* sp. as uncommon natural enemies of larvae only found while dissecting infested berries.

3.14.2 Fungal Entomopathogens

The mode of action of fungal entomopathogens involves spore attachment to the insect cuticle, followed by germination and cuticle penetration (Vega *et al*., 2012b). Insect death is caused by hyphal growth and proliferation throughout the hemocoel, a process that depletes nutrients used by the insect and disrupts internal tissues; production of secondary metabolites could also contribute to death (Vega *et al*., 2012b).

In recent years, molecular research has vastly altered the phylogenetics and systematics of fungal entomopathogens, with major changes for *Beavueria* (Rehner *et al*., 2011) as well as *Metarhizium* (Bischoff *et al*., 2009), the two best-known fungal entomopathogens. In addition to these changes, the reader should become familiar with the new "one fungus, one name" concept (Taylor, 2011) that no longer uses two different scientific names for the same fungus based on sexual (teleomorphic) or asexual (anamorphic) reproduction (Gams *et al*., 2012). Being familiar with this change will help figure out what the new—and correct—scientific names are, and how they relate to the previously used names.

With one exception, all fungal entomopathogens attacking the coffee berry borer belong to the Phylum Ascomycota, Class Sordariomycetes, Order Hypocreales, Family Cordycipitaceae: *Beauveria bassiana* (Balsamo-Crivelli) Vuillemin, *Metarhizium anisopliae* (Metschn.) Sorokin, *Isaria farinosa* (Holmsk.) Fr. (formerly known as *Paecilomyces farinosus* (Holmsk.) Brown and Smith), *Isaria fumosorosea* Wize (formerly known as *Paecilomyces fumosoroseus* (Wize) Brown and Smith), and *Lecanicillium lecanii* (Zimm.) Zare and Gams (formerly known as *Verticillium lecanii* (Zimm.) Viégas). The exception is *Ophiocordyceps entomorrhiza* (Dicks.) Sung, Sung, Hywel-Jones and Spatafora (formerly known as *Hirsutella eleutheratorum* (Nees) Petch), which belongs to the Family Ophiocordycipitaceae (Bustillo *et al*., 1998, 2002; Vega *et al*., 1999).

Some papers list *Nomuraea rileyi* (Farlow) Samson (Clavicipitaceae) as a fungal entomopathogen of the coffee berry borer (Moore and Prior, 1988; Waterhouse and Norris, 1989; Klein-Koch, 1989; Murphy and Moore, 1990; Waterhouse, 1998; Damon, 2000). The reports are likely based on Le Pelley (1968), who stated that *N. rileyi* occurs in Brazil, while citing Averna-Saccá (1930). In actuality, what Averna-Saccá (1930) reported was the isolation of the fungus, at the time known as *Botrytis rileyi* (Farlow), from a twig borer attacking *Melia azedarach* L., followed

by attempts to inoculate the coffee berry borer. Finding *N. rileyi* attacking the coffee berry borer would be highly unusual, as it is a common pathogen of Lepidoptera (Humber, 2012).

Beauveria bassiana has been the most commonly reported fungal entomopathogen infecting the coffee berry borer worldwide (Figure 11.8A–C): Brazil (Averna-Saccá, 1930; Drummond-Gonçalves, 1940; Mesquita, 1944; Villacorta, 1984; Costa *et al*., 2002); Cameroon (Pascalet, 1939); Colombia (Vélez-Arango and Benavides-Gómez, 1990); Costa Rica (Echeverría Beirute, 2006); Cuba (Pérez León *et al*., 2009); Democratic Republic of the Congo (Steyaert, 1935); Ecuador (Klein-Koch *et al*., 1988); Guatemala (Monterroso Mayorga, 1981); Honduras (Lazo A., 1990); India (Haraprasad *et al*., 2001); Indonesia (Friederichs, 1922b; Friederichs and Bally, 1922, 1923); Mexico (Méndez-López, 1990; Sampedro-Rosas *et al*., 2008); Nicaragua (Monzón *et al*., 2008); Puerto Rico (Gallardo-Covas *et al*., 2010); and Venezuela (Bautista, 2000), among others.

In the first paper related to *Beauveria* and the coffee berry borer, Friederichs (1922b) reported a large natural epidemic in the field in Java, which greatly reduced infestation levels. In the Democratic Republic of the Congo, Steyaert (1935) found much higher *B. bassiana*-induced mortality in insects originating in green berries (highest monthly level: 64%) than in red berries (highest monthly level: 29%), a result he ascribes to females becoming infected while walking on the surface of the green berry, and moving among these, before eventually selecting a suitable berry. Pascalet (1939) concurs in that infection only occurs while females are outside the berry and while in the process of boring into the berry. In contrast to Steyaert's (1935) results, *B. bassiana* infection in green berries in

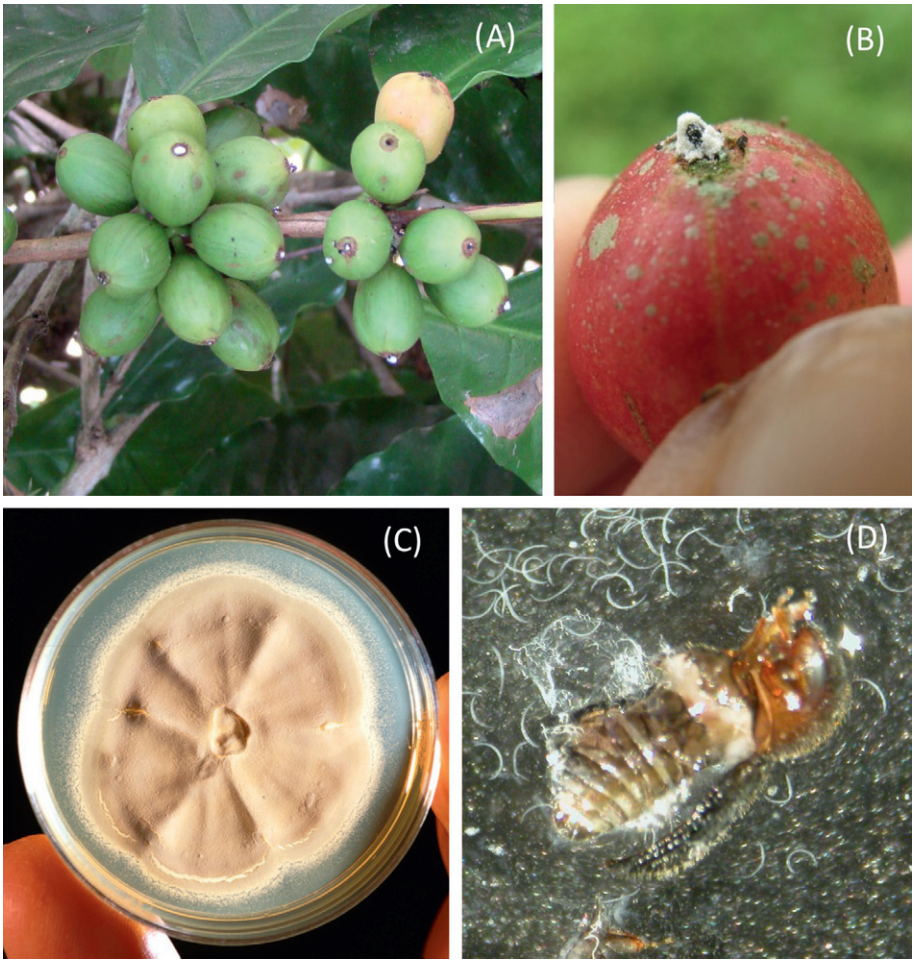

FIGURE 11.8 (A) Coffee berries, some of which show coffee berry borers infected with the fungal entomopathogen *Beauveria bassiana* (white areas on disc). (B) Red berry showing posterior part of the coffee berry borer abdomen infected with *B. bassiana*. (C) *B. bassiana* growing in culture. (D) Third-stage juveniles of the nematode *Metaparasitylenchus hypothenemi* emerging from an adult coffee berry borer. *Photos by: (A) Fernando E. Vega; (B) Aixa Ramirez Lluch (Departamento de Agricultura, Puerto Rico); (C) Keith Weller (USDA), and (D) Alfredo Castillo (ECOSUR).*

Ecuador was 15.9% vs. 13.1% in red berries, and 5% in black berries (Molinari, 1988).

Steyaert (1935) also found highest *B. bassiana*-induced mortality in insects in shaded (8.2–13.6%) vs. unshaded plots (1.8–3%), which is in agreement with Friederichs (1922b) and Friederichs and Bally (1923). Pascalet (1939) observed that *B. bassiana* was more widespread in forest areas than in the savanna and that shade was favorable for the development of the fungus. This is likely a result of higher fungal survival due to reduced ultraviolet light and higher moisture.

Coffee berry borer mortality levels caused by natural occurrences of *B. bassiana* in the field can vary widely (percentages given are highest levels reported in each study): 71% in Cameroon (Mbang *et al.*, 2012); 63% in the Democratic Republic of the Congo (Steyaert, 1935); 60% in India (Balakrishnan *et al.*, 1994); 44% in Nicaragua (Monzón *et al.*, 2008); 42% in Colombia (Posada-Flórez *et al.*, 1993); 30% in Ecuador (Klein-Koch *et al.*, 1988); <10% in Mexico (Méndez-López, 1990; Córdova-Gámez, 1995); and <1% in Brazil (Costa *et al.*, 2002) and Puerto Rico (Gallardo-Covas *et al.*, 2010).

In the field, *B. bassiana*-infected females can often be seen covered with white sporulating mycelia while fixed at the entrance hole in the berry, with the anterior part of the body sticking out of the hole (Pascalet, 1939; Villacorta, 1984; Figure 11.8A, B). Several possibilities exist for this situation. It is possible that females might have become infected while selecting a berry into which they can oviposit, and that they die in the process of boring the hole, followed by fungal sporulation on the cadaver. Another possibility is that described by Pascalet (1939). He mentions that in some cases, depending upon stage of infection, females move to the entrance hole and die, while the progeny continues its development inside the berry, free of infection. This argument presents the quandary that the progeny has to emerge from the berry through the entrance hole, which would then be blocked. A third possibility is that this phenomenon is the result of fungal manipulation of the insect to an area where the spores have a higher chance of finding a host, as has been reported for other fungal entomopathogens (Krasnoff *et al.*, 1995).

Several papers have reported results of laboratory bioassays aimed at testing the pathogenicity of *B. bassiana*: Fernandes *et al.* (1985); Jiménez-Gómez (1992); González G. *et al.* (1993); de la Rosa *et al.* (1997); Varela Ramírez (1997); Bustillo *et al.* (1999); Haraprasad *et al.* (2001); Samuels *et al.* (2002); Posada and Vega (2005); Neves and Hirose (2005); Sampedro-Rosas *et al.* (2008); and Vera *et al.* (2011). A common goal in these bioassay studies is to select the most virulent isolates for subsequent spraying and testing in the field, even though the bioassays are conducted under ideal conditions (e.g., constant temperatures, 100% RH, protection from ultraviolet light) that do not mimic field conditions. Thus, it is questionable whether laboratory results will be similar in the field. In addition, there are many parameters that are not considered in most laboratory bioassays. For example, Posada and Vega (2005) conducted bioassays using 50 different *B. bassiana* isolates from coffee berry borers collected in Cameroon, Ivory Coast, Kenya, Togo, Brazil, Mexico, and Nicaragua. In addition to determining normal parameters assessed in usual bioassay studies (percent mortality, survival time), they assessed spore germination, length of duration of the fungal life cycle in the insect, and spore production in the insect cadaver.

Other studies have focused on the enzymes produced by *B. bassiana* infecting the coffee berry borer (Rivera M. *et al.*, 1997; Varela-Ramírez, 1997; Castellanos Domínguez, 1997; Ito *et al.*, 2007; Dias *et al.*, 2008; Sassá *et al.*, 2008, 2009; Varéa *et al.*, 2012). Enzymatic action by the fungus is needed to breach the cuticle and enter the insect. In one study (Bridge *et al.*, 1990), enzymatic band patterns were used in an attempt to determine if 16 *B. bassiana* isolates attacking the coffee berry borer in 10 countries had disseminated with the insect, or whether isolates attacking the insect throughout the world were similar, with inconclusive results. In a similar study using molecular markers, Rehner *et al.* (2006) assessed the phylogenetic diversity of 34 coffee berry borer-infecting *B. bassiana* isolates from four African countries and five Neotropical countries. Results revealed that *B. bassiana sensu lato* is comprised by cryptic species, with four distinct lineages infecting the insect in Africa and the Neotropics. Also using molecular markers, Gaitan *et al.* (2002) detected low genetic variability among 49 *B. bassiana* isolates from coffee berry borers from Colombia, the Philippines, Brazil, Ecuador, and Guatemala.

Various papers have examined coffee berry borer infection levels in the field after spraying *B. bassiana* conidial suspensions (Vélez-Arango and Benavides-Gómez, 1990; Bustillo *et al.*, 1991, 1999; Tobar H. *et al.*, 1998; de la Rosa *et al.*, 2000; Haraprasad *et al.*, 2001; Montilla *et al.*, 2006). Unfortunately, these studies did not include cost to benefit analyses. Obtaining answers to the following questions is essential in order to determine whether a recommendation to the grower is warranted: (1) Is there increased insect mortality in sprayed plots compared to plots that were not sprayed?; (2) Are yields higher in sprayed plots?; (3) What costs, in terms of labor and material, are incurred when spraying?; and (4) Is spraying cost effective?

In a novel approach to using fungal entomopathogens, Cruz *et al.* (2006) developed the concept of using mixtures consisting of different *B. bassiana* strains. They conducted laboratory bioassays based on 10 *B. bassiana* strains from eight different hosts in four countries, all characterized for genetic diversity using different molecular methods (internally transcribed spacer region, β-tubulin gene, and

AFLP). Based on single strain bioassay results, five *B. bassiana* mixtures were designed to hypothetically take advantage of genetic diversity. Results revealed co-infections were prevalent when mixtures were used, and if strains in a mixture were genetically similar, virulence was similar to that obtained when single strains were used. In a very interesting twist, if strains in the mixture were not genetically similar but had caused similar virulence when individually tested, antagonism was observed if virulence was individually high and synergism if individual virulence was low. A field test using artificial infestations (i.e., insects were introduced into entomological sleeves) confirmed the synergism when a mixture of low virulence strains was used (Cárdenas-Ramírez *et al*., 2007; Benavides *et al*., 2012). Gene expression profiles of *B. bassiana* germinating conidia and growing hyphae on coffee berry borers was studied by Mantilla *et al*. (2012).

Coffee berry borer field and laboratory bioassays have also been conducted using *M. anisopliae*: D'Antonio and de Paula (1979); Lecuona *et al*. (1986); Bernal U. *et al*. (1994); de la Rosa-Reyes *et al*. (1995); de la Rosa *et al*. (2000); Bustillo *et al*. (1999); and Samuels *et al*. (2002). Pava-Ripoll *et al*. (2008) expressed a scorpion neurotoxin coding sequence in transformed *M. anisopliae*, resulting in higher virulence against the coffee berry borer.

Overall, there are many constraints to the effective use of fungal entomopathogens using traditional spraying methods. These include the inherent susceptibility of the fungus to low moisture levels and to UV light (Vega *et al*., 2012b). Edgington *et al*. (2000) tested 22 substances as *B. bassiana* UV protectants, and two that were tested in the field did not improve coffee berry borer control. In addition, spraying fungal suspension requires ready access to water throughout the plantation, which can be difficult. Carrying a five-gallon (18.9 liters) back-sprayer over steep hills can quickly become a burden based on weight alone, i.e., 41.7 lb (18.9 kg). More importantly, spraying to reach an insect that has a cryptic life cycle is a great challenge and spraying must be done when the insect is boring the berry, i.e., ca. 90–120 days after flowering, but this is complicated by numerous flowering periods induced by rain.

The cost of a commercial product, which could be prohibitive for a grower, is another factor to consider, although artisanal production methods have been developed. These are usually based on using rice as a solid substrate inside glass bottles, where the fungus can be grown (Antía-Londoño *et al*., 1992; Posada F. and Bustillo P., 1994). Production of large amounts of fungal entomopathogens would require a production facility, whose cost can be quite high (Grimm, 2001). Growing *B. bassiana* in liquid culture, followed by inoculating solid substrates such as cooked rice, has been demonstrated by Posada Flórez (2008), but the amounts of rice needed to produce high levels of inoculum for field application are too high to be practical.

3.14.3 Fungal Endophytes

A non-traditional method for using *B. bassiana*, as well as other fungal entomopathogens, is to attempt to establish them as fungal endophytes, i.e., as fungi that live internally in the plant (Posada and Vega, 2006; Posada *et al*. 2007; Vega *et al*. 2008b, c; Vega, 2008b). Various fungal entomopathogens have been reported as endophytes (see Vega *et al*., 2008b) and three methods used to inoculate coffee plants with *B. bassiana* (spraying, injecting, and drenching the soil) were partially effective (Posada *et al*., 2007), as recovery was confirmed but establishment was not long lasting. This lack of establishment was hypothesized to be due to the presence of other fungal endophytes that outcompeted *B. bassiana* (Posada *et al*., 2007). In the coffee-producing world, where seedlings are constantly grown in nurseries for subsequent transplant in the field, it would be ideal to develop a methodology effective in inoculating the seedlings with fungal entomopathogens.

The endophyte research also revealed the presence of bacterial endophytes in coffee plants (Vega *et al*., 2005), and that coffee plants growing in the field in Hawaii, Colombia, Mexico, and Puerto Rico can harbor hundreds of fungal endophytes (Vega *et al*., 2010), including *B. bassiana*.

3.14.4 Nematodes

Two vastly different groups of nematodes could be used as biological control agents against the coffee berry borer. The first group includes the entomopathogenic nematodes and the second group is the insect-parasitic ones. The entomopathogenic nematodes are in the genera *Steinernema* (Rhabditida: Steinernematidae) and *Heterorhabditis* (Rhabditida: Heterorhabditidae), and are mutualistically associated with bacteria in the genera *Xenorhabdus* and *Photorhabdus*, respectively. The mode of action of both nematode–bacteria complexes is similar. It involves infection of the hemocoel with infective juveniles followed by release of mutualistic bacteria that produce toxins that kill the insect (Lewis and Clarke, 2012). On the other hand, insect parasitic nematodes do not kill their hosts but reduce fecundity and/or sterilize females, and may reduce their longevity.

With entomopathogenic nematodes, laboratory bioassays using either coffee berry borer-infested coffee berries or specific insect stages exposed to *Steinernema* or *Heterorhabditis* infective juveniles have shown variable levels of mortality (Allard and Moore, 1989; Castillo and Marbán-Mendoza, 1996; Molina A. and López N., 2002; Molina Acevedo and López Núñez, 2003; Sánchez and Rodríguez, 2007, 2008; Manton *et al*., 2012). In addition to laboratory bioassays, Manton *et al*. (2012) conducted field bioassays in Hawaii. Infested berries were placed on the soil surface around coffee plants, covered with leaf

litter, followed by *S. carpocapsae* (Weiser) applications; resulting mortality was 4.7% in adults and 17% in larvae. In Colombia, Lara G. *et al.* (2004) also conducted field experiments using infested berries placed around coffee trees, followed by treatments consisting of various concentrations of *Steinernema* sp. or *Heterorhabditis* sp. (nematodes were not identified to species). Realpe-Aranda *et al.* (2007) developed a method for rearing *S. colombiense* López-Nuñez, Plichta, Góngora-Botero and Stock and *H. bacteriophora* Poinar in *Galleria mellonella* (L.) for use against the coffee berry borer. It remains unclear whether the use of entomopathogenic nematodes would be practical in the field, taking into consideration various constraints faced by coffee growers, such as the cost and proper storage of the product, labor costs, proper spray coverage, and ready access to water.

An area that might be more promising than the use of commercially available entomopathogenic nematode species is field sampling for parasitic nematodes infecting the coffee berry borer, followed by identification and subsequent studies aimed at determining their biocontrol potential. Varaprasad *et al.* (1994) reported on a *Panagrolaimus* species (Rhabditida: Panagrolamidae) attacking the coffee berry borer in India. However, most *Panagrolaimus* species are free-living nematodes and the parasitic nature of this species needs to be confirmed. In Mexico and Honduras, a new nematode species, *Metaparasitylenchus hypothenemi* Poinar, Vega, Castillo, Chavez and Infante (Tylenchida: Allantonematidae; Figure 11.8D) was found attacking the coffee berry borer in the field (Castillo *et al.*, 2002; Poinar *et al.*, 2004), the first such report in the Americas. *Metaparasitylenchus hypothenemi* appears to affect the female reproductive organs, reducing fecundity (Castillo *et al.* 2002).

3.14.5 Parasitoids

Murphy and Moore (1990) stated that parasitoids are probably the most promising biological control agents against the coffee berry borer. Approximately 12 species of parasitoids have been reported to attack the coffee berry borer (Morallo-Rejesus and Baldos, 1980; Benassi, 1995; Waterhouse, 1998; Pérez-Lachaud, 1998; Bustillo *et al.*, 2002), but only six species, all in the Hymenoptera, have been confirmed. This section will focus on the six parasitoids, four of them originating in Africa: (1) *Prorops nasuta* Waterston (Bethylidae); (2) *Cephalonomia stephanoderis* Betrem (Bethylidae); (3) *Phymastichus coffea* LaSalle (Eulophidae), and (4) *Heterospilus coffeicola* Schmiedeknecht (Braconidae). Two of the six parasitods originate in the Americas: (1) *Cryptoxilos sp.* Viereck (Braconidae), and (2) *Cephalonomia hyalinipennis* Ashmead (Bethylidae). A hyperparasitoid, *Aphanogmus dictynna* (Waterston) (Hymenoptera: Ceraphronidae), has been reported in Kenya (Jaramillo and Vega, 2009; Buffington and Polaszek, 2009).

3.14.5.1 Prorops nasuta

Prorops nasuta, also known as the Uganda wasp, was the first reported natural enemy of the coffee berry borer. Even though Hargreaves (1926) states that it was "discovered early in 1923" attacking the coffee berry borer in Kampala, Uganda, the specimens described by Waterston (1923) as the new species *P. nasuta* were provided to him by Hargreaves in May of 1922. The species name, *nasuta*, denotes the elongated frontal process, described by Hargreaves (1926) as "a short median snout-like projection" (Figure 11.9D). This parasitoid appears to be indigenous to Uganda, Tanzania, and the Congo (Le Pelley, 1968); however, it has also been collected in Kenya, Cameroon, Ivory Coast, and Togo (Klein-Koch *et al.*, 1988; Barrera *et al.*, 1990a). This species has been used in several biological control programs throughout Latin America, the Caribbean, Asia, Madagascar, and the Pacific Islands (Klein-Koch *et al.*, 1988; Barrera *et al.*, 1990a; Infante, 1998; Baker, 1999; Waichert and Azevedo, 2012).

Females are minute wasps (ca. 2.3 mm long) with few body sculptures. They are blackish brown, with pale brown antennae and legs (Hargreaves, 1926). The males are similar to females but smaller (ca. 1 mm long). The head is nearly quadrate, with an elongated frontal process covering the clypeus and the antennal base (Figure 11.9D). The mandibles have three teeth and are strongly developed and especially large when compared to other bethylid species (Evans, 1964). The ocelli are arranged in an equilateral triangle and the antennae have 12 segments. The wings have long radial veins that lack closed cells with the exception of the subcostal vein. The forewings are faintly tinted and the hind wings are hyaline. The abdomen is smooth with a very short petiole. The females have a short ovipositor with about six to eight short bristles (Waterston, 1923; Hargreaves, 1926).

The immature stages of *P. nasuta* have been poorly studied. Eggs are comparatively large (0.53×0.18 mm), elongated, sausage-shaped, translucent, and white (Figure 11.9A). The larva is ca. 1.8 mm long, white and faintly segmented (Hargreaves, 1926) (Figure 11.9B, C). There are three instars in the larval stage (de Toledo, 1942). The pupa is initially white and gradually becomes dark brown as metamorphosis proceeds (Hargreaves, 1926).

Prorops nasuta is an idiobiont (stops development of the host after parasitizing it) solitary parasitoid. The female wasp enters an infested coffee berry, kills the adult borer and seals the entrance of the berry with the body of the insect, impeding the entry of other natural enemies (Hempel, 1933; Infante *et al.*, 2005). It usually spends the remainder of its life inside the berry. The preoviposition

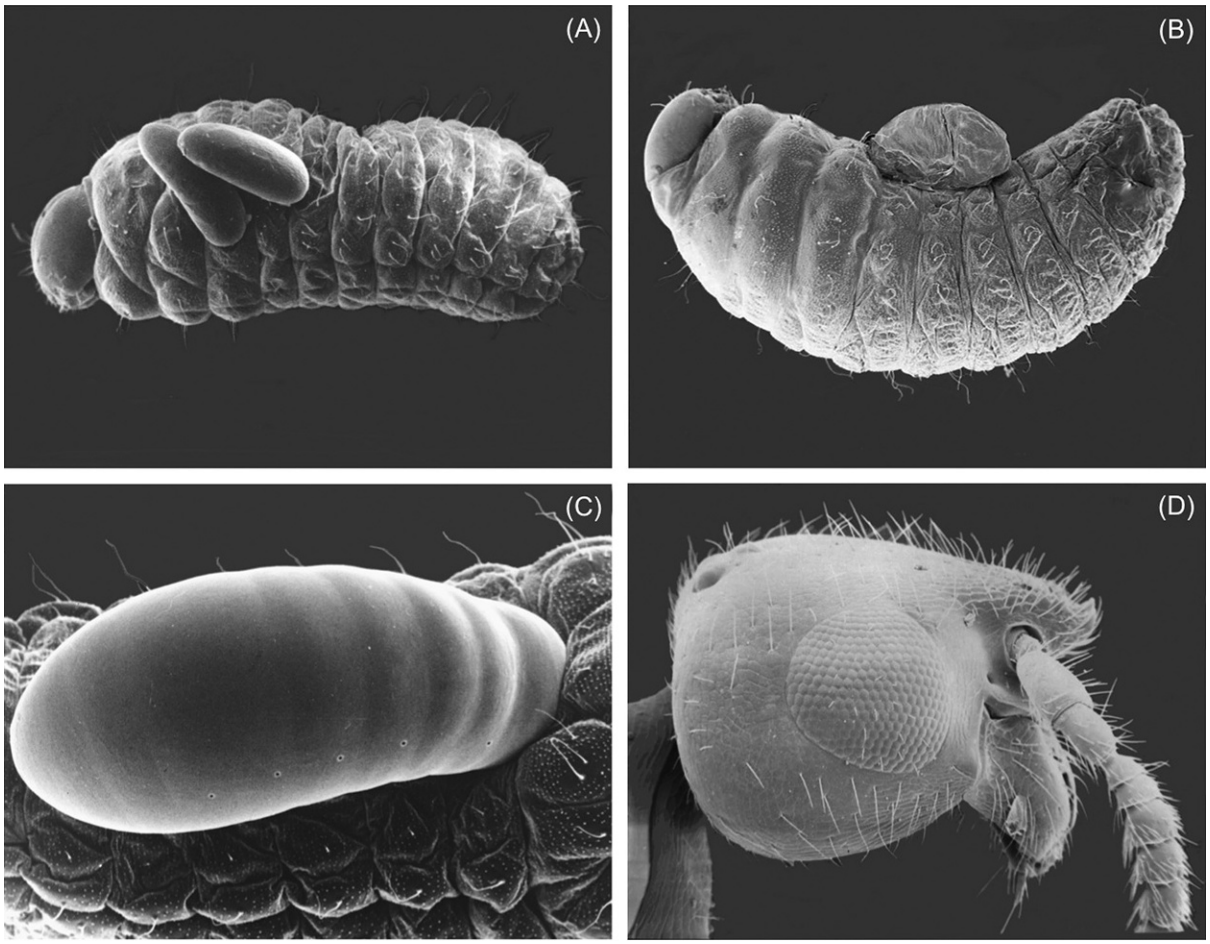

FIGURE 11.9 **Life stages of the parasitoid *Prorops nasuta*.** (A) An exceptional case of two eggs on a coffee berry borer larva; (B) a newly emerged larva on its host; (C) *P. nasuta* larva feeding on its host; and (D) the adult stage.

period ranges from 3 to 14 days. During this time, females feed on eggs and larvae, and paralyze fully grown larvae and pupae. The adult female is able to feed on all juvenile stages of the coffee berry borer (Infante *et al.*, 2005). Eggs are laid singly and externally on the insect cuticle, and in exceptional cases, two eggs can be laid (Figure 11.9A); when oviposition occurs on a pupa, the egg is placed in the dorso-abdominal region, while on larva, it is placed on the ventral surface (Figure 11.9B) (Hargreaves, 1926; de Toledo, 1942; Abraham *et al.*, 1990). The rate of egg laying varies between one and two eggs per day. Immediately after hatching, the larva starts to feed externally (Figure 11.9B, C) and slowly ingests the host fluids, leaving only a shriveled integument and cranial capsule (Abraham *et al.*, 1990). Each *P. nasuta* larva only consumes one host during its development. When completely mature, it spins a cocoon in which pupation occurs. Egg incubation lasts ca. 3 days and larval development ca. 4.5 days, passing through three instars. The prepupal stage lasts ca. 8 days and the pupal stage ca. 13 days. The life cycle from egg to adult lasts on average 28 days at a constant temperature of 22°C and at 75% RH, but adults remain in the berry for a few days in order to mate. In total, 297 degree-days are required to complete the development from egg to adult (Infante, 2000). As with other bethylids, males emerge 2–3 days before their sisters, with whom they mate (Hargreaves, 1926, 1935; Hempel, 1933; de Toledo, 1942; Abraham *et al.*, 1990). The proportion of sexes is one male to four females. Eggs laid by unfertilized females hatch and develop normally. In such instances, the resultant progeny are all males. The median longevity of *P. nasuta* adult females is 28 days when they feed on immature stages of the coffee berry borer but if no food is provided, longevity is drastically reduced to ca. 2.5 days (Infante *et al.*, 2005).

Rearing Methods The rearing method for *P. nasuta* in the laboratory is dependent on the availability of its host, which can be obtained from infested ripe coffee berries collected regularly in the field or from insects reared in artificial diet. Field-collected fresh berries are taken to the laboratory and placed for 3 days on trays lined with tissue paper to reduce humidity. *Prorops nasuta* cultures can then be established

in circular plastic jars with ventilated mesh lids, at a ratio of one female parasitoid per 1.5 infested berries. Once inside the berry, the female parasitoid will feed and reproduce on its host. To avoid proliferation of saprophytic fungi, only a single layer of berries should be placed in each jar (approximately 200 berries). Three weeks after the culture has been initiated and just before progeny are expected to emerge, frass must be removed from the container to facilitate the emergence and collection of parasitoids. The jars are then placed under fluorescent lights and checked several times daily to collect and record the emerging adult parasitoids. In Mexico, *P. nasuta* has been reared for many years using fluctuating temperatures, ranging from 18 to 30°C (16 and 8 h, respectively), 60–85% RH, and a 12 h light:dark photoperiod (Barrera *et al.*, 1991; Infante *et al.*, 2005). In 10 years, more than three million parasitoids were produced in the laboratory (Infante *et al.*, 2005).

An alternative rearing method for *P. nasuta* was developed in Colombia using parchment coffee, which is rehydrated and treated with a fungicide and miticide to avoid contaminants. The parchment coffee is then placed in trays and infested in the laboratory with coffee berry borer females at a rate of two individuals per seed. Twenty-five days after infestation, 200 coffee seeds are placed in containers with ventilated lids and offered to 200 *P. nasuta* females. Parasitoid cultures are stored in the dark at 25°C and 70% RH. The progeny usually emerges 30 days later. This methodology results in an average of 3.7 wasps per seed and 20,000 wasps per month (Portilla and Bustillo, 1995).

Results of Cage Releases Cage exclusion or inclusion techniques are especially valuable because they provide a preliminary assessment of the impact of natural enemies upon pest populations, and also give quantitative information that can be used to understand the insect population dynamics (Luck *et al.*, 1999; Kidd and Jervis, 2005). To our knowledge, only one study has evaluated *P. nasuta* through the use of parasitoid inclusion field-cages techniques. In a preliminary evaluation in Ecuador in which 1605 adult parasitoids were released in sleeved cages, only 1430 individuals were recovered the following generation (Delgado and Sotomayor, 1991). Parasitism rates in the localities where the parasitoid was tested ranged from 2.3 to 38% in coffee berries on the plant, and 6% in coffee berries on the ground (Delgado *et al.*, 1990).

Results of Field Releases *Prorops nasuta* has been imported for biological control purposes to at least 14 coffee producing countries (Table 11.4). Unfortunately, classical biological control attempts using *P. nasuta* have, in almost all cases, not been satisfactory. There are various reasons for this. For instance, in Mexico (importation of 1988) and India (Table 11.4), the introductions failed due

TABLE 11.4 Introductions (in Chronological Order) of the Parasitoid *Prorops nasuta* to Countries outside Africa

Imported to:	Year	Exported from:	Reference
Indonesia	1924	Uganda	Le Pelley, 1968
Brazil	1929	Uganda	Hempel, 1933
Sri Lanka (Ceylon)	1938	Uganda	Le Pelley, 1968
Peru	1962	Brazil	de Ingunza, 1964
Ecuador	1987	Kenya and Togo	Klein-Koch *et al.*, 1988
Mexico	1988	Kenya and Togo	Barrera *et al.*, 1990c
Indonesia	1989	Togo	Murphy and Moore, 1990
Colombia	1990	Ecuador and Brazil	Baker, 1999; Bustillo Pardey, 2005
Mexico	1992	Brazil	Infante *et al.*, 2005
Guatemala	1993	Mexico	Infante, 1998
Honduras	1993	Mexico	Infante, 1998
El Salvador	1993	Mexico	Infante, 1998
India	1995	Mexico	Sujay *et al.*, 2010
Jamaica	1999	Honduras	Trejo S. and Fúnez, 2004
Costa Rica	2003	Colombia	Borbón-Martínez, 2007
Panama	2006	not stated	Contreras and Camilo, 2007

to problems with the rearing system. In these countries, *P. nasuta* was found to be difficult to maintain in a laboratory-rearing system and the colony collapsed. As a consequence, parasitoids could not be released (Barrera *et al.*, 1990c; Infante, 1998). In other cases, such as the introductions to Mexico (importation of 1992), Indonesia, Sri Lanka, Peru, and El Salvador (Table 11.4), the parasitoid never became established in the field after several releases (de Ingunza, 1964; Murphy and Moore, 1990; Infante *et al.*, 2001). It is assumed that in these cases the parasitoid only had a temporary effect on the coffee berry borer population, immediately after the release. *Prorops nasuta* has been recorded as established in Brazil, Ecuador, Colombia, Guatemala, and Honduras (Heinrich, 1965; Ruales, 1997; Trejo S. and Fúnez, 2004; Maldonado-Londoño and Benavides-Machado, 2007). However, parasitoid population levels have been barely perceptible and the parasitoid did not provide good control of the pest. In these countries, coffee growers typically use other methods to manage the coffee berry borer (Infante *et al.*, 2001).

It is apparent that *P. nasuta* is only able to maintain high populations in the field if there are multiple releases through the coffee season. In places where there was a constant rearing-release system, parasitism levels were acceptable but after several years with no releases, parasitoid populations decreased dramatically. In Brazil, reports following the introduction of *P. nasuta* introduction were very optimistic (Hempel, 1933; de Toledo, 1942, 1948; Yamamoto, 1948). Subsequently, it was demonstrated that although present in the country, *P. nasuta* populations were extremely low. Only 2% of the coffee berry borer infested berries were parasitized by *P. nasuta* (Heinrich, 1965; Ferreira and Bueno, 1995). Such low parasitism appears to have little impact on the pest population. A similar situation occurred in Ecuador. After its importation in 1987 (Table 11.4), average parasitism levels were 27% in berries on the plant and 25% in berries that had fallen on the ground (Cisneros and Tandazo, 1990). Unfortunately, 7 years later, the parasitoid was reported as barely present in some regions of the country (Ruales, 1997).

The best results obtained with *P. nasuta* have been reported in Colombia, where parasitoid releases started in 1991. The number of released individuals has been impressive. From 1994 to 2000, ca. 516 million *P. nasuta* were released in coffee plantations (Maldonado-Londoño and Benavides-Machado, 2007). Although parasitoid releases have decreased drastically in the recent years, the establishment of this species is evident in most coffee plantations (Bustillo Pardey, 2006). For example, Morales P. *et al.* (2011) reported the establishment of *P. nasuta* in 15 coffee farms 8 years after their release. The parasitoid was found in 80% of the farms evaluated, with parasitism between 0.2 and 11.6%. Another evaluation carried out 15 years after releases in 80 farms revealed that although *C. stephanoderis* was not recovered, *P. nasuta* was recovered in 65% of the locations sampled, where the percentage of parasitism ranged from 0.25 to 50% (Maldonado-Londoño and Benavides-Machado, 2007). These results indicate that *P. nasuta* is well adapted to the environmental conditions of the Colombian coffee-growing areas, contributing in some degree to the control of the coffee berry borer. In fact, from the three African species introduced into Colombia for the biological control of the coffee berry borer, *P. nasuta* is considered the most promising species (Maldonado-Londoño and Benavides-Machado, 2007; Rivera-España *et al.*, 2010).

3.14.5.2 Cephalonomia stephanoderis

Ticheler (1961, 1963) discovered *Cephalonomia stephanoderis* (Figure 11.10) parasitizing the coffee berry borer by the end of 1950s in coffee plantations in Ivory Coast. He considered this species to be the most important natural enemy of the coffee berry borer in that country. Subsequently, Betrem (1961) described it as a new species. *Cephalonomia stephanoderis* is widely disseminated in Togo, Ivory Coast, Democratic Republic of the Congo, Burundi, Benin, and Cameroon (Koch, 1973; Damon, 1999; Barrera *et al.*, 2000). In a recent study, Jaramillo *et al.* (2009b) confirmed the presence of *C. stephanoderis* in coffee plantations in Kenya, although at low levels. It has been introduced to at least 16 countries (Table 11.5) in an attempt to use it as a biological control agent against the coffee berry borer (Klein-Koch *et al.*, 1988; Barrera *et al.*, 1990a; Bustillo *et al.*, 1998; Baker, 1999).

Cephalonomia stephanoderis is a macroptereous shiny black wasp (Figure 11.10F). Adult females are ca. 2 mm long and males ca. 1.4 mm long. The eggs are slightly curved and shiny white (Figure 11.10A, B). The eclosed larva is curved and looks like the egg because its segmentation is not apparent. The precise number of larval instars is unknown, but there are at least three larval instars (Infante *et al.*, 1994a). The pupal stage is similar to the adult in size and shape (Figure 11.10E). For a detailed description of the insect, see Betrem (1961) and Infante *et al.* (1994a).

Cephalonomia stephanoderis is a solitary ectoparasitoid of the coffee berry borer. A female wasp enters an infested coffee berry in search of potential hosts and will remain inside the berry for the rest of her life if there are enough hosts to feed on and parasitize (Koch, 1973). Females are synovigenic parasitoids that feed on all biological stages of the coffee berry borer, but have preference for eggs and adults (Koch, 1973; Lauzière *et al.*, 2001a). Lauzière *et al.* (2000) described in detail the behavior and daily parasitic activity, including host examination, adult feeding, paralysis, and oviposition. The preoviposition period usually takes 2 to 3 days and females feed during their entire lifetime (Lauzière *et al.*, 2001b). Ovipositing females

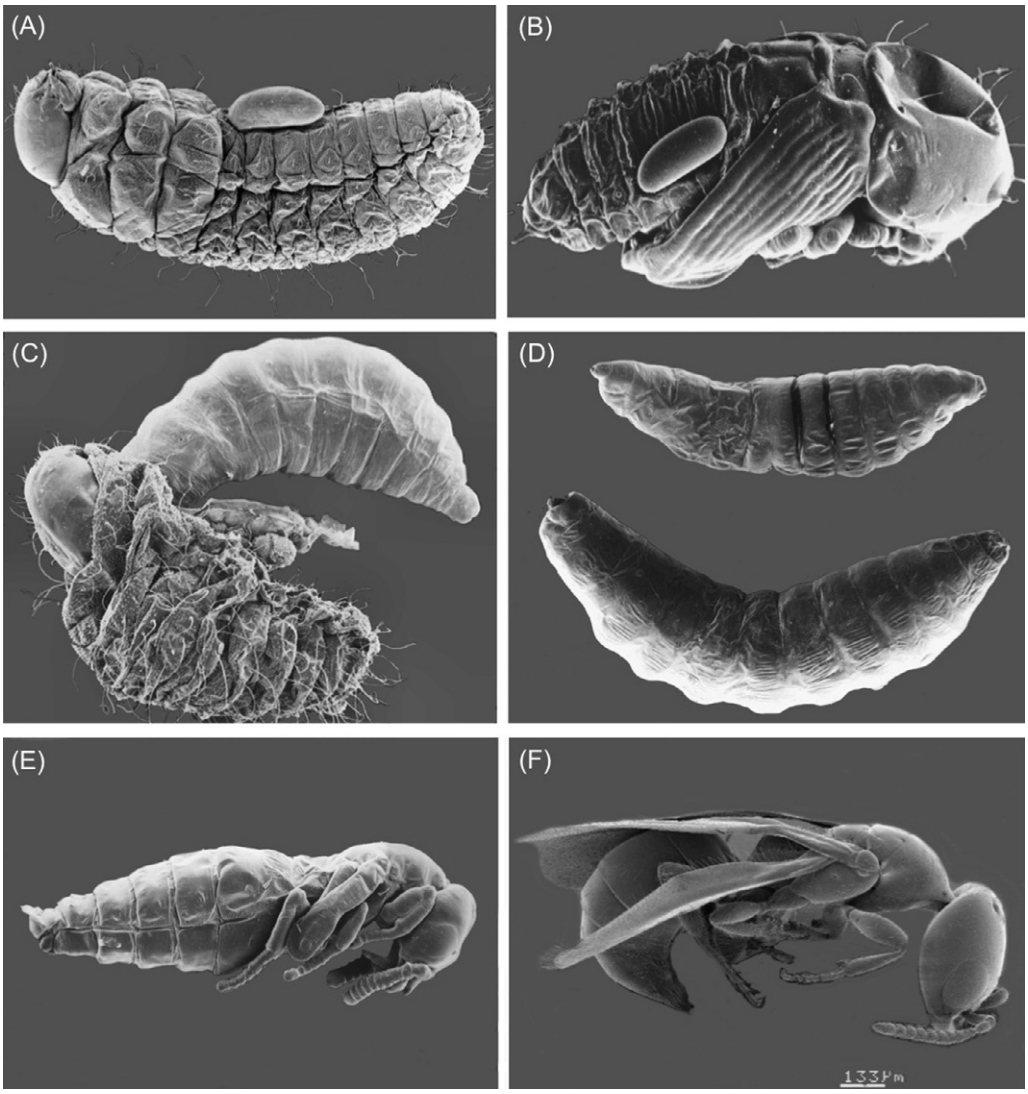

FIGURE 11.10 **Life stages of *Cephalonomia stephanoderis*.** (A) Parasitoid eggs laid on the prepupa and (B) pupa; (C) larva feeding on host; (D) fully grown male (top) and female (bottom) larvae; (E) pupa after removing the silk cocoon; and (F) the adult stage.

permanently paralyze full-grown coffee berry borer larvae, prepupae (Figure 11.10A), and pupae (Figure 11.10B) prior to oviposition and subsequently parasitoid eggs are laid singly and externally on these biological stages (Infante *et al*., 1994a; Lauzière *et al*., 2000). Individual wasps can parasitize two to three hosts per day for several weeks if there are enough hosts (Barrera *et al*., 1989; Abraham *et al*., 1990). Individual females can oviposit up to 63 eggs under optimal conditions in the laboratory (Infante and Luis, 1993). Upon hatching, the larva inserts its mouthpart into the host body and commences feeding externally until it has consumed the tissues of the host (Figure 11.10C). Once feeding is complete the larva detaches from the remains of the host and spins a cocoon. Adult parasitoid males emerge 1 day before females and sibling mating occurs inside the berry (Abraham *et al*., 1990; Infante *et al*., 1994a). The females exhibit arrhenotokous parthenogenesis (Koch, 1973; Infante *et al*., 1993). In nearly all aspects, the biology and habits of *C. stephanoderis* is similar to *P. nasuta* (Abraham *et al*., 1990). There is a skewed sex ratio favoring females: 4.8:1 (Ticheler, 1961, 1963); 3.5:1 (Koch, 1973); and 7:1 (Barrera *et al*., 1993b). At 27°C, the developmental time for egg, larva, and pupa is 1.7, 4.2, and 12.7 days, respectively, while the development from egg to adult requires about 252 degree-days (Infante *et al*., 1992a).

For a long time, both *C. stephanoderis* and *P. nasuta* were considered to be parasitoids specific to the coffee berry borer (Abraham *et al*., 1990). However, Arcila *et al*. (1997) reported that *C. stephanoderis* also attacks *H. obscurus* in Colombia. In the laboratory, both parasitoid species can feed and reproduce on two curculionid species:

TABLE 11.5 Introductions (in Chronological Order) of the Parasitoid *Cephalonomia stephanoderis* to Countries outside Africa

Imported to:	Year	Exported from:	Reference
Ecuador	1988	Togo	Klein-Koch *et al.*, 1988
Mexico	1988	Togo	Barrera *et al.*, 1990a
Indonesia	1989	Togo	Murphy and Moore, 1990
New Caledonia	1989	Togo	Murphy and Moore, 1990
Colombia	1989	Ecuador	Benavides and Portilla, 1991
Guatemala	1990	Mexico	Barrera *et al.*, 1990b
El Salvador	1990	Mexico	Barrera *et al.*, 1990b
Honduras	1990	Mexico	Barrera *et al.*, 1990b
Nicaragua	1992	El Salvador	López *et al.*, 1993
Bolivia	1993	Ecuador	Sirpa-Roque, 1999
Brazil	1994	Colombia	Benassi, 1995
India	1995	Mexico	Sujay *et al.*, 2010
Dominican Rep.	1997	Honduras	Trejo S. and Fúnez, 2004
Jamaica	1999	Honduras	Trejo S. and Fúnez, 2004
Cuba	2003	Mexico	Peña *et al.*, 2006
Venezuela	2003	Dominican Rep.	Torrealba and Arcaya, 2005

Caulophilus oryzae (Gyllenhal) and *Sitophilus* sp. (Pérez-Lachaud and Hardy, 2001).

Rearing Methods Based on the similarity of their life cycles, the rearing methods for *P. nasuta* and *C. stephanoderis* are the same (Abraham *et al.*, 1990; Barrera *et al.*, 1991; Infante *et al.*, 2005). Therefore, no additional details for rearing *C. stephanoderis* will be presented in this section. The rearing methodology developed for *C. stephanoderis* in Mexico has been successful and this species has been reared uninterruptedly for over 25 years.

As in the case of *P. nasuta*, a rearing method based on parchment coffee (described above) has been developed in Colombia for *C. stephanoderis* (Portilla and Bustillo, 1995). This methodology has been reported as very successful, producing up to 10 million *C. stephanoderis* adults per month (Baker, 1999).

Results of Cage Releases Not much information is available on the field evaluation of *C. stephanoderis* in caged conditions. In Ecuador, Delgado *et al.* (1990) released *C. stephanoderis* in caged branches and caged plants after berries had been artificially infested with the coffee berry borer. Parasitization rates reached up to 86% in berries on the plant and 87% in berries on the ground.

In Mexico, field cages were placed individually on eight coffee plants and adult *C. stephanoderis* females were released inside the cages at a rate of 200 individuals per plant (Damon and Valle, 2002). One month later, berries were taken to the laboratory to estimate parasitism rates, with poor results. A high proportion of parasitoids were unable to find the infested berries, resulting in low levels of parasitism (4–37%). It became evident that *C. stephanoderis* has poor host searching capabilities and that a large numbers of parasitoids are needed to obtain high parasitism rates. Therefore, the use of *C. stephanoderis* in Mexico is not economically feasible (Damon and Valle, 2002).

Results of Field Releases Three papers from Africa have reported encouraging parasitism rates by *C. stephanoderis* (Ticheler, 1961, 1963; Koch, 1973; Borbón-Martinez, 1989). In Ivory Coast, the percentage of berries infested by the coffee berry borer and with presence of *C. stephanoderis* reached up to 50% at the end of the harvest (Ticheler, 1961, 1963). Also in Ivory Coast, Koch (1973) suggested that coffee harvesting considerably affects coffee berry borer population levels and, consequently, *C. stephanoderis*

too. However, he mentioned that this parasitoid might be responsible for a 20–30% reduction in coffee berry borer population levels in berries remaining on the plant after harvest. In Togo, Borbón-Martinez (1989) reported 47% coffee berry borer mortality due to *C. stephanoderis*.

Cephalonomia stephanoderis has been introduced in at least 16 countries outside Africa for classical biological control purposes (Table 11.5). However, field evaluations have not been conducted in most countries, and therefore little information on parasitism levels is available in the literature. The parasitoid has been studied in Ecuador, Mexico, and Colombia and the results are quite different from those reported in Africa.

The first releases of *C. stephanoderis* in Ecuador were done in 1989 and resulted in parasitism rates of 9 to 52% (Delgado *et al.*, 1990). In another release, 10,000 parasitoids were released on four dates followed by monthly sampling of berries for parasitism assessments. The highest parasitism rate was 12% 3 months after release. The effect of the parasitoid decreased as time after release increased. Eight months after parasitoid release, parasitism levels were 1.3% (Delgado *et al.*, 1990). Also in Ecuador, Sponagel (1994) conducted an evaluation of *C. stephanoderis* after releasing 17,500 parasitoids in nine farms. Three months after release, the parasitoid was only detected in six farms. The parasitoid could not be detected 10 months after release. Sponagel (1994) concluded that *C. stephanoderis* is very susceptible to the humid conditions of the Ecuadorian Amazon region, where up to 25 days of rain per month are common.

In Mexico, a preliminary evaluation of the introduction of *C. stephanoderis* found that it could be detected in up to 81% of the infested berries; however, parasitism levels decreased to 3.2% after coffee was harvested (Barrera *et al.*, 1990c). In another study carried out in 26 localities in Chiapas, it was reported that the parasitoid was established in all of them, reaching parasitism rates between 0.5 and 19.6%, 3 years after being released (Barrera, 1994). Gómez *et al.* (2010) conducted a survey to evaluate the establishment of the three African parasitoids that have been released in Mexico. Sampling was conducted in 31 coffee plantations during the intercropping period. *Cephalonomia stephanoderis* was found in 67% of the plantations, with parasitism ranging from 0.3 to 26%. The highest level of parasitism was found in *C. canephora* plantations. The study confirmed the establishment of *C. stephanoderis* in Mexico 20 years after its first release. In Mexico, Dufour *et al.* (1999) reported a reduction of 22–56% in coffee berry borer infestation after releasing 35,000–40,000 wasps/ha during the intercropping period.

In Colombia, *C. stephanoderis* has become established in all the sites where it has been released. Parasitism rates between 2.2 and 13.8% have been reported (Portilla and Bustillo, 1995). Generally, field parasitism is lower than 10% and consequently not enough to reduce the pest population below the economic threshold (Bustillo *et al.*, 1998). Salazar and Baker (2002) conducted a field experiment to determine ensuing parasitoid infestation rates when different densities of the parasitoid were released based on the number of infested berries. A ratio of 100:1 (parasitoids:infested berries) resulted in an average of five coffee berry borer infested berries per tree. The 50:1 ratio had an average of 30 infested berries per tree, while the 10:1 ratio had 53 infested berries per tree. The control (no parasitoids) had 82 infested berries per tree (Salazar and Baker, 2002). In another experiment, Aristizábal *et al.* (1998) reported a significant reduction in the number of infested berries when using *C. stephanoderis*. The experimental plots, containing 2200 coffee plants, were treated with 30,000, 32,000, or 80,000 parasitoids, resulting in 3 to 28% parasitism. The conclusion was that very high numbers of parasitoids are required to improve parasitism levels (Aristizábal *et al.*, 1998). A similar conclusion was reached in Mexico by Damon (1999).

A tritrophic simulation model by Gutierrez *et al.* (1998), which included the coffee plant, the coffee berry borer, and their natural enemies, predicted that bethylid parasitoids, singly or in combination, have little impact on coffee berry borer population levels. Among other factors, poor control is predicted because these species have a low numerical response and their attack is limited to a single berry.

3.14.5.3 Phymastichus coffea

This parasitoid (Figure 11.11) was discovered parasitizing adult coffee berry borers in Togo in 1987 (Borbón-Martínez, 1989) and was described as a new genus and species in the family Eulophidae (LaSalle, 1990). *Phymastichus coffea* has been collected in Benin, Burundi, Cameroon, Ivory Coast, Kenya, and Togo (Infante *et al.*, 1992b) and is believed to be present in all African countries infested with the coffee berry borer (López-Vaamonde and Moore, 1998). *Phymastichus coffea* has been introduced in at least 12 countries (Table 11.6). It was introduced to Colombia in 1995 (Table 11.6) after being quarantined in England (López-Vaamonde and Moore, 1998). From Colombia it has been exported to Brazil, Ecuador, Honduras, Guatemala, India, and Costa Rica (Table 11.6).

Adults (Figure 11.11E) are dark brown wasps with reddish eyes and shiny wings (LaSalle, 1990; Vergara-Olaya *et al.*, 2001a). Adult females are ca. 1 mm long, and males are half that size (for a detailed description, see LaSalle, 1990). Sex in immature stages can be differentiated based on pupal size, with females being twice as large as males (Feldhege, 1992; Vergara-Olaya *et al.*, 2001a; Espinoza *et al.*, 2002, 2009).

Pymastichus coffea is a primary, gregarious, idiobiont endoparasitoid of coffee berry borer adults (Feldhege,

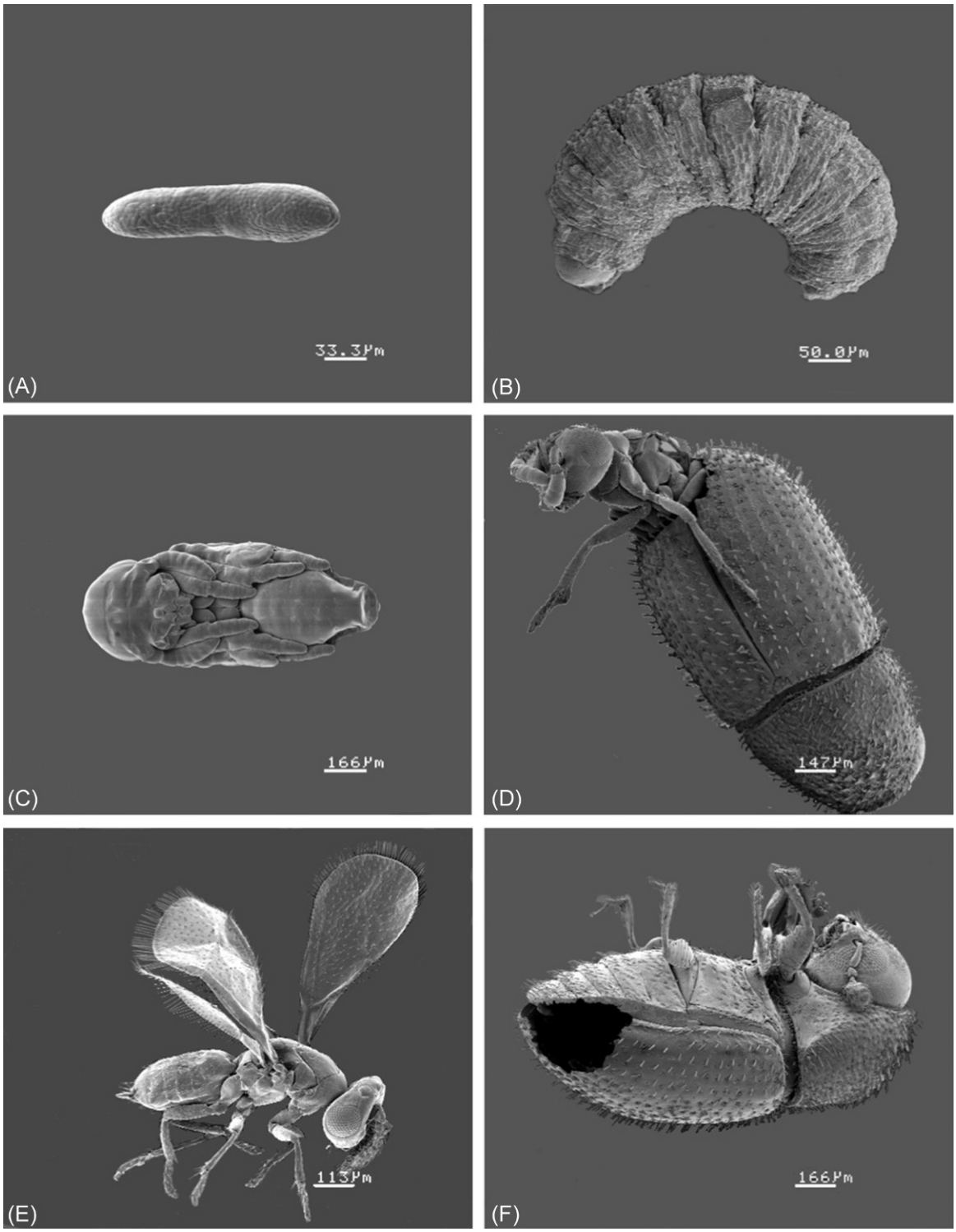

FIGURE 11.11 **Life stages of the parasitoid *Phymastichus coffea*.** (A) Egg; (B) larva; (C) pupa; (D) an adult emerging from coffee berry borer; (E) the adult female; and (F) a typical hole made by the female parasitoid, after emerging from its host.

1992; Infante *et al*., 1994a; López-Vaamonde and Moore, 1998). Adult females start to search for hosts immediately after emergence and do not have a preoviposition period. Parasitization can occur within the first hours after the wasp reaches the adult stage (Infante *et al*., 1994a). Females oviposit in the abdomen of coffee berry borer adults (Figure 11.12C), allocating two eggs per host, one of which will become a male and the other a female.

TABLE 11.6 Introductions (in Chronological Order) of the Parasitoid *Phymastichus coffea** to Countries outside Africa

Imported to:	Year	Exported from:	Reference
Colombia	1995	Kenya	López-Vaamonde and Moore, 1998; Baker, 1999
Brazil	1998	Colombia	Cantor *et al.*, 1999
Ecuador	1999	Colombia	Delgado A. *et al.*, 2002
Honduras	1999	Colombia	García, 2000
El Salvador	1999	Honduras	Baker *et al.*, 2002
Jamaica	1999	Honduras	Baker *et al.*, 2002
Guatemala	1999	Colombia	García, 2000
India	1999	Colombia	Bustillo Pardey, 2005; Sujay *et al.*, 2010
Mexico	2000	Guatemala	García, 2000
Cuba	?	Mexico	Vázquez-Moreno, 2005
Costa Rica	2003	Colombia	Borbón-Martínez, 2007
Panama	2006	?	Armuelles, 2007

There is some evidence that P. coffea has also been introduced to Bolivia, Peru, Venezuela, Nicaragua, and the Dominican Republic. However, there are no reliable sources to support this information.

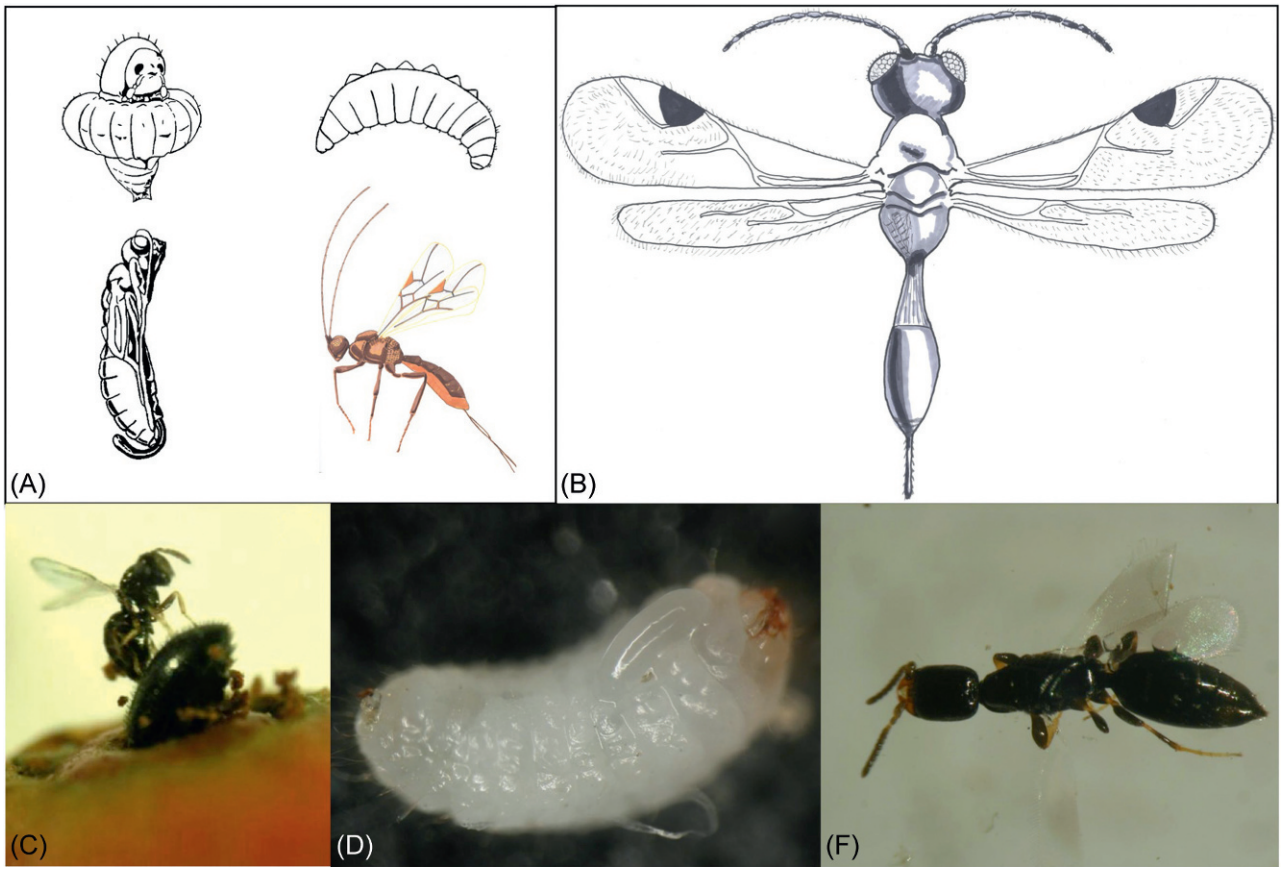

FIGURE 11.12 (A) Life stages of *Heterospilus coffeicola*: larva feeding on the pupal stage of the coffee berry borer (upper left); fully grown larva (upper right); pupa (lower left); and an adult female (lower right). No photographs are known for the biological stages of this species. *Redrawn from Fonseca and Araujo (1939). (B) Adult female of the* Cryptoxilos sp. *Redrawn from Deyrup (1981). No photographs are known for the biological stages of this parasitoid. (C) An adult female* Phymastychus coffea *at the moment of parasitizing the coffee berry borer, which is boring into a berry. (D) An egg of the parasitoid* Cephalonomia hyalinipennis *laid on a prepupa of the coffee berry borer and (E) adult female* C. hyalinipennis.

Sometimes it is possible to find more individuals in a single host, but only two will survive due to intense intraspecific competition (Castillo *et al*., 2004a; Espinoza *et al*., 2009). Upon hatching, parasitoid larvae feed on the internal tissues of the host's abdomen. After feeding for several days, the male larva migrates to the prothorax where it continues to feed, while the female larva remains feeding on the abdominal region. Pupation occurs inside the host without the formation of a cocoon. Males pupate in the prothorax, while females pupate in the abdomen. The female parasitoid makes an exit hole in the exoskeleton of the host in order to emerge (Figure 11.11D, F). The male comes out immediately afterwards, using the same hole made by the female. The sex ratio is close to 1:1, and presumably there is sibling mating just before emergence from the host (Espinoza *et al*., 2009). The life cycle from egg to adult is ca. 30 days at 27°C and 70–80% RH (Feldhege, 1992). In the field, the life cycle from egg to adult is completed in 47 days at an average temperature of 23°C. The adult longevity is at most 3 days. Hosts parasitized by *P. coffea* do not live longer than 15 days (Espinoza *et al*., 2009).

Some reports indicate that *P. coffea* can attack other scolytids in the laboratory. For example, in no-choice tests, *P. coffea* was able to parasitize and complete its development on *H. obscurus*, *H. seriatus*, and *Araptus* sp. (López-Vaamonde and Moore, 1998), three bark beetle species common in Colombian agroecosystems. In another laboratory host-specificity test, Castillo *et al*. (2004b) assessed parasitism on *H. crudiae*, *H. eruditus*, *H. plumeriae*, *Scolytodes borealis* Jordal, and *Araptus fossifrons* Wood. There were ovipositions attempts by *P. coffea* on all species tested, but parasitization and development of progeny was only completed in *H. crudiae* and *H. eruditus*. Both findings confirm the oligophagic behavior of *P. coffea*, although there are no field reports on parasitization of species other than the coffee berry borer.

Early studies suggested that attack by *P. coffea* occurred just while the coffee berry borer was initiating fruit perforation (Borbón-Martínez, 1989; Feldhege, 1992; López-Vaamonde and Moore, 1998). However, berries that had been infested with the coffee berry borer for 7 days were successfully parasitized by *P. coffea* (Echeverry-Arias, 1999; Jaramillo *et al*., 2006; Espinoza *et al*., 2002, 2009). Thus, it appears that *P. coffea* is able to attack the coffee berry borer at any time after fruit colonization. This could have important practical implications, as it would allow for field releases of the parasitoid at any vegetative period of the coffee plant, as long as infested berries are available.

Rearing Methods A method for rearing *P. coffea* was developed in Mexico by Infante *et al*. (1994b, 2003). Non-infested green coffee berries are collected in the field and taken to the laboratory. Berries are placed in a plastic container filled with water, in order to separate the floating berries, as they are not useful for rearing. Berries are washed and dried in trays for 2 or 3 days. To facilitate penetration by the coffee berry borer, the disc is slightly pierced with a dissecting needle. Immediately afterwards, berries are placed in a plastic container covered with a fine mesh lid. If the container has a one-liter capacity, a maximum of 50 berries should be used, distributed in a single layer. Adding more than 50 berries could lead to fungal proliferation due to increased moisture. A ratio of about 10 coffee berry borer females per berry are placed in the container and allowed to bore for ca. 2 hours, followed by introduction of parasitoids previously fed with honey. The container should not be moved to avoid injuring the parasitoids. At this stage, coffee berry borers will have about half of their bodies inside the berry, which makes parasitoid attack easier. Insects that do not bore the berries are also susceptible to attack. The containers can be kept at room temperature in the laboratory, keeping in mind that optimal ambient conditions for rearing are 80–90% RH, a 12:12 L:D photoperiod, and 26°C. Collection of the new generation of parasitoids should be done 25 days after initial set-up. Berries are brushed to remove dust and any fungal growth present, and transferred to a clean plastic container. Coffee berry borers that did not bore into berries should also be placed in these containers as they might have been parasitized. Generally, the parasitoids start emerging from the berries 1 month after set-up. The new generation of parasitoids will emerge on a daily basis for about 7 days. It is important to keep the containers under a light source to stimulate emergence (Infante *et al*., 1994b, 2003).

As is the case for *P. nasuta* and *C. stephanoderis*, the rearing of *P. coffea* in Colombia is based on parchment coffee artificially infested with adult coffee berry borer (López-Vaamonde and Moore, 1998; Orozco Hoyos, 2002). Parasitoid colonies are held at 24°C, and 75% RH in total darkness. This methodology has been reported to be very successful, producing an average of one million parasitoids per month (Baker, 1999).

Results of Cage Releases Parasitoid inclusion experiments with *P. coffea* under field-cage conditions or entomological sleeves have been very promising for the control of the coffee berry borers. For instance, Echeverry-Arias (1999) evaluated releases of *P. coffea* in experimental plots in Colombia using different densities of parasitoids released on infested coffee berries inside entomological sleeves. Parasitism varied from 8 to 49% when releasing a 1:13 and 1:1 parasitoid:host ratio, respectively. Releasing parasitoids at a 1:1 ratio in entomological sleeves 5 days after the coffee berry borers had infested the berry resulted in up to 83% parasitism. Using a 1:1 parasitoid:host ratio, Jaramillo *et al*. (2005) observed that parasitism was significantly affected by the age of the berries at the time of infestation. They reported a maximum parasitism of 32% in

210-day-old berries and parasitism increased to 85% and 76% when berries were 150 and 90 days old, respectively.

Similar levels of parasitism were obtained in Mexico when evaluating *P. coffea* using different densities of parasitoid:host ratios in field-cage experiments. At the 1:30 parasitoid:host ratio, parasitism was ca. 12%. The pest population was significantly reduced when *P. coffea* was released at a 1:5 or 1:10 parasitoid:host ratio. The highest level of parasitism (62%) occurred at the 1:5 parasitoid:host ratio, with a significant reduction in damage to the seeds. These studies demonstrate that the use of *P. coffea* resulted in a 2.2–3.1-fold lower coffee berry borer damage to the coffee seeds' weight (Infante *et al.*, 2013).

Results of Field Releases Due to the short longevity of adult *P. coffea* (2–3 days), releases in Mexico have been carried out using the pupal stage. The entire rearing culture containing berries and coffee berry borers parasitized by *P. coffea* are taken to the field 3 days before the expected date of adult parasitoid emergence. Coffee berries are placed inside 10×15 cm metallic cages and hung on a coffee branch. The wire from which the cage is hung is covered with grease to avoid the interference of ants or other predators. The amount of individuals released is estimated by leaving 10% of the infested berries in the laboratory, to quantify the total emergence of parasitoids (Infante *et al.*, 2003).

Reports on the field performance of *P. coffea* have only been published in Colombia and Mexico. The first release in Colombia occurred in 1997 (Baker, 1999). The parasitoid was recovered from coffee plots the following year, with ensuing parasitism levels ranging between 41 and 67%. In a more extensive study comprising 33 coffee farms, ca. two million adult parasitoids were released, resulting in overall parasitism of 2–6% (Benavides *et al.*, 2002). Despite the low parasitism levels, the parasitoid appears to be adapted to the environmental conditions of the country (Benavides *et al.*, 2002). Echeverry-Arias (1999) carried out artificial infestations of coffee berries and released adult parasitoids at different densities. He reported parasitism rates of 47, 41, 22, 21, 13, 10, and 6% when using parasitoids:host ratios of 1:1, 1:3, 1:5, 1:7, 1:9, 1:11, and 1:13, respectively.

Vergara-Olaya *et al.* (2001b) reported on an augmentative release of 30,000 *P. coffea* adults in a 70×130 m plot with a 13% natural coffee berry borer infestation. Following the release of wasps in the center of the plot, samples were collected 25 days later at different distances from the center of the experimental plot. Results revealed that parasitism by *P. coffea* decreased gradually as the distance from the release point increased. There was a parasitism rate of 61, 63, 37, 25, and 27% at a distance of 0–10, 10.1–20, 20.1–30, 30.1–40, and 40.1–54 m from the release point, respectively. The overall mean parasitism was 47%. These results confirm that high levels of parasitism can only be achieved if there are releases with high numbers of parasitoids. In Colombia, sampling for *P. coffea* to assess its establishment only resulted in detection for the first 3 years after its release (Bustillo Pardey, 2006).

In Mexico, *P. coffea* was released in 14 coffee farms at different elevations with the goal of having it established permanently (Galindo *et al.*, 2002). At least 9000 female parasitoids were released at each farm. Samples of 200 infested berries collected at random from each farm on a monthly basis resulted in parasitoid recovery from all farms for the first 6 months following release. The highest levels of parasitism occurred the first month (32–55%) following release. At 6 months, parasitism declined 10 to 28%. At eight to 12 months after release, no parasitoids were recovered. The following coffee season, parasitism was barely detected in three of the sites, and afterwards, the parasitoid was never recovered from any site (Galindo *et al.*, 2002). It is assumed that as is the case with the bethylid parasitoids, the coffee harvest has a severe effect on the survivorship of parasitoids and acts as a mortality factor. At present, *P. coffea* is not considered to have become established in Mexico.

3.14.5.4 Heterospilus coffeicola

Information on this species is very scarce and most data were published more than 80 years ago. *Heterospilus coffeicola* (Figure 11.12A) was discovered in Uganda in 1923 (Hargreaves, 1926, 1935) and has also been recorded in Tanzania, the Democratic Republic of the Congo, and Cameroon (Le Pelley, 1968). The adult female is a dark brownish wasp, ca. 2.5 mm long. There is sexual dimorphism, with males being smaller than females and having a small dark area (stigma) near the base of each hind wing (Fonseca and Araujo, 1939). The eggs are small and white, measuring approximately 0.39×0.13 mm, and can be confused with the eggs of the coffee berry borer. The size of first instar larvae is ca. 0.5 mm long, but fully developed larvae are 1.2 mm. The pupal stage can be found inside a white cocoon (Fonseca and Araujo 1939; Le Pelley, 1968).

In contrast with *P. nasuta* and *C. stephanoderis*, adult *H. coffeicola* spend little time inside infested berries (Fonseca and Araujo, 1939). A single egg is deposited per berry and the incubation period is about 6 days. After eclosion, the larva is able to feed on eggs and larvae of the coffee berry borer over a period of 18–20 days. The predatory rate of the parasitoid larva can reach 15 individuals during its entire life. By the end of the larval stage, a cocoon is formed in the gallery, where pupation occurs. Complete development from egg to adult takes about 40 days. Females prefer to oviposit in ripe berries that are attached to the plant. Berries that have fallen on the ground are not susceptible to be parasitized by *H. coffeicola*

(Hargreaves, 1926, 1935; Fonseca and Araujo, 1939; Le Pelley, 1968).

Hargreaves (1926, 1935) reported that, based on the large amount of individuals consumed by *H. coffeicola*, it could be the most important natural enemy of the coffee berry borer in Africa. In addition, *H. coffeicola* attacks the coffee berry borer shortly after it colonizes the berry, in contrast to the bethylids, which attack later. Fonseca and Araujo (1939) proposed that *H. coffeicola* could be complementary to *P. nasuta*. However, additional observations revealed that *H. coffeicola* larvae also feed on *P. nasuta* larvae, thereby reducing the efficacy of *P. nasuta* (Le Pelley, 1968). Thus, although *H. coffeicola* exerts some mortality over the coffee berry population in several countries in Africa, there is no evidence to suggest that its presence is sufficient to control the pest. Waterhouse (1998) stated that the biological control potential of *H. coffeicola* requires further study because it is not specific to the coffee berry borer. All attempts to rear *H. coffeicola* under laboratory conditions have been unsuccessful (Le Pelley, 1968).

3.14.5.5 Cryptoxilos sp

The genus *Cryptoxilos* (Figure 11.12B) belongs to the Braconidae subfamily Euphorinae. Species in this genus are characterized by brownish black color and small size (<2 mm) (Muesebeck, 1936). A wasp belonging to this genus was found parasitizing the coffee berry borer in a coffee plantation in Antioquía, Colombia (Cárdenas, 1995; Bustillo *et al.*, 2002). This finding constituted the first braconid parasitizing the coffee berry borer outside Africa. However, the species was never fully identified and there is very little information on this insect. According to Bustillo *et al.* (2002), *Cryptoxilos* enters coffee berries using the same hole made by the coffee berry borer. Female wasps are endoparasitoids of coffee berry borer adults. A single egg of the wasp is deposited internally in the coffee berry borer. After eclosion, the larva feeds and kills the adult host. When the larval stage is completed, the mature larva leaves the coffee berry borer cadaver and pupates in a gray cocoon that blocks the entrance tunnel bored into the berry by the colonizing female, presumably to avoid the entrance of potential predators. The adult wasp emerges through the entrance tunnel. Many individuals of this species have been collected in Colombia from coffee berry borers. Attempts to rear this species in the laboratory have been unsuccessful (Bustillo *et al.*, 2002).

Cryptoxilos has been recorded as parasitoids of adult scolytids (Deyrup, 1981; Jordal and Kirkendall, 1998; Kenis *et al.*, 2004). Therefore, it is possible that *Cryptoxilos* sp. is a native parasitoid of an unidentified scolytid inhabiting coffee plantations of Colombia and that it also attacks the coffee berry borer. Generally, this type of parasitism is considered incidental and with no important consequences in reducing pest population levels.

3.14.5.6 Cephalonomia hyalinipennis

Pérez-Lachaud (1998) reported *Cephalonomia* near *waterstoni* parasitizing the coffee berry borer in Chiapas, Mexico. The species was later confirmed to be *C. hyalinipennis* (Figure 11.12D, E) (Pérez-Lachaud and Hardy, 1999), which has been recorded attacking several coleopteran species in several countries throughout North America, South America, and Europe (Evans, 1978).

Females are dark wasps (Figure 11.12E), ca. 1.7 mm long, and males are smaller. This species feeds on all immature stages of the coffee berry borer and oviposits one to three eggs per host on the cuticle of last instar larva, prepupae (Figure 11.12D), or pupae. Most of these individuals are able to reach the adult stage, although the size of the progeny is reduced if there is more than one parasitoid on a host (Pérez-Lachaud, 1998). It takes ca. 20 days from egg to emergence of adults at 28°C. Emergence of males occurs earlier than females and there is sibling mating. Longevity of adult females is ca. 57 days and average fecundity per female is 88 eggs (Pérez-Lachaud, 1998; Pérez-Lachaud and Hardy, 1999).

In Brazil, Benassi (1989) reported the presence of an unidentified species of *Cephalonomia* attacking larvae of the coffee berry borer. Although there is no further information on this discovery, this species could be *C. hyalinipennis*, whose geographical range comprises all of South America (Evans, 1978). *C. hyalinipennis* is known to be a generalist parasitoid attacking larvae and pupae of several species of Coleoptera, especially Scolytinae and Anobiidae (Evans, 1964, 1978). Under laboratory conditions it is also capable of parasitizing several species of Curculionidae, Bostrichidae, and Bruchidae (Pérez-Lachaud and Hardy, 2001). Pérez-Lachaud *et al.* (2004) has shown that *C. hyalinipennis* can be a facultative hyperparasitoid of *C. stephanoderis* and *P. nasuta* and that its presence may have a negative effect on these parasitoids (Batchelor *et al.*, 2006). Consequently, it is not recommended for use in coffee berry borer biological control programs.

3.14.6 Predators

3.14.6.1 Ants

One of the first reports of ants (Hymenoptera: Formicidae) preying on the coffee berry borer was published by Leefmans (1923) in Java, where he showed 9.3% lower coffee berry borer infestation rates in coffee plants with *Dolichoderus bituberculatus* Mayr (current name: *D. thoracicus* (Smith)) than in plants without ants. In Brazil, Fonseca and Araujo (1939) concluded that *Crematogaster curvispinosus* Mayr, which uses dry berries as nests, was only an occasional predator of immature stages of the coffee

berry borer. Almost 60 years later, Benassi (1995) found *C. curvispinosus* at low levels throughout coffee plantations in northern Espírito Santo (Brazil). The presence of the ant can be recognized based on the ant enlargement of the hole originally made by the coffee berry borer (Fonseca and Araujo, 1939; Benassi, 1995).

Varón *et al.* (2004) reported on *Solenopsis geminata* (F.), *Pheidole radoszkowskii* Mayr, and *Crematogaster torosa* Mayr as highly effective predators of the coffee berry borer in laboratory experiments with up to 100% predation, depending on insect growth stage provided. In contrast, predation levels in the field were much lower, not exceeding 25%, a result ascribed to the generalist diet of the ants and the lack of attraction towards coffee berry borer infested berries placed next to ant nests. These results point at the generalist nature of ants and the fact that in order for ants to be effective sources of mortality for the coffee berry borer they would have to enter the berry and consume life stages contained within. Even though Varón *et al.* (2004) observed the three ant species (as well as others) entering the berries placed near the ants nests, the size of the tunnel in the berry could be a limiting factor, impeding ant entrance based on ant size (see discussion in Varón *et al.*, 2004).

In Cuba, Vázquez Moreno *et al.* (2009) concluded that *Tetramorium bicarinatum* (Nylander) enters infested coffee berries and expands the galleries built by the colonizing female. The presence of immature ant stages inside the berry indicates that in addition to preying on the coffee berry borer, the ant uses infested berries for nesting.

Most papers reporting effects of ants on the coffee berry borer base their conclusions on observations of ants carrying coffee berry borers in their mandibles, predation of free living stages of the coffee berry borer offered in the field or laboratory, or on methods that allow or prevent ants to access the infested berries (bags with different mesh sizes) followed by subsequent sampling for assessment of coffee berry borer presence (Leefmans, 1923; Varón *et al.*, 2004; Gallego Ropero and Armbrecht, 2005; Vélez *et al.*, 2006; Vélez-Hoyos *et al.*, 2006; Perfecto and Vandermeer, 2006; Armbrecht and Gallego, 2007; Larsen and Philpott, 2010). Some studies have been conducted on coffee berry borers infesting parchment coffee, although it is not clear how the results relate to actual field situations involving infested coffee berries (Gallego Ropero and Armbrecht, 2005; Vélez *et al.*, 2006; Vélez-Hoyos *et al.*, 2006). For example, in a laboratory study Gallego Ropero and Armbrecht (2005) reported that *Solenopsis picea* Emery could enter coffee berry borer-infested parchment seeds but *Tetramorium simillimum* Smith did not do so, even though it had been observed to go into parchment seeds in the field. It is necessary to conduct molecular gut content analysis of ants (as done by Chapman *et al.* (2009) and Jaramillo *et al.* (2010b) for thrips; discussed below) to determine if ants play an important role as coffee berry borer predators under natural field conditions involving infested berries on plants.

It is also important to consider that manipulating ants to increase coffee berry borer predation would be quite difficult, not to mention that ants can be a serious nuisance to coffee pickers (Vrydagh, 1940; Vandermeer *et al.*, 2002; Vera-Montoya *et al.*, 2007). Additionally, some ants tend other insects (e.g., coccids) that might create problems in coffee plantations (Leefmans, 1923; Vandermeer *et al.*, 2002). Leefmans (1923) found that even though a lower coffee berry borer infestation level was found in berries to which *D. bituberculatus* had access, greater damage was done to these berries by the ant-reared green scale of coffee, *Lecanium viride* (current name: *Coccus viridis* (Green); Coccidae), which prefers the stalks of the berries. He concluded, "...it is clear that by enticing ants to the coffee plants means more damage by the green coccids than is done by the borer." On the other hand, Perfecto and Vandermeer (2006) found a negative relationship between the number of ant-tended coccids and coffee berry borer damaged berries on a plant basis but not on a branch basis, presumably as a result of ant predation of the coffee berry borer. Ants were observed carrying coffee berry borers in their mandibles. For an in-depth discussion of this topic, see Philpott and Armbrecht (2006).

3.14.6.2 Birds

Coffee plantations, particularly when shaded, are important habitats for birds (Perfecto *et al.*, 1996; Moguel and Toledo, 1999; Sherry, 2000; Somarriba *et al.*, 2004). A few papers have examined bird predation on the coffee berry borer. Leefmans (1923) observed swallows (*Callocalia* sp.) feeding on swarming coffee berry borers in Java, and Sherry (2000) observed American redstarts (*Setophaga ruticilla* (L.)) eating coffee berry borers.

In Jamaica, Kellermann *et al.* (2008) identified 17 species of birds as potential coffee berry borer predators. Using coffee berry borer infested plants from which birds were excluded and contrasting them to plants to which birds had access resulted in a reduction in coffee berry borer infestation. They concluded: "These services likely result from avian predation of adult female borers as they search for an oviposition site or bore into the endosperm, which can take up to 8 h." Predation by birds as the insect searches for an oviposition site and starts boring the berry is possible, but not when the insect bores into the endosperm (seed), as this event occurs within the berry. Kellermann *et al.* (2008) cite an unpublished study that revealed the presence of coffee berry borers in the stomach contents of three bird species. They also mention that the bird exclosures do not exclude lizards, which were observed in both treatments. Johnson *et al.* (2010) conducted a similar

experiment in Jamaica as the one conducted by Kellermann *et al.* (2008), with the exception that they examined responses in coffee plantations at full sun and in shaded plantations. Their results also show reduced coffee berry borer infestations in plants where birds were not excluded, and even though there were more birds in shaded plantations, their effect was not greater in shade than in sun grown coffee.

Using molecular methods for coffee berry borer DNA detection, Karp *et al.* (2013) confirmed the predatory status of five bird species after analyzing 469 fecal samples from 75 species of birds, and 53 samples from 13 bat species. Exclusion of birds from coffee plants increased coffee berry borer infestation levels from 4.6 to 8.5% in the wet season, and from 2.7 to 4.8% in the dry season. Presence or absence of bats did not have an effect on coffee berry borer infestation levels.

3.14.6.3 Thrips

Using molecular gut content analysis, Chapman *et al.* (2009) and Jaramillo *et al.* (2010b) confirmed that the black thrips, *Karnyothrips flavipes* (Jones) (Thysanoptera: Phlaeothripidae), serves as a predator of coffee berry borer eggs and larvae in Kenya. The study involved the collection of almost 18,000 coffee berry borer infested berries and of over 3000 thrips emerging from the berries. It serves as a model to confirm the predatory status of an organism based on detection of coffee berry borer DNA in the predator gut. The thrips is cosmopolitan and it could possibly be preying on the coffee berry borer in other countries.

3.14.6.4 Other predators

Leptophloeus sp. near *punctatus* Lefkovitch (Coleoptera: Laemophloeidae) collected in Togo and Ivory Coast has been observed preying on coffee berry borer larvae (Vega *et al.*, 1999). In Java, *Dindymus rubiginosus* (F.) (Hemiptera: Pyrrhocoridae), which preys on bark beetles in the forest, was observed feeding on coffee berry borers inside the berry as well as outside (Wurth, 1922; Sladden, 1934). Adults move among berries and insert their proboscis, which can be 9 mm long, in the galleries within the berry, sucking the contents of the insect (Wurth, 1922; Sladden, 1934). The insect can kill six coffee berry borers in an hour, but is not considered an important predator due to the small number of insects it can kill.

In sometimes-conflicting field observations and laboratory results in Colombia, nymphs and adults of unidentified species of *Calliodes*, *Scoloposcelis*, and *Xylocoris* (Hemiptera: Anthocoridae), *Cathartus quadricollis* (Guérin-Méneville) and *Monamus* sp. (Coleoptera: Cucujidae), and *Prometopia* sp. (Coleoptera: Nitidulidae) have been reported to feed on immature stages of the coffee berry borer (Cárdenas, 1995; Bustillo *et al.*, 2002; Vera-Montoya *et al.*, 2007). In laboratory studies in Costa Rica, *C. quadricollis*, *Ahasverus advena* (Waltl) (Coleoptera: Silvanidae) and *Lyctocoris* sp. (Hemiptera: Anthocoridae) preyed on various stages of the coffee berry borer (Rojas Barrantes, 2009; Rojas *et al.*, 2012).

Working in Mexico, Henaut *et al.* (2001) placed coffee berry borers on the webs of four spiders (*Cyclosa caroli* (Hentz), *Gasteracantha cancriformis* (L.), *Leucauge mariana* (Keyserling), and *L. venusta* (Walckenaer)) and concluded that preference for the insect was low when compared to other prey placed on the webs.

3.15 Cultural Control

Many authors have suggested that after the harvest, all berries in the field should be collected, including those left on trees and those that have fallen on the ground, to interrupt the life cycle of the insect. This method, known as rampassen in Dutch (Friederichs, 1922a), repasse in Portuguese (Bergamin, 1944a), repase in Spanish (Bustillo P. *et al.*, 1998), and re-picking in English, is the only method that would be guaranteed to eliminate the insect. Nevertheless, as discussed in Section 3.6.3, the number of insects that could be present on fallen berries is daunting; therefore, unless the insect presence is very limited, re-picking might be difficult to implement due to associated costs, the need for all growers to participate, and the requirement that absolutely all berries should be collected, both on the plant and on the ground. According to Pamplona (1927), finding an uninfested tree in the state of São Paulo (Brazil) was an unusual event in 1924, but after a large-scale re-picking effort just 228 infested berries were found in ca. 22,000 sampled trees.

Cultural control could also be used to reduce passive dispersal, which occurs when materials contaminated with the insect are moved from one place to another. These materials include coffee bags used during harvesting, agricultural implements, vehicles, workers clothing, and infested beans or coffee seeds for domestic use (Corporaal, 1921; Leefmans, 1923; Wilkinson, 1928). In Colombia, the dissemination of the insect from the southwest border with Ecuador to the main coffee growing areas has been ascribed to the movement of coffee pickers (Benavides *et al.*, 2006). Cultural control methods to avoid passive dispersal include tightly closing the bags containing harvested berries to prevent insect dispersal during transportation; placing screens covered with grease or other sticky substance over the areas where coffee is placed before initiating the wet processing; and properly managing pulp after depulping the berry to prevent insect dispersal (Bustillo P. *et al.*, 1998). The insect could also survive the drying process (Bustillo P. *et al.*, 1998). In coffee stores in Yemen, dead coffee berry borers were found in coffee beans imported from Ethiopia (Mahdi, 2006).

Another mechanism for passive dispersal is via animals. An experiment conducted by Leefmans (1923) found that 5.75 lb of coffee seeds in the feces of the Asian palm civet *Paradoxurus hermaphroditus* Pallas contained 17 coffee berry borer eggs, 11 newly hatched living adults, eight living old adults, seven dead adults, 33 living pupae, and 62 living larvae for a total of 114 live insects. Survival of coffee berry borers after being excreted by the palm civet was also confirmed by Gandrup (1922).

The use of cover crops could be an effective method to reduce insect levels inside berries that have fallen on the ground. According to Vázquez-Moreno (2005), coffee plantations in Cuba with *Zebrina pendula* Schnizl. (current name: *Tradescantia zebrina* var. *zebrina* Bosse; Commelinaceae) as a cover crop have a lower number of berries on the ground in the interseason period (i.e., between harvests). This is due to a faster decomposition of berries when the cover crop is present, which reduces survival of coffee berry borers within these berries. The decomposition of berries also makes dispersal of insects less successful due to the reduced number of suitable berries that they can find on the ground. In Mexico, Pohlan (2005) and Pohlan *et al.* (2008) found lower coffee berry borer levels in plantations with *Canavalia ensiformis* (L.) DC (Fabaceae) as a cover crop.

3.16 Climate Change

Jaramillo *et al.* (2009c) determined that 14.9 and 32°C were the upper and lower thresholds for coffee berry borer development, with 26.7°C being the optimal development temperature. According to Jaramillo *et al.* (2009c, 2011, 2013), increases in average daily temperature (global warming) in coffee-growing areas where temperatures have not reached 26.7°C could result in faster developmental time, increased number of generations, as well as an expanded distribution of the insect to elevations where it might not be able to otherwise survive. Bark beetles and climate change is covered in detail in Chapter 13.

4. CONCLUSIONS

There is very little information on the biology and ecology of the vast majority of *Hypothenemus* species. A reason for this is the difficulty in identifying the species and the difficulty in conducting the fieldwork that is essential to better understand them. The authors hope that this chapter will result in new research programs among entomologists and ecologists that will result in new and novel insights in the genus *Hypothenemus*.

As for the coffee berry borer, even though more than 100 years of research have been conducted on the insect, it remains the most economically important insect pest of coffee worldwide. This is likely due to a narrow focus on pest management approaches that have been repeatedly attempted in many different countries. For example, the use of methanol:ethanol traps has resulted in dozens of papers notwithstanding its lack of effectiveness in reducing population levels. Similarly, the use of parasitoids and fungal entomopathogens has been implemented in many countries, with mixed results, which have only slightly or temporarily alleviated the problem. In the same vein, it is unlikely that additional fungal entomopathogen field and laboratory bioassays will solve the problem, or that further studies on the predatory effects of ants or birds will suddenly reveal major insights over what has already been reported.

Currently available pest management strategies require collective action among coffee growers, a very difficult task. If one coffee grower implements one or several available strategies and the neighbor does not, then all the effort by the enterprising grower might be lost due to insect dispersal from the neighbor's field. A better understanding of basic biology issues related to the coffee berry borer that are just beginning to be elucidated, such as the genome and microbiota, might reveal novel strategies for pest management. Nevertheless, these possible strategies remain a distant dream. What is needed today is a novel strategy that dramatically reduces coffee berry borer population levels in the field. Such a strategy could involve the deployment of coffee berry borer-specific attractants and/or repellents. In order for these to be adopted, they need to be effective and repeatedly shown to reduce damage and consequently to increase yields. Another possibility is the use of fungal entomopathogens as endophytes. If a successful method can be developed to introduce fungal entomopathogens into coffee seedlings with long-term establishment or induced effects against insects, then they might become a feasible option for growers. After more than 100 years of dealing with the coffee berry borer, coffee growers deserve a novel pest management breakthrough that improves their economies and consequently their lives.

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