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From forest to plantation? Obscure articles reveal alternative host plants for the coffee berry borer, *Hypothenemus hampei* (Coleoptera: Curculionidae)

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The coffee berry borer, *Hypothenemus hampei* (Coleoptera: Curculionidae: Scolytinae), is the most devastating insect pest of coffee throughout the world. The insect is endemic to Africa but can now be found throughout nearly all coffee-producing countries. One area of basic biology of the insect that remains unresolved is that of its alternative host plants, i.e. which fruits of plants, other than coffee, can the insect survive and reproduce in. An in-depth survey of the literature revealed an article by Schedl listing 21 genera in 13 families in which the insect was collected, mainly in the Democratic Republic of Congo. This overlooked reference, together with information provided in other early articles, suggests that *H. hampei* is polyphagous, and could provide, if confirmed in the field, critical information on the evolution of this insect's diet, ecology and host range. *Biological Journal of the Linnean Society*, 2012, **107**, 86–94.

ADDITIONAL KEYWORDS: *Coffea* – ecology – evolution – insect host range – speciation.

INTRODUCTION

The coffee berry borer, *Hypothenemus hampei* (Ferrari, 1867) (Coleoptera: Curculionidae: Scolytinae), an insect endemic to Africa (Vega *et al*., 2009; Gauthier, 2010), was first reported in exported coffee (*Coffea* L.) seeds ('beans') by Ferrari (1867), described as *Cryphalus hampei*. It was first collected in the field in 1897 in Mount Coffee, Liberia, classified as *Stephanoderes cooki* (Hopkins, 1915), which subsequently became a synonym for *H. hampei* (Schedl, 1959; Wood, 2007). In 1901 it was reported as a pest of *Coffea canephora* Pierre ex. A. Froehner in the Republic of Congo (Fleutiaux, 1901), and ever since the insect has disseminated throughout nearly all coffee-producing countries in the world, and has become the most devastating insect pest of the two commercial *Coffea* species, *C. arabica* L. and *C. canephora*, causing an estimated $500 million in losses yearly (Vega, Franqui & Benavides, 2002).

Hypothenemus hampei has a cryptic life cycle, with an adult female boring a hole in the coffee berry (botanically known as a drupe) and then a tunnel in the endosperm (i.e. the major component of a coffee seed), in which eggs are laid. Upon hatching, larvae commence to feed on the endosperm, thereby producing small galleries throughout the seed, reducing the yield and quality of the marketable product. To complicate matters, there is sibling mating inside the berry, and once adult females emerge from the berry, they are already inseminated and ready to oviposit in other berries. The cryptic life cycle inside the berry makes the insect quite difficult to control by both chemical and biological methods. The use of biological control agents such as parasitoids, predators, and fungal entomopathogens is a pest management alternative that has been practiced in several countries (Jaramillo, Borgemeister & Baker, 2006; Vega *et al*.,

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2009), and yet the insect continues to pose a formidable challenge to coffee growers throughout the world.

The natural habitats of *C. arabica* and *C. canephora* are the humid, evergreen forests of Africa (Davis *et al*., 2006): the former is a high-altitude species (900–2000 m a.s.l.) of south-western Ethiopia and the surrounding regions; the latter is a predominately lowland plant (50–1500 m a.s.l.) found throughout much of tropical Africa, west of the Rift Valley (Davis *et al*., 2006). One aspect of paramount importance in dealing with the basic biology of *H. hampei* has been determining its alternative host plants in Africa, i.e. are there plants other than *C. arabica* and *C. canephora* that, in their natural habitat, are suitable for the reproduction and development of the insect?

Recently, as part of a project aimed at locating alternative host plants for *H. hampei* in Africa, we compiled a list of *Hypothenemus* species that have been reported in Africa together with the host plants for these species, when known. We identified 94 *Hypothenemus* species out of 179 described species as having been recorded in Africa (F. E. Vega, unpubl. data). This process required keeping track of old names for *Hypothenemus* species, based on Wood & Bright (1987, 1992), Bright & Skidmore (1997, 2002), and Wood (2007), and consulting the literature reviewed in these works. During this review, and to our great surprise and excitement, we discovered three obscure studies, either not previously cited or undervalued by subsequent researchers working in our field. These works have important consequences for the study of alternative hosts of *H. hampei*.

MATERIAL AND METHODS

Three articles have revealed important aspects of the biology of the coffee berry borer: Beille (1925), Ghesquière (1933), and Schedl (1960). The most significant was Schedl's (1960) article, which was found while tracking records for *Hypothenemus* species in Africa (see previous paragraph), and was cited by Wood & Bright (1987). It appears the importance of this article was not recognized because of its title, *Insectes nuisibles aux fruits et aux graines* (*Insect pests of fruits and grains*), which does not give any indication about its coverage of *H. hampei*.

RESULTS

The first significant finding we came across was a article by Beille (1925), in which he writes:

> Le début de la maladie a coïncidé avec la destruction de la forêt; il semble que le *Stephanoderes*, privé des végétaux sur lesquels il pullulait, ait trouvé dans les nouvelles plantations de Caféiers, des conditions favorable à son évolution. [The onset of the disease coincided with the destruction of the forest; it appears that *Stephanoderes* (i.e. *Hypothenemus hampei*), lacking the plants that it frequents, has found in the new coffee plantations, conditions that are favourable to his evolution.]

This article is significant because, as far as we know, it is the first mention of plants in the forest being original host plants for the insect, and ascribes forest destruction as a contributor to the insect moving into coffee plantations. Before being commercially planted, *C. canephora* was endemic to humid, evergreen forests in Africa (Davis *et al*., 2006), and Beille's statement would require the insect to have used *C. canephora* (or other wild *Coffea* species) as one of its many host plants in the forest, in order to make it plausible for the insect to have then been able to exploit coffee plantations.

The second significant finding comes from an article by Schedl (1960), in which he reports results of a field survey he conducted in the Belgian Congo (present-day Democratic Republic of Congo, DRC), together with findings from other scientists. Karl E. Schedl (1898–1979) was a world-renowned bark beetle taxonomist who published 342 articles dealing with bark beetle taxonomy (Wood & Bright, 1992). What is quite striking about Schedl's (1960) article is that *H. hampei* was recovered from 20 plant genera (other than *Coffea*) in 13 families (Table 1). Some examples of damaged fruits presented by Schedl (1960) are shown in Figure 1. The valid name for the coffee berry borer at the time of publication was *Stephanoderes hampei*, and what Schedl (1960) reports as *Stephanoderes punctatus* was later re-classified as *H. hampei* by Wood (1972). Concerning *H. hampei*, Schedl (1960: 13) writes:

> Il est intéressant, du point de vue biologique, de noter que, d'après les recherches faites par l'auteur à Yangambi et d'après les données bibliographiques au sujet de *Stephanoderes hampei* Ferr., il existe dans la forêt ombrophile toute une série d'hôtes naturels du parasite qui lui donnent la possibilité de se développer indépendamment des plantations de caféiers. Il est certain que cet insecte est une espèce endémique de la forêt ombrophile; il ne s'établit que secondairement dans les plantations de caféiers. [It is interesting, from the biological point of view, to note that after the investigations conducted by the author in Yangambi and after the bibliographical data on the subject of *Stephanoderes hampei* Ferr., there exists inside the rainforest a series of natural hosts for the parasite that give it the possibility to develop independently from coffee plantations. It is certain that this insect is an endemic species of the rainforest; it becomes established only secondarily in coffee plantations.]

Schedl (1960) specifically mentions that the forest plants provide the insect with 'the possibility to

Table 1. Plants in which Schedl (1960) reported the coffee berry borer (*Hypothenemus hampei*) as attacking fruits or seeds. *Stephanoderes punctatus* and *Stephanoderes hampei* are synonyms for *H. hampei*. A total of 21 genera in 13 families are reported. Host plant names in parentheses indicate the current name

Family	Host plant (current name)	*H. hampei* reported as:	Reported location	Plant habit	Plant distribution	Plant Ecology	Fruit	Seeds	Seed fat content
Achariaceae	*Caloncoba* aff. *crepiniana*	*Stephanoderes punctatus*	DRC	Tree (rarely a shrub), 10(–25) m tall	Tropical West and Central Africa	Humid forest; 850–1500 m.a.s.l.	Capsule, subglobular, (5–)7(–8) × 5–6(–8) cm, orange; with numerous seeds	Seeds angular, 0.7–0.8 × 0.5–0.6 mm	Unknown. Other species in genus said to be 'oil rich'
Apocynaceae	*Pleiocarpa tubicina* Stapf (*Pleiocarpa pycnantha* (K. Schum) Stapf)	*Stephanoderes hampei*	DRC	Tree 20(–30) m tall; bole up to 50 cm in diameter	Tropical West and Central Africa, and western East Africa	Humid forest, primary and secondary; up to 2300 m.a.s.l.	Composed of several basally joined carpels, each carpel globose to ellipsoid, 1.3–2.3(–3) cm long, yellow to orange; each carpel 2-seeded	Seeds ellipsoid to oblong, 6.5–13.5 mm long	Unknown
Bignoniaceae	*Spathodea campanulata* P. Beauv.	*S. hampei*	DRC	Tree, 25(–35) m tall; bole up to 60 cm in diameter	Tropical West and Central Africa, and western East Africa	Humid forest and savanna, primary and secondary; up to 2000 m.a.s.l.	Woody capsule, dehiscing by 2 valves, narrowly ellipsoid, 15–27 × 3.5–7 cm; seeds numerous	Seeds thin and flat, very broadly winged, ~1.5 × 2 cm	Unknown
Calophyllaceae	*Mammea africana* Sabine	*S. hampei*	DRC	Tree, 30–45 m tall; bole up to 125 cm in diameter	Tropical Africa	Humid forest, primary and secondary, up to 1000 m.a.s.l.	Drupe, with 1–4 (one seeded) pyrenes, globose to pear-shaped, 7–18(–30) × 10 cm	Seeds 1–4, flattened, ~3 cm long	Seeds: ~10% oil (9.6% oil: consisting of a mixture of oleic acid 34.9%, palmitic acid 32.3%, linoleic acid 22.9%) [palmitic acid (28%), stearic acid (27.5%), myristic acid (1.5%), lauric acid (1%)]
Clusiaceae	*Allanblackia floribunda* Oliv.	*S. hampei*	DRC	Tree, ~30 m tall; bole ~50 cm or more in diameter	Tropical West and Central Africa	Humid forest, primary and secondary; up to 1000 m.a.s.l.	Berry, ellipsoid, 20–50 × 5–14 cm (colour); 40–80-seeded, each enclosed in a pinkish aril	Seeds ovoid, 2.5–3 × 1.5–2 cm	Kernel (~60% seed mass): ~72% fat (stearic acid 45–58% and oleic acid 40–51%)
Combretaceae	*Terminalia superba* Engl. & Diels.	*S. punctatus*	DRC	Tree, up to 45(–50) m tall; bole 120(–150) cm in diameter	Tropical West and Central Africa	Humid forest, primary and secondary; up to 1000 m.a.s.l.	Winged nut (indehiscent), transversely oblong-elliptical in outline, 1.5–2.5 × 4–7 cm; 1-seeded	Seed ~1.5 × 7 cm	Unknown

Leguminosae	*Phaseolus lunatus* L.	*S. hampei*	Uganda	Climbing, trailing or more or less shrubby, annual or perennial; stems up to 4.5(–8) m long	Cultivated throughout the world, in tropical and temperate regions; introduced from Tropical South America	Cultivated under various conditions	Pod, [?dehiscent], oblong, (4.5–)5–10.5(–13) × 1–2(–3) cm; 2–4(–5)-seeded	Seeds kidney-shaped to rhomboid or globose, 8–11 × 6–7 mm	Edible portion [per 100 g (immature bean)]: water 66.3 g, protein 8.3 g, carbohydrate 23.1 g, fibre 1.0 g ~0.7% fat
Leguminosae	*Cathormion altissimum* (Hook f.) Hutch & Dandy (*Albizzia altissima* Hook f.)	*S. punctatus*	DRC	Tree, 15–35 m tall; bole up to 80 cm in diameter	Tropical West and Central Africa	Humid and subhumid forest, primary and secondary forest; 10–1000 m.a.s.l.	Pod, breaking up into 1-seeded segments, narrowly oblong, 10–28 × 1–2 cm, red-brown to blackish; up to 20-seeded	Seeds oblong to lens-shaped, flattened, 0.6–0.9 × 0.6–0.7 mm	Fermented seeds: 25.3% protein, 16.9% fat and 10% carbohydrate
Leguminosae	*Caesalpinia pulcherrima* (L.) Sw.	*S. punctatus*	DRC	Shrub or small tree, up to 5 m tall	Probably native to tropical America (though often alleged to be Asiatic); widely cultivated in the tropics	Cultivated under various conditions in tropical and subtropical regions	Pod, dehiscing down both sides, obliquely oblong to oblanceolate, flattened, 6–12 × 1.4–2.5 cm; several seeded	Seeds, obovate or obtriangular, compressed, 9–10 × 7–8 × 3 mm	Unknown
Leguminosae	*Dialium lacourtianum* Vermoesen (*D. englerianum* Henriq.)	*S. hampei, S. punctatus*	DRC	Tree 8–23 m tall, or shrub 1–3 m tall	Tropical West and Central Africa	Humid forest; 900–1450 m.a.s.l.	Pod, indehiscent, ± obovoid, 2.2–3.7 × 1.4–2.5 cm; 1- or 2-seeded, each embedded in a floury pith	Seeds ± lenticular, 8–13 × 7–8.5 × 3.5–5 mm	Unknown
Leguminosae	*Oxystigma oxyphyllum* (Harms) Leonard	*S. hampei*	DRC	Tree, up to 45 m tall; bole 130(–180) cm in diameter	Tropical West and Central Africa	Humid and subhumid forest; up to 800 m.a.s.l.	Pod indehiscent, samara-like (leaf-like, very flattened), 3.5–13 × 2.2–8 cm; 1-seeded	Seeds flattended-ellipsoid, 2–5 × 2–4 cm	Unknown. Other species in genus said to be 'oil rich'
Malvaceae	*Cola griseiflora* De Wild.	*S. punctatus*	DRC	Tree, up to 22(–35) m tall; bole up to 30 cm in diameter	Gabon and DRC	Humid and subhumid forest; up to 800 m.a.s.l.	Fruit consisting of follicles, ovoid, 6 × 3.5 cm; 3–7-seeded	Seeds plano-convex, ~0.2 × 0.15 cm	Unknown
Malvaceae	*Hibiscus* sp.	*S. hampei*	DRC	Specific information not available					
Malvaceae	*Theobroma cacao* L.	*S. hampei*	DRC	Tree, 4–20 m tall	Native to Tropical South America; cultivated throughout Tropical Africa	Cultivated under various conditions	Berry-like drupe, commonly called a pod, globose to cylindrical, 10–32 × 6–12 cm, 20–60-seeded, seeds embedded in mucilageous, whitish, sugary, acidic pulp	Seeds globose to ellipsoid, 2–4 × 1–2 cm	Seeds: ~50% fat

Table 1. *Continued*

Family	Host plant (current name)	*H. hampei* reported as:	Reported location	Plant habit	Plant distribution	Plant Ecology	Fruit	Seeds	Seed fat content
Meliaceae	*Trichilia gilgiana* Harms	*S. hampei*	DRC	Tree, up to 30 m tall; bole up to 100 cm in diameter	Tropical West and Central Africa	Humid and subhumid forest; up to 950 m.a.s.l.	Capsule, dehiscent, pear-shaped (obovoid) to fig-shaped, 3–3.5 cm in diameter; up to 6-seeded	Seeds, ± angular ellipsoid, ~2 × 1.2 cm	Seeds: reported as 'oily'
Myristicaceae	*Pycnanthus angolensis* (Welw). Warb.	*S. hampei*	DRC	Tree, 25–35(–40) m tall; bole 120(–150) cm in diameter	Tropical West and Central Africa	Humid and subhumid forest; 1200 (–1400) m.a.s.l.	Drupe, splitting longitudinally with 2 valves, ellipsoid to oblong or globose, 3–4.5 × 2–4 cm, 1-seeded	Seed ellipsoid, 1.5–3 × 1–1.5 cm	Seeds: 45–70% fat
Rhizophoraceae	*Anopyxis klaineana* (Pierre) Pierre ex Engl.	*S. punctatus*	DRC	Tree, ~45 m tall; bole ~120 cm in diameter	Tropical West and Central Africa	Humid forest; 200–500 m.a.s.l.	Capsule, 5-valved, obovoid, 2.6–3.2 × 2–2.4 cm; several seeded	Seeds ± ellipsoid, flat end on one side, winged at apex, 0.8–1 × 0.5 cm	Unknown
Rosaceae	*Rubus* sp.	*S. hampei, S. punctatus*	Tanzania	Specific information not available					
Rubiaceae	*Coffea* sp., *C. arabica, C. canephora, C. excelsa* (*C. liberica* var. *dewevrei* (De Wild & T. Durand) Lebrun), *C. liberica* Bull. ex Hiern	*S. hampei, S. punctatus*	DRC, Uganda, Angola, Tanzania, Liberia, Ivory Coast	Treelet, small tree or bush (in cultivation), 3–10 m tall	Tropical West and Central Africa; cultivated throughout Tropical Africa	Humid to subhumid forest; 0–2200 m.a.s.l.; cultivated under various conditions in humid and subhumid regions	Drupe, with (1–)2 pyrenes, each pyrene 1-seeded, oblong-elliposoid, 0.9–2.2 × (0.6–)0.9–1.6 cm	Seeds, hemi-ellipsoid, (0.7–)1.3–1.6 × 0.4–0.7 cm	Seeds (endosperm): 7–17% fat
Rubiaceae	*Nauclea diderrichii* (De Wild.) Merr.	*S. hampei*	DRC	Tree, 30–40(–50) m tall; bole 90–150 cm in diameter	Tropical West and Central Africa	Humid to subhumid forest; 0–500 m.a.s.l.	Syncarp, fleshy, globose, 1.8–2.5 cm in diameter; many seeded	Seeds ± ellipsoid, ~1.2 × 0.8 mm	Unknown
Rubiaceae	*Oxyanthus* sp.	*S. hampei*	Uganda	Shrubs and small trees, (1–)2–5(–12) m tall	Tropical Africa	Humid to subhumid forest; 0–2000 m.a.s.l.	Drupe, spherical to ovoid, 1–4 × 1–2 cm; several seeded	Seeds, ± lenticular, 5–11 × 2–6 mm	Unknown

DRC, Democratic Republic of Congo.

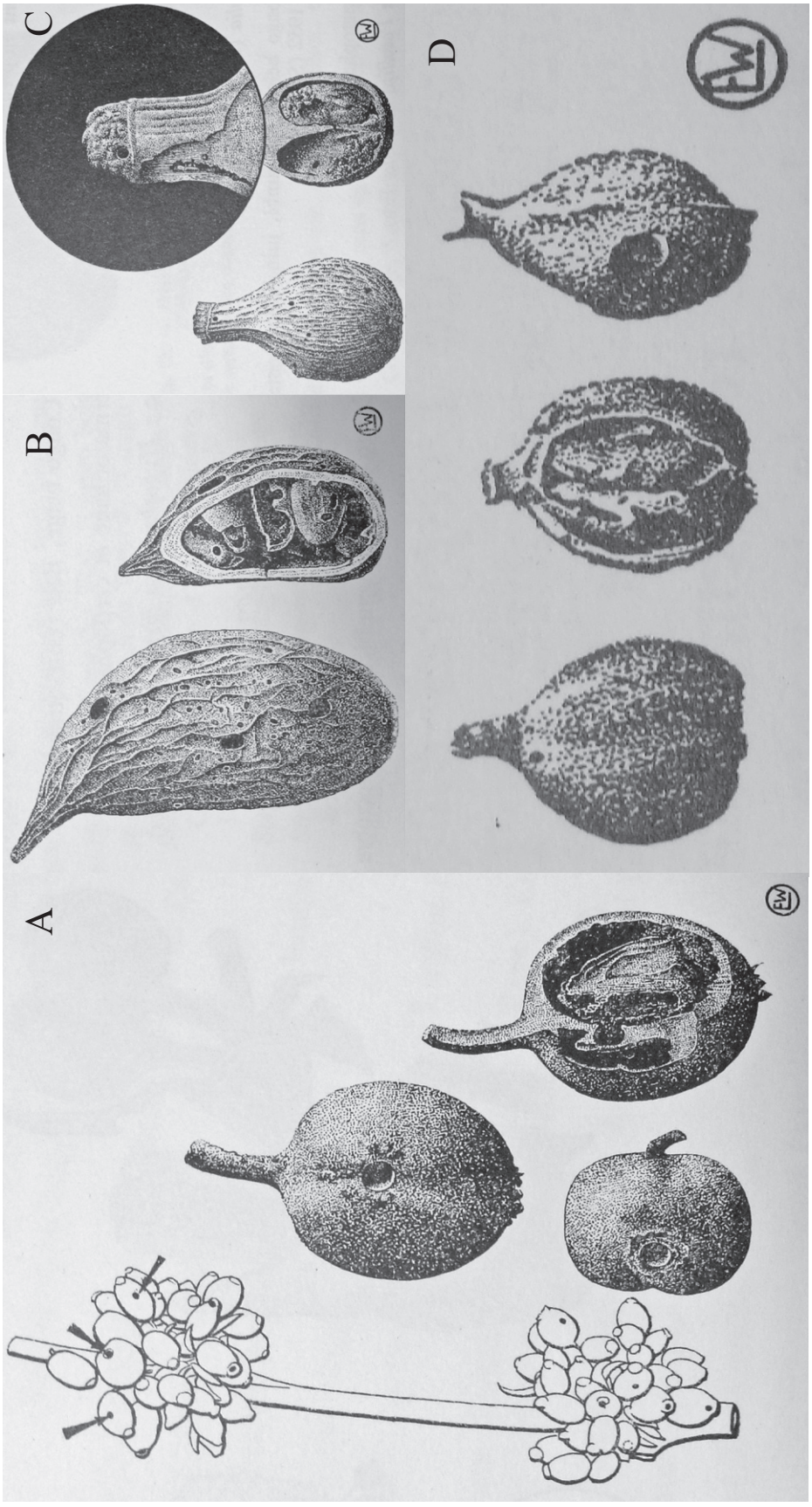

Figure 1. Some examples of damaged fruits presented by Schedl (1960). A, damage caused by *Hypothenemus hampei* on *Coffea* sp. B, damage caused to *Cola griseiflora*: the small holes on the left were made by *H. hampei* and the large holes were made by a Curculionidae; the fruit on right shows damage by both insects. C, *Trichilia gilgiana* damaged by *H. hampei* and *Poecilips* sp., another bark beetle. D, *Pleiocarpa pycnantha*: left and middle fruits show damage caused by *H. hampei*; right fruit shows damage caused by a Curculionidae.

develop independently from coffee plantations', thus implying that the insect could possibly complete its life cycle in these plants (i.e. they could be alternative host plants). Furthermore, Schedl (1960: 13) also states:

> Comme le caféier est également cultivé en dehors de la forêt ombrophile typique, il y a lieu de considérer que dans ces autres situations, *S. hampei* Ferr. possède également des hôtes naturels à partir desquels il infeste les plantations de caféiers, même lorsque la lutte menée contre lui est intense. [As coffee is also cultivated outside of the typical rainforest, it should be considered that in these other situations, *S. hampei* Ferr. also has natural hosts from which it infests plantations of coffee, even when the struggle against it is intense.]

This indicates that in areas where there is coffee outside the vicinity of a rainforest (more correctly termed humid, evergreen forest), it is possible that other plants might serve as hosts for the insects.

The article by Schedl (1960) is also significant because it suggested that *H. hampei* could be polyphagous ('generalists that exploit plants in more than one family'; Price *et al*., 2011). In his landmark book on coffee pests, Le Pelley (1968) discussed *H. hampei* host plants, and after mentioning several reports of the insect having been found in plants other than *Coffea*, he concludes that 'In none of the above cases was breeding found in the plants and they can be considered as occasional food plants only; some of the records may even be erroneous through misidentification of the insect found in them' (p. 118). Interestingly, even though Le Pelley (1968) cites Schedl (1960), he does not include the host plants listed in that publication. It should be emphasized that Schedl's expertise in bark beetle taxonomy makes it highly unlikely that he would have been mistaken in identifying *H. hampei*, and therefore his identifications must be considered reliable based on subsequent work by Wood & Bright (1987, 1992) and Wood (2007). The only caveat is that as mentioned above, what he classified as *S. punctatus* was later re-classified as *H. hampei* by Wood (1972).

Sixteen of the 21 genera listed in Table 1 were reported by Waller, Bigger & Hillocks (2007), based on a subsequent article by Schedl (1961). Waller *et al*. (2007), in reference to the list of plants they compiled, wrote: '. . . it has been assumed by many authors (e.g. Le Pelley, 1968; Hill, 1975) that these are either exploratory attacks by the beetle on plants in which it cannot breed or that the beetle has been confused with other, similar species of Scolytid'. This means that Schedl's (1960) article was unknown to Waller *et al*. (2007), as it is not cited by them, and furthermore, as mentioned above, their assumption that these beetles had been confused with similar species is unlikely given that Schedl was an expert on the identification of *H. hampei*. It is clear then that Schedl (1960) reveals important information on possible alternative host plants for *H. hampei*, for which field confirmation is now urgently required. At this point, it is important to observe that Schedl (1960: 14) mistakenly reported that Roepke (1919) reported host plants for *H. hampei* in Indonesia. Roepke (1919: 21–22) actually reported that none of the beetles bored into the branches of the plant species tested, and that all of *H. hampei* had died within 2–3 days in the various seeds tested.

The third significant article reporting alternative host plants for *H. hampei* was published by Ghesquière (1933). In this article, he stated:

> Le *Stephanoderes hampei* Ferr. est certainement, au point de vue économique, le plus dangereux, il a toujours été considéré, jusqu'a présent, comme un sténomère spécifique des Coffea. Il y a une vingtaine d'années cependant, notre collègue R. Mayné signalait que cet insecte fréquentait, outre le *Coffea robusta* son hôte habituel, des *Hibiscus* et diverses Légumineuses. Cette assertion mise en doute par d'autres entomologistes, est actuellement confirmée par les résultats de nos recherches sur Cacaoyer, *Caesalpinia pulcherrima*, et *Dialium lacourtianum*. Les récoltes de larves, nymphes et adultes sur ce dernier, surtout, ne peuvent laisser subsister aucun doute, cette Légumineuse croissait, par bosquets, dans les savanes boisées du Kasai, loin de toute plantation et de galerie forestière quelconque. L'utilisation du *D. lacourtianum* comme plante-piège serait sans doute à préconiser, il murit ses fruits tardivement en saison sèche, à une époque différente des Caféiers et fournirait en même temps on ombrage léger nécessaire aux plantations équatoriales. [*Stephanoderes hampei* Ferr. is certainly, from an economic point of view, the most dangerous, and it has always been considered, until now, like a specific stenomere (old term used in classification of Coleoptera) of *Coffea*. It has been 20 years since our colleague R. Mayné (see Mayné, 1914) noted that this insect frequented, in addition to its habitual host *Coffea robusta* (valid name: *C. canephora*), *Hibiscus* and various Leguminosae. This assertion, doubted by other entomologists (Ghesquière, (1933), includes a footnote to specify that these doubts by other entomologists are based on possible mistakes in taxonomic determination), is currently supported by the results of our research on cocoa, *Caesalpinia pulcherrima*, and *Dialium lacourtianum* (valid name: *D. englerianum*). The collection of larvae, pupae and adults on the latter, above all, can leave no doubt, that this Leguminosae growing in groves in the woodlands of the Kasai, away from all plantations and any gallery forest. (Our interpretation of this apparently incomplete sentence is that all stages of the insect were found on this plant away from coffee plantations and the forest, thus indicating that the insect does not need coffee or other forest plants to survive.) The use of *D. lacourtianum* as a trap plant should be advocated because its fruits ripen late in the dry, at a time different from coffee, while providing at the same time the light shade needed in equatorial plantations.]

Ghesquière's (1933) article confirms the presence of other plants on which *H. hampei* can reproduce.

Habit, distribution, and ecology of the plants listed in Table 1, as well as information of the fruit and seeds, were obtained from the herbarium at the Royal Botanic Gardens, Kew, and from various literature sources (Burkill, 1985, 1994, 1997; PROTA, 2012).

CONCLUSIONS

The articles by Beille (1925), Ghesquière (1933), and particularly Schedl (1960), raise important issues, which if resolved, would greatly expand our knowledge of *H. hampei*. For example, were wild *Coffea* species the original host plants for the insect in addition to those plants reported by Schedl (1960), and did forest disturbances push the insect towards areas where food resources, in the form of *C. canephora* plantations, were readily available, resulting in pest status, as implied by Beille (1925)? To our knowledge, *H. hampei* is the only insect pest that completes its life cycle in *Coffea* seeds, even though eight additional *Hypothenemus* species have been collected from *Coffea* plants: *Hypothenemus areccae* (Hornung), *Hypothenemus crudiae* (Panzer), *Hypothenemus eruditus* Westwood, *Hypothenemus grandis* Schedl, *Hypothenemus liberiensis* (Hopkins), *Hypothenemus plumeriae* (Nordlinger), *Hypothenemus seriatus* (Eichoff), and *Hypothenemus solitarius* (Schedl) (F. E. Vega, unpubl. data). Nevertheless, the use of coffee seeds as food by *H. hampei* requires biochemical mechanisms to break down the alkaloid caffeine, known to be toxic to other insects (see Vega *et al.*, 2003).

Our assessment of the species listed by Schedl (1960) shows that many of the proposed alternative hosts for *H. hampei* have similar biological characteristics. The first of these, and one that immediately appears at odds with the *Coffea* host, is the height of the plant species listed in Table 1. Fifteen of the 20 (75%) species (i.e. excluding *Coffea*) can attain a height greater than 15 m; and 13 (65%) are trees of more than 25 m in height, with several of these attaining heights between 30 and 45 m (Table 1). Thus, this list includes many canopy trees and canopy emergents. A canopy existence has not previously been suggested for *H. hampei*. *Coffea* species rarely attain heights of greater than 10 m. Secondly, a large number of the species listed possess seeds with a high oil/fat content. Eight of the 20 species (40%; excluding *Coffea*, and including two genera without specific information) are reported to have seeds with high oil or fat content. This percentage could be considerably larger, as the oil/fat content of many of the listed species are unknown to us. Significantly, the seeds (endosperm) of *Coffea* are also rich in fats, having a fat content between 7 and 17% (Speer & Kölling-Speer, 2006). This relationship is, however, by no means universal for the species listed by Schedl (1960), as some species, notably *Phaseolus lunatus*, are low in oil/fat; we also have a considerable quantity of missing data for seed composition. Thirdly, large seed size figures prominently in the list. Thirteen of the 20 species (65%; excluding *Coffea*, and including two genera without specific information) have seeds with at least one dimension (e.g. length or width) greater than 1 cm. For *Coffea* species reported as hosts of *H. hampei* (Table 1), the seeds are hemi-ovoid, and usually between 0.9 and 1.4 cm long. In summary, a high proportion of the alternative hosts reported by Schedl (1960) are substantial rainforest trees, and the majority have large, nutritious seeds capable of providing a worthwhile food source for *H. hampei*. It is also evident from Table 1 that there are three species listed as cultivated and introduced from South America [*Caesalpinia pulcherrima* (L.) Sw., *Phaseolus lunatus* L., and *Theobroma cacao* L.]. It is clear that in at least the latter two species (lima bean and cocoa, respectively), *H. hampei* is not a significant pest, as it would have been widely reported as such for these significant crop species.

Another interesting issue that would need to be elucidated is whether a field survey would reveal the insect in *Dialium englerianum*, and if so, whether the plant can be used as a trap, as proposed by Ghesquière (1933). Finally, another important implication of finding the alternative host plants for *H. hampei* is that these plants might reveal previously unreported biological control agents (i.e. predators, parasitoids, pathogens) that might be more effective in controlling the insect than those currently being used.

Based on the findings presented here, the pursuit of *H. hampei* in the field in the alternative host plants listed in Table 1 is being planned, under the leadership of J. Jaramillo, as part of a project funded by the German Research Foundation (Deutsche Forschungsgemeinschaft). Once these alternative host plants are located it will be essential to determine if *H. hampei* can be found naturally infecting and completing its life cycle in the fruits produced by these plants. This will be the only way to ascertain whether these plants do indeed serve as host plants for *H. hampei*, and not as exploratory or temporary hosts in which reproduction and development does not occur. It will also be important to determine whether *H. hampei* insects taken from these alternative plants can complete their development in coffee berries: this information will provide insights on how the insect might have become adapted to thrive on *Coffea* fruits.

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