REVIEW

Feeding by lepidopteran larvae is dangerous: A review of caterpillars' chemical, physiological, morphological, and behavioral defenses against natural enemies

HF Greeney[1] LA Dyer[2], AM Smilanich[2]

[1]Yanayacu Biological Station & Center for Creative Studies, Cosanga, Napo, Ecuador c/o Foch 721 y Juan Leon Mera, Quito, Ecuador
[2] Department of Biology, University of Nevada, Reno, NV 89557 USA

Abstract

Larval lepidopterans (hereafter, caterpillars) protect themselves from natural enemies with a diverse suite of defenses which are employed before, during, or after encounters with enemies. Some strategies help caterpillars avoid detection, while others function to repel or escape attackers. Post-attack strategies attempt to remove or destroy the eggs or larvae of parasitoids. In this review we focus on some of the best documented chemical, physiological, morphological, and behavioral characters which protect caterpillars from predators, parasitoids, and pathogens.

Introduction

Aptly expressed by Bernays (1997), "feeding by lepidopteran larvae is dangerous." The list of challenges faced by the larval stages (caterpillars) of butterflies and moths (Lepidoptera) is extensive, and includes both top-down and bottom-up pressures which vary temporally, spatially, and ontogenetically between and within species (Zalucki *et al.*, 2002). From the moment caterpillars emerge from their eggs and begin searching for food, they must overcome abiotic dangers such as wind, rain, temperature, and constantly shifting microenvironments, while simultaneously contending with the defenses of their potential hostplants, which include leaf trichomes, surface waxes, silica crystals, glands or tissues with allelochemicals, and feeding-induced plant responses (Zalucki *et al.,* 2001; Massad *et al.,* 2011). Meanwhile, evading the dangers from top-down pressures is equally important for caterpillars, as they are actively sought out by a plethora of pathogens, parasitoids, and predators (Baker, 1970; Scoble, 1995; Hawkins *et al.*, 1997; Karhu and Neuvonen, 1998; Salazar and Whitman, 2001; Kalka *et al.*, 2008) (Figs 1, 2).

Caterpillars respond to the defenses of their food-plants in a variety of ways including modifying plant tissue to avoid chemical and physical plant defenses, changing location to feed on less defended

tissues, and physiologically or chemically processing defensive chemicals (Bowers, 1988, 1992, 1993; Dussourd and Denno, 1994; Lill and Marquis, 2003). While the responses of caterpillars to these bottom-up "attacks" are arguably of equal importance to the ecology and evolution of herbivores, this review focuses only on the responses of caterpillars to the top-down forces exerted by predators, parasitoids, and to a lesser extent pathogens (hereafter "enemies"). Despite the enormous diversity of both vertebrate and invertebrate species preying upon caterpillars, parasitoids are probably the most important source of mortality for most species of phytophagous insects (Godfray, 1994; Hawkins *et al.*, 1997; Quicke, 1997). Both guilds of enemies, however, have the potential to act as strong selective agents on the evolution of caterpillar defenses that are effective before, during and after attack by their enemies. Not surprisingly, natural enemies of caterpillars have evolved a similar diversity of behavioral, chemical, and morphological responses designed to circumvent caterpillar defenses (Loan, 1964; Askew, 1971; Danks, 1975; Damman, 1986; Herrebout, 1969; Stamp, 1984; Mellini, 1987; Yeargan and Braman, 1989). Gross (1993) reviewed insect defense mechanisms against parasitoids and divided defenses into three broad categories: 1) characteristics which reduce encounters with enemies; 2) behavioral and morphological traits; 3) physiological defenses.

The literature on caterpillar defenses was large when Gross (1993) provided a review of countermeasures against parasitism. In the
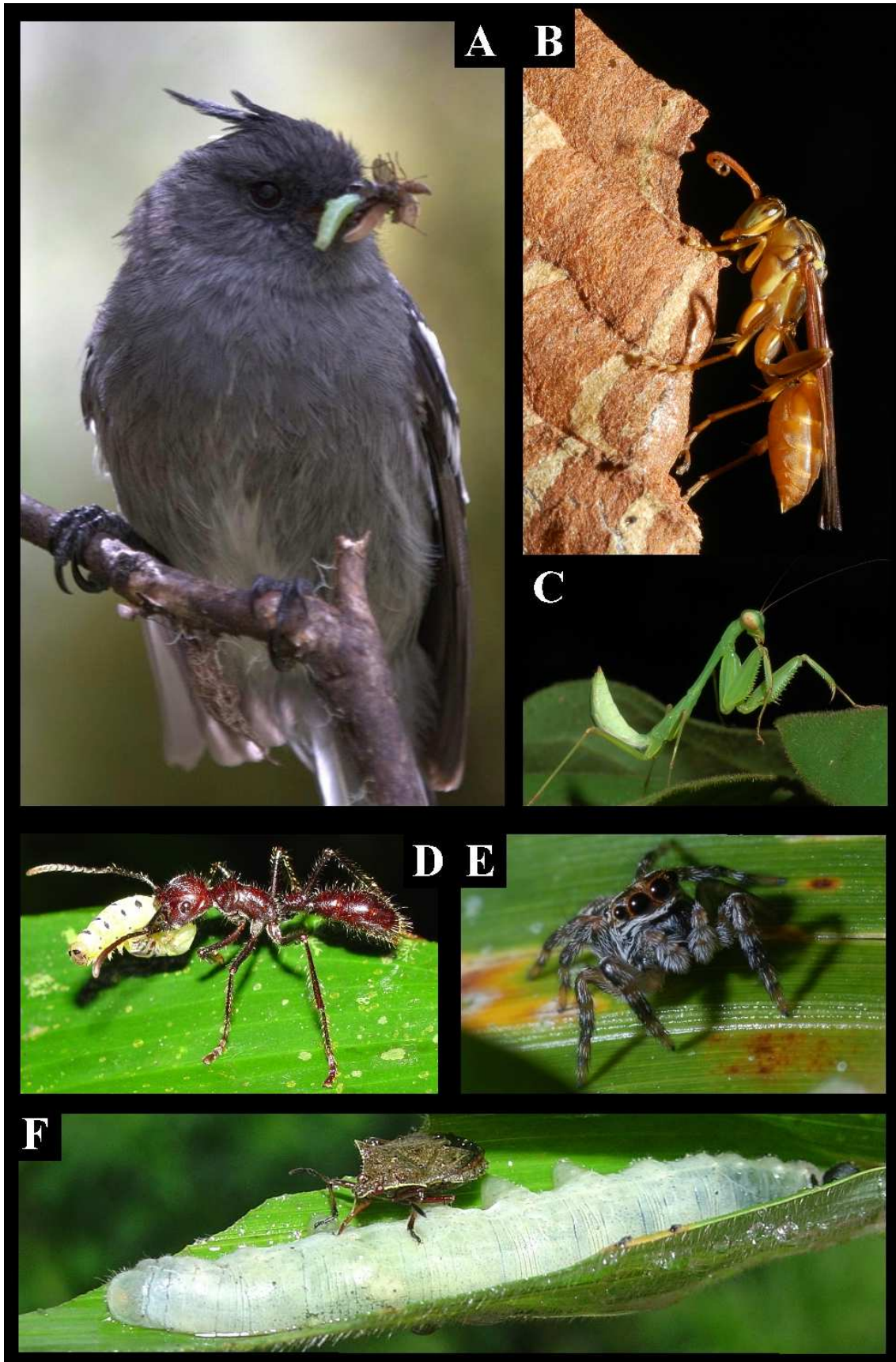
Corresponding Author:
Harold F Greeney
Yanayacu Biological Station & Center for Creative Studies
Cosanga, Napo, Ecuador c/o Foch 721 y Juan Leon Mera
Quito, Ecuador
E-mail: revmmoss@yahoo.com

Fig. 1 Examples of caterpillar predators: a) *Anairetes alpinus* (Tyrannidae) bringing lepidopteran larvae to its nestlings; b) wasp (Vespidae); c) mantid (Mantidae); d) *Paraponera* ant (Formicidae) carrying larval lepidopteran; e) jumping spider (Salticidae); f) stink bug (Pentatomidae) feeding on hesperiid larva killed while still within its larval shelter.

intervening two decades, this literature has grown exponentially, along with studies of caterpillar defenses against other natural enemies. We cannot, therefore, promise the reader an exhaustive review of this fascinating topic. Instead we have made every effort to at least touch upon all known defenses or defensive categories, but focus the bulk of our discussion on themes which more directly impact our own studies. Shifting slightly from Gross's (1993) defensive mechanisms for all insects, we have organized our review of caterpillar defenses on four slightly different categories of defense within the Lepidoptera: 1) chemical, 2) physiological, 3) morphological, and 4) behavioral.

Chemical defenses

Secretory glands, regurgitated plant extract, *de novo* production of chemical defenses, and sequestration of toxic compounds are the main chemical defenses used by caterpillars. While many excellent descriptive and empirical studies investigate each of these (Schulze, 1911; Bourgogne, 1951; Eisner and Meinwald, 1965; Davis and Nahrstedt, 1979; Weatherstone *et al.,* 1986; Pasteels *et al.,* 1983; Damman, 1986; Bowers, 1992, 1993; Dyer, 1995, 2001; Sime, 2002; Rayor *et al.,* 2007), we will focus here on the most wide-spread and best-studied strategy: sequestering secondary plant compounds as a defense against natural enemies.

The study of chemically mediated trophic interactions, such as fungus-plant-herbivore, plant-herbivore-predator, and prey-predator-parasite, has provided key concepts for the development of ecological and evolutionary theory. Host plant chemistry, especially allelochemistry, is known to play an important role in these interactions (Ehrlich and Raven, 1964; Jones *et al.,* 1987; Stamp and Bowers, 1996; Singer and Stireman, 2003; Dyer *et al.*, 2004; Ode, 2006), particularly in mediating the interaction of caterpillars with their predators and parasitoids. One mechanism for this mediation is caterpillar sequestration of hostplant allelochemicals, which serves as a defense against natural enemies (Duffey, 1980; Brower, 1984; Bowers, 1991; Dyer and Bowers, 1996). Although this relationship has been described for some species, the relative efficacy of this defense against predators (reviewed by Bowers, 1990; Witz, 1990) or parasitoids (Gross, 1993; Godfray, 1994; Hawkins, 1994) remains under-investigated (Witz; 1990, Gentry and Dyer, 2002; Stireman and Singer, 2003; Ode, 2006). In particular, there are very few studies that have examined the importance of sequestered plant allelochemicals as mediators of herbivore-parasitoid interactions (but see Singer *et al.*, 2004). A recent review (Ode, 2006) pointed out that, while many studies have shown that the identity of plant species eaten by herbivorous insects affects the growth and development of parasitoids, very few (*e.g.*, Barbosa *et al.*, 1986, 1991; Ode *et al.,* 2004) have directly measured plant chemistry. Furthermore, most of these studies have been conducted in agroecosystems (Ode, 2006).

There is considerable evidence that specialists are better able to sequester plant secondary metabolites, presumably as defenses, than generalists (Bowers, 1990, 1992, 1993; Dyer, 1995; Nishida, 2002). Experimental evaluations of putative caterpillar defenses suggest that both vertebrate and invertebrate predators are important selective forces in the evolution of dietary specialization and the sequestration of plant allelochemicals and that these sequestered compounds negatively affect predators (Brower, 1958; Bowers 1980, 1981; Bernays and Cornelius, 1989; Bowers and Farley, 1990; Dyer and Floyd, 1993; Dyer, 1995, 1997; Dyer and Bowers, 1996; Stamp and Bowers, 1996; Theodoratus and Bowers, 1999). Although there are far fewer studies on the effects of sequestered compounds on parasitoids, they may be even more important as selective agents than predators (Hawkins *et al.*, 1997). The effects of sequestered compounds on parasitoids are not well understood, but one view is that the effects on parasitoids will be similar to that on predators: sequestered compounds will be toxic to parasitoids and act in a dose-dependent manner (*e.g.*, Duffey *et al.,* 1986; Sime, 2002; Singer and Stireman, 2003; Singer *et al.,* 2004). The other view is that sequestration of plant compounds turns a host into enemy free space for parasitoids; sequestering hosts are protected from predators and thus so is the parasitoid (Dyer and Gentry, 1999; Dyer, 2001; Gentry and Dyer, 2002; Lampert *et al.,* 2011; Reudler *et al.,* 2011). This "safe haven" hypothesis (Lampert *et al.,* 2010) predicts that higher concentrations of sequestered compounds will be beneficial to parasitoids that can tolerate the host compounds. For example, parasitism rates of a sequestering leaf beetle, *Chrysomela lapponica* were higher when the beetles were fed on willow species with high levels of salicyl glucosides (Zvereva and Rank, 2003). Several studies (see section on physiological defenses) suggest that sequestered host plant compounds may affect the ability of the host caterpillar to encapsulate parasitoids. Thus, plant allelochemicals used by caterpillars to make themselves unpalatable may not only provide parasitoids with enemy free space, but may increase the probability of successful parasitoid attack.

Plant allelochemicals may have both direct and indirect effects on natural enemies (Gauld and Gaston, 1994; Ode, 2006). Direct effects occur when the host is able to sequester the plant allelochemicals so that predators, pathogens, or parasitoid larvae are exposed to these sequestered compounds during development. Indirect effects occur when the allelochemicals in the caterpillar hostplant affect the quality of the caterpillar as food for the parasitoid, thereby impacting the parasitoid's growth and development. In sequestering caterpillars, there may be both direct and indirect effects because the sequestered compounds may also affect host quality, either positively or negatively (Duffey *et al.*, 1986). Comparisons of related sequestering and non-sequestering caterpillar hosts, combined with varying chemical content of sequestering hosts have supported these
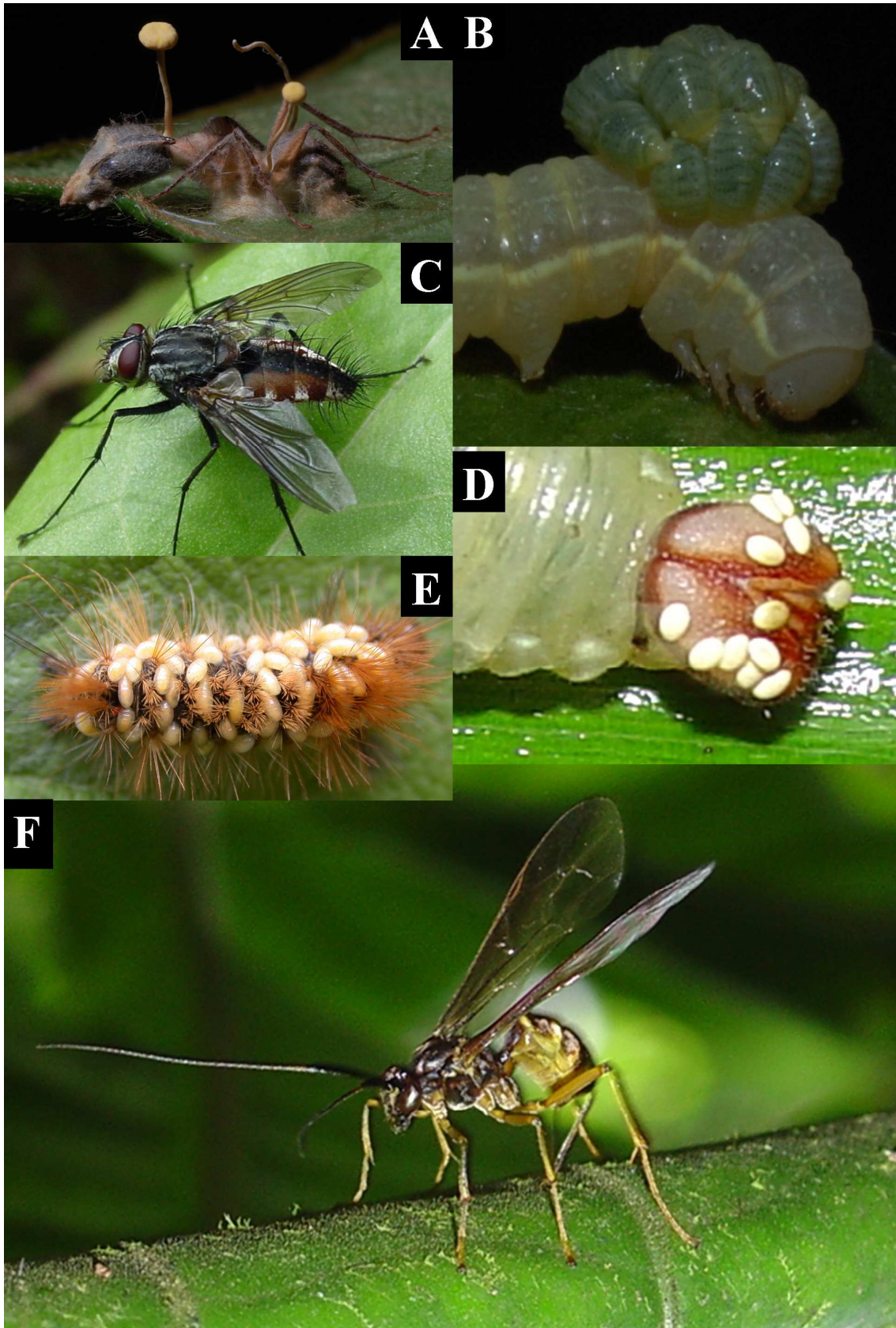
Fig. 2 Examples of caterpillar parasitoids: a) *Cordyceps* fungus attacking an ant (Formicidae); b) ectoparasitoid wasp larvae (Eulophidae) attached to the outside of a caterpillar; c) adult parasitoid fly (Tachinidae); d) eggs of parasitoid fly (Tachinidae) attached to the head capsule of a caterpillar (Hesperiidae); e) parasitoid wasp larvae (Braconidae) emerging from their caterpillar host (Erebidae) prior to pupation; f) adult parasitoid wasp (Ichneumonidae) piercing a caterpillar leaf shelter with its ovipositor to find the larvae within.

hypotheses (Bowers 2003; Ode, 2006; Lampert *et al.*, 2010, 2011).

There may also be differences in how different parasitoid taxa, or parasitoids with varying host ranges, are affected by sequestered allelochemicals. Barbosa (1988) hypothesized that specialized parasitoid wasps (braconids and ichneumonids) can tolerate the associated chemicals of their hosts but that generalist flies (tachinids) cannot. Mallampalli *et al.* (1996) however, found that the tachinid fly, *Compsilura concinnata,* was unaffected when host caterpillars were fed on condensed tannins or the iridoid glycoside, catalpol, and thus suggested that generalist flies may be resistant to allelochemicals. The study did not look at a host species that sequestered plant allelochemicals. Interestingly, Harvey *et al.* (2005) found that two species of specialist wasp parasitoids (a braconid and an ichneumonid) responded differently to host caterpillars reared on diets differing in iridoid glycoside content. The braconid was unaffected by host diet, while the ichneumonid developed more quickly in hosts reared on diets higher in iridoid glycosides (Harvey *et al.,* 2005). Although the caterpillar species in the study sequesters iridoid glycosides (Suomi *et al.*, 2001), levels of iridoids were not quantified. A few studies suggest that some parasitoids may be more tolerant of toxins than previously thought, and in some cases parasitoids sequester chemicals from their hosts (Duffey *et al.*, 1986; Gauld and Bolton, 1991; Rossini *et al.*, 2000; Bowers, 2003).

In summary, several different classes of allelochemicals are sequestered by herbivorous insects, including alkaloids, amides, cardiac glycosides, aristolochic acids and iridoid glycosides, and all of these compounds can be deterrent to predators (Bowers, 1990; Nishida, 2002). However, investigations of the importance of these sequestered compounds for the interaction of herbivorous insects and their parasitoids are rare and their results conflicting: 1) A few examples show that sequestered host plant allelochemicals negatively affect parasitoid wasps, and suggest that these chemicals may act as both pre- and post-oviposition defenses (*e.g.*, Barbosa *et al.,* 1991; Isman and Duffey, 1983; Turlings and Benrey, 1998; Sime, 2002). 2) Bourchier (1991) and Mallampalli *et al.* (1996) found that generalist tachinid larvae were not directly affected by host associated chemicals but were affected indirectly by changes in overall host quality. 3) Some studies suggest that sequestered allelochemicals may encourage and facilitate attack by parasitoids (*e.g.*, Sheehan 1991; Cornell and Hawkins, 1995; Dyer and Gentry, 1999; Gentry and Dyer, 2002; Zvereva and Rank, 2003; Smilanich *et al.*, 2009a, b).
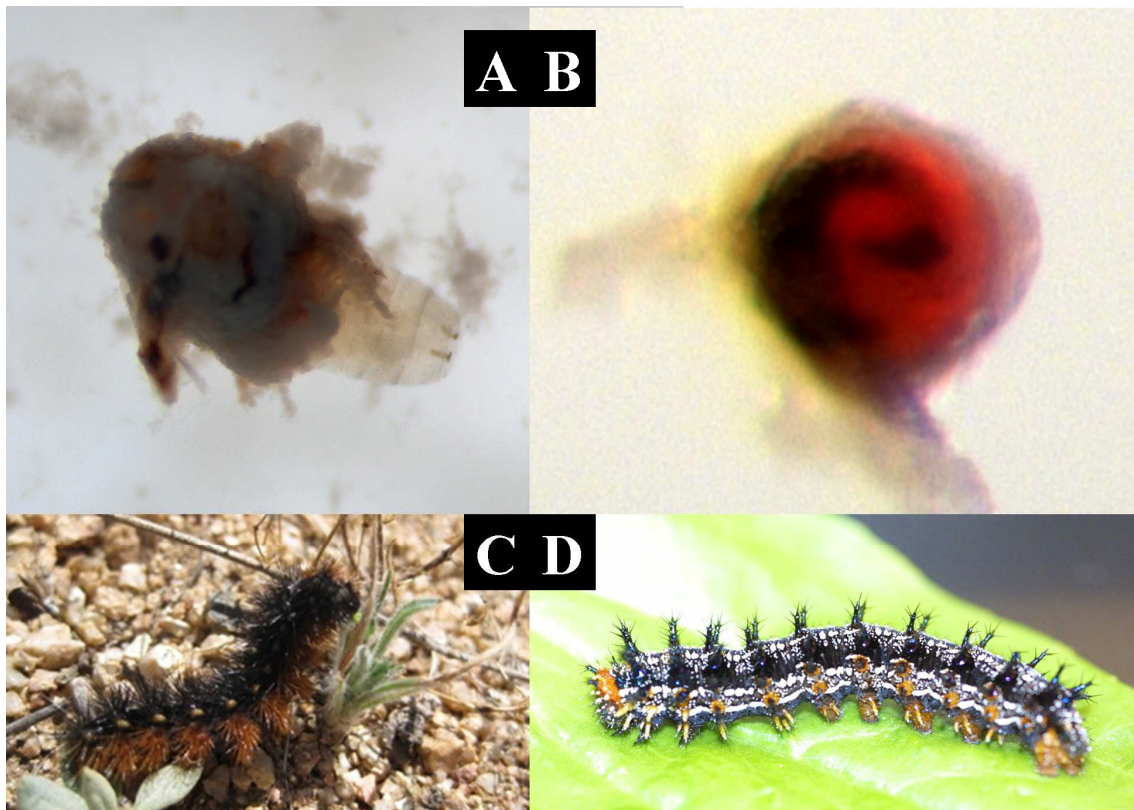
Physiological defenses

The insect immune response

Physiological defenses consist of 3 sublevels and are used primarily to combat pathogens, parasites, and parasitoids (reviewed by Gillespie *et al.,* 1997; Carton *et al.,* 2008; Strand, 2008; Beckage, 2008). The 3 sublevels include: (1)

integument and gut as physical barriers to infection, (2) coordinated action of several subgroups of hemocytes when physical barriers are breached and, (3) induced synthesis of antimicrobial peptides and proteins, mostly by the fat body (Gillespie *et al.,* 1997). This section focuses on the last two sublevels which compose the insect immune response, as these have been the best studied over the past two decades. The immune defense in insects is considered one of the most effective defenses against parasitoids and pathogens (Godfray, 1994; Smilanich *et al.,* 2009a).

Prokaryotic invaders and small eukaryotic cells (*e.g.*, protists, fungi) are recognized as non-self by the many recognition protein molecules that create the humoral response. Antimicrobial and lysozyme proteins attack these smaller invaders, and in some cases the cellular action of phagocytosis engulfs and digests the foreign object (Carton *et al.,* 2008; Strand, 2008). For larger objects such as parasitoid eggs, encapsulation is a key defense. The encapsulation response is carried out by several groups of specialized cells (*e.g.*, hemocytes). The encapsulation response is immediate and takes place inside the host's hemolymph. Encapsulation is generally composed of both the humoral and cellular response, although they do not always occur together (Strand, 2008). In Lepidoptera, the primary circulating hemocytes are plasmatocytes, granulocytes, oenocytoid, and sperule cells. Precursors for these cells are produced by the hematopoeisis organs located in the meso- and meta-thorax (Lavine and Strand, 2002; Strand, 2008). Immediately following a parasitoid attack, the recognition proteins of the humoral response function to recognize non-self objects and activate the hemocytes. The cellular response continues with hemocytes attacking the foreign object and beginning the process of encapsulation, in which cells adhere to the foreign object and begin to build layers of cells, which eventually die and harden onto the surface (Figure 3a, b). In some insects, when the cells die, they undergo the chemical process of melanization, which includes the production of the cytotoxic molecule, phenoloxidase, and other free radicals such as quinones. Since phenoloxidase is cytotoxic, it is usually stored as the precursor, prophenoloxidase. The parasitoid eggs or larvae are killed through the asphyxiating effects of the encapsulation process and through the cytotoxic effects of the phenoloxidase cascade (Nappi and Christensen, 2005; Carton *et al.*, 2008).

Measuring the immune response

Experiments seeking to understand the variation in immune parameters use a variety of methods to measure immunity. A common method for measuring encapsulation and melanization is injection or insertion of a synthetic object into the insect's hemocoel (Lavine and Beckage, 1996; Klemola *et al.,* 2007). The immune response is quantified by measuring the color change and/or cell thickness around the object (Diamond and Kingsolver, 2011). Other measurements rely on quantifying the protein activity of the humoral response by determining the concentration of the

Fig. 3 Physioloical defenses: a) a partially encapsulated tachinid larva (*Chetagena* sp.) dissected from the generalist Woolly Bear caterpillar, *Grammia incorrupta* (Erebidae);b) a partially encapsulated and melanized sephadex bead used to challenge the immune response of the specialist Buckeye caterpillar, *Junonia coenia* (Nymphalidae); c) *Grammia incorrupta* caterpillar (photo: P. Mason); d) *Junonia coenia* caterpillar.

enzyme, phenoloxidase, which catalyzes the melanization cascade, or quantifying the activity of antibacterial lysozyme activity (Adamo, 2004a). Still other measures include hemocyte counts (Ibrahim and Kim, 2006), hemolymph protein concentration (Adamo, 2004a), and gene expression (Freitak *et al.,* 2009). Studies measuring the response of multiple immune parameters show that they do not always respond in the same way (Adamo, 2004b). Many examples show that the phenoloxidase activity can be affected differently from the encapsulation, lysozyme, or hemocyte response (Bailey and Zuk, 2008; Freitak *et al.,* 2009; Shikano *et al.,* 2010), indicating different adaptations depending upon the identity of the attacker. For example, not only will a bacterial infection induce a specific component of the immune response that is different from a parasitoid infection, but the response will also be specific to the type of invading bacteria (Riddell *et al.,* 2009).

Host plants and the immune response

Host plant diet is a major source of variation in the immune response (Smilanich *et al.,* 2009b; Diamond and Kingsolver, 2011). The effects of host plants on immune responses can depend on plant chemistry, herbivore health, both herbivore and plant genotype, and the specific immune parameter being measured (*i.e.*, PO activity, encapsulation of

inert object, lysozyme activity, etc.). Certain plant secondary metabolites can alter the effectiveness of immune responses. For example, ingestion of diets containing carotenoids enhances immune function due to their free-radical scavenging properties (de Roode *et al.,* 2008; Babin *et al.,* 2010). In contrast, ingestion of other secondary metabolites (*e.g.*, iridoid glycosides) can negatively affect the immune response (Haviola *et al.,* 2007; Smilanich *et al.,* 2009b). Macronutrients can also affect the immune response. Protein and carbohydrates not only boost immune parameters (Lee *et al.,* 2008; Srygley *et al.,* 2009; Cotter *et al.,* 2011), as does plant/diet quality (Yang *et al.,* 2008; Bukovinszky *et al.,* 2009; Diamond and Kingsolver, 2011), but also is preferred by immune challenged herbivores (Lee *et al.,* 2006; Povey *et al.,* 2009). In most cases high plant quality (*i.e.*, low secondary metabolite concentration and high nitrogen content) translates to increased immunity (but see Klemola *et al.,* 2007).

Counter adaptations to the immune response

Since the immune response is one of the most effective defenses against parasitic enemies (Smilanich *et al.,* 2009a; Godfray, 1994), it is evolutionarily fitting that these enemies will have evolved counter adaptations to cope with or suppress the immune response. Indeed, the best
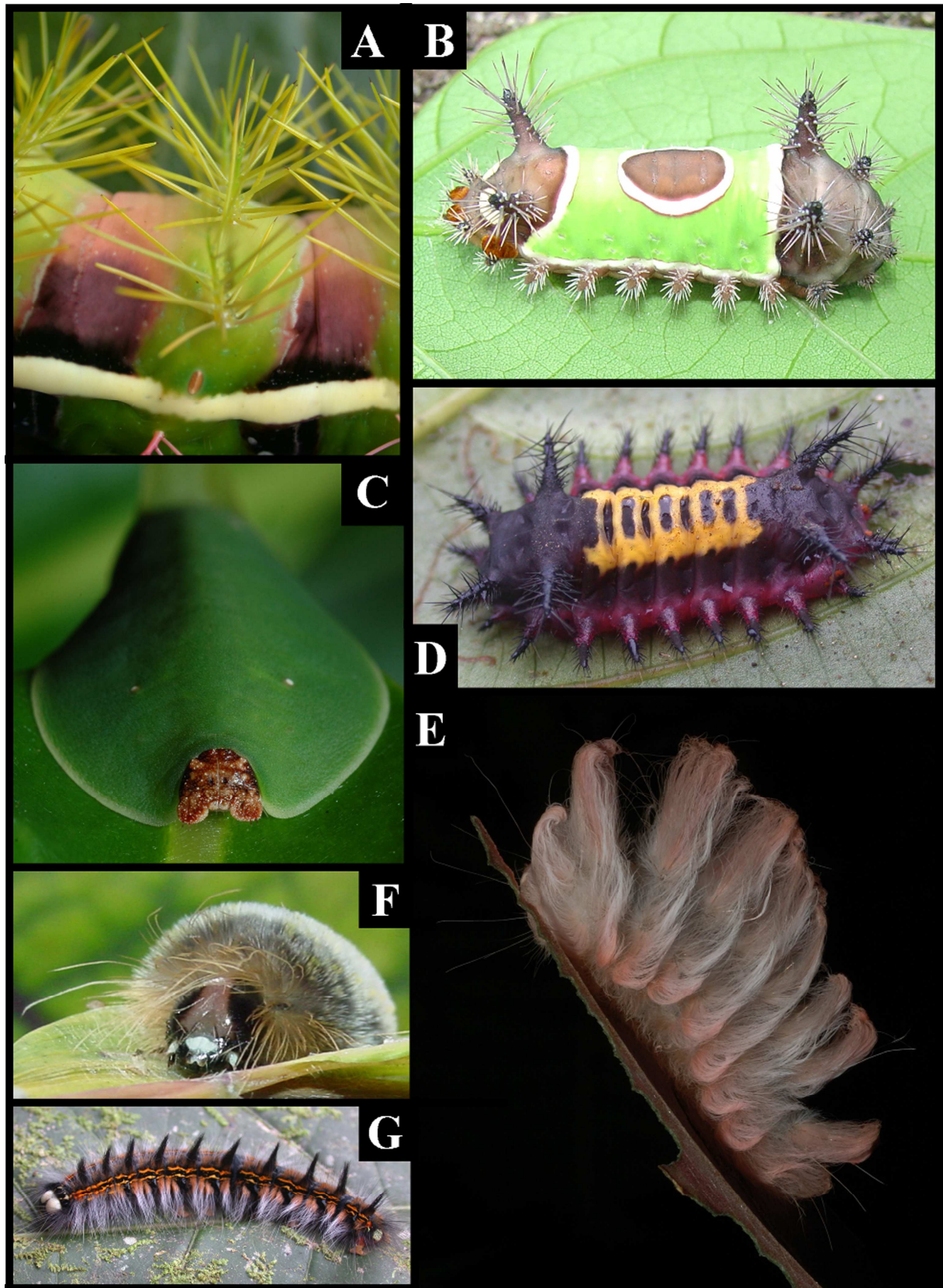
Fig. 4 Morphological defenses of caterpillars: a) detail of stinging spines (Saturniidae); b & d) saddle-back moth *Acharia* caterpillars (Limachodidae) with stinging spines; c) *Menander* (Riodinidae) with thickened exoskeleton and body shape allowing it to retract and protect head and legs; e) *Megalopyge* (Megalopygidae) caterpillar with long hairs covering urticating spines; f) tiger moth caterpillar (Erebidae) with dense hairs; g) *Olcelostera* caterpillar (Apatelodidae) with short hairs which cause intense skin irritation.

example of a counter adaptation to the insect immune response is exhibited by hymenopteran parasitoids in the families, Braconidae and Ichneumonidae (Strand, 2009). Species in these two families harbor polydnaviruses, which have become integrated into the wasp's genome and are passed vertically through the germ line to offspring (Strand, 2009). The virus replicates in the reproductive tract of the female wasp and is injected into the host during oviposition (Beckage, 2008). Once inside the host's hemocel, the virus infects immune functioning cells, enzymes, and tissues such as hemocytes, phenoloxidase, and fat body, and thereby suppresses the immune response (Strand, 2009). Another example of counter adaptation to the immune response is found in certain species of tachinid flies. Bailey and Zuk (2008) found a positive correlation between the phenoloxidase activity of the field cricket, *Teleogryllus oceanicus*, and the melanization of the respiratory funnel in the attacking tachinid fly, *Ormia ochracea*. Since the respiratory funnel is the means by which many tachinid flies receive oxygen, a stronger funnel that is less likely to break is beneficial. In this way, these flies may be co-opting the immune response for their own benefit as the funnel is strengthened by the encapsulation process. Other species of tachinids have evolved a behavioral counter adaptation to the immune response. The broad generalist tachinid, *Compsilura concinnata*, hides from the host immune response by developing between the peritrophic membrane and the midgut, where the immune response has limited access (Carton *et al.*, 2008). Similarly, other tachinids reside in certain tissues, such as fat bodies, to avoid the immune response (Salt, 1968).

Morphological defenses

A wide array of morphological characteristics may act as defensive mechanisms (reviewed by Edmunds, 1974; DeVries, 1987; Evans and Schmidt, 1991; Gross, 1993; Godfray, 1994; Dyer, 1995; Eisner *et al.,* 2007), and these are generally divided into two categories: A) caterpillar integumental processes, such as spines or hairs; or B) caterpillar coloration, such as brightly colored (aposematic) or visually cryptic. Caterpillar size or developmental rates may also influence predation (Evans, 1983; Gaston *et al.,* 1991; Montllor and Bernays, 1993). In many cases, simply being larger (*i.e.*, later instars) may provide protection through increased effectiveness of their behavioral or physical defenses because they are larger relative to their attacker (Iwao and Wellington, 1970; Schmidt, 1974; Stamp, 1984; Martin *et al.,* 1989). This topic, however, has recently been reviewed by Remmel *et al.* (2011), and we do not further consider size and developmental rate here.

Integumental structures

Possessing tough or thickened exoskeletons may prevent attack from some enemies (Malicky, 1970; Schmidt, 1974; Breckage and Riddiford, 1978), and may be widespread among caterpillars

forming associations with ants (Pierce *et al.,* 2002). In some taxa, for example, the neotropical genus *Menander* (Riodinidae), this is accompanied by a dorso-ventrally flattened, tank-like body form (DeVries, 1997) which allows caterpillars to press themselves tightly to the leaf surface and protect exposed appendages which might otherwise be vulnerable to attack (Fig. 4c). A variety of integumental structures may also function in defense (Epstein *et al.,* 1994; Eisner *et al.,* 2007), but here we focus on spines and hairs, two structures found in taxa across the lepidopteran phylogeny and for which the effectiveness has been studied in a variety of systems (Dyer, 1995, 1997; Lindstedt *et al.,* 2008; Murphy *et al.,* 2010).

Urticating or stinging spines (multicellular processes with poison glands) and hairs (hollow trichogens with poison glandsassociated with the tormogen) are familiar defenses to anyone who has worked with caterpillars in the field (Figs 4a-b, d-e) They are found in at least six families of Lepidoptera (Kephart, 1914; Foot, 1922; Bishopp 1923; Valle *et al.,* 1954; Jones and Miller, 1959; Beard, 1963; Wirtz, 1984; Gibbons *et al.,* 1990; Deml and Dettner, 2003; Bohrer *et al.,* 2007), yet there are surprisingly few studies examining their effectiveness against predators (Murphy *et al.,* 2010). The effectiveness of hairs (Figs 4 e-g), which may have irritating properties (Beard, 1963; Wagner, 2009), are less obvious, and generalizations such as, "hairs are a good defense against invertebrate predators," are predictably, unreliable. Predators vary in their propensities to reject prey based on defensive structures, and each predator is influenced by a different assemblage of caterpillar defenses (both physical and otherwise). However, while individual caterpillar-enemy interactions are highly variable, and largely unknown, one study comparing the effectiveness of defenses against different predators provides us with some basic generalizations. An experimental comparison of caterpillar predation by ants (Formicidae), wasps (Vespidae), and bugs (Hemiptera) showed that the effectiveness of morphological defenses depended on the predatory guild (Dyer, 1997). Large size, for example, was an effective defense against the two solitary predators (bugs and wasps) but not against ants. Ants, which are able to recruit other individuals, are often able to subdue larger prey items. Thick coverings of hairs (Figs 4e-f) are important deterrents for bug predators as they inhibit insertion of proboscis (Dyer, 1997; Bowers, 1993), and are likely also effective against any predators which have mouthparts specialized for sucking. Interestingly, an alternative function of hairs may be warning the caterpillar of an advancing predator or parasitoid before it actually has a chance to catch the caterpillar (Tautz and Markl, 1978; Castellanos *et al.,* 2011), with some species bearing setae apparently modified specifically for such a purpose (Rota & Wagner, 2008). Hairs are not as effective against other predators, such as birds and wasps, which are often able to remove hairs (Bowers, 1993) or to simply digest them in the crop.
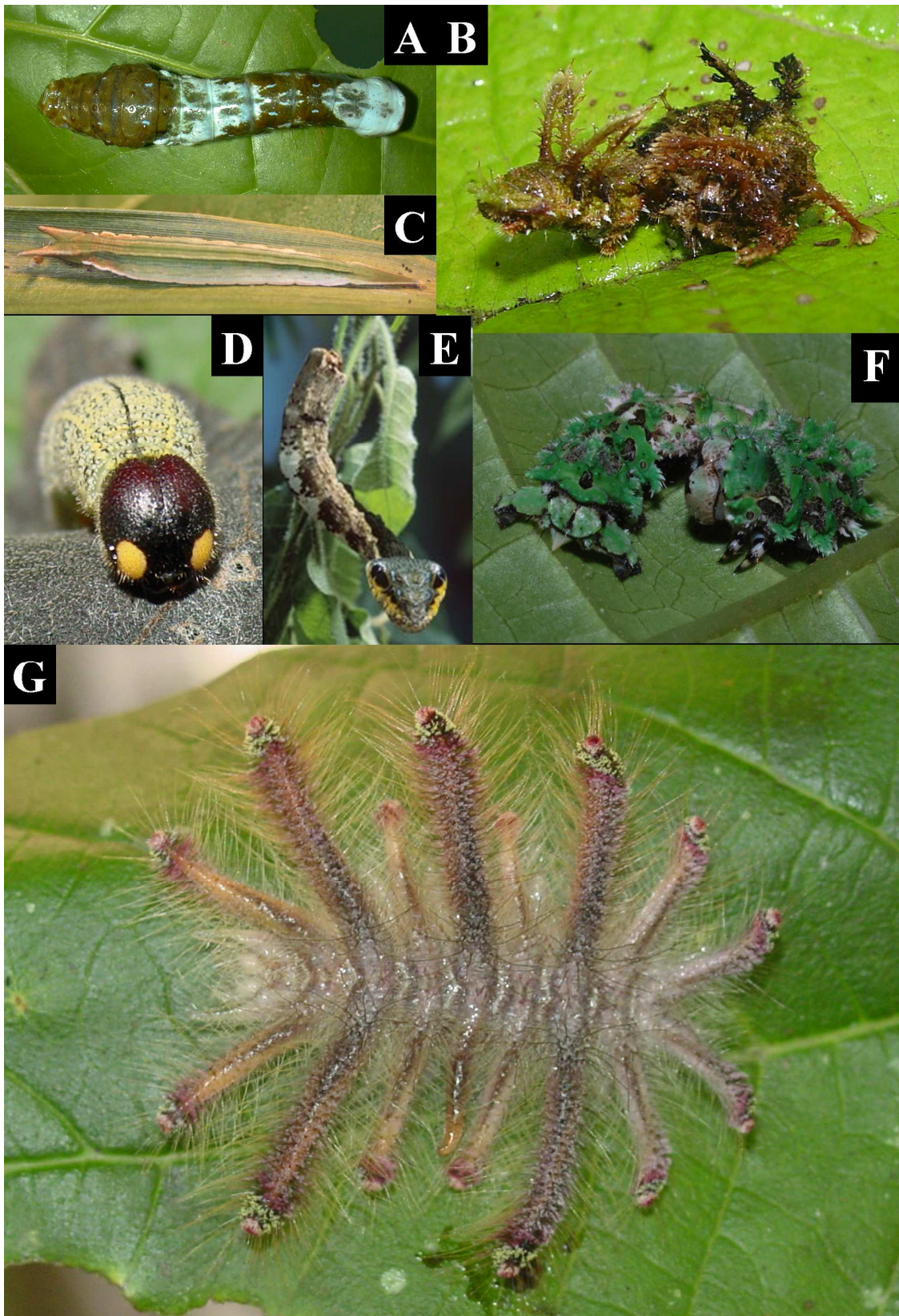
Fig. 5 Coloration as a defense in caterpillars: a) *Papilio* caterpillar (Papilionidae) resembling a bird dropping; b) an *Adelpha* caterpillar's (Nymphalidae) resemblance to moss is enhanced by distinctive resting posture; c) *Corades* caterpillar (Nymphalidae) with color patterns matching the leaves of its hostplant; d) *Urbanus* caterpillar (Hesperiidae) with yellow "eye-spots" on its head; e) *Hemeroplanes ornatus* caterpillar (Sphingidae) with thorax lifted and inflated to expose paired "eye-spots," increasing its resemblance to a snake's head; f) caterpillar (Geometridae) increasing its resemblance to lichen with a partially curled resting posture; g) caterpillar (Megalopygidae) with long, fleshy protuberances giving it the appearance of a tarantula spider.

Coloration

Caterpillar coloration as a defense strategy generally falls into three categories; (1) bright warning coloration (Figs 4d, 7a), (2) cryptic patterning matching their substrate (Figs 5c, 6a, c-d, g), (3) mimicry of inedible objects (Figs 5b, f), or resemblance to organisms considered dangerous to their predators (Figs 5e, g). Some species exhibit ontogenetic shifts between different color strategies (Grant, 2007; Sandre *et al.,* 2007), or may change which portion of their plant they are cryptic on between instars (Greeney *et al.,* 2010b, 2010c, 2011) or even seasons (Greene, 1989). One example pointed out by Wagner (2005) is *Papilio troilus* (Papilionidae), which mimics a bird dropping for several instars and then resembles a snake once it is reaches later instars.

Aposematic coloration

Aposematic (warning) coloration (*e.g.*, Figs 4d, 7a) may be important for visual predators, such as wasps, birds, and mantids, but is likely less important for ants or other species which are more chemically oriented. When predators are deterred by brightly colored prey, it provides support for the long-standing belief that aposematism is an adaptive explanation for bright colors and striking patterns (Cott, 1940; Ruxton and Sherrat, 2006). However, there are many visually oriented predators, such as reduviids and pentatomids (Johnson, 1983), and some parasitoids, that are not deterred by brightly colored prey (Dyer, 1997; Gentry and Dyer, 2002). A correlation between palatability and coloration is widely assumed to exist in the animal kingdom (*e.g.*, Cott, 1940; Edmunds, 1974; Harborne, 1988), and coloration has even been used as an indicator of palatability (Sillén-Tullberg, 1988). However, as more predation studies accumulate, it appears that this correlation is often overstated.

Crypsis

Many species of caterpillars are patterned to closely match the portion of the plant where they feed or rest, allowing them to blend into the background and avoid detection (DeVries, 1987; Greene, 1989; Stamp and Wilkens, 1993; Allen, 1997) (Figs 5c, 6a). Often in conjunction with cryptic coloration, many caterpillars are "behaviorally cryptic," and assume resting or feeding postures which mimic a portion of the hostplant or the damage caused to it by the caterpillar itself (Figs 6a, c-d, g). Such behavior is especially well developed and effective within the Geometridae (McFarland, 1988, Wagner, 2005), which can either freeze and mimic straight twigs, or can contort and twist to drastically alter the outline of their bodies (Figs 6a, d, g).

Mimicry

In a very similar manner to crypsis, some caterpillars resemble "unpalatable" items that are common in the habitat such as bird feces (Fig. 5a), lichen (Fig. 5f), moss (Fig. 5b), or detritus (DeVries, 1987; Lederhouse, 1990; Wagner, 2005). This strategy is particularly widespread and effective in later instars of caterpillars in the neotropical genus

Adelpha (Nymphalidae), most of which appear as little more than a piece of moss while resting on the dorsal surface of the leaf (Moss, 1927, 1933; Aiello 1984; Willmott, 2003) (Fig. 5b). Many species of papilionids are excellent mimics of bird droppings and, like the *Adelpha* caterpillars, behaviorally enhance the resemblance by resting prominently on the dorsal surfaces of leaves where bits of moss or bird feces might naturally occur (DeVries, 1987; Allen, 1997; Wagner, 2005) (Fig. 5a). Resemblance to unpalatable items is taken a step further by some species of papilionids (or by later instars of the same), whereby large eyespots on the thorax and the accompanying behavior of rearing up onto their prologs to resemble a predatory snake (DeVries, 1987; Wagner, 2005), a resemblance enhanced in some species by the eversion of their snake-tongue-like osmeteria (see *Eversible glands*). With regards to realism, however, this performance is far surpassed by several genera of sphingid caterpillars which do the same, simultaneously expanding parts of the abdomen and all or portions of the thorax to form the shape of a snake's head (Moss, 1920; Curio, 1965; Hogue, 1982) (Fig. 5e). Realism, however, may not be very important in the evolution and maintenance of eye-spots in caterpillars, which is a widespread phenomenon. Janzen *et al.* (2010) speculate that even markings that have the vaguest resemblance to eyes (Fig. 5d) would be selected for if they triggered innate startle-flee responses in visually oriented predators.

Although eye-spots as anti-predator adaptations have been examined in various contexts, in both adult and larval Lepidoptera (Blest, 1957; Shirota, 1980; Stevens *et al.,* 2007, 2008; Kodandaramalah *et al.,* 2009), studies gathering further empirical data to test the robustness of this hypothesis would surely prove rewarding. The extremely convincing patterns and behaviors of many of the species mentioned above leave little doubt that eye-spots are an effective defense against some predators. From extensive personal experience (HFG) observing caterpillar coloration, behavior, and habits, as well as avian foraging tactics, however, the validity of even the tiniest spots on > 1 cm, immobile pupae being perceived as "dangerous" eyes to vertebrate predators, seems weak, despite the arguably sound evolutionary theory supporting the overall argument.

Behavioral defenses

Behavioral defense strategies are ubiquitous, diverse, and often spectacular in their complexity and ingenuity (Awan, 1985; Damman, 1986; DeVries, 1991c; Hunter, 2000; Machado and Freitas, 2001; Aiello and Solis, 2003; Reader and Hochuli, 2003; Castellanos and Barbosa, 2006; Grant, 2006; Lill and Marquis, 2007; Greeney, 2009). In a fascinating twist of the caterpillar-enemy interaction story, some endobiont microgastrine wasp parasitoids (Braconidae) actually usurp caterpillar behavioral defenses, causing their host to respond protectively to their own enemies including both hyper-parasitoids and predators (Brodeur and Vet, 1994; Tanaka and Ohsaki, 2006;
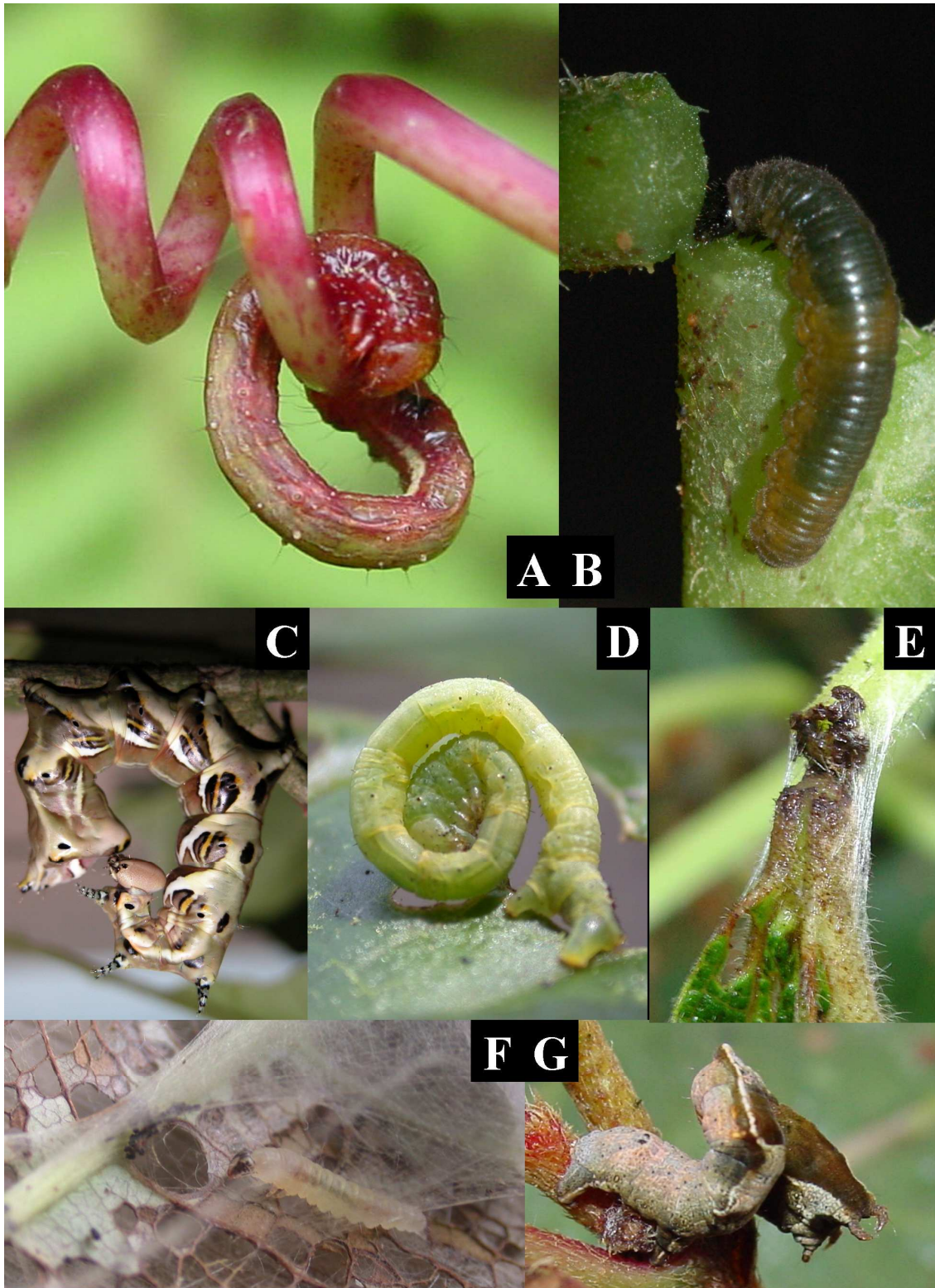
Fig. 6 Behavioral defenses of caterpillars: a) caterpillar (Geometridae) with coloration and resting position which make it resemble the tendrils of its hostplant; b) *Oleria* (Nymphalidae) caterpillar in the process of severing the petiole of a hostplant leaf, preparing to drop with it to the ground to feed; c) caterpillar (Notodontidae) hanging from a leaf edge with coloration and posture resembling a damaged portion of the hostplant; d) caterpillar (Geometridae) in a resting position which mimics a leaf tendril of its host plant; e) partially severed leaf petiole secured with silk to prevent it from falling from the plant and allowing the *Urbanus* caterpillar (Hesperiidae) to hide on the wilted leaf and escape some crawling predators; f) caterpillar (Choreutidae) resting inside a silken shelter spun across the bottom of a leaf, resting to the right of an "escape" hole in the leaf, through which it will crawl if threatened; g) caterpillar (Geometridae) assuming a resting position which enhances its resemblance to a piece of dead leaf.

Grosman *et al.*, 2008; Harvey *et al.*, 2008a; Tanaka and Ohsaki, 2009). For reviews of this topic see Harvey *et al.* (2008b; 2011). Most species exhibit several defensive behaviors, as exemplified by *Urbanus esmeraldus* (Hesperiidae) caterpillars, which build architecturally complex shelters, alter plant tissue position and coloration to make their resting places more cryptic, throw fecal pellets away from their bodies, as well as bite and regurgitate upon potential threats (Moraes *et al.,* in press). With most species still lacking even basic descriptions of their life history strategies, there are undoubtedly numerous tactics still to be discovered. Here we provide an overview of a few of the best studied and widely utilized behavioral defenses. For a discussion of resting or feeding postures or other behaviors which enhance crypsis see *Coloration*.

Of the four behavioral defense categories considered by Gross (1993), three are commonly exhibited by caterpillars. The applicable categories considered by Gross (1993) were: 1) evasive; 2) aggressive; 3) associative (*i.e.*, myrmecophily, group feeding). We are not aware of any cases of parental care within the order, Gross's (1993) fourth category. With only slight modification of Gross's (1993) organization of insect defenses, with regards to caterpillars we have organized our discussion of behavioral defenses into two categories A) behaviors which presumably reduce encounters and attacks from enemies and B) behaviors exhibited upon encountering or being attacked by an enemy. Both categories include many variations, combinations, and modifications of innumerable potential life history strategies and behaviors, the expression or employment of which may shift during larval ontogeny (Stamp, 1984; Cornell *et al.,* 1987; Allen, 1990). We discuss some of the most commonly observed variations of these categories below.

Avoiding detection and capture

Here we consider three taxonomically wide-spread behaviors that fall within the suite of life history strategies designed to evade detection and attack by enemies: a) associative behaviors with con- or heterospecifics; b) behaviors designed to disassociate caterpillars with cues used by predators for prey location; and c) shelter building.

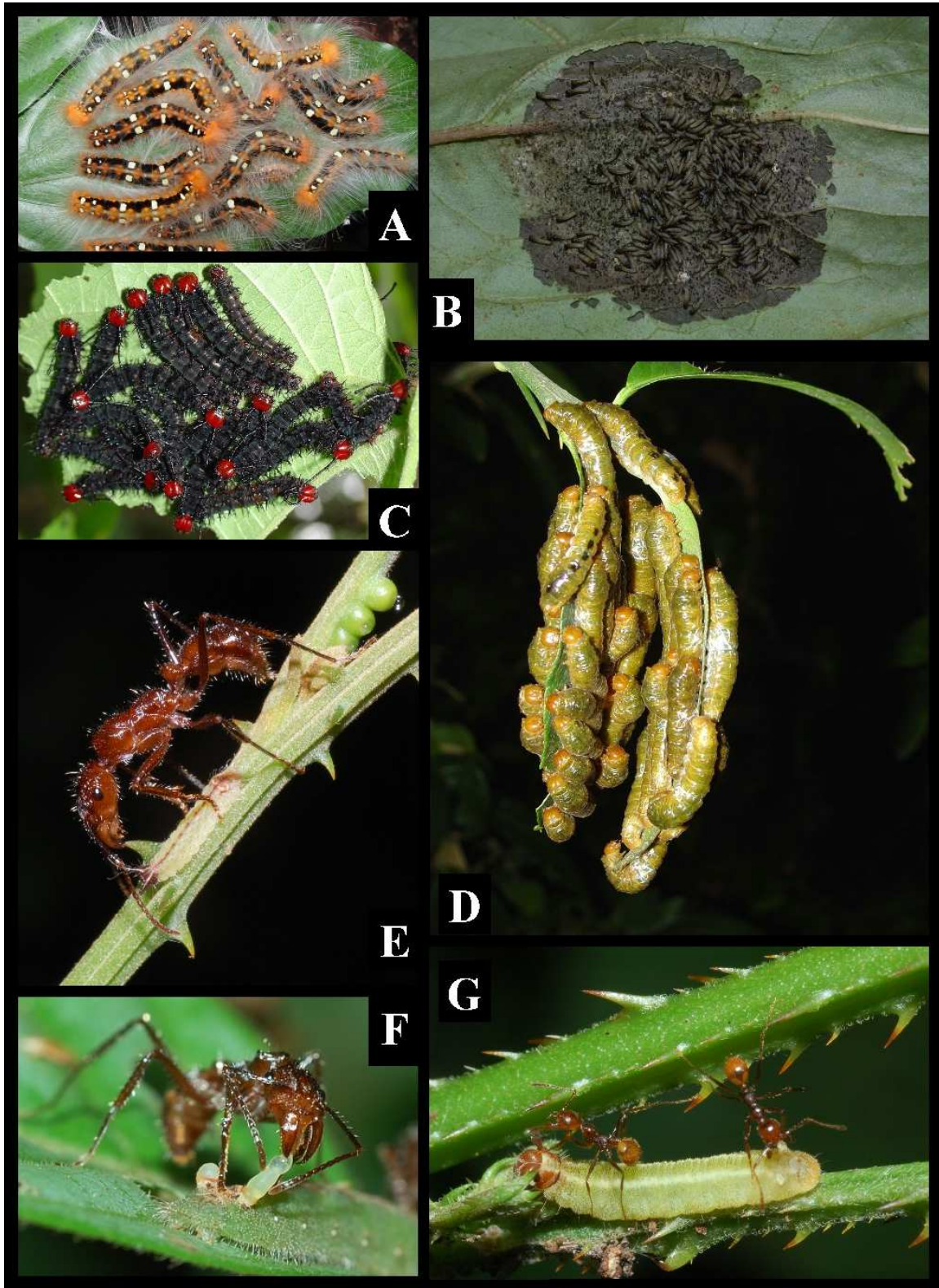**Association with other individuals or organisms**

A working definition of gregarious behavior in larval Lepidoptera is feeding or moving, at some point in their development, in tight groups of at least three individuals (Fitzgerald and Costa, 1999). Gregarious caterpillar feeding behavior is exhibited by species in many families of Lepidoptera (Hogue. 1972; DeVries, 1987, 1997; Allen, 1990; Clark and Faeth, 1997; Fordyce and Agrawal, 2001) (Figs 7a-d, 8a, c) and, in some, has been shown to be an effective defense against a variety of enemies (Myers and Smith, 1978; Lawrence, 1990; Parry *et al.,* 1998; McClure and Despland, 2011). Groups may be formed by siblings from a single clutch or conspecific individuals of differing instars from several clutches, and such groups may feed exposed (DeVries, 1987, 1997; Fordyce and

Agrawal, 2001) or within large silken shelters (see *Natural or engineered shelters*). Gregariousness may also serve to augment the effectiveness of chemical or behavioral defenses such as osmeteria (Fig. 7d), vomiting (Fig. 8c), head thrashing (Fig. 8a), or spine waving (Fig. 7c) (Hays and Vinson, 1971; Hogue, 1972; Prop, 1960; Stamp, 1982; Tulberg and Hunter, 1996), and in aposematic caterpillars may augment the warning signal (Aldrich and Blum, 1978; Pasteels *et al.*, 1983; Beatty *et al.*, 2005) (Figs 7a, c). Additionally, though to the best of our knowledge this has not been studied, aggregations and group behaviors may also serve a camouflaging function (see *Coloration*). In the case of some *Actinote* (Nymphalidae) caterpillars (Fig. 7b), the combination of tight aggregative behavior and distinctive feeding damage of early instars might function to give the otherwise exposed group the appearance of old leaf damage or disease. In other cases, such as the early instars of *Daedalma* (Nymphalidae) (Fig. 8a), the simultaneous head-rearing of linearly aggregated caterpillars may give the appearance of a larger, spine-defended caterpillar.

A second, and perhaps more widely studied associative behavior of caterpillars, is living in association with ants (DeVries, 1990, 1991b; Fiedler, 1991; Pierce *et al.,* 2002). The exact nature of these interactions varies from species to species, but is most commonly mutualistic, whereby caterpillars provide secreted nutritional rewards to their associates, who remain nearby and protect the caterpillar from enemies (DeVries, 1991a; Pierce *et al.,* 2002; Pierce and Easteal, 1986; Travasos and Pierce, 2000) (Figs 7e-g). In the Riodinidae and Lycaenidae, many species have evolved specialized caterpillar organs to elicit protective behaviors from their attendant ants using vibrations or sounds (DeVries 1988, 1990, 1991b) or volatile alarm pheromones (Fiedler 1991; Fiedler *et al.*, 1996). Another extreme is exhibited by some species whose caterpillars chemically mimic their associative ant species and are actually carried into the ant nest and fed and cared for by their hosts (Henning, 1983; Elmes *et al.,* 1991). The associative benefits may vary between different ant species (Wagner, 1993), but may also be maintained by additional fitness benefits such as faster growth (Pierce *et al.,* 1987; Wagner and del Rio, 1997). Some associations are obligate, in other cases these protective associations appear to be predominantly facultative, at all or several portions of the larval cycle (Pierce *et al.,* 2002). The majority of species known or suspected to form associations with ants, however, have yet to be studied (DeVries, 1997; DeVries and Penz, 2000).

Avoiding encounters in space and time

Other life history strategies which help caterpillars avoid encounters with enemies include feeding from hidden positions such as under leaves or in leaf shelters (see below) and temporal or spatial alterations of feeding activity, location, or even food plant (Rothschild *et al.,* 1979; Heinrich, 1979; DeVries, 1987; Stireman and Singer, 2003).

Fig. 7 Protective associations of caterpillars with other individuals and organisms; a) aposematic caterpillars (Apatelodidae) increasing the magnitude of their warning signal by resting together on the dorsal surface of a leaf; b) young *Actinote* caterpillars (Nymphalidae) resting in a tight group and surrounded by feeding damage which makes them less apparent to visually oriented predators; c) aposematic *Hamadryas* (Nymphalidae) caterpillars improving the effectiveness of head scoli thrashing by resting in a group; d) *Papilio* caterpillars (Papilionidae) resting in groups, resembling damaged plant tissue and increasing the effectiveness of their chemical defenses (osmeteria); e) *Synargis* caterpillar (Riodinidae) protected by large *Ectatomma* ant (Formicidae); f) *Ectatomma* ant receiving edible secretions from specialized caterpillar gland (Riodinidae); g) *Nymphidium* caterpillar (Riodinidae) attended by *Azteca* ants.

Many species of caterpillars partially sever or "trench" a portion of their food plant (*e.g.*, leaf vein or petiole), isolating the portion of the plant where they are feeding and resting, a behavior which may facilitate the ingestion of chemically defended plants by cutting off the supply of toxins (Dussourd, 1999; Clarke and Zalucki, 2000; Chambers *et al.,* 2007). This behavior also frequently facilitates the manipulation of plant tissues into larval shelters (see below) or adds to the crypsis or isolation of the caterpillars' resting or feeding location (*e.g.*, Greeney and Warren, 2004, 2009; Ide, 2004; Moraes *et al.,* in press), and consequently reduces encounters by predators (Freitas and Oliveira, 1992, 1996; Djemai *et al.,* 2004; Oliveira and Freitas, 2004). Recently, Walla and Greeney (in press) described the behavior of a nymphalid caterpillar which takes this behavior one step further, completely severing the petiole prior to feeding (Fig. 6b) and falling with the leaf to the ground below the plant, presumably avoiding encounters with enemies searching on (or using cues from) their food plant. Similarly, some caterpillars remain on the hostplant but sever leaves which they have previously fed upon, removing physical or chemical cues which may be used by enemies to locate them (Heinrich, 1979; Cornelius, 1993).

Shelters

Many species of caterpillars construct shelters in part or entirely out of hostplant tissue (Figs 6 f, 9c, f) (DeVries, 1987; Stehr, 1987; Scoble, 1995; Greeney and Jones 2003; Wagner, 2005). Shelter architecture varies from loosely curled leaves to intricately cut and folded patterns or even large, silken shelters built by many individuals and enveloping many hostplant leaves (Stamp 1982, 1984; Fitzgerald and Willer, 1983; Fitzgerald *et al.*, 1991; Fitzgerald and Clark, 1994; Fitzgerald 1995; Greeney, 2009; Ide, 2004; Weiss *et al.,* 2003). Although here we focus on shelter construction as a defensive tactic, shelters are also thought to serve a variety of additional functions such as preventing dislodgement and desiccation, or increasing host tissue quality (Damman, 1987; Hunter and Willmer, 1989; Sagers, 1992; Loeffler 1993, 1996; Larsson *et al.,* 1997). In fact, shelter-building lepidopterans are well known to suffer from heavier parasitism than non-shelter building caterpillars in the same community (Hawkins and Sheehan, 1994; Dyer and Gentry, 1999; Gentry and Dyer, 2002). Though it has been proposed that this is due to the enemy-free space provided for parasitoids by caterpillars protected from predators (Gentry and Dyer, 2002), very few empirical data are available to test these ideas and, as shelters appear to vary in their effectiveness at ameliorating predation of caterpillars by ants and wasps (Raveret-Richter, 1988; Eubanks *et al.,* 1997; Jones *et al.,* 2002; Weiss *et al.,* 2004; Abarca and Boege, 2011), the degree to which shelter-dwelling caterpillars provide safe hosts for parasitoids deserves further investigation. Furthermore, shelter-building is a time-consuming endeavor (Fitzgerald *et al.,* 1991; Berenbaum *et al.,* 1993, Fitzgerald and Clark, 1994;

Lind *et al.,* 2001) and the process of construction may make caterpillars more visible and susceptible to predation (Bergelson and Lawton, 1988; Loader and Damman, 1991). The physiological costs of shelter-building, however, are unclear (Damman, 1987; Hunter and Willmer, 1989; Loeffler, 1996; Lill *et al.,* 2007, Abarca and Boege, 2011). In summary, the complex interactions of top-down and bottom-up forces potentially shaping shelter construction and use, such as food plant species or tissue choice, development time and energy expenditure, and exposure to or protection from different natural enemies, provide a rich and intriguing field of investigation for students of life history evolution (Clancey and Price, 1987; Dussourd and Denno, 1994; Williams, 1999; Lill and Marquis, 2001; Kursar *et al.,* 2006; Dussourd, 2009; Greeney *et al.,* 2010d; Abarca and Boege, 2011).

While not strictly a "shelter," many species of caterpillars, particularly within the Nymphalidae, construct and rest on frass-chains (Figs 9a-b) (Muyshondt, 1973a, b, c, 1974, 1976; Casagrande and Mielke, 1985). These structures are built by silking frass pellets into a narrow chain protruding from the leaf (Aiello, 1984), and appear to deter crawling predators (Freitas, 1999; Freitas and Oliveira, 1992; Machado and Freitas, 2001). In a similar fashion, some caterpillars rest on the tips of plant tendrils or thin, isolated portions of leaf tissue that remain after feeding (Benson *et al.,* 1976; Bentley and Benson, 1988; Greeney *et al.,* 2010a). Many frass-chain builders do both, and leave a vein or narrow portion of the leaf intact while feeding, and then further extend this by silking frass onto its end (Freitas *et al.*, 2000; Greeney *et al.,* 2010a). Some caterpillars create strings of hanging frass near their resting or feeding location, and Aiello and Solis (2003) suggested that these provide "landmarks" within their complex shelter, facilitating the location of escape routes. Unlike the many shelter-dwellers which expel frass away from the shelter (see below), many species leave fecal pellets strewn throughout their webs or allow large quantities to build up within their shelters. As volatiles from caterpillar frass may act as chemical or visual cues to natural enemies (Agelopoulos *et al.,* 1995; Stamp and Wilkens, 1993; Ravert-Richter, 2000; Weiss 2003, 2006; Stireman *et al.,* 2006), resting on, or surrounding the body with feces seems counterintuitive, and there are likely a variety of explanations which have yet to be explored.

In contrast to the above, many species of Lepidoptera whose caterpillars build shelters also actively eject their frass from their shelters (Figs 9d-e) (Frohawk, 1892, 1913; Scoble, 1995; Caveney *et al.,* 1998; Weiss, 2003). Although few empirical studies have been performed, at least in the case of the hesperiid *Epargyreus clarus*, frass ejection behavior seems an effective defense against predation by wasps, which attacked significantly more caterpillars that were in close proximity to frass (Weiss, 2003). Similarly, the presence of frass on the ground below caterpillars of the hesperiid *Urbanus esmeraldus* induced ants to climb nearby stems, and expulsion of frass away from the base of the food plant presumably decreases caterpillar vulnerability to ant predation (Moraes *et al.,* in press).
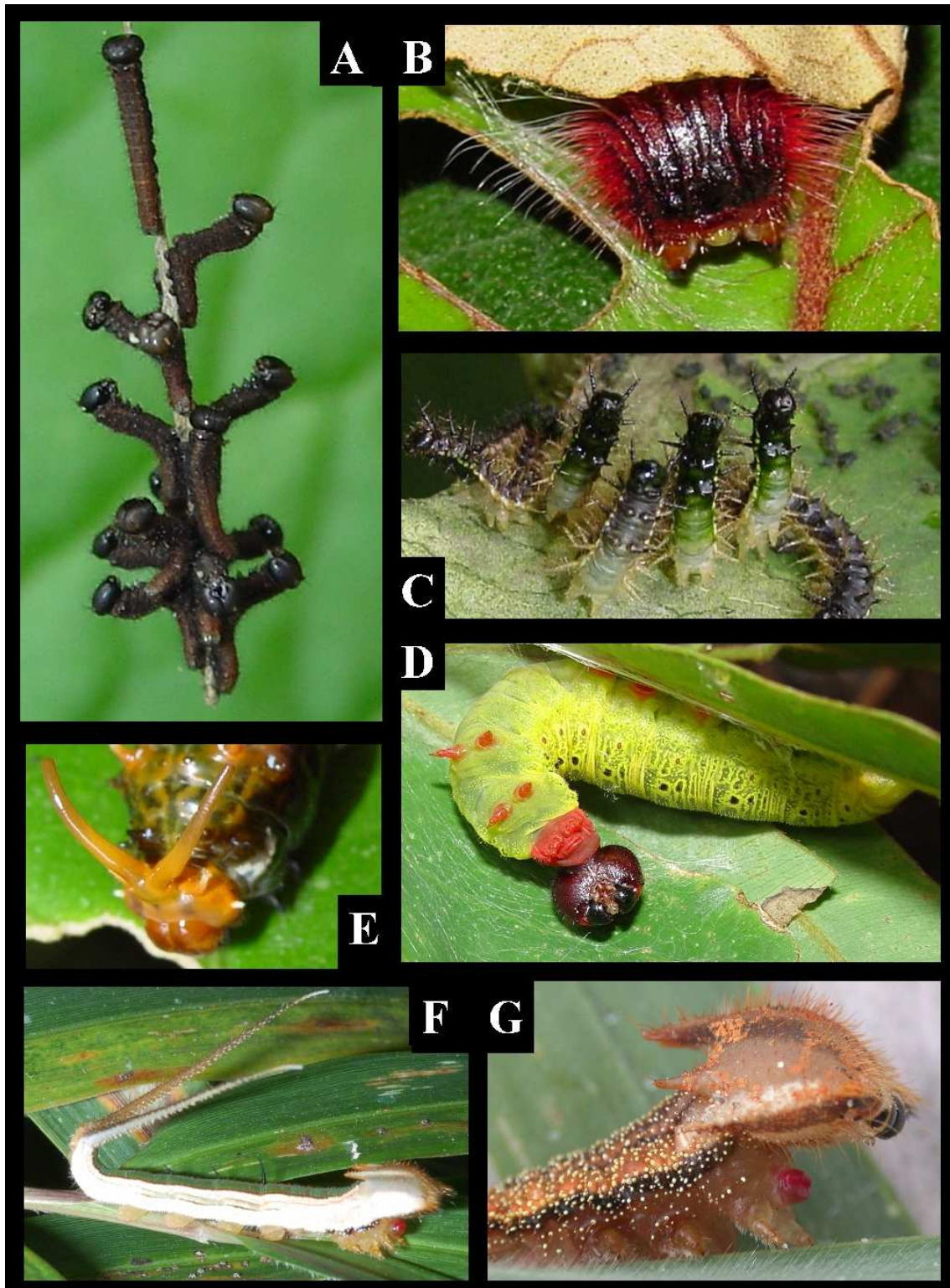
Fig. 8 Behavioral defenses of caterpillars upon encountering an enemy: a) *Daedalma* caterpillars (Nymphalidae) resting gregariously on a skeletonized leaf vein and rearing their heads, perhaps to increase the resemblance of the group to a larger, spine-defended caterpillar; b) *Pyrrhopyge* caterpillar (Hesperiidae) blocking the entrance to its shelter with its head and attempting to bite approaching enemies; c) Actinote caterpillars (Nymphalidae) feeding as a group, rearing and regurgitating simultaneously; d) *Epargyreus* caterpillar (Hesperiidae) rearing out of its shelter, exposing warningly colored legs and pro-thorax, while everting its cervical gland and attempting to bite; e) *Papilio* caterpillar (Papilionidae) secreting defensive chemicals through its osmeterium; f) *Eryphanis* caterpillar (Nymphalidae) rearing its head while everting its cervical gland and thrashing its long, spiny caudal tails over its back to knock away potential enemies; g) detail of *Eryphanis* caterpillar with cervical gland everted (reddish cylinder below head).

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Upon encounter with an enemy

Upon detection or contact with a potential enemy or after parasitoid oviposition, caterpillars show a wide array of behavioral defenses designed to aggressively repel or remove attackers (or parasitoid eggs/larvae), or to escape capture (Heads and Lawton, 1985; Cornell *et al.*, 1987; Gross, 1993; Gauld and Gaston, 1994; Godfray, 1994; Freitas and Oliveira, 1996; Gentry and Dyer, 2002; Oliveira and Freitas, 2004; Sendoya *et al.*, 2009). Aggressive behaviors include biting, thrashing and twisting, vomiting, and tail or scoli thrashing (Danks 1975; Myers and Smith, 1978; DeVries, 1987; Stamp and Bowers, 1990; Rhainds *et al.*, 2011; Greeney *et al.*, 2011). Evasive responses include thrashing or twisting, cessation of movement, and dropping from the foodplant (Dyer, 1995, 1997; Gentry and Dyer, 2002). Responses may also include the eversion of osmeteria or secretion of noxious chemicals (see *Eversible Glands*).

The function of these behaviors varies between specific prey-enemy interactions. For example, thrashing or rolling may function as an escape mechanisim, an aggressive counterattack, or both. With some enemies, violent movements may increase handling time and help to avoid contact with ovipositors or mandibles (Hopper, 1986; Schmidt, 1974). Particularly within shelter building species, the same movements may function to move the caterpillars into inaccessible areas of the shelter to avoid probing ovipositors or grasping structures (Salt, 1938; Powell, 1973). Against some parasitoids, which require immobility of the host for opposition (Tobias, 1967), violent movements may be especially effective, allowing caterpillars to escape before paralysis can set in (Gross and Price, 1988). Species with integumental spines or hairs may increase the effectiveness of these defenses by waving them about and striking potential enemies.

Aggressive behaviors

Biting

The powerful mandibles (Figs 8b, d) of many caterpillars can be effective weapons against small enemies, even resulting in the severing of enemy appendages (Salt, 1938; Brubaker, 1968; Herrebout, 1969; Danks, 1975; Martin *et al.,* 1989; Allen, 1990; Potting *et al.,* 1999). Many caterpillars combine a head-flick with biting (Danks, 1975; Gross, 1993). Hesperiid caterpillars, while resting in their shelters, will often block the entrance with their head capsule, attempting to bite any object which approaches (Fig. 8b).

Regurgitating

When handled, or when contacted by a potential enemy, many species of lepidopteran larvae regurgitate a drop of fluid (Fig. 8c) (Common and Bellas, 1977; Peterson *et al.,* 1987; Smedley *et al.,* 1993; Rhainds *et al.,* 2011). Although the toxic properties of regurgitates and their degree of effectiveness against enemies is largely unexplored for most species, most or all have repellent or deleterious effects on potential attackers, and are likely toxic to some degree (Hays and Vinson, 1971; Eisner *et al.*, 1980; Blum *et al.*, 1981; Brower 1984, Stamp, 1984, Peterson *et al.*, 1987; Freitas and Oliveira, 1992; Salazar and Whitman, 2001; Gentry and Dyer 2002; Oliveira and Freitas, 2004). In at least one case, larval regurgitate was used to dislodge parasitoid eggs attached to the exoskeleton (Brubaker, 1968).

Eversible glands

While actually a chemical defense, the defensive response of some papilionid caterpillars is eversion of a forked, tube-like gland on the prothorax (osmeterium) (Fig. 8e) (Schulze, 1911; Scoble, 1995). Secretory cells on this gland produce odiferous chemical repellents (Eisner and Meinwald, 1969), the smell of which has been likened by some authors to "fresh vomit" (Wagner, 2005), though its effect on other natural enemies has been little investigated. Similarly, the caterpillars of many families possess an eversible secretory gland, or cervical gland, (usually ventral) between the head and prothorax (Figs 8d, f-g) (Scoble, 1995; DeVries 1997). We observe these glands in many of the species we have studied throughout the Americas (Greeney and Warren, 2009; Greeney *et al.*, 2009, 2011), though few studies have investigated their function or effectiveness against enemies (Weatherstone *et al.,* 1986; Marti and Rogers, 1988).

Evasive behaviors

Thrashing and twisting

Anyone who has collected caterpillars in the field is familiar with this behavior, though its effectiveness is rarely investigated (Dyer and Gentry, 1999; Gentry and Dyer, 2002). The severity and manner of violent movement varies between species, with some violently curling and uncurling, rapidly twisting, or even undulating their entire body in a wave-like motion which causes the caterpillar to flip about the substrate (Wagner, 2005). Other species may lift only the anterior or posterior segments and thrash the elevated portion back and forth, using either head scoli or caudal tails to strike or dislodge enemies (Fig. 8f) (DeVries, 1987; Greeney and Gerardo, 2001, Greeney *et al.*, 2009, 2010a, 2011). In some cases thrashing, though likely a predominantly evasive response, may function to aggressively dislodge or injure attackers (Myers and Smith, 1978; Stamp, 1982; Heinz and Parella, 1989), and the sudden spasmodic movements of silk moth caterpillars (Saturniidae), often serve to bring their urticating spines into contact with the enemy before they drop from the hostplant (see *Dropping*).

A less dramatic, but similar, evasive maneuver is "head flicking" whereby caterpillars twitch their heads in response to potentially dangerous stimuli (Myers and Campbell, 1976; Myers and Smith, 1978). Such movements presumably deter oviposition by parasitoids, or may startle and confuse potential predators. Some species of shelter-dwelling hesperiid caterpillars rapidly flick their head up and down, striking the upper and lower surfaces of their shelters to produce a rattling
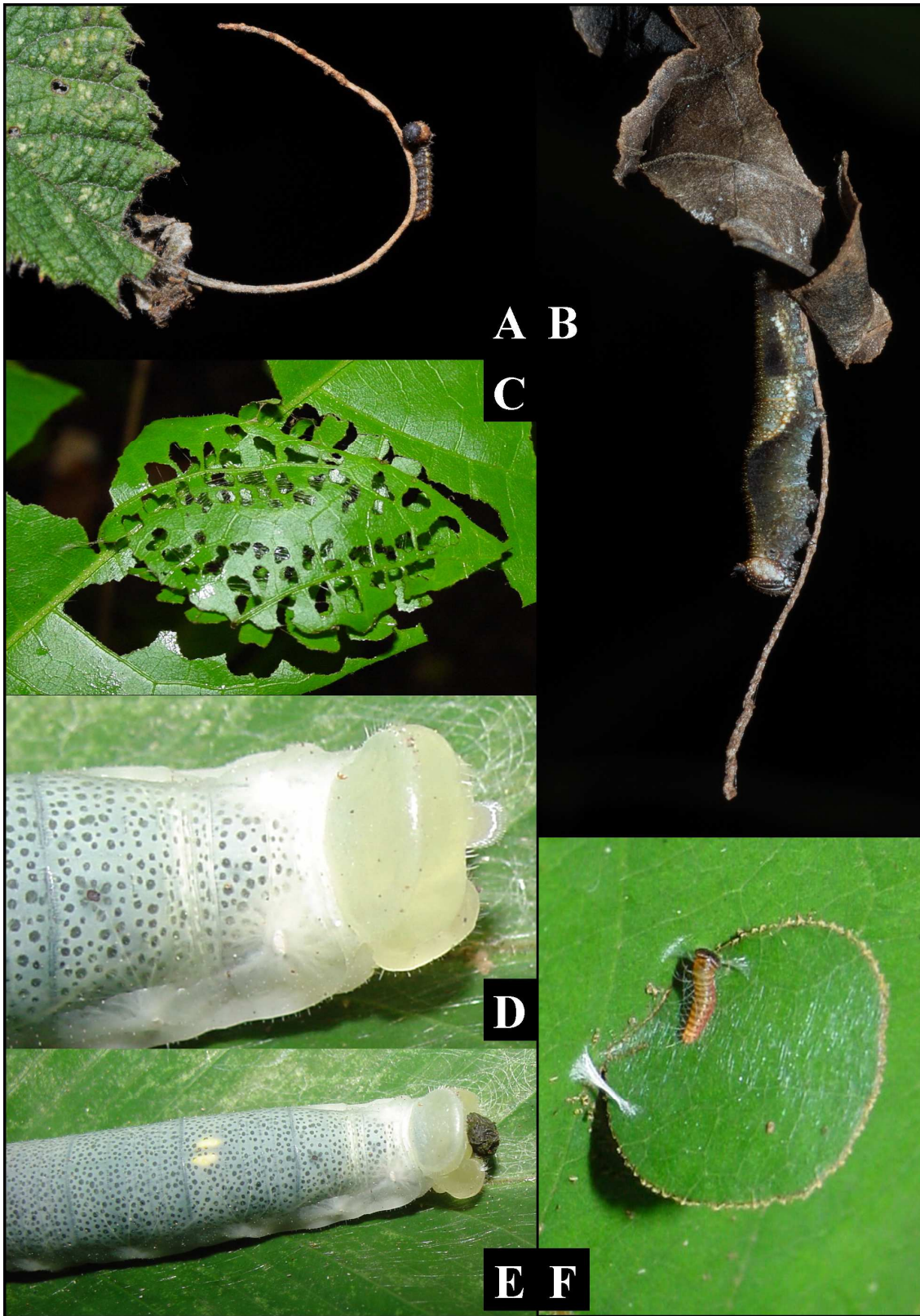
Fig. 9 Engineered caterpillar refuges and associated behaviors: a) young *Adelpha* caterpillar (Nymphalidae) resting on a "frass-chain" built by extending a skeletonized leaf vein with silk and fecal pellets; b) *Memphis* caterpillar (Nymphalidae) resting on a "frass-chain" and cryptically patterned to match damaged leaf tissue created by its feeding near the base of the chain; c) complex caterpillar leaf shelter (Hesperiidae) built by cutting, perforating, and tying leaves together with silk; d) detail of terminal segments of *Saliana* caterpillar (Hesperiidae) shown just after expelling a frass pellet away from its shelter and showing the "anal comb" which facilitates this process; e) same caterpillar as in previous, just prior to expelling frass; f) *Myscelus* caterpillar (Hesperiidae) in the process of using silk ties to manipulate an excised portion of hostplant leaf into a shelter.

sound, while others thrash their head back and forth, scraping their mandibles across the leaf surface to create a rasping sound (pers. observ.). In these cases, as the caterpillar is hidden from view while doing this, the noises produced may function to startle potential predators or perhaps cause sound or vibrational interference for enemies using substrate-borne vibrations for locating caterpillars. Though some sphingid caterpillars produce hissing or squeaking noises when disturbed (Wagner, 2005), apart from the substrate-borne calls of ant-attended caterpillars (see *Associations*), sound production by caterpillars is relatively unstudied.

Dropping

For externally feeding species, violent movements such as those described above frequently lead to dropping from the plant, quickly removing them from the presence of the enemy (Powell, 1973; Gross, 1993; Castellanos *et al.,* 2011). Dropping is likely an effective defense, whether accomplished by simply releasing the substrate or through thrashing, and was suggested by Gross (1993) to be the most common defense found across insect taxa, and our personal observations in the field suggest this claim may be true for caterpillars as well. In Lepidoptera, dropping is frequently accompanied by the spinning of a silk "life-line" which allows the caterpillar to later climb back up to the host plant (Sugiura and Yamazaki, 2006). In response to dropping, at least some parasitoids have evolved a remarkable countermeasure, whereby they find the silk support line and glide gracefully down it to the doomed caterpillar (Yeargan and Braman, 1986, 1989).

In contrast to the active defenses described above, some caterpillars react to contact by remaining motionless and retracting any exposed appendages (Benson, 1950; Loan, 1964; Herrebout, 1969; DeVries, 1997), a behavior which may increase susceptibility to parasitism but which may nonetheless be selected for by visually oriented predators (Rotheray, 1981), and vulnerability may also be reduced in species with protective morphologies (see *Morphological Defenses*).

Future research on caterpillar defenses

Caterpillar defenses include chemical, physiological, morphological, and behavioral characters that function against a variety of natural enemies (also reviewed by Eisner, 1970; Edmunds, 1974; Godfray, 1994; Dyer 1995, Gentry and Dyer, 2002; Beckage 2008). In this review, we were able to only touch upon a few of the large number of strategies used by larval Lepidoptera. It is likely that there are thousands of undocumented defensive strategies and that most known strategies are used by many more species than has been reported. Wagner (2005) aptly describes the abundance and redundancy of defenses by observing that most species "stack strategy upon strategy, ruse upon ruse, in order to win the battle between predator and prey." In fact, based on the pervasiveness of such statements in the literature, and our own cumulative field experience of over half a century,

we venture to say that all caterpillars have multiple tricks up their sleeve. These may be applied in concert, or their use may vary ontogenetically, temporally, or in response to different enemies. Thus, while the literature on caterpillar defenses is extensive, the number of unstudied species, defenses, and interactions ensures that sweeping ecological and evolutionary generalizations made today are, at best, premature. Although the gaps are many, below we suggest a few areas of investigation which might be particularly rewarding.

There are several problems that currently present difficulties for synthesis: 1) Defenses are typically thought to be equally effective against the entire suite of natural enemies (or the differences in defensive efficacies for various mechanisms are ignored), 2) The utility of any category of defense against parasitoids and pathogens has scarcely been tested in natural systems (Price *et al.,* 1980; Gauld and Gaston, 1994), and 3) gross generalizations about defenses persist (e.g., aposematic coloration is always assumed to be indicative of toxicity or invulnerability to predation; Bowers, 1993; Dyer, 1995). These problems have been partly addressed by studies examining multiple species (Dyer 1995, 1997; Gentry and Dyer, 2002; Smilanich *et al.,* 2009a, b), but even these barely touch upon the sample of interactions needed to address broader questions.

To address these problems and gaps in are knowledge of the ecology and evolution of caterpillar defenses, there are several genres of hypotheses about defenses that can help guide research in ecology and evolution, including: 1) hypotheses about the effectiveness and the evolution of a suite of defenses against specific predatory guilds or against single species, 2) hypotheses about effectiveness and the evolution of specific defenses against a suite of predatory guilds or against multiple species, 3) hypotheses about the genetics underlying specific defenses or suites of defenses, 4) hypotheses about the effects of variation in caterpillar defenses on community dynamics or ecosystem processes, and 5) hypotheses about the role of multitrophic interactions, caterpillar defenses, and plant chemistry in the evolution of diet breadth in the Lepidoptera.

These problems have been acknowledged by various authors and our suggested hypotheses have been tested by some studies, but it is surprising that there have been few attempts to characterize important components of lepidopteran larval defenses, either by conducting multiple-species experiments or through literature reviews (Witz, 1990; Dyer and Floyd 1993; Gross, 1993; Godfray, 1994; Dyer, 1995, 1997; Gentry and Dyer, 2002; Smilanich *et al.,* 2009a, Remmel *et al.,* 2011; Rhainds *et al.,* 2011). While multiple-species approaches are generally not as thorough as experiments on focal taxa, they allow for different generalizations on insect defenses which can ultimately provide a framework for both basic and applied research questions with specific systems. For example, Bernays and Cornelius (1989) demonstrated that a number of species of leaf rollers were extremely palatable to ants; their

generalization that trade-offs could exist between chemical defense and concealment from predation provides guidelines for more focused studies on sister taxa with and without these defenses or for molecular ecology approaches to understanding variation in chemical defense within and between clades.

We conclude by reiterating the obvious: the basic natural history of most caterpillars is still unknown, especially in the tropics (DeVries, 1987, 1997; Hespenheide, 2011). Thus, with ever-increasing rates of habitat loss (e.g., Henderson *et al.*, 1991) and the current academic devaluation of descriptive taxonomic and natural history research (Greene, 1994; Noss, 1996; Futuyma, 1998; Dayton, 2003), many fascinating interactions between caterpillars and their enemies will forever remain unknown. If we hope to address some of the ecological and evolutionary questions mentioned in the preceding paragraphs, future research on caterpillars must include additional documentation of life-history traits such as behavior, diet, morphology, and defense strategies. The deflowering of our world (Janzen, 1974) continues, and in the trophic collapse that follows the loss of plant diversity, we are also losing caterpillars and their enemies, and all of the beautiful interactions that unite them.

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