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Thomas J. Hossie[a], Thomas N. Sherratt[b], Daniel H. Janzen[c] & Winnie Hallwachs[c]

[a] Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, ON, Canada

[b] Department of Biology, Carleton University, Ottawa, ON, Canada

[c] Department of Biology, University of Pennsylvania, Philadelphia, PA, USA

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An eyespot that "blinks": an open and shut case of eye mimicry in *Eumorpha* caterpillars (Lepidoptera: Sphingidae)

Thomas J. Hossie[a]*, Thomas N. Sherratt[b], Daniel H. Janzen[c] and Winnie Hallwachs[c]

[a]*Ottawa-Carleton Institute of Biology, Carleton University, Ottawa, ON, Canada;* [b]*Department of Biology, Carleton University, Ottawa, ON, Canada;* [c]*Department of Biology, University of Pennsylvania, Philadelphia, PA, USA*

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We describe the final instars of two tropical Sphingidae caterpillars – *Eumorpha phorbas* and *Eumorpha labruscae* – from Area de Conservacion Guanacaste, northwestern Costa Rica, whose anal horn has become a posterior eyespot structure capable of rapid palpitation. When approached or harassed, the caterpillars palpitate this eyespot and produce the effect of a blinking vertebrate eye. We propose that this "blinking" is an extension of eye mimicry or at least draws attention to the eyespot, functioning to startle or intimidate would-be predators. As snakes lack eyelids and do not blink, this suggests that the blinking eye represents a more generalized (or possibly mammalian) eye. Eyespot "blinking" is probably controlled by the same musculature used to wave the anal horn in earlier instars. The extent to which this eyespot is perceived as a blinking eye, and the degree of protection from the caterpillars' suite of potential predators, remain to be discovered.

Keywords: blink; blinking eyespot; eye mimicry; anti-predator; mimic; Area de Conservacion Guanacaste; Costa Rica

Introduction

Eyespots are circular or elliptical markings that occur on the bodies of many animals. To varying degrees, these markings resemble either a single or pair of vertebrate eyes (reviewed by Stevens 2005; Kodandaramaiah 2011). The function typically ascribed to eyespots is protection from, or during, a predatory attack (Edmunds 1974; Ruxton et al. 2004; Janzen et al. 2010), although other (or additional) processes can also generate and maintain similar markings including sexual selection when the eyespots are on adults (e.g. Breuker and Brakefield 2002; Oliver et al. 2009). The eyespots of many animals are kept concealed, then revealed suddenly when the prey is approached by an another animal that is perceived as a potential threat, possibly functioning to startle, confuse, frighten (Janzen et al. 2010), threaten, or otherwise intimidate a predator. Indeed, the sudden appearance of eyespots probably augments their protective value (Vallin et al. 2005, 2006). In contrast, (and occasionally in concert), some species possess constantly displayed eyespots that also appear to prevent attack, possibly through predator fright or intimidation (Karplus and Algom 1981; Kodandaramaiah et al. 2009; Janzen et al. 2010).

*Corresponding author. Email: thomashossie@cmail.carleton.ca

Naturalists have long recognized that a variety of Lepidoptera caterpillars possess eyespots, and that some of these species possess traits that resemble features of snakes, lizards, mammals and birds (Bates 1862; Weismann 1882; Poulton 1890; Janzen et al. 2010). Such resemblance may be generated morphologically or behaviourally by various traits acting independently or synergistically to convey the impression of a snake or other predatory vertebrate. Henry Walter Bates described his encounter with one such caterpillar as "The most extraordinary instance of imitation I ever met with . . ." (Bates 1862, p.509). As naturalists continue to discover additional species, and describe previously undocumented larval stages of known species, it has become apparent that eyespots are frequent among tropical caterpillars. This is illustrated graphically in Janzen et al. (2010), as well as in images in the Area de Conservacion Guanacaste (ACG) caterpillar database (Janzen and Hallwachs 2012).

It seems to be generally accepted that caterpillar eyespots mimic the eyes of a snake or other threatening vertebrate (e.g. Edmunds 1974; Pough 1988; Lederhouse 1990; Janzen et al. 2010), thereby causing a predator to flee or hesitate in a strike, giving the caterpillar an escape opportunity (e.g. by dropping off the host plant or by simply causing the potential predator to not return to the microlocation of the caterpillar to verify its initial reaction; Janzen et al. 2010). The natural history of tropical birds and caterpillars argues strongly that the plethora of caterpillars with eyespots is the product of natural selection imposed by a set of avian predators, encompassing a variety of species, that innately respond to eye-like or face-like stimuli by adopting a range of risk mitigation measures including hesitation and abruptly fleeing (Janzen et al. 2010). The ubiquitous danger associated with close proximity to a predator's eyes (i.e. regardless of predator species) has probably favoured the generalized avoidance of eye-like features by birds (Janzen et al. 2010). That the markings on a given caterpillar do not seem to mimic any specific model predator (Rothschild 1984; Pough 1988; Janzen et al. 2010), in contrast to the frequent case with Batesian and Müllerian wing-pattern mimicry, further supports this idea.

Many of the most impressive, and perhaps best known, eyespot caterpillars are members of the family Sphingidae (Weismann 1882; Poulton 1890; Edmunds 1974; Janzen et al. 2010). Caterpillars from this group can be as long as 10 cm, and 2 cm in diameter, and possess a distinctive mid-dorsal horn on the posterior end of their body (segment A8). This horn has sometimes been modified to be an eyespot or hardened button-like structure, especially in the caterpillar's ultimate instar (Heinrich 1979; Wagner 2005).

As part of ongoing research in Costa Rica we closely examined a *Eumorpha phorbas* (Cramer 1775) caterpillar (Sphingidae: Macroglossinae). In the ultimate instar this caterpillar's caudal horn has been reduced to a single eyespot capable of movement such that it appears to "blink" when the caterpillar is approached or harassed. That is, the fleshy exoskeleton around the posterior eye-like spot contracts then is quickly released creating what looks like a blinking eye. *Eumorpha labruscae* (Linnaeus 1758) is a closely related species collected previously in the same and adjacent forests in ACG (see below), and is similarly capable of "blinking" the posterior eyespot during the final instar (DHJ, personal observation). What follows is a description of the *E. phorbas* and *E. labruscae* caterpillars, our thoughts on the function of a "blinking" eyespot, and the implications of these observations for eyespot function. Although this is the first published description of *E. phorbas* caterpillars (but see multiple images at Janzen and Hallwachs 2012), the specimen descriptions provided here are focused on describing features linked to the caterpillars' anti-predator strategy rather than being an attempt to describe taxonomically relevant features.

Material and methods

The *E. phorbas* caterpillar was collected and reared within Sector San Cristobal by parataxonomists based at the rain forest Estacion San Gerardo (10.8809 N, 85.3887 W, elev. 575 m) of ACG, Costa Rica, as part of an ongoing long-term caterpillar inventory (Janzen et al. 2005; Smith et al. 2008; Janzen and Hallwachs 2011; Janzen and Hallwachs 2012). The specimen is indexed within the ACG caterpillar database (11-SRNP-2980; Janzen and Hallwachs 2012). As is standard protocol for rearing caterpillars for the project, the caterpillar was maintained in an inflated plastic bag along with fresh foliage of its host plant, in this case *Sarcopera sessiliflora* (Marcgraviaceae), a canopy-level large woody vine (that was rendered accessible by the 25-m tall tree being uprooted). The description of the *E. labruscae* caterpillar is based on the following caterpillars collected within the dry forest Sector Santa Rosa of ACG and indexed in the same database (but this species also occurs in ACG rain forest): 78-SRNP-35, 84-SRNP-1316, 87-SRNP-560, 92-SRNP-1514.

Preliminary observation had revealed that the ultimate instar of the *E. phorbas* caterpillar "blinked" its posterior eyespot in response to tactile stimulus and to motion (see video in the online supplemental material). Here, a "blink" is characterized by a quick localized depression of the posterior section of the eyespot, resulting in a greater portion of the black "button" being revealed. To gain further insight into how this caterpillar might respond to an attacker, we carefully removed the caterpillar from its rearing bag and after approximately 1 minute of acclimation we prodded the specimen three times on the anterior segments; each prod was separated by ~ 5–6 s. The caterpillar was then placed back into its rearing bag with trimmings of its host plant. After 1 h, the specimen was again removed and similarly prodded on the posterior end. Notes on the behaviour of *E. labruscae* are based on observations of specimens made previously by DHJ and WH in the course of the ongoing inventory of the ACG between 1978 and 1992 (see dates in rearing records at http://janzen.sas.upenn.edu).

Results

Description of **Eumorpha phorbas** *caterpillar*

Penultimate instar

The body is largely a uniform green colour that (to human eyes) qualitatively matches the foliage of its host plant. The lateral sides of the caterpillar are further textured with small irregularly shaped blue-white dashes, nearly all of which occur above the spiracles (see images of 11-SRNP-2980 at http://janzen.sas.upenn.edu). The contrast of these markings is enhanced by the dark charcoal-coloured edging that surrounds each marking, and they appear similar to small spots of insect damage on a leaf. One pair of such markings is particularly distinct and occurs on each side of the first abdominal segment. A red anal horn protrudes from the posterior margin of a single dorsal eyespot on the A8 segment; this eyespot is composed of a dark oval-shaped outer ring surrounding a single dark central spot. Both the inner and outer margins of the outer ring are highlighted by a lighter green, and the area between the ring and the central

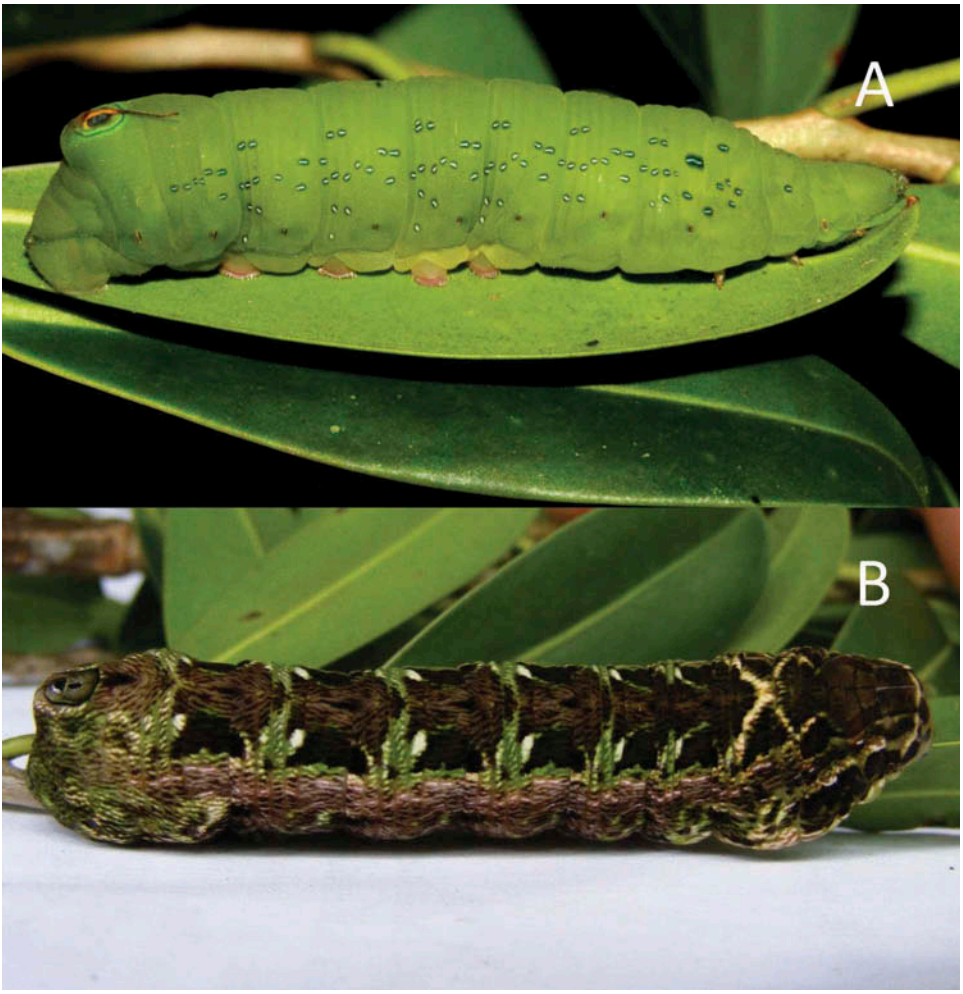

Figure 1. Lateral view of *Eumorpha phorbas* caterpillars. (A) During the penultimate instar; (B) during the ultimate instar.

spot is the same green as the body, having transitioned from the black-brown colour of the central spot (Figure 1A). This caterpillar in nature perches on the leaves themselves when diurnally resting (Elda Araya, personal observation).

Ultimate instar

The specimen was 60 mm in length and 12 mm in diameter at the middle of the body. When undisturbed the caterpillar appears to human eyes especially cryptic against a naturally heterogeneous brown bark-coloured background. We assume that during the daytime, this caterpillar rests on the tree bark under the epiphytic vine-like food plant, as is the case with other ACG caterpillars with this colour pattern. Dorsally, the caterpillar's colouration was dominated by light and dark brown patterning (Figure 1B). The first abdominal segment possessed a pale yellow cross dorsally (Figure 2A),

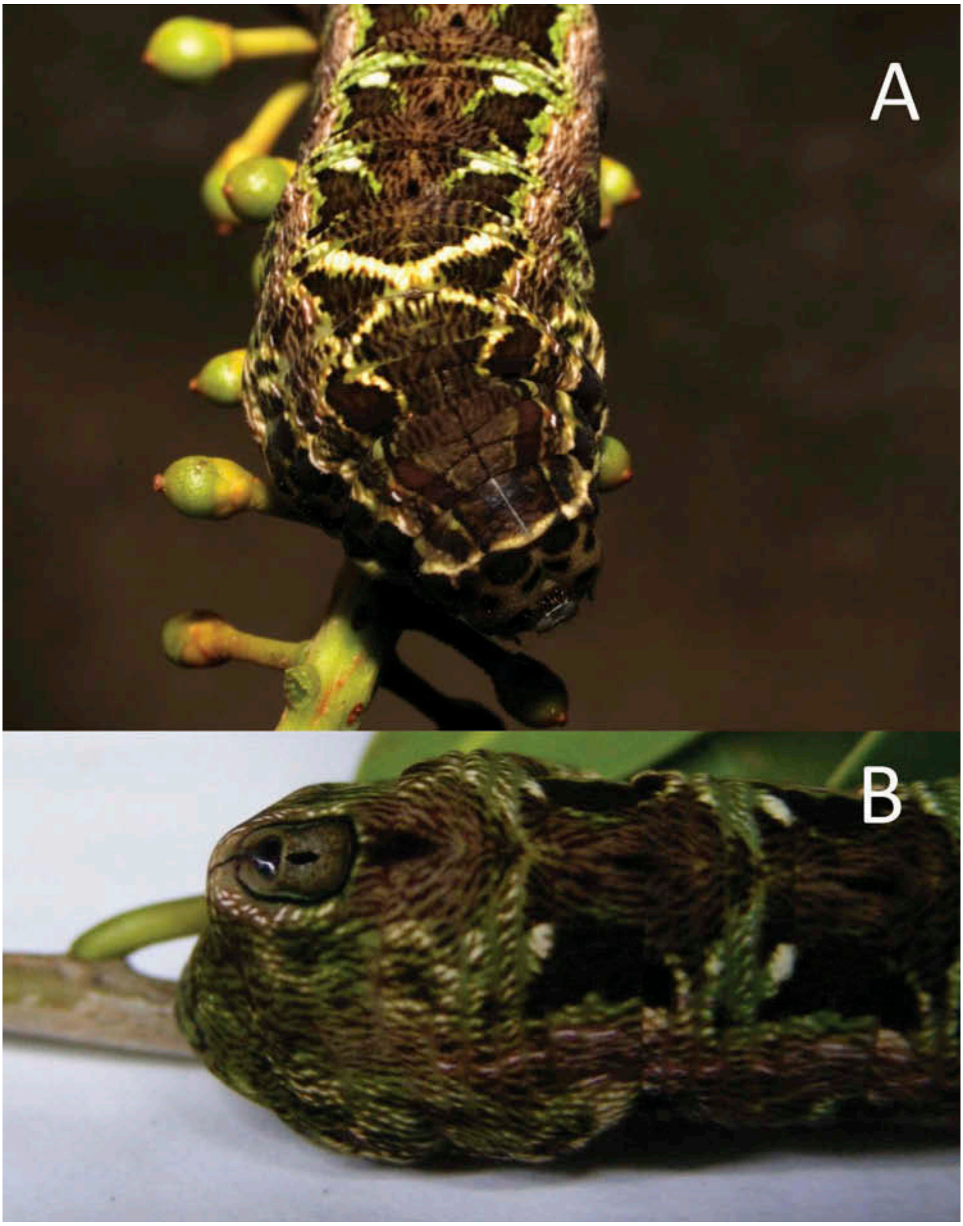

Figure 2. Close-up views of *Eumorpha phorbas* caterpillars. (A) Dorsal view of the anterior body segments; (B) dorsolateral view of posterior eyespot that replaces the anal horn present in the penultimate instar.

whereas abdominal segments possessed textured green stripes extending towards the dorsal midline (Figure 1B). A pair of small cream-coloured spots (1.6 × 0.7 mm) appeared on most of the abdominal body sections, located dorsolaterally adjacent to the green markings (Figure 1B). Additional textured green markings bordered a reasonably sharp contrast between the caterpillar's dorsal and lateral colouration, where a much lighter brown patterning, with flashes of light green and dark brown, predominate on the lateral side of the abdominal segments (Figure 1B). When this colour morph pulls its head into its thorax and expands the thorax, the frontal view is that of an arboreal viper such as the dark morph of *Bothrops schlegeli* (see images DHJ493714 through DHJ493719 for voucher code 11-SRNP-2980 at Janzen and Hallwachs 2012).

However, an equally striking feature is the posterior eyespot of the ultimate instar. The characteristic anal horn of a sphingid caterpillar has been modified into a shiny black, hardened "button" partially covered by fleshy tissue. This "button" is located within an oval-shaped marking (3 × 3.5 mm) surrounded by a thin black border and otherwise filled with a dark cream colour (Figure 2B). The eyespot also contains an additional small, black, oval-shaped marking (0.8 × 0.4 mm) at its centre (Figure 2B).

Behaviour

When initially disturbed, the caterpillar pulls its head into its thorax, expanding the thorax and rendering it much like the head of an arboreal cryptically coloured viper, with somewhat developed eyespots on the thorax (see above). When in this defensive posture both terminal ends are wider than the mid-body sections, the anterior reaching a diameter of 14 mm and the posterior end widening to a diameter of 13 mm. The caterpillar thrashes its anterior body laterally in response to the first anterior prod, and "blinks" in response to all three anterior prods (see video in ESM 2). Similarly, the caterpillar flicks its posterior body in response to the first posterior prod, and "blinks" in response to all three prods (see video in ESM 3). Notably, "blinks" were more frequent and rapid in response to the posterior prods than to the anterior prods (14 versus 6 "blinks" in total; see ESM 2 and 3).

Description of* Eumorpha labruscae *caterpillar

Penultimate instar

In contrast to the penultimate instar of *E. phorbas*, the body of the *E. labruscae* penultimate instar is largely a textured brown colour with green pear-shaped ovals on the flanks of the abdominal segments A2–A7 and distinct eyespots on the first abdominal segment (A1, Figure 3A). The dorsal body colour is, on average, a darker brown than the flanks and the sides of the thoracic segments are coloured light yellow-brown. The combination of these colours renders the caterpillar cryptic when on tree bark, where it rests when not feeding on the foliage of its vine-like food plant. The eyespots on the A1 segment occur just above the spiracle and are composed of a black ring surrounded by a highly contrasting light yellow ring, with a dark white-speckled centre. In addition, there is a distinct white spot within the black eyespot just above, and anterior to, the centre. The long red anal horn extends upwards from the posterior margin of a black spot on the A8 segment (Figure 3A). This spot is surrounded by a highly contrasting orange ring, which is in turn is bordered by a dark brown ring (Figure 3A).

Ultimate instar

About 80 mm long and with a similar colour pattern to that of *E. phorbas*. The eyespots on segment A1 are present but less distinctive in comparison with the

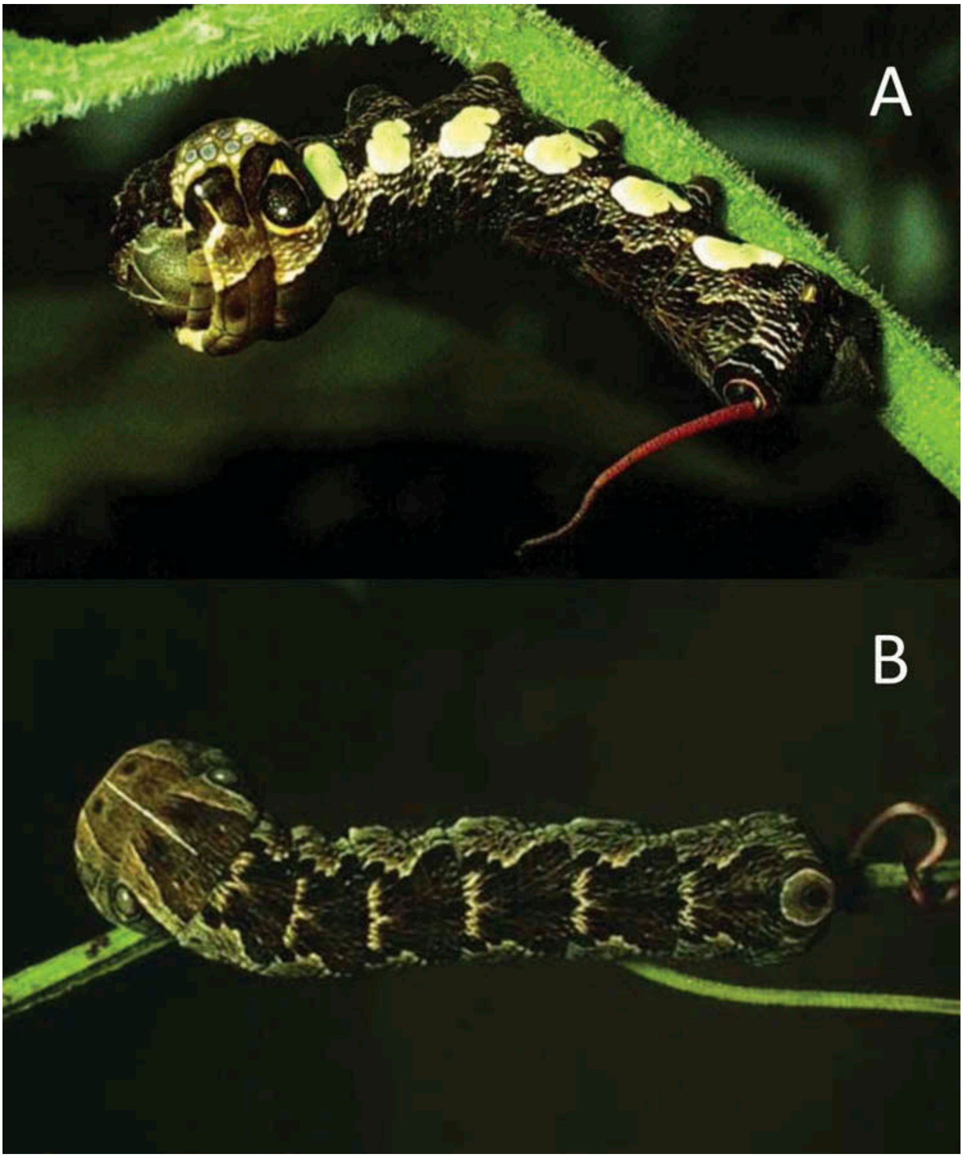

Figure 3. *Eumorpha labruscae* caterpillars. (A) Lateral view of the penultimate instar; (B) dorsal view of the ultimate instar.

penultimate instar (Figure 3B). The distinct black ring remains, inside which is a grey-brown base colour. The white spot remains within the centre of each eyespot and is itself surrounded by a fine black ring (Figure 4A). An additional white spot may occur within the eyespot (e.g. images of 92-SRNP-1514 at Janzen and Hallwachs 2012). The eyespots contain several smaller oval markings, which also occur on segment A1 outside the eyespot (Figure 4A). The dorsal colour of abdominal segments A2–A7 is similar to that of *E. phorbas*, but *E. labruscae* is distinct in having short light yellow-brown streaks that extend from the anterior margin of each segment (Figure 3B). A pair of small faint spots can be seen on the dorsal side of segments

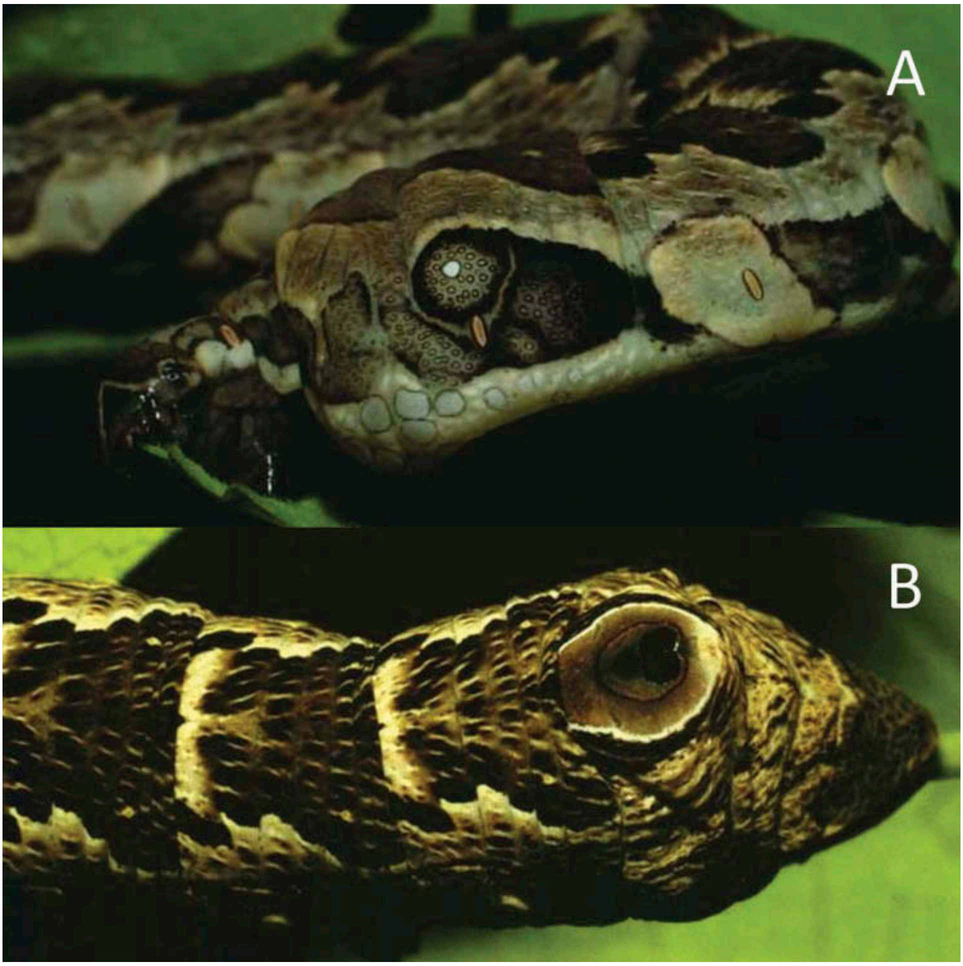

Figure 4. Close-up views of *Eumorpha labruscae* caterpillars. (A) Lateral view of the anterior body segments; (B) dorsal view of posterior eyespot that replaces the anal horn present in the penultimate instar.

A1–A7, towards the posterior side of each segment. The anal horn on segment A8 is reduced to a hardened "button" and is similar to that of the ultimate instar of *E. phorbas* (Figure 4B). It differs in being more circular, having an outer pale yellow ring, and containing an additional internal ring that surrounds the hardened button (Figure 4B).

Behaviour

When harassed both the ultimate and penultimate instars of this caterpillar have an effective snake-like display during which they telescopically pull the head into the thoracic segments, which in turn inflates the caterpillar's anterior segments. This behaviour creates a shape similar to that of a snake's head and increases the conspicuousness of the pair of eyespots on the first anterior body segment. Penultimate instar caterpillars flick the red anal horn when harassed, whereas the ultimate instar "blinks" the posterior eyespot.

Discussion

We have described the *E. phorbas* and *E. labruscae* caterpillars which, during the ultimate instar, respond to close approach and tactile stimulation by contracting a localized portion of the posterior eyespot; to human observers such palpitation produces the effect of a blinking eye. Eyespot "blinking" involves a constantly displayed eyespot that appears to close and open and is thereby distinct from well-known cases where concealed eyespots are suddenly revealed upon attack (e.g. the eye spots on the wings of many Lepidoptera). Although, suddenly revealing otherwise hidden eyespots may produce a greater startle effect, a "blinking" eyespot probably mimics a real vertebrate eye more closely. When approached or harassed, the described *Eumorpha* caterpillars also inflate their thoracic segments to form a diamond shape similar to the head shape of dangerous, co-occurring snakes. These traits may work independently or in combination with eyespots to deter predators from attacking once they have detected the caterpillar and the facultative expression of these traits probably minimizes any costs associated with signal expression (e.g. via reduced crypsis, energetic expenditure or lost foraging opportunity).

The rear eyespot is only contracted upon close approach or harassment, suggesting that "blinks" are directed towards a perceived threat and we suggest that this "blinking" is an extension of eye mimicry. Quickly concealing/revealing the dark central "pupil" of an eyespot upon harassment ought to make a more convincing "eye". Furthermore, the response of a small insect-eating bird that finds itself very close to what appears to be a blinking eye would almost certainly be to distance itself from that object (Janzen et al. 2010). As such, it seems to us that the "blinking" behaviour described here probably protects the caterpillar from attackers by mimicking a vertebrate eye.

Both *E. labruscae* and *E. phorbas* caterpillars possess a long red anal horn during the penultimate and pre-penultimate instars, attached just posterior to the site of the hardened button (Figures 1A and 3A). When disturbed during the pre-penultimate instar, *E. labruscae* (and perhaps also *E. phorbas*) caterpillars rapidly beat or whip this long anal horn (Moss 1912). Whipping the anal horn may fend off parasites (Moss 1920), intimidate attackers by resembling a snake tongue (Curio 1965), or function as part of a generalized startle display. The ability to "blink" the rear eyespot during the ultimate instar is probably produced by the same musculature used formerly for whipping the anal horn in the intermediate instars. As the observed specimens were part of the ongoing ACG inventory project, which involves rearing to adulthood, lethal sampling and dissection were not possible.

Other published accounts of a "blinking" eyespot include Moss (1912) who describes the ultimate instar of *Pholus labruscae* (now: *Eumorpha labruscae labruscae*, the same species as observed in ACG) collected in Peru, Hayward (1929) who described an ultimate instar *P. labruscae* (*E. labruscae*) caterpillar from Villa Ana, Argentina, and Curio (1965) who described an ultimate instar *P. labruscae* (now: *E. labruscae yupanquii*) collected on Isla Santa Cruz (Indefatigable) in the Galápagos. All three descriptions emphasize the snake-like appearance of the anterior segments, as well as the posterior spot that oscillates with muscular action. Notably, Moss (1912) suggests that both ends of the caterpillar resemble the head of a snake, and Hayward (1929) observed that the caterpillar "... is reminiscent of certain poisonous snakes, and the natives refuse to touch it".

Interestingly, the posterior spot on the ultimate instar of *E. labruscae* was described by Moss (1912) as "... capable of rapid palpitation, catching the light and flashing like a serpent's eye when molested". However, although snakes are, almost exclusively, cited as the model for caterpillars with eyespots (e.g. Pough 1988; Lederhouse 1990), snakes have transparent eye scales ("brilles") in place of eyelids and therefore do not blink or flash (Mead 1976). It is unclear whether Moss's use of "flashing" refers to the blinking action of the spot, or simply that the white spot appears as though there is light reflected from a black spot as it would a snake's eye. We emphasize that for small insect-eating birds the ubiquitous threat associated with proximity to an eye suggests that eyespots need not mimic the eye of any specific model species to provide some degree of protection (Janzen et al. 2010). A fear response would be similarly generated by the fear of other co-occurring lizards, mammals and birds that do blink and also pose a considerable threat to insect-eating birds. As the anterior end of *E. labruscae* and *E. phorbas* possesses features that mimic a snake, and the "blinking" spot on the posterior end mimics the eye of a different enemy (suggested also by Curio 1965), such a feature probably extends the range of predators that can be deterred from attack upon detecting caterpillars.

To date, *E. phorbas* and *E. labruscae* are the only species known to be capable of "blinking" an eyespot, and are the only *Eumorpha* species known to have evolved this specialized posterior eyespot. It remains to be seen whether *E. capronnieri*, a closely related species, also possess this specialized posterior eyespot. The other reared ACG *Eumorpha* (*E. obliquus*, *E. satellitia*, *E. vitis*, *E. megaeacus*, *E. fasciatus*, *E. triangulum*, *E. anchemolus*) are all cryptic green to yellow to pink in coloration with various sizes of white diagonal side slashes, but lack the specialized "blinking" eyespot (see images at Janzen and Hallwachs 2012). We propose that the "blinking" eyespot observed in these final instar *Eumorpha* caterpillars intimidates would-be predators from attack. However, the extent to which caterpillar predators perceive the rear eyespot as an eye blinking and the degree of protection conferred remains unknown. We are not aware of any reported observations of bird responses to these caterpillars. Unfortunately, the rarity of these *Eumorpha* species currently precludes direct examination of ecologically relevant predators responding to the "blinking" eyespots of these caterpillars. Future collection of *E. labruscae* for more detailed study may be possible outside its primary habitat where it is ephemerally abundant (but of course where the relevant predators may be absent).

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Supplemental material

Supplemental material is available online DOI: 10.1080/00222933.2013.791935

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