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A new gall-inducing shining leaf beetle (Coleoptera: Chrysomelidae) from Thailand and its relevance to the evolution of herbivory in leaf beetles

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Abstract. Extremely few gall-inducing Coleoptera attack Monocotyledonae. We describe and report on a new species of true shining leaf beetle, whose larvae form complex, multilayered galls on the host plant. During a field survey in Western Thailand, a galling member of the genus *Oulema* (Criocerinae) was discovered in a premontane rainforest attacking *Commelina paludosa,* a member of the monocotyledonous dayflowers (Commelinaceae). Our report is the first instance of a galling member of the genus *Oulema* and is described herein *O. reclusa*. The galler's adult habitus exhibits the general traits typical of the genus *Oulema*: front of the head between the eyes narrow, with the sides forming an angle of more than 90°; emarginate pronotum, moderately constricted below the middle; antennae filiform, longer than half the body length; two small protuberances on the vertex, almost touching; claws connate; 9th elytral stria with a complete row of punctures. The larva is extremely reduced, lacking discernable setae, a dorsal anus, ambulatory warts and ocelli. Our observation of a coleopterous gall-inducer may be the first on a monocot. Despite the fact that the putative sister taxa of the Criocerinae are the Sagrinae and the Bruchidae, gall-inducers and seed feeders respectively, we believe that gall-induction, as well as leaf mining in *Oulema,* are derived trophic habits within the Criocerinae. We discuss the relevance of this discovery to the evolution of ecto- and endophagy in the Criocerinae, a very basal subfamily within the broad Chrysomelidae radiation.

Keywords. gall, *Oulema, Commelina,* Monocotyledonae, Chrysomelidae, Criocerinae.

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1. Introduction

Extremely few gall-inducing Coleoptera attack the Monocotyledonae. Here we report on a true shining leaf beetle, whose larvae form complex, multilayered galls on its monocotyledonous host plant. During a field survey in Thailand, the second author discovered a galling member of the chrysomelid subfamily Criocerinae associated with a monocot in the dayflower genus *Commelina* (Commelinaceae). The Criocerinae are a cosmopolitan group of nearly 2000 species distinguished by their brilliant, often colorful appearance, narrow, sometimes hour-glass shaped pronotum, and excrement-covered, folivorous larvae. Subsequent inspection suggested that this is the first instance of a galling member of the genus *Oulema* De Gozis, and is described herein. With the exception of the mining *Oulema pumilo* Vencl and Aiello, and *Lema quadrivittata* Boheman, the putatively galling *Ortholema samalkotensis* Heinze and *O. abnormis* Heinze, and several stem bores (Schmitt pers. com.; Vencl and Aiello 1997; Vencl *et al.* 2004), the larvae of the vast majority of shining leaf beetles are external grazers on leaf surfaces of both Monocotyledonae and Dicotyledonae (Monrós 1960; Schmitt 1988; Jolivet and Hawkswood 1995; Vencl *et al.* 2004). The present case represents a notable exception and as such, an interesting problem for our understanding of the selective factors that influenced the evolution of trophic modes in larval Criocerinae in particular, and in exophytic phytophagous insects in general. Here we ask if internal foraging behaviors, such as galling, boring and mining, were the progenitors of the leaf surface trophic mode, which now predominates within the Criocerinae, or, alternatively, whether internal feeding represents a highly derived habit, perhaps reflecting a retreat from the high costs associated with the invasion of the leaf-surface adaptive zone (sensu Simpson 1953). We present below our understanding of this remarkable discovery.

2. Study site and habitat

Galls were found on a dayflower *Commelina paludosa* Blume (Commelinaceae), at 962 m at Thong Pha Phum National Park (14°41´29.7N, 098°24´04.5˝E). The Park is located in Kanchanaburi Province, Thailand, which borders Myanmar (Fig. 1). The study site, a large bamboo thicket at bottom of a hill, was shaded, very humid and the ground was moist at the time of the investigation (Plate 29 A). The climate in this area is tropical pre-montane rain forest, with a southeastern monsoon rainy season lasting from May to July, and a northeastern monsoon with a distinct dry season lasting from November to January (Thong Pha Phum National Park 2004).

3. The host plant

A perennial, *C. paludosa* Blume has erect, sometimes smooth, distally branched stems, which grow to 1 m. The leaves are lanceolate to ovate-lanceolate, sessile,

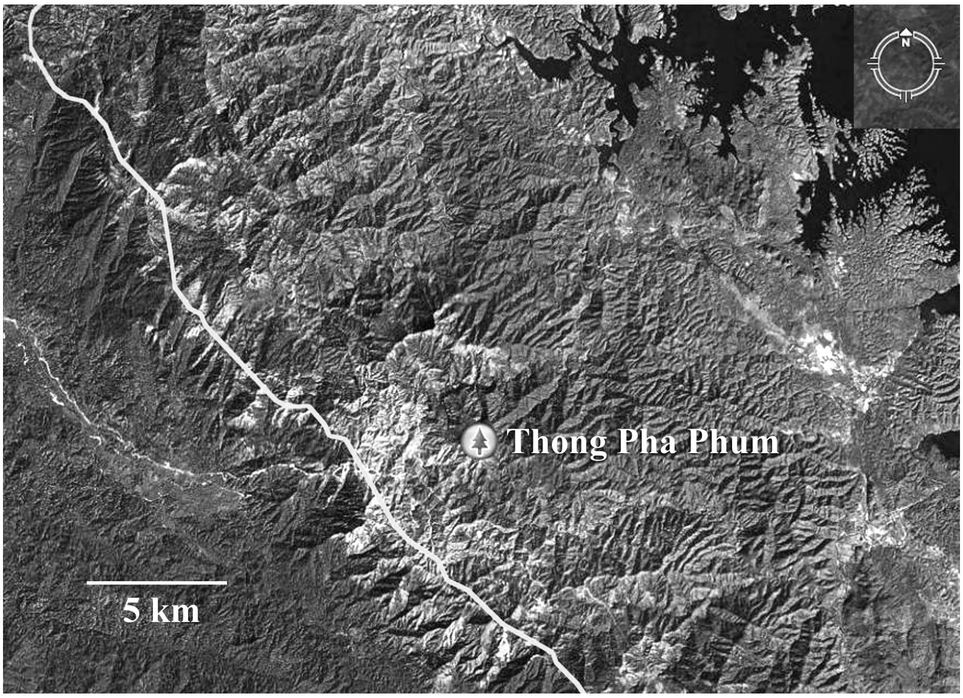

Figure 1. Collection site of *Oulema reclusa*, *sp. nov.*, Thong Pha Phum National Park, located in Kanchanaburi Province, Western Thailand (14°41´29.7˝N, 98°24´4.5˝E).

generally glabrous, with sheathing petioles, reaching a length of 6 cm. The chief characteristics of *C. paludosa* are a three stamen-three staminoid configuration, two blue enlarged upper petals, and connate, spath-like involucral bracts (Plate 29 B). Galls may induce branching as they were frequently found at stem junctions. Growing in well-drained areas at mid-elevations, *C. paludosa* is distributed broadly from South Central China, Nepal to Malaysia (Shu 2000).

4. The gall

Galls were collected at the beginning of the dry season in late October and early November 2005. Galls occurred on the host's stems and induced stem branch points at leaf bases of the sheathing petioles and axillary shoots, possibly causing formation of a new shoot. Although the host plants were common along the bamboo thicket, galls were uncommon and no plants had more than one gall. Of the seven at our disposal, mature galls were globose to spindle shaped, with an average (± SE) length × width of 22.19 ± 2.44 × 15.79 ± 0.083 mm (Plate 29 C, D). The un-galled part of the stem (normal stems) averaged 2.5 to 3.0 mm in diameter. The outer surface was reddish in color and cracked in some galls (Plate 29 C). Each gall contained a single, narrow chamber with an average (± SE) chamber length of 8.06 ± 0.71 mm, containing a single larva, pupa or adult. A relatively irregular margin of large, succulent white to translucent ‘nutritive’ tissue surrounded the chamber, which appears to be modified parenchyma (Plate 29 E, F). The mature gall which contained a pupa or an adult had a brown (dried) circular, thin layer of the plant epidermis at the exit orifice. It is most likely that the mature larva constructs this circular exit orifice prior to pupation.

5. The adult

Oulema reclusa Vencl and Nishida, new species
Plate 29 G
Diagnosis The adult habitus is 5.26 mm in length and of a uniform, pale yellowish-tan. The head is divided and distinctly bituberculate at the vertex. The head and pronotum are narrower than elytra; front of the head between the eyes narrow, with the sides forming an angle of more than 90°; the claws are connate; the elytra lack any color patterning; and the 9th stria of elytral punctation is complete.
Description: Form sub-cylindrical. *Head*: yellowish tan, shiny, moderately constricted behind the eyes and head much narrower than the width of the pronotum; clypeus, labrum and mouth parts with pale tannish-yellow ground color and finely setose; frons separated from the vertex by deep grooves forming an ‘X’ with the angle between them less than 90°; front of head between the eyes narrow, with sides forming an angle of more than 90°; the antennal tubercles almost touching and much closer together than the vertex-frons intersection; vertex weakly divided by a broad, longitudinal depression; antennae are of a uniform tan color, filiform, with 11 segments and longer than 1/2 the body length; segments 5 and 6 equal in length; eyes black, deeply notched to 1/3 their diameter; mandibles black at apices. *Pronotum*: Pale yellowish-tan, shiny, glabrous and emarginate, with a shallow, submedial constriction, 96% of apical width, near base; disc with a long, curved lateral seta projecting from each corner; a fine median pit in sulcus. *Elytra*: Shiny, uniformly yellowish-tan, with a pronounced basal depression; punctation coarse and uniformly spaced, becoming somewhat irregular to obsolete toward the apex; punctation of the 9th stria complete; scutellum tan. *Venter*: Uniformly yellowish-tan, evenly setose; minutely and evenly punctose; legs uniformly pale yellowish-tan; metafemora slightly swollen; two apical metatibial spurs; tibiae and tarsi very finely setose; claws connate and black.
Holotype Female: Reared from a stem gall on *Commelina paludosa*, Thong Pha Phum National Park (14°41′29.7″N, 098°24′04.5″E), 962 m, Thailand, 2005. The pinned holotype is deposited in the U.S. National Museum with its gall voucher (dried).
Emergence phenology The single gall to produce an adult was collected on 21 October 2004 and eclosed 25 days later.
Host plant *Commelina paludosa* Blume (Commelinaceae).
Distribution The only location known so far is the holotype locality, a mid-elevation, pre-montane rainforest above 500 m.

Etymology Derived from Middle English, from Old French *reclus*, meaning hidden or secretive from the world; originally from the Latin *reclasus*, past participle of *recludare*, to shut up or to close.

Remarks Although there is no general agreement as to whether *Oulema* De Gozis (1886) is a bona fide genus, or rather a subgenus within *Lema* (see Mohr 1985), our use of *Oulema* follows that of Monrós (1960), White (1993) and Vencl *et al.* (2004). The *sp. nov.* should belong in Lacordaire's (1845) division I because it has a complete row of punctation in the 9th elytral stria and is a denizen of the Old World. However, due to its very small size and uniform light coloration, we were unable to assign it to any of Lacordaire's groups within that division. Although two *Lema* species share a complete ninth stira of punctations, the solid pale yellowish tan habitus and Oriental location of *Oulema reclusa*, *L. indica* J. can be readily distinguished from it by its much larger size (+8 mm), antennae longer than 1/2 the body length, while *L. chinensis* J. is easily distinguished by its black antennae, clypeus, base of eyes, and legs. We thus are confident of its novelty to science.

6. The larva

The larval habitus is extremely reduced. It is cylindrical, un-sclerotized, somewhat dorso-ventrally flattened at the extremes, with tapering fore-and-aft. Coloration is semi-translucent, creamy white, and a creamy opaque white after preservation in live early- to mid-instars. With a length of 4.5 mm, the larva is legless, lacks ambulatory warts, ocelli, and has an extremely thin, easily deformed, transparent cuticle (Plate 29 F). The head capsule is tan in color and prognathous. The terminal abdominal segment is tan in color. The larvae do not posses the dorsally oriented anus typical of the subfamily, hence, they are shield-less. The anus is instead positioned in the upper half of the tan-colored terminal abdominal segment, a location typical of other galling chrysomelid species. The larva also lacks a complex system of dorsal setae typical of their shield-forming, surface-feeding relatives. Material: one early to mid-instar larva in EtOH deposited in the U. S. National Museum.

7. Parasitoids and inquilines

Larvae of two species of parasitoid wasps parasitizing the *Oulema* larvae were observed in two galls. One of them was a large, solitary ectoparasitic idiobiont parasitoid, which appears to be an Ichneumonidae. This parasitoid larva was apparently feeding on the gall 'nutritive tissue' after feeding on the *Oulema* larva, possibly being an inquiline. This behavior has been observed in a pimpline ichneumonid (Gauld *et al.* 2002; K. Nishida pers. obs.). The other parasitoid was a species of small, gregarious, ectoparasitic idiobiont parasitoid (possibly Eulophidae) on mid-instar *Oulema* larva. Material: two larvae in EtOH deposited in the U. S. National Museum.

8. Discussion

The *Oulema* described herein is, we believe, new to science. Although its host appears widespread, the galls may be extremely rare. Despite the fact that we base its description on a limited amount of material, *Oulema reclusa* is an exemplar of an important trophic habit in a basal family within the Chrysomelidae and as such, deserves recognition. A severe shortage of material was a typical problem confronted by 19th Century chrysomelid workers, who acknowledged their limitations. Numerous species were described on the basis of a single specimen. Otherwise, most species would remain completely unknown today. We thus feel compelled to use the limited information now at our disposal in the hope that other investigators will verify our proposal and add more detailed information about the biology of this exceptional leaf beetle. Obviously, we cannot make definitive statements about the range of phenotypic variation, but nevertheless, we hope future workers using these preliminary findings will expand upon our report of this unusual, and perhaps significantly exceptional trophic behavior.

The larva of *Oulema reclusa* is highly specialized for galling, with extremely reduced larval morphology. It is probably confined to its *Commelina* host plant, since clades with endophytic larvae, like gallers, tend to have very much more restricted host ranges than their externally feeding relatives (Raman 1996; Raman *et al.* 2005). In general, the internal-feeding chrysomeloid beetles, like our *Oulema,* posses reduced, vestigial, or have completely lost morphologies such as legs, light-sensing ocelli, thick cuticles, rotund bodies, and complex setation. In contrast, external feeders (exophytes) are much more robust, possess ocelli, fully functional legs with grasping claws and are externally embellished with setae along or more specialized projections, many of which function as defenses (Crowson 1981; Stehr 1987). As noted above, criocerine larvae retain feculae on the dorsum, which serves as an anti-predator defense based on host-derived primary and secondary chemicals (Morton and Vencl 1998). The galling mode would seem to obviate the need for such a shield defense and the orientation of the larval anus appears consistent with this trait loss in the present instance.

The taxonomic position of *Oulema* is an important context for our hypotheses about the evolution of the gall-inducing trophic habit. Monrós (1960) transferred some New World species traditionally placed in *Lema* to *Oulema,* a scheme corroborated by White (1993) and elaborated by Vencl *et al.* (2004), which expanded the host records for *Oulema sensu lato,* to include mainly Poaceae in the Old and Commelinaceae in the New Worlds. If valid, our observation would be the first for a species of *Oulema* on host in the Commelinaceae from South East Asia, and would thus further support the idea that *Oulema* is cosmopolitan, probably ancestral within its subfamily, whose hosts chiefly are limited to the above mentioned monocotyledonous families.

Galls come in an astonishing diversity of forms and are produced by a variety of mechanisms. We define a gall as any modifications in host tissue or organ growth induced by the parasite's chemical or mechanical stimuli that are partially or totally utilized by the to parasite to complete its life cycle. As Mani (2000) noted, most types of gall growths can be recognized by hypertrophy and hyperplasy of host cells, tissues, and organs, including the regeneration of new leaves (K. Nishida, pers. obs.). Rather than complex, multi-layered galls, larval Sagrinae appear to form feeding chambers in the pith of the host's stems. There are however scattered reports of true galling in other Chrysomelidae. For example, *Psylliodes napi* F. on young stems of *Cardamine flexuosa* With. (Brassicaceae), and *Schematiza cordiae* Barber (Galerucinae) on *Cordia* (Boraginaceae) (Barber 1947; Freude *et al.* 1965). To date, only *Ortholema samalkotensis* Heinz and perhaps *O. abnormis* Heinz are reported to form galls on Poaceae (Heinze 1943; Schmitt pers. com.). Since it was synonymized under *Oulema* in the most recent revision of the Criocerinae (Monrós 1960), *Ortholema*'s exact systematic position is problematic. The extremely orthognathous head and unconstricted pronotum makes it distinct from the present species, but other characters do place *Ortholema* closer to the Criocerinae than to the putatively galling Sagrinae (Schmitt pers. com.). Despite these systematic uncertainties, the present observation of a gall-inducing criocerine is the first for *Oulema sensu stricto,* and as such, may shed light on the origins of folivory and endophagy within Criocerinae, a basal subfamily within the impressive radiation of the Chrysomelidae. Incidentally, only four other gallers have been reported from the Commelinaceae in Asia: one from a clear-wing moth (Sesiidae), *Aegeria uniformes* Snellen, and the remainder formed by unknown Lepidoptera (Houard 1922). Our observation represents one of an extremely few reported instances of a coleopterous gall-inducer from the Monocotyledonae.

As described above, larval *Oulema reclusa* form multilayered galls of diversified tissues. Because the plant receives no benefit, galling is a parasitic relationship (Price *et al.* 1987; Redfern and Shirley 2002). Resembling tumors, gall formation induces the host to provide shelter, nourishment and perhaps also protection from the galler's enemies. Gall insects induce unique patterns of tissue differentiation, which normally do not occur in plant morphogenesis. Although galls are plant tissue, they nevertheless are extended phenotypes of the gall-inducing insect, and as such, represent a manipulation by the insect to improve the nutritional and/or protective qualities of the host's tissues. However, unlike cancerous growths, galls are structurally complex. In fact, the galler may not only manipulate the distribution of nutrients adjacent to the galler's chamber, but also the distribution of the plant's own defensive chemicals. Galls induced by thrips for instance, have a 'nutritive' zone of high metabolic activity comprised of meristematic cells with dense cytoplasm, enlarged nuclei and high levels of protein and lipid synthesis (Raman and Ananthakrishnan 1983; Ananthakrishnan and Gopichandran 1993; Raman 2007). Near to the gall's exterior and away from its nutritive inner zone, the host tissues often accumulate high levels of phenolic by-products of tissue degradation, tannins and other putative defensive chemicals. In at least one case, it is clear that the host plant is differentially allocating its defensive chemicals to the exterior of the galled tissue. The oak galling cynipid wasp, *Andricus petiolicolus* Basse, induces its host to re-distribute plant defensive chemicals to the outer layers of the gall, evidently by elevated total peroxidase activity. By so doing, it might enhance the gall's effectiveness as a sanctuary against the galler's enemies. At the same time, the wasp is inducing the plant to produce nutrient-rich tissue nearby its gall chamber, perhaps via reduced peroxidase activity. The cynipid evidently not only elicits the host to produce nutritious tissue by the gall, but can manipulate the host to re-allocate defensive allelochemicals from the vicinity of its feeding chamber to the outer walls of the gall (Allison and Schultz 2005). However, bioassays of these remarkable observations are required to confirm the efficacy of the proposed allocation events, and their fitness consequences for host and galler. Because the Sagrinae lack these complex gall-induced host tissue manipulations, and the galls of *Ortholema* have not been properly examined in detail, we suspect that their larvae do not reside in true galls, but rather are specialized stem bores.

The vast majority of gall-makers are flies and wasps, and the vast majority of galls occur on dicotyledonous plants (Abrahamson and Weis 1997). Our report of a true galling criocerine is notable for three reasons: 1) with the exception of the reports above, including those from the putative galling subfamily Sagrinae, gall induction is rare in beetles generally but it is extremely rare in leaf beetles in particular; 2) *Oulema* induces galls on a monocotyledonous plant. The vast majority of galls are formed on dicotyledonous plants, and; 3) *Oulema* produces a complex, multilayered gall; gall-induction is a highly specialized trophic habit expressed in only 6 of 27 insect orders. As noted above, most criocerine larvae are leaf surface feeders. Yet their sister taxa, the Bruchinae and Sagrinae, have seed-feeding and possibly gall-forming larvae respectively. The present galler represents a conundrum: did gallicoly in the Criocerinae originate before, or after larval surface folivory? Galling as a retained trait would be consistent with the plesiomorphy of endophagy for the criocerine's closest relatives. On the other hand, larval galling may be a highly derived condition, evolving in response to high vulnerability to natural enemies, to numerous competitors experienced by surface-feeding counterparts, or perhaps as a response to stressful abiotic factors on leaf surfaces, such as desiccation and insolation. Numerous experimental studies support the idea that leaf feeding is dangerous, particularly from the perspective of vulnerability to natural enemies (Vencl and Morton 1998; Stamp 2001 and references therein). Galling, as a derived trait, would be consistent with the transformation series proposed by Price (2005), which posits that gallicoly arose from an ancestral exophagous habit to increasingly more concealed trophic modes.

When we considered the other sister gall/non-gall comparisons in sawflies and aphids for which phylogenetic hypotheses are available, we detected a discernable trend in the galling habit from superficial, *i.e.*, open galls on leaves, toward more central, richer resources, such as buds and stems (Price 2005). If the galling pattern from peripheral-to-central is a general one, as we suspect here, then galling may be derived from the boring mode and seems the most parsimonious account for the present instance. In the case of our *Oulema*, galls are found at the growing meristematic apex and induce new stem formation as well as apparently diversified nutritive and encapsulating layers. Despite the fact that the putative sister taxa of the Criocerinae, the Sagrinae and the Bruchinae, gallers and seed feeders respectively, we believe that gall-induction, as well as leaf mining in *Oulema,* are derived habits within the Criocerinae (Vencl and Aiello 1997; Farrell and Sequira 2004). As pointed out earlier, gall-induction, and perhaps mining, probably arose from the boring habit (Rohfritsch and Shorthouse 1982; Farrell and Sequira 2004), this despite the fact that the majority of larval Criocerinae are exophytic. The galling habit is generally considered to be derived in other groups for many reasons (Raman *et al.* 2005). Chief among these are the fact that: 1) the galling habit is rare and does not occur in all lineages of herbivorous insects. For example, of the 9 herbivorous orders, six have gall-inducing taxa; 2) only a few derived taxa, even among related groups, are gall inducers (*e.g.*, within Hemiptera, only Aphididae, Psyllidae, Coccidae, and Aleyrodidae include gall inducers), and; 3) even within the predominantly gall-inducing families, several closely related taxa are exclusively non-gall inducers. For example, within several families, gall-induction has evidently evolved independently several times.

As noted above, gall-induction is believed to be derived from two trophic modes: (1) from the mining habit, as in the dipteran Agromyzidae and microlepidopteran Nepticulidae (Dempewolf 2005) and Gracillariidae (Kumata 1982; Kumata, *et al.* 1988; K. Nishida, unpublished), and; (2) from the boring habit, as in the lepidopteran Tortricidae and the coleopteran Curculionidae. Herbivory, of which gall-induction is perhaps the most specialized form has clearly evolved from detritus-feeding (Labandeira 1997; Raman *et al.* 2005). Furthermore, cecidogeny (*i.e.* gall-induction) is considered to be derived from mycophagy, which itself is thought to be a derivation of detritus feeding (Rohfritsch 1992). For example, within gall midges (Cecidomyiidae), a few unrelated taxa (*e.g.*, Asphondylini, Lasiopterini, and Alycaulini) do not in fact feed on plant tissues but instead on the fungi growing within the galls (Raman *et al.* 2005 and references therein). As suggested above, our hypothesis is consistent with the latter trend.

Trophic specialization is believed to foster both the processes of adaptive radiation and of speciation (Schluter 2002). Specialized diets are frequently found in lineages that feed inside plant tissues or that form galls (Gaston *et al.* 1992; Frenzel and Brandl 1998). However, beetles with externally feeding larvae are much more diverse than their sister groups with concealed-feeding larvae (Price 1980). A recent phylogenetic analysis of the Chrysomelidae including its most basal subfamilies, the Bruchinae and Sagrinae, indicates that rates of host shifts are faster for exophagous lineages than for those consuming different plant tissues, such as stems, seeds and leaf interiors (Farrell and Sequeira 2004). Similar patterns were found in nematine sawflies, also represented by internally and externally feeding larvae (Nyman *et al.* 2006). Moreover, the surface-feeding Chrysomelidae, Criocerinae, and cassidoid Cassidinae each have more than two fold the number of species than their internally-feeding Bruchinae and Sagrinae basal counterparts combined. These exophytic chrysomelids collectively use a much broader spectrum of hosts than their endophytic sister taxa do. For example, the Bruchinae and Sagrinae are largely specialists on legumes and palms (Jolivet and Hawkswood 1995). However, within the Cassidinae at the δ level, the internally feeding hispine-Hispinae lineages attack nearly 40 plant families, while the externally feeding cassidoid-Hispinae, with three-fold greater diversity, are found on only five dicotyledonous plant families (Windsor *et al.* 1992; Hsiao and Windsor 1999). It is hypothesized, but as yet unsubstantiated, that exophytes shift hosts more frequently than do related endophytes. This could be due to factors mentioned before, such as the multiple biotic and abiotic obstacles encountered on exposed leaf surfaces. Chief among these hazards must be counted the threat from natural enemies. Under an escalation scenario, natural enemies might select for shifts to hosts that provide enhanced 'enemy-free space', wherein vulnerability is reduced through the expropriation of more potent or higher levels of host-derived defensive precursors that enhance the effectiveness shields, glands or other host-dependent anti-predator defenses (Jefferies and Lawton 1984; Bernays and Graham 1988; Hawkins 1994; Vencl *et al.* 2005). Losses to natural enemies are higher among externally feeding herbivores (Hairston *et al.* 1960; Lawton and Strong 1981; Hawkins 1994). Consequently, competition is low among exophages (Denno *et al.* 1995). Consistent with the 'enemy-free space' idea is the fact that ectophagous chrysomelids have evolved an astounding diversity of putative defenses, such as gregarious larval behavior, eversible glands, fecal shields and the many associated metabolic pathways for the retention and secretion of *de novo* and host-derived chemicals (Vencl and Morton 1998; Termonia *et al.* 2001; Kuhn *et al.* 2007). These primary lines of defense are sometimes augmented by further adult commitments, such as maternal care or oviviparity (Windsor and Choe 1994; Trillo and Vencl in press). With reduced susceptibility to natural enemies desiccation, and competition etc., the 'enemy-free' space scenario may also explain the secondary invasion of the boring, mining and galling adaptive zone by erstwhile exophytic larvae. However, for reasons that are not altogether clear, the endophytic 'adaptive zone,' entails the costs of reduced speciation rates and curtailed adaptive radiations at the macro-evolutionary level (Santiago-Blay 2004; Nyman *et al.* 2006). All of these various traits support the idea that feeding upon plants is a dangerous occupation, with serious evolutionary consequences. Unfortunately, phylogenetic analyses contrasting related exo- and endophagous lineages are still lacking. They could reveal the factors favoring the repeated evolution of gallicoly and perhaps the processes responsible for its maintenance, despite the evident macro-evolutionary costs in terms of depauperate diversity.

Finally, two species of *Commelina*, *C. benghalensis* L. and *C. diffusa* Burn., are listed under Plant Threats to Pacific Ecosystems (PIER 2006). At present, gall-inducing Lepidoptera and Coleoptera are especially preferred as agents in integrated biological control programs of invasive weeds because they are thought to be monophagous (Muniappan and McFadyen 2005). Thus, gall-inducing *Oulema* could be a candidate control agent for several weedy *Commelina* species.

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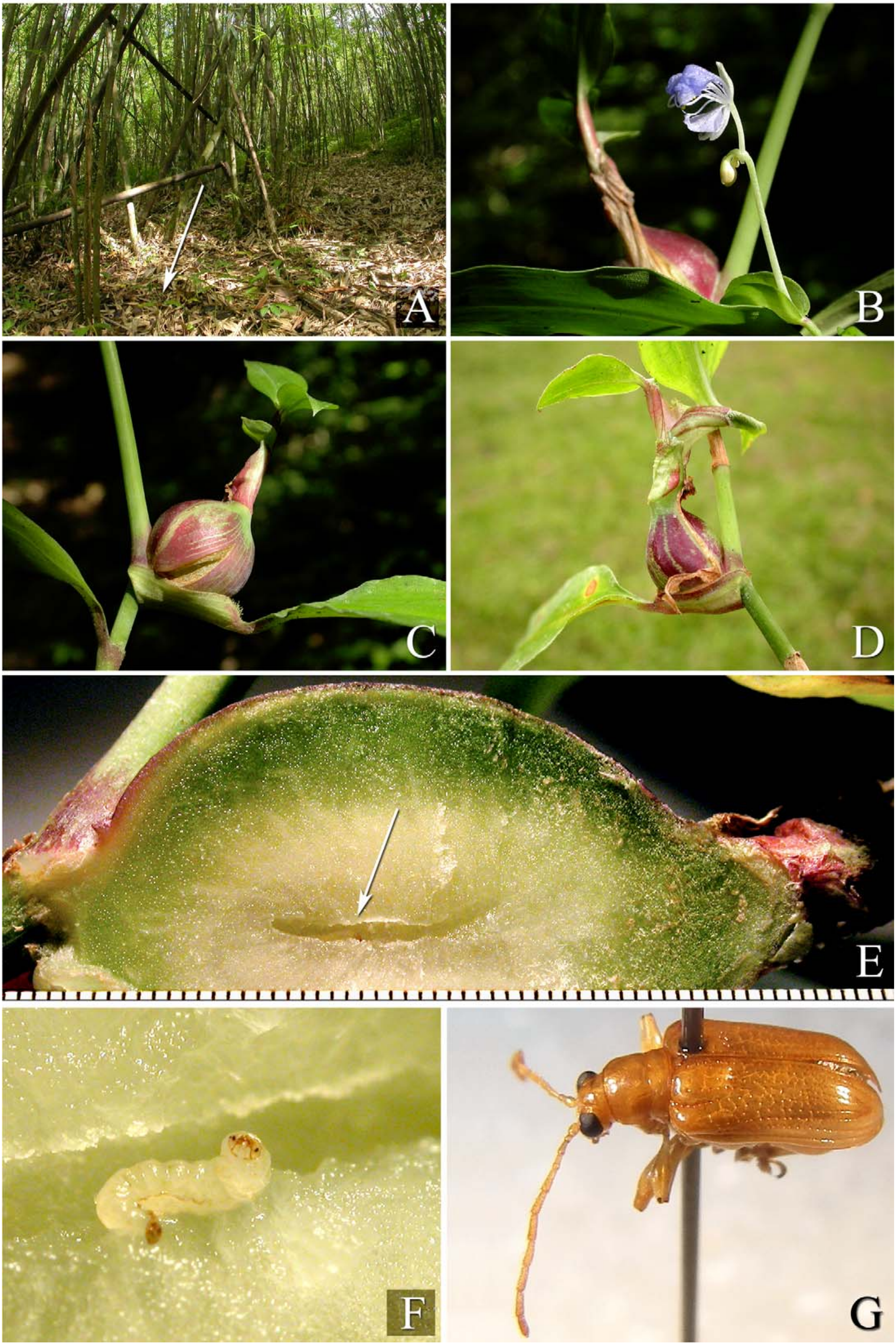
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Plate 29 [PREVIOUS PAGE]. **A.** Habitat of *Oulema reclusa*'s host, *Commelina paludosa* with a gall (arrow), in a bamboo thicket in pre-montane rainforest in Thailand.

B. A *Commelina paludosa* Blume (Commelinaceae) flower and a gall. Flowers posses three stamens and three staminoids.

C. Gall of *Oulema reclusa* in *Commelina paludosa.* Note the split in the exterior of the gall.

D. Exterior of *Oulema reclusa* gall in *Commelina paludosa.*

E. Longitudinal section of *Oulema reclusa* gall showing different layers of transformed tissues. Note that the gall chamber is located longitudinally in the center part of the gall. The arrow indicates the anterior end of an *Oulema reclusa* larva (scale: 0.5 mm).

F. *Oulema reclusa* larva *in situ* within a gall chamber surrounded by ‘nutritive' tissue and denser exterior tissue.

G. Lateral view of adult *Oulema reclusa* female (length: 5.26 mm).