

Maternally inherited architecture in tertiary leaf beetles: paleoichnology of cryptocephaline fecal cases in Dominican and Baltic amber

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Abstract Complex ethological adaptations and intraspecific interactions leave few fossil traces. We document three Dominican (20 million years old [myo]) and Baltic (45 myo) amber fossils that exhibit firm evidence of highly integrated interactions between mothers and offspring in the diverse camptosomate lineage of beetles (Chrysomelidae, leaf beetles). As in contemporary species, these hard cases were initially constructed by mothers, then inherited and retained by offspring, which then elaborate this protective domicile with an unusual but economical building material, their feces. The three fossils are classified in the Subfamily Cryptocephalinae; two are classified in the tribe Chlamisini based on morphological evidence—the flattened head lacking a sharp keel and long legs with simple recurved untoothed claws. These diagnostic features are not clearly visible in the third specimen to permit more refined identification. These fossils provide more precise paleontological dating of tribal nodes within the cryptocephaline radiation of leaf beetles. These fossils are the first and

earliest evidence of mother–offspring interaction, building behavior, and fecal recycling in Camptosomata beetles and of inheritance of architectural structures in beetles.

Keywords Larvae · Maternal care · Amber · Animal architecture · Behavior

Introduction

Behavioral characters can be valuable in recognizing evolutionary relationships among organisms, as well as in understanding their ways of life (Darwin 1859). Sometimes, behavior may be used as a supplement to or proxy for morphological or molecular evidence of relationships. An early example was the well-known study of ducks by Konrad Lorenz (1935). The origin and antiquity of behaviors are rarely known because behavior does not fossilize. However, constructs resulting from behavior sometimes do fossilize.

Among beetles, the largest diversification of animal life at over 300,000 described species, the leaf beetles (family Chrysomelidae, *ca.* 40,000 species) exhibit a broad range of maternal behaviors (Hilker 1994; Chaboo 2007). Most remarkable is that of mothers which provide an unusual form of care by using their own feces to build hard egg-protecting cases (Hislop 1871; Cockerell 1891; Spruyt 1925; Fiori 1950; Erber 1969, 1988; Lawson 1976; LeSage 1982; LeSage and Stiefel 1996; Flinte and Macêdo 2004; Reu and Del-Claro 2005; Brown and Funk 2005; Chaboo 2007; Chaboo et al. 2008). These cases are inherited by the hatching larvae, retained as domiciles, and enlarged by the subsequent larval instars using their own feces (Fig. 1a), then sealed as a pupation chamber. The cases are exceptionally sturdy, do not break down easily, and

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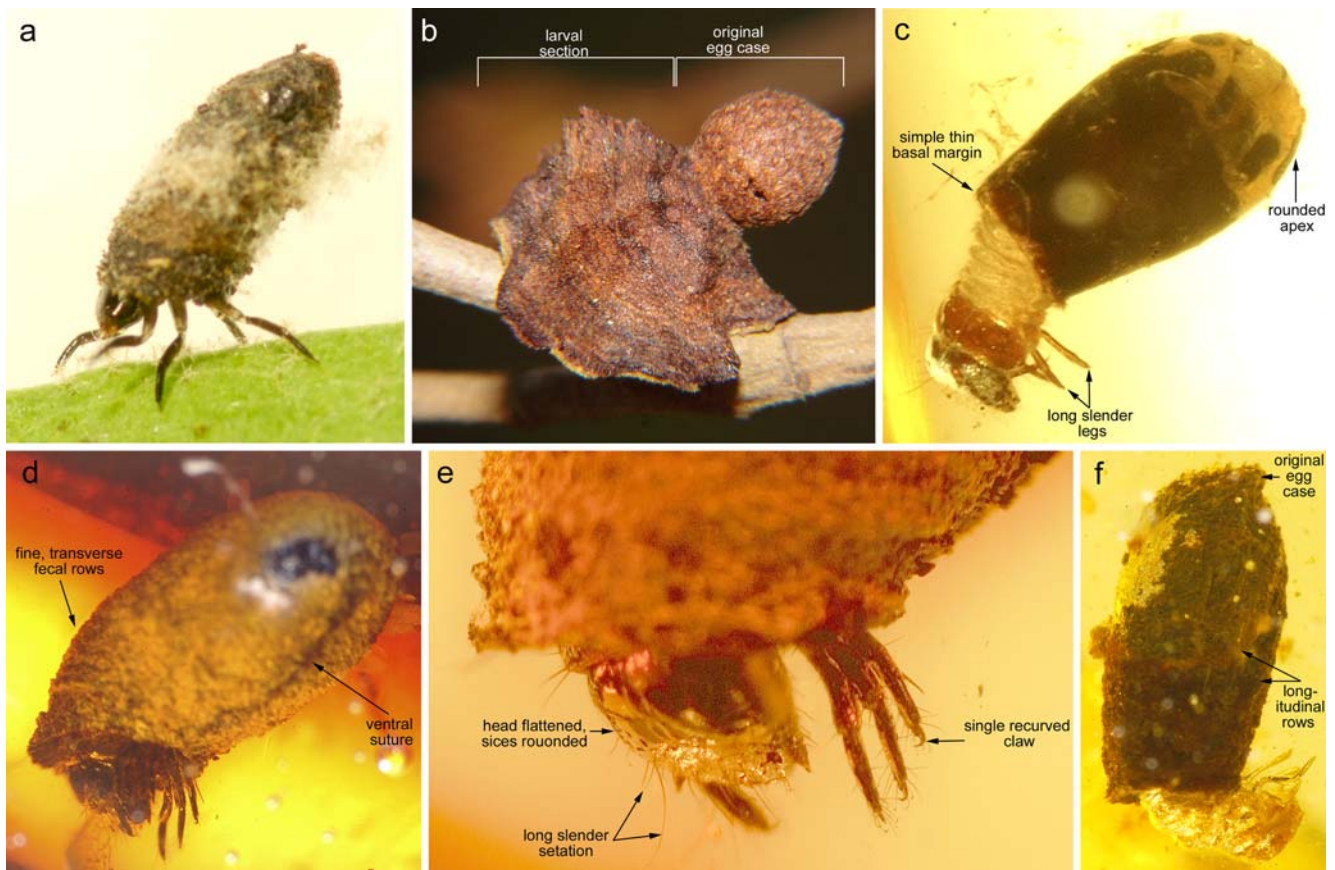


Fig. 1 Photomicrographs of Cryptocephaline leaf beetle immatures and their fecal cases. Modern larvae enclosed in cases of (a) *Neochlamisus* in North America and (b) *Fulcidax* in Brazil, and

remains of three ancient cryptocephaline larvae and their fecal cases in (c–e) Early Miocene (ca. 20 myo) Dominican amber and (f) middle Eocene (ca. 45 myo) Baltic amber

regularly provide secondary homes to other animals such as spiders, ants, and bugs (Schöller 1999). This remarkable protective adaptation has been evidence for treating two subfamilies, Cryptocephalinae and Lamprosomatinae, as a distinctive group, collectively known as the Camptosomata. We describe here three fossils of immature cryptocephalines preserved in amber along with their fecal cases, representing the earliest direct evidence of these elaborate behaviors and indirectly documenting the transfer of fecal architecture from mother to offspring as early as the middle Eocene [45 million years ago (mya)].

The remains of two larval camptosomates were identified in Early Miocene Dominican amber (Fig. 1d–e) and a single specimen in middle Eocene Baltic amber (Fig. 1f). These individuals are unquestionably members of the subfamily Cryptocephalinae as evidenced by the absence of wooden splinters that characterize cases in the subfamily Lamprosomatinae (Erber 1988) and lack the elongate apical segment on the antennae of larval lamprosomatines (Reid 1990; Kimoto and Takizawa 1997). The approximately thirty fossils documented in Cryptocephalinae comprise primarily adults and three larvae (Santiago-Blay 1994;

Santiago-Blay and Craig 1994; Santiago-Blay et al. 1996; Grimaldi and Engel 2005). The three fossils we describe here are a valuable window into the evolutionary history of Cryptocephalinae and offer critical data on the distribution, natural history, morphology, case architecture, and the timing of origin of their strange scatological habits.

Materials and methods

The two Dominican amber pieces, AMNH DR-10-1833 and AMNH DR-14-18, were collected in the Dominican Republic and are housed in the American Museum of Natural History. Dominican amber has been dated to the early Miocene (Iturralde-Vinent and MacPhee 1996, 1999). The single Baltic amber specimen (LCLC-0001) is in the collection of Chamorro-Lacayo. This piece also contains stellate trichomes, distinctive of Baltic amber, and *Microtelenomus angulatus* Brues, an Eocene species of scelionid wasp. Baltic amber is of middle Eocene (Lutetian) age, slightly more than twice that of Dominican amber (Engel 2001; Grimaldi and Engel 2005). The larvae in AMNH DR-10-1833 and LCLC-

0001 are unnaturally extended out of their cases, with the abdomen partially exposed. As far as is known, only the head and legs are exposed in live animals. Amber flow or a slow death may explain the altered position of these larvae within their cases. The larva in AMNH DR-14-18 is more naturally positioned, with the abdomen in situ and completely encased.

The Dominican amber specimens were stabilized in epoxy and viewed under mineral oil. Specimens were measured using a Lasico digital ocular micrometer, examined with a Nikon SMZ800 microscope, and photographed using a Nikon D1x digital camera attached to an Infinity® K2 lens.

All camptosomate cases share fundamental landmarks due to their construction and carriage. Cases are initiated by the mother to protect the egg. This egg case is inherited by the natal larva, turned upside down (and worn as a hat) and elaborated by fecal additions to the base (producing dorso-ventral lengthening) and by periodically splitting the case longitudinally to insert feces (producing lateral expansion). The uppermost section of larval cases is therefore actually equivalent to the maternal egg case construction while the basal sections are built by each subsequent larva. Detailed descriptions of this construction behavior from the mother through the pupal stage are described (e.g., Brown and Funk 2005; Reu and Del-Claro 2005). Chaboo et al. (2008) reviewed, defined, and illustrated these typical architectural features: apex = dorsal surface in larval case; ventral suture = the longitudinal break created, filled in with feces, and sealed as the case is expanded; the basal opening = where the larval body protrudes and contacts the substrate; and basal margin = the edge of the case that is pressed to the substrate when the animal retracts into the case.

Systematic paleontology

Family Chrysomelidae Latreille, 1802; Subfamily Cryptocephalinae Gyllenhal, 1813

Tribe Chlamisini Gressitt, 1946

Dominican Amber Morphospecies #1

Material AMNH DR-10-1833 (Fig. 1c); Early Miocene (Burdigalian) amber from the Dominican Republic; a single larva and case preserved in a piece of amber with the following case dimensions: maximum length 2.41 mm, maximum width 0.93 mm, maximum depth 0.45 mm. The amber is a rectangular fragment that is light orange-yellow with the single inclusion positioned about one-third along its length.

Description Larval case: maximum length 1.05 mm, maximum width (in lateral aspect) 0.94 mm, width at opening = 0.35 mm. Case dark brown to black, unevenly colored; egg case distinguishable from new larval section by width,

color, wall thickness and texture, trichome placement, and patterning of fecal deposit (as described below); egg case mostly intact except for dark triangular insertion basally and ventral suture; stalk absent; larval section of case slightly wider and thicker than that of egg case; feces granular, deposited in rows, not in plates, with trichomes protuberant; trichome density higher than in egg case; ventral wall with suture continuous, extending subapically from egg case through larval section to base; fecal rows few in number, positioned obliquely; dark triangular wedge spanning suture; lateral and dorsal walls with transverse fecal rows; base opening slightly oblique in lateral view; apical margin simple, not flared, trichomes not apparent in apical margin. Larva: length of exposed section of body 0.50 mm, maximum width of head capsule 0.29 mm. Head capsule exposed, prognathous, as wide as pronotum, broadly flattened, edges rounded; epicranial suture Y-shaped, frontal arms broadly divergent, curved; clypeus broadly fused to labrum; labrum hemispherical shaped, margin continuous, rounded; mandibles elongate, symmetrical, curved along labral edge; leg slender, podites rounded in cross-section, surfaces generally smooth; all coxae elongate, five times longer than broad; trochanter short, wider than long; femur with single seta apparent in dorso-apical position; tarsungulus single, slender, oriented laterad, tapered, surface smooth, without basal dens.

Remarks In addition to being unnaturally extended out of its case, the larva in AMNH DR-10-1833 (Fig. 1c) has been turned 90° anti-clockwise from the ventral suture of the case. Living larvae maintain a position such that the suture is always in a medio-ventral position relative to the body (14, 15).

Tribe Chlamisini Gressitt, 1946

Dominican Amber Morphospecies #2

Material AMNH DR-14-18 (Fig. 1d–e); Early Miocene (Burdigalian) amber from the Dominican Republic; a single larva and case preserved in a piece of amber with the following dimensions: maximum length 13.92 mm, maximum width 4.82 mm. The amber piece is elongate oval containing a single inclusion. The amber is evenly colored and deep burgundy orange.

Description Larval case: maximum length 3.13 mm, maximum width (along midline) 1.52 mm. Case dark brown to black, uneven; shape barrel-like, width of apex and base opening similar, sides sub-parallel; egg case not intact, broadly joined to larval section, distinguishable by surface texture, egg stalk absent; wall material granular, arranged in rows, not in plates; trichomes not apparent; rows oriented longi-laterally on ventral surface, transverse on lateral and

dorsal surfaces; apex somewhat flattened, surface with sharp protuberant plants; larval sections with material arranged in fine rows; base opening slightly oblique in lateral view; apical margin simple, not flared; wall thickness narrow. Larva: length of exposed section of body 0.52 mm, maximum width of head capsule 1.12 mm. Head capsule exposed, prognathous, as wide as pronotum, broadly flattened, edges rounded; epicranial suture Y-shaped, frontal arms broadly divergent, curved; frons with four pairs of setation, arranged in two longitudinal rows; setation simple, sparse, long, slender, tapered; antenna small, two-segmented; spatulate setation absent; clypeus broadly fused to labrum; labrum hemispherical shaped, margin continuous, rounded; mandibles elongate, symmetrical, curved along labral edge; legs of similar sizes, long and slender; leg setation similar, long, slender, and tapered; spiniform setae absent; tarsungulus gently tapered and sharply recurved.

Tribe undetermined

Baltic Amber Morphospecies #1

Material LCLC-0001 (Fig. 1f); middle Eocene (Lutetian) Baltic amber; a single larva among other organic inclusions in an amber piece with the following dimensions: maximum length 38 mm, maximum width 15 mm, maximum depth 7 mm. The amber is elongate with the beetle larva, the largest of the inclusions, laterally positioned in one half of the piece.

Description Larval case: maximum length 2.61 mm, maximum width (in lateral aspect) 1.32 mm, width at opening = 0.67 mm. *Shape* elongate; basal opening circular, edges slightly flared. *Maternal egg case* forming apical nipple. *Larval-built sections* approximately three, based on the color variations. *External surface* coarse, feces granular, arranged in fine transverse rows; apex with spiny appearance. *Trichomes* not apparent. Larva: *size*: exposed up to 1st abdominal segment; length of exposed section of body = 1.2 mm; head capsule exposed laterally, maximum length = 0.64 mm. Head capsule and pronotum sclerotized; head prognathous, flattened, edges sharply demarcated; setation radially arranged along edge, evenly spaced apart; other setation sparse, simple, not spatulate; legs slender, podites rounded in cross-section, surfaces generally smooth, setation sparse; all coxae elongate, five times longer than broad; trochanter longer than wide; tarsungulus single, slender, oriented laterad, tapered, surface smooth, without basal dens.

Remarks On the basis of the position and shape of the egg case, three distinct color variations in the larval sections, and elongate shape of the case, this specimen appears to represent an early third-instar larva, before the renovation that produces a barrel-shaped case that accommodates the fourth instar in contemporary species.

Discussion

The fossils discussed herein are unquestionably Cryptocephalinae since the cases lack the wooden splinters that characterize lamprosomatine cases (Fiori 1950). Within the Cryptocephalinae, we used the diagnoses of Kasap and Crowson 1976) to place the two Dominican amber specimens in the tribe Chlamisini as these larvae exhibit a flattened head with rounded margins, and lack the sharply keeled head that characterizes members of the tribe Cryptocephalini. Another diagnostic chlamisine feature, leg with tibiae showing more than four spatulate ventral setae, is very clearly seen in AMNH DR-14-18 (Fig. 1d–e) but not in AMNH DR-10-1833 (Fig. 1c). It is difficult to refine the identification of the Baltic specimen, LCLC-0001, since its head, claw, and setal features are not clearly visible. The three previously documented cryptocephaline larvae are either undescribed and unidentified (Grimaldi and Engel 2005: 393) or have been described in a limited way and classified in the tribe Cryptocephalini (Santiago-Blay et al. 1996). Without a comprehensive phylogenetic analysis of Camptosomata and additional information on the diversity of larval forms across the subfamily, we cannot estimate more exact nodal placements of each fossil to the genus level. Nonetheless, all six fossil larvae provide a unique and remarkably clear window into the evolutionary history of the subfamily Cryptocephalinae and permit a minimum age estimate for the origin of fecal recycling and architecture in at least two tribes, Cryptocephalini and Chlamisini.

While the multi-colored adults of camptosomates are solitary free-living herbivores, the more ecologically versatile larvae live on plants, in soil, and even in ant colonies (Erber 1988; Selman 1962; Jolivet and Hawkeswood 1995). Larval adaptability, and thus the evolutionary success of camptosomates, is likely due to the hardened cases they live in. Detailed natural history studies of cryptocephaline species provide a context for evaluating the paleobiology of these fossils (Wood 1966; Root and Messina 1983; Flinte and Macêdo 2004; Reu and Del-Claro 2005). Entrapment in amber suggests that the species were exposed and therefore arboreal and free-living, not myrmecophilous or submyrmecophilous (living with ants), or symphiles (living inside thorns), or living in roots as do some camptosomates. Arboreal cryptocephalines eat pollen, leaves, and stems of a single host species, related host species, or may be widely polyphagous.

Although most of the body is hidden in these fossils (as in life), the flattened heads and long, exposed legs are widely recognized synapomorphies of Camptostomata (Crowson 1955; Lawson 1991; Lawrence and Britton 1991). The flattened head potentially permits the larva to retract it more easily and shelter itself when under attack or

stress. The elongate legs give the larva considerable mobility while retaining the case over most of its body. By comparing the fossilized legs with the available information on larval leg structure across Cryptocephalinae it has been possible to refine our understanding of this synapomorphy. The lengthening of cryptocephaline larval legs is due to several factors: (1) well-developed and elongate coxae and trochanters (in contrast to reductions), and (2) a vertical or perpendicular re-orientation of the coxae (in contrast to a horizontal orientation). Given the size of the larvae relative to their respective cases, it appears that the larvae occupy the entire case cavity. This indicates that the case lacks internal partitions, with the larva occupying only certain partitioned sections, a condition seen in extant species of *Fulcidax* (Fig. 1b; Bokerman 1964).

Evidence for the age of these larvae can be inferred by comparison with living species, from the complete abrasion of the egg stalk (instar I may have the stalk), the complete abrasion of the egg case flange (instars I and II have remnants), the barrel-shape (tubiform in earlier instars), the presence of a complete ventral suture (incomplete in earlier instars), the apex shape (the egg case is completely distorted), and the relative quantity of the maternal and larval fecal additions (the larval section is very long relative to the egg case). Accordingly, these larvae appear to be early third and early fourth instars. Within the penultimate instar, the case is transformed from tubular to barrel shape, while within the final larval instar, the sides of the case become rounded and the overall shape becomes more rounded so as to hold the pupa.

Camptosomate case architecture can vary in material composition and in architecture within the life cycle, between host plant forms, and among species (Erber 1988; Chaboo et al. 2008). In the fossils, the egg case section that was inherited from the mother is completely split by the ventral suture, and the two hemispheres are widely separated and broadly joined to the section built by the larvae. Modern cases have a distinct ventral suture that extends completely from the basal opening (where the animal protrudes) to the apex. A broad triangular wedge, represents the feces inserted each time the ventral suture is separated to expand the case as in *Neochlamisus*. The fossilized cases appear to have this arrangement though the suture is not discernible owing to positioning within the amber. The cases also lack the external ribbing seen in some modern genera of Cryptocephalinae and overall the form is relatively generalized and putatively plesiomorphic.

Materials incorporated in the cases appear to be primarily feces, lacking plant or soil debris, and is consistent with what is known of modern cryptocephalines. The presence of trichomes, a common secondary material in modern cases (Fig. 1a), cannot be determined since only SEM analysis of broken cases can reveal the lattice

arrangement formed when trichomes are incorporated. Unfortunately, the color of the cases has apparently changed over time becoming more uniform brown-black and losing the typical striated patterns of extant taxa that results from layering of fecal rows and soil particles that appear in extant taxa; therefore, we cannot determine the presence of soil inclusions.

Like the preservation of dinosaurs brooding their nests, or fossil leaves cut by leaf-cutter bees, these specimens provide a minimum age for the unique ethological complex of mother–offspring interaction and building behavior in Camptosomata. This distinctive biological repertoire was likely well established by at least 45 mya. This age determination is consistent with hypothesized Eocene age of this clade (Hunt et al. 2007; Gómez-Zurita et al. 2007). Our larvae represent the earliest and only fossil evidence of intricate case-building behavior for which the Camptosomata is famed and named. Additionally, they are the first fossil evidence for maternal inheritance of architectural structures in the most diverse lineage of animal life—the beetles.

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