

Ovoviviparity in carabid beetles of the genus *Pseudomorpha* (Insecta: Coleoptera)

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Ovoviviparity is reported for the first time in the ground beetle family Carabidae. Eclosed larvae and fully developed embryos are found within the expanded lateral oviducts, bursa copulatrix and vagina of the putative myrmecophiles *Pseudomorpha angustata* and *P. hubbardi*. Eclosed larvae do not appear to be active while held inside the female prior to larviposition. Maximum larval numbers occur from mid-July to early September in these Arizona species, implying that larviposition is timed to coincide with summer rains. Larviposition is hypothesized as a means to eliminate egg mortality due to predation by ant hosts.

Introduction

The vast majority of insects are oviparous, with eggs laid singly or in masses, and embryogenesis occurring after oviposition. As a modification of simple oviparity, the eggs may be retained for various amounts of time within the female reproductive tract, resulting in a shortened incubation period after laying. In ovoviviparous species, eggs are retained within the female for the entire embryogenic period. Egg-hatch may occur just after oviposition, or larvae may hatch inside the female followed by larviposition.

Ovoviviparity occurs in a variety of insect lineages, including cockroaches (Blattodea) (Riley 1891, McKittrick 1964, Roth 1982), caddis flies (Trichoptera) (Wood-Mason 1890), tineid moths (Lepidoptera: Tineidae) (Sharp 1899, Common 1970), and various families of flies (Diptera) (Colless and McAlpine 1970). It is a common reproductive strategy in plant lice and scale insects (Homoptera: Aphidoidea, Coccoidea). In cases of ovoviviparity, the egg chorion is thick enough to prevent nutrients from passing from mother to developing embryo. The principal requirements for such a reproductive strategy include the ability of the female to hold maturing eggs, adequate provision for the hatching of larvae inside the female, and the ability of the female to larviposit on to a substrate on which the larvae can survive.

The most sophisticated maternal-egg relationships in the Insecta are the various forms of viviparity (Hinton and Mackerras 1970). In viviparous species the egg chorion is thin enough or specially modified to permit nutrients to pass from the mother to the developing embryo. Examples of this developmental strategy can be found in

cockroaches (McKittrick 1964), book lice (Psocoptera) (Smithers 1970), aphids and scales (Woodward *et al.* 1970), parasitic earwigs of the genus *Hemimerus* (Dermaptera) (Hansen 1894), and various flies, e.g. the tsetse flies, *Glossina* spp. (Diptera: Muscidae) (James and Harwood 1969).

In Coleoptera, several lineages possess ovoviviparous development. The termitophilous aleocharine Staphylinidae, *Corotoca melantho* Schiødte and *Spirachtha eurymedusa* Schiødte, were the first beetle species found to be ovoviviparous (Schiødte 1856). Subsequently, Wasmann (1915) reported several ovoviviparous aleocharine myrmecophiles, including *Lomechusa strumosa* F. and several species of *Atemeles*. Among chrysomelid leaf beetles, montane phytophagous species of the genera *Orina* (Perroud 1855, Weise 1885, Champion and Chapman 1901), *Chrysomela* (Rupertsberger 1870, Holmgren 1904, Rethfeldt 1924), and *Phytodecta* (Henneberg-Geissen 1926, Scheidter 1926) have been found to be ovoviviparous. Females of two South African species of Tenebrionidae, *Eurynotus capensis* (F.) and *Melanopterus marginicollis* Muls., have been found to contain a single, large, well-developed larva within the bursa copulatrix or vagina (Tschinkel 1978).

Recently we were pursuing studies on the form and structure of the female reproductive tract of a variety of ground beetle taxa (Carabidae). During these studies we discovered that females of several species of *Pseudomorpha* carry hatched larvae in their bursa copulatrix, vagina and lateral oviducts. This is the first instance of ovoviviparity reported for the Carabidae. *Pseudomorpha* beetles are known to be myrmecophilous with known larvae characterized by a physogastric body shape and the presence of peculiar mushroom-shaped setae over much of the body surface (Lenko 1972, Erwin 1981). The characteristics of the larvae have been attributed to their myrmecophilous habits (Erwin 1981).

In this paper we describe the occurrence of ovoviviparity in two species of *Pseudomorpha* from Arizona: *P. angustata* Horn and *P. hubbardi* Notman. We describe the manner in which the eggs, developing embryos and hatched larvae are carried by the females; the general form of the larvae; and the seasonality of larval occurrence in the females. The characteristics of *Pseudomorpha* ovoviviparity are compared to what is known of other cases of ovoviviparity in beetles.

Materials and methods

Specimens were dissected following two protocols. Initially, whole abdomens of *Pseudomorpha* females were cleared in 10% cold potassium hydroxide overnight. The genitalia and reproductive tract were dissected in 70% ethyl alcohol following a dilute acetic acid wash. The dissected tracts were stained in chlorazol black dissolved in 70% ethyl alcohol. Eggs and larvae were subsequently removed from the chitinized portions of the lateral oviducts, bursa copulatrix and vagina. In later dissections, after ovoviviparity had been discovered, whole specimens were boiled in distilled water, and dissected in 70% ethyl alcohol. By this protocol, the entire reproductive tract could be examined.

For closer examination of genital tracts and larvae, specimens were critical-point dried, sputter-coated with gold/palladium, and studied with an AMR 1000A scanning electron microscope.

Females of *Pseudomorpha angustata* and *P. hubbardi* from throughout the breeding season were dissected. The capture data for specimens used to study the seasonality of larval abundance in the females are presented in the Appendix.

Results

Ovoviviparity in Pseudomorpha

Hatched larvae can be found within the lateral oviducts, bursa copulatrix and vagina of *Pseudomorpha hubbardi* and *P. angustata*. Larvae may be completely free of the egg chorion, or the head and fore parts of the body may be free with the caudal segments still surrounded by the egg. Fully developed embryos can be distinguished while still in the egg by their fully sclerotized mouthparts and frontal ecdysial spines (Fig. 1A); both visible through the chorion.

Females that contain hatched larvae and eggs with fully developed embryos also have eggs with no apparent embryos visible. Eggs with undeveloped embryos are situated at the anterior ends of the greatly inflated lateral oviducts, the basal germarial strand of the ovarioles passing forward into the metathorax. Full-sized eggs are found at least as far forward as the second visible abdominal segment, with the mass of eggs and larvae occupying much of the volume of the abdomen. If a female is carrying hatched larvae and eggs with fully developed embryos, these are always found closer to the genital opening than are eggs without apparent embryos.

Eggs and hatched larvae are surrounded and separated from each other by a gelatinous matrix that does not dissolve upon treatment with cold 10% potassium hydroxide. This matrix constrains larval movements, but its disposition at the time of larviposition, and its chemical constitution remain unstudied.

Form of first instar larvae

First instar larvae of *P. angustata* and *P. hubbardi* have an orthosomatic body shape, and are *c.* 1.5 mm long. The body is cylindrical, with convex tergites and sternites. Stemmata are absent. The antennae are short and stout, and held appressed to the frontal region of the head (Fig. 1A). The head and sclerites of the thorax and abdomen bear the trumpet-shaped setae characteristic of other known *Pseudomorpha* larvae (Fig. 1). These relatively stout setae are often associated with depressions in the integument (Fig. 1B), indicating that larvae are neither fully inflated nor fully sclerotized while in the female. The legs are relatively short, and the tarsungulus bears two unequal claws. The basal abdominal segments are of the same diameter as the metathorax, with segments VII, VIII and IX of gradually decreasing diameter. Segment X is a small button-like segment without urogomphi.

Seasonality of larval occurrence in females

Totals of the number of eggs without visible embryos, the number of eggs with fully developed embryos visible, and the number of free larvae were recorded for eight *P. hubbardi* and 17 *P. angustata* females from throughout the collecting season (Fig. 2, Appendix). Presence of larvae from of the egg chorion is restricted to the latter portion of July, August and early September. This is the period of summer rains in southern Arizona, where the specimens were taken. The total number of eggs plus free larvae found per female averages 32.6 ($s=15.0$, $n=17$) for *P. angustata*, and 34.9 ($s=15.0$, $n=8$) for *P. hubbardi*. Females may contain only eggs without visible embryos, or they may carry eggs without embryos plus eggs with embryos and/or free larvae. The constant occurrence of the most fully developed larvae closest to the genital opening implies that larvae may be deposited in sequential batches as they hatch from the egg. Whether unhatched eggs are also laid after larviposition is completed is unknown, but this would appear unlikely given the occurrence of ovoviviparity in the first place.

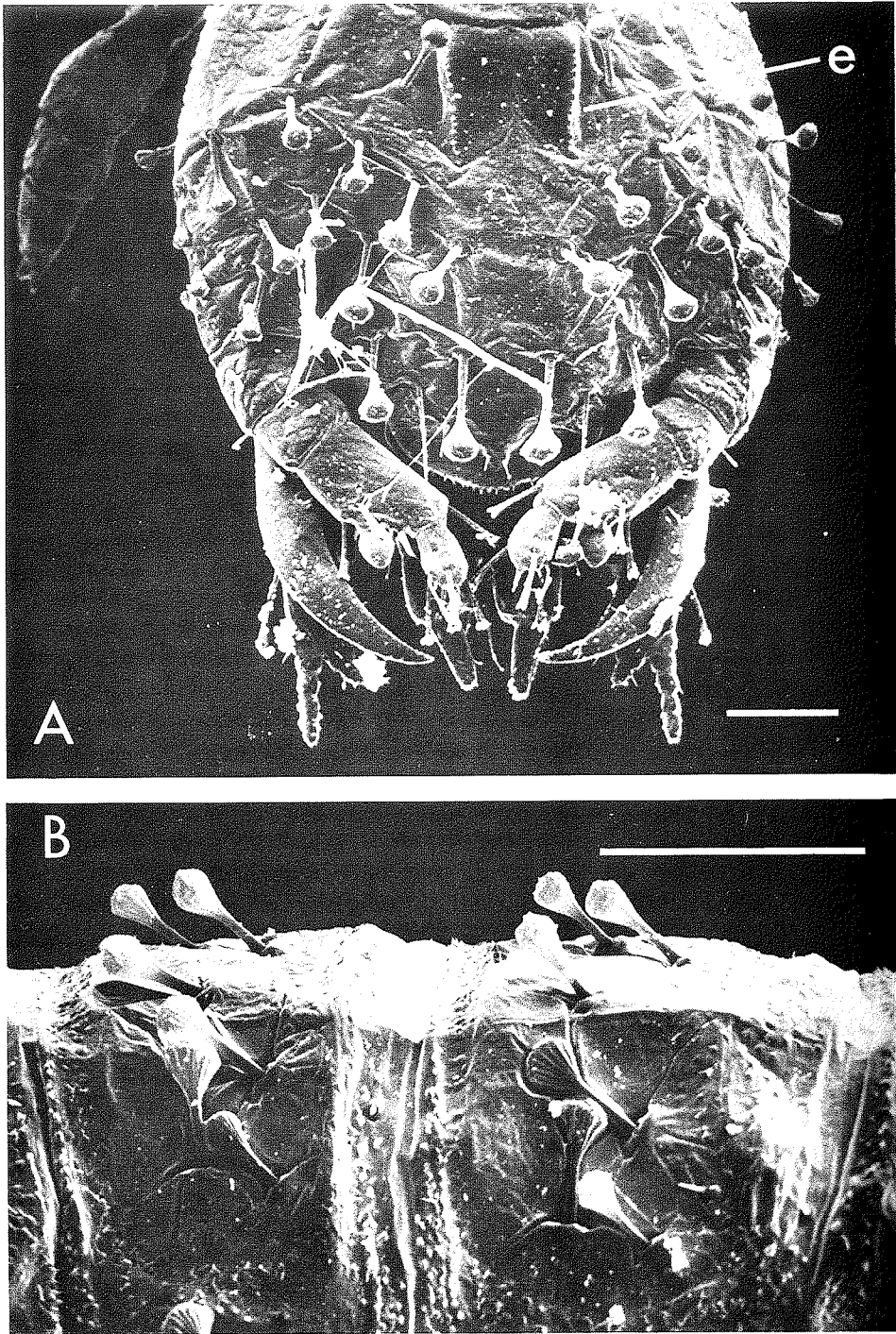


FIG. 1. Scanning electron micrographs of first instar larvae of *Pseudomorpha hubbardi*. A, dorsal view of head. e, Ecdysial ridge. Scale bar = 0.05 mm. B, Lateral view of setae on first and second abdominal tergites. Scale bar = 0.1 mm.

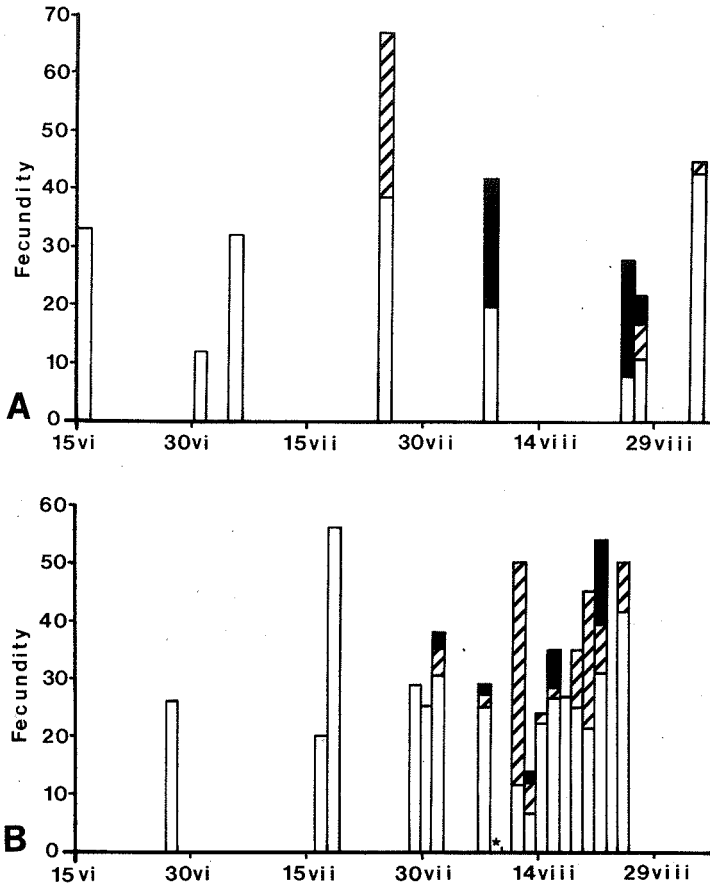


FIG. 2. Totals of hatched larvae (■), mature embryos (□), and eggs without visible embryos (▨) dissected from female *Pseudomorpha*; for date-locality data see Appendix. A, *P. hubbardi*, B, *P. angustata* (asterisk indicates female without eggs).

Discussion

Larvae of most carabid beetles are active aggressive predators, and are often cannibalistic when confined together. Larvae carried by *Pseudomorpha* females differ from free-living carabid larvae in the orientation of their antennae; the antennae being held close to the head, not porrect as in active larvae. The impressions in the cuticle associated with the trumpet-shaped setae imply that these larvae are not fully sclerotized. Thus, even though these larvae have eclosed, they are not a functionally active life stage before larviposition.

First instar larvae of *P. angustata* and *P. hubbardi* possess an orthosomatic body shape, with the mushroom-shaped setae found over the entire body surface (Fig. 1B). The first instar larvae of a myrmecophilous *Pseudomorpha* sp. described from Nevada (Erwin 1981) differs by having a physogastric body shape, and having the mushroom-shaped setae concentrated on the head region. The differences between the first instar

larvae of *P. hubbardi* and *P. angustata*, and those of the *Pseudomorpha* sp. from Nevada may indicate differences in life history strategies within the genus. Retention of the more plesiotypic character states of orthosomatic body shape and generalized setal distribution in *P. hubbardi* and *P. angustata* may indicate selective pressures acting against physogastry in first instars of these species. The most probable constraint on body shape would involve the larvae hatching inside the gelatinous matrix in which the eggs are carried in the female.

In *Pseudomorpha hubbardi* and *P. angustata* females, eggs mature within the greatly expanded median and lateral oviducts. In a gravid female, the ovarioles are reduced to thin strands at the anterior of the abdomen, the eggs being packed alongside each other within the oviducts. In the chrysomelid beetle *Orina vittigera* Suffr., eggs mature while still in the individual ovarioles (Champion and Chapman 1901). Larger larvae are found near the base of the ovarioles, with smaller, less mature larvae found distally. The tenebrionids *Eurynotus capensis* and *Melanopterus marginicollis* have a single large egg or larva within the bursa copulatrix or vagina of females (Tschinkel 1978). The different manner in which maturing eggs are held in *Pseudomorpha*, *Orina*, *Eurynotus*, and *Melanopterus* indicates fundamental differences in the physiological bases for ovoviviparity among these taxa.

In myrmecophilous Staphylinidae, the chief benefit of the female holding the eggs until larviposition is the elimination of potential egg mortality caused by foraging or nest-cleaning ant hosts. In *Lomechusa* and *Atemeles* the adult beetles enter the nest to larviposit (Hölldobler 1970). In these groups the larvae can appease, as well as solicit regurgitated food from their ant hosts (Hölldobler 1967, 1971). In *Pseudomorpha* species that have adopted ovoviviparity, it may be hypothesized that the phenomenon has likewise evolved to reduce egg mortality due to ant predation. By this reckoning, female *Pseudomorpha* beetles should also enter ant nests to larviposit. Such a strategy would require appeasement behaviour by both the adult and larval stages of ovoviviparous *Pseudomorpha* species.

The occurrence of ovoviviparous Chrysomelidae, which are not intimately associated with ants, indicates that termitophily or myrmecophily are not prerequisites for the evolution of ovoviviparity in Coleoptera. The ovoviviparous chrysomelids are chiefly montane and subarctic species. Larviposition may increase the larval survival rate by eliminating external incubation in a fluctuating or marginal environment. Internal incubation of eggs by female beetles basking in sunny areas of habitat could also shorten the incubation period, improving the chances that the next generation could be completed before environmental conditions deteriorate.

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Appendix

Date locality data and deposition of material for *P. hubbardi*. AZ: Pima Co., Santa Rita Mts, Madera Cyn., 4400 ft, 15.vi.1963 (CUIC); AZ: Cochise Co., Huachuca Mts, Miller Cyn., 5000 ft, 1.vii.1974 (CUIC); AZ: Santa Cruz Co., Santa Rita Mts, Madera Cyn., 4880 ft, 4.vii.1963 (CUIC); AZ: Cochise Co., San Bernardino Rch., 25.vii.1949 (MCZ); AZ: Santa Cruz Co., Capitan Mt., 8.viii.1933 (CAS); AZ: Cochise Co., Huachuca Mts, 5600 ft, 26–27.viii.1981 (CUIC); AZ: Pima Co., Quijotoa, 27.viii.1927 (CISC); AZ: Coconino Co., 6.3 miles EESE Flagstaff, Walnut Cyn., 6500 ft, 5.ix.1964 (CUIC). Data for *P. angustata*: AZ: Cochise Co., Huachuca Mts, Miller Cyn., 5000 ft, 25.vi.1974 (CUIC), 30.vii.1974 (CUIC); AZ: Cochise Co., Portal, 18.vii.1963 (CISC), 9.viii.1958 (CISC); AZ: Chiricahua Mts, 20.vii.1944 (CISC); AZ: Santa Cruz Co., Patagonia, 1.viii.1924 (CAS), 2.iii.1924 (CAS); AZ: Gila Co., Globe, 8.viii.1933 (CAS); AZ: Cochise Co., Texas Colony, 12.viii.1974 (AMNH); AZ: Pima Co., Tucson, 14.viii.1924 (CAS); AZ: Cochise Co., near Chiricahua National Monument, 17.viii.1952 (CAS); AZ: Cochise Co., Douglas, 19.viii.1940 (CAS), 20.viii.1940 (2, CAS); AZ: Cochise Co., 7 miles south of Gleason, 20.viii.1977 (2, AMNH); AZ: Pima Co., Baboquivari Mts, 23.viii.1949 (MCZ).

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