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**BIOLOGY OF THE MYRMECOMORPHIC PLANT BUG  
*ORECTODERUS OBLIQUUS* UHLER  
(HETEROPTERA: MIRIDAE: PHYLINAE)**

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*Abstract.*—The basic biology of the myrmecomorph *Orectoderus obliquus* Uhler (Heteroptera: Miridae: Phylinae) is described, including details of its growth, morphology, phenology, distribution and behavior. We document the temporal relation of *O. obliquus* to its host plant, *Penstemon procerus brachycanthus* (Pennell) Cronq., as well as to species of ants and visual predators that may serve as models and operators in a Batesian mimicry system including *O. obliquus*. The morphological and behavioral correspondence between various stages of the myrmecomorph and the six most common species of potential ant models is described.

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*Orectoderus obliquus* Uhler (Miridae: Phylinae) is a myrmecomorphic plant bug traditionally placed in the tribe Hallodapini (Carvalho, 1958; Knight, 1968). New evidence suggests, however, that *Orectoderus* and its New World relatives *Coquillettia* Uhler and *Teleorhinus* Uhler form a monophyletic group distinct from other hallodapines (R. T. Schuh, pers. comm.). The less ant-like Nearctic genus *Pronotocrepis* Knight and the Palearctic genus *Ethelastia* Reuter also seem to belong to this group.

*Orectoderus* is a North American genus comprised of ten species, of which only *O. obliquus* is found east of the Rocky Mountains. The genus was reviewed by Knight (1968), who described six new species and provided a key to adult males. Our determination of *obliquus* for the present study was based on information in Knight's review in conjunction with an examination of type specimens at the National Museum of Natural History, Washington, D.C. *Orectoderus obliquus* is distinguished from other species of the genus by the large size (length: male 6.7–8.2 mm; female 5.3–5.8 mm), shiny luster of the pronotum and hemelytra, weakly convex calli of the male, and by the structure of the male genitalia.

*Orectoderus obliquus* has a transcontinental distribution in southern Canada and northern United States with deep southward penetration into the Rocky Mountains (Fig. 1). This species is typically associated with grasses and herbaceous flowering plants throughout its range (Knight, 1923, 1941; Kelton, 1980, also gives *Rosa acicularis* Lindl. as host). Knight (1941) reported that it "occurs on the ground" and is "associated with ants." In the western Cascades of Oregon, *obliquus* is strictly associated with *Penstemon procerus brachycanthus* (Pennell) Cronq., which we have identified as a breeding host of this species. Although adults are sometimes found on other herbaceous plants of the subalpine meadow community to which *obliquus* belongs, they do not appear to use these plants for oviposition or as an important food resource.

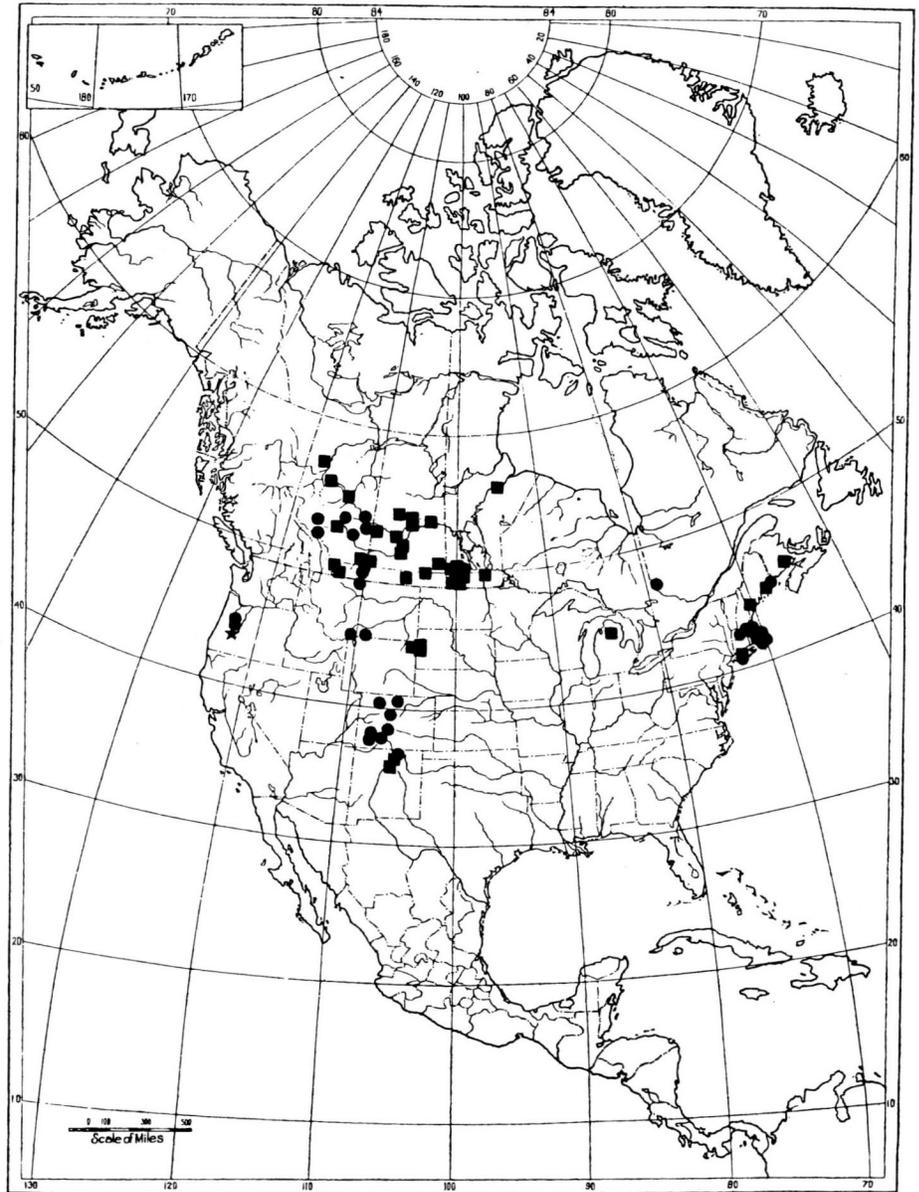


Fig. 1. Distribution of *Orectoderus obliquus* Uhler: ●, records from our examination of museum specimens; ■, other published records (also reported from Connecticut, Illinois, Kansas, Ontario, Pennsylvania, and Washington, without specific locality data); ★, Carpenter Mt. study area in west-central Oregon.

The adults of *obliquus* are sexually dimorphic, with a brachypterous and ant-like female (Fig. 2a). The major myrmecomorphic features of the female are: 1) brachyptery—hemelytra very small, pointed, strongly upturned; 2) elongation and lateral rounding of the thoracic tergites, especially the pronotum; 3) bulbous, petiolate abdomen with the anterior two segments strongly constricted and the lateral margins (connexiva) abruptly upturned; 4) large, elongate head with greatly enlarged gular region; and 5) long, thin legs. The male is macropterous and much less ant-like, lacking most of the thoracic and abdominal modifications of the female (males have weakly constricted anterior abdominal segments). In populations east of and including the Rocky Mountains, the hemelytra of males are sometimes totally black. However, males usually have white markings on the hemelytra, especially in western populations (Fig. 2b). Knight (1923) described the black form as a color variety (*O. obliquus* var. *ferrugineus*), known only from the state of New York. We have examined uniformly black specimens from Colorado, Montana, Massachusetts, New York, and Alberta and Manitoba.

The nymphs of both sexes are fair to good myrmecomorphs, becoming more slender and ant-like with age. Late instar males are less ant-like because of the greatly increased size of the meso- and metathoracic wing pads. Nymphs have extensive pale markings on the first two abdominal segments, that may serve to enhance the petiolate appearance of the abdomen.

*Orectoderus* species all bear a convincing resemblance to ants, and yet there is no published information on their basic biology and ecological relation to ant models and to potential operators. The purpose of this paper is to describe the basic biology of *obliquus* and to identify potential models and operators associated with it. This study, along with a companion paper on *Coquillettia insignis* Uhler (McIver and Stonedahl, 1987) will serve as a base upon which more detailed studies of ant-mimicry will depend.

#### STUDY AREA AND METHODS

*Study area.* The research was conducted from June through August 1983 and 1984 in the H. J. Andrews Experimental Forest, near Blue River, Oregon (122°21'W; 44°10'N). *Orectoderus* populations were studied in four subalpine meadows located on the southern flank of Carpenter Mt., at elevations ranging from 1,370 to 1,465 meters. These steep, well-drained, rocky meadows harbor a rich assemblage of low-growing herbaceous plant species, including the small-flowered penstemon, *Penstemon procerus brachycanthus* (Scrophulariaceae). Individual penstemon plants grow in dense mats and produce tall flowering stalks (15–30 cm) terminating in a dense cluster of small, tubular, blue flowers. Budbreak occurs just after snowmelt (usually early June) and blooming begins in late June to early July. Sampling evidence suggests that *obliquus* occurs primarily on *P. p. brachycanthus*, particularly in the early season. We therefore focused our attention on this plant species to study *Orectoderus* biology, and to examine the relations among *obliquus* individuals, their presumed ant models, and potential operators.

*Methods.* Individuals of *obliquus* ranging from 3rd instar to adult were collected in the four meadows to provide material for description, illustration, and fecundity

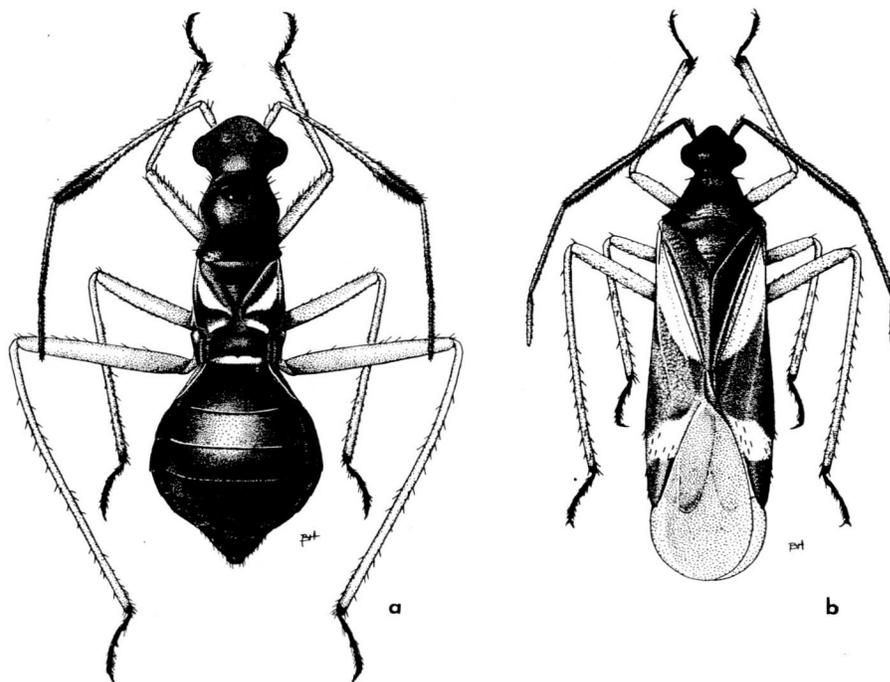


Fig. 2. Adults of *O. obliquus*, dorsal habitus. a. Female. b. Male.

estimates. Forty of these specimens were reared on a penstemon diet at approximately 25°C to obtain information on durations of the 4th and 5th nymphal stadia. Estimates of fecundity (estimated as egg-load) were obtained by dissecting six field-collected and four laboratory-reared females.

A cassette tape recorder was used to record continuous behavioral activity of *O. obliquus* and a time budget was constructed using these observations. A total of 18 hours of observations on 3rd, 4th, and 5th instar nymphs and on adult females were recorded in this manner. These data provide important information on basic habits. Casual observations of behavior (especially predatory and ovipositional behavior) were made throughout each field season to supplement the time budget data.

Penstemon plants in all four meadows were sampled regularly for arthropods from snowmelt in early June to the onset of plant senescence in mid-August 1983 and 1984. Samples were taken with both sweep-net and D-vac device (Echo Power Blower®) and provided information on the phenological relation of *O. obliquus* to its host plant, as well as the temporal correspondence of the myrmecomorph to its potential ant models and arthropod operators. We identified all possible ant models and the common species of potential operators (visual arthropod predators and birds) that occurred on or around the penstemon plants during the active portion of the life cycle of *obliquus*.

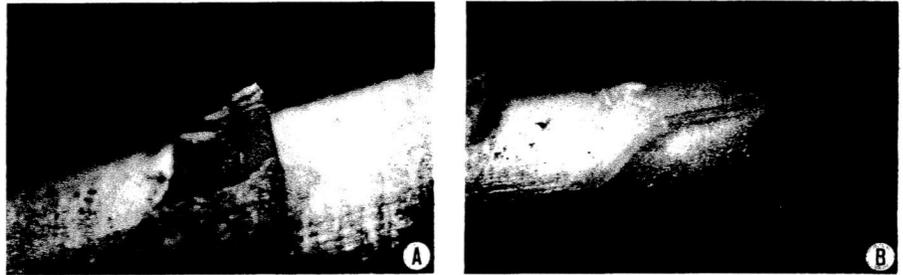


Fig. 3. Eggs of *O. obliquus* in penstemon stem. a. Eggs with neck and operculum exposed. b. Stem with elongate oviposition scar and single well-embedded egg.

#### RESULTS AND DISCUSSION

*The life cycle.* Females of *O. obliquus* deposit their eggs just under the surface of the flowering stems of *P. p. brachycanthus*. The eggs are inserted obliquely to the stem surface, leaving the operculum and chorionic rim collar exposed (Fig. 3). The eggs overwinter in the dried-out, persistent stems and hatching occurs immediately after snowmelt the following spring, usually between late May and late June. Hatching occurs prior to penstemon bloom with early instars remaining in the dense, matted foliage of the plant, making it difficult to collect them by sweep-net or D-vac techniques. We have observed second through fifth instars running on upper parts of the plant.

Nymphs require an average of 5.55 days ( $N = 62$ ,  $SE = 0.22$ , range 2.5–10) to complete a stage, with the fourth and fifth instars requiring 5.57 days ( $N = 21$ ,  $SE = 0.42$ , range 2.5–10) and 6.48 days ( $N = 25$ ,  $SE = 0.21$ , range 3–9), respectively. Thus, total developmental time from eclosion to adult is about four weeks. Hatching date and postembryonic developmental speed thus place *obliquus* on its host plant during peak flowering period, from mid-June to late July. This temporal relation agrees with our observation that *Orectoderus* spends a substantial amount of time feeding on penstemon flowers. The adult is the dominant stage by late July, with mated females ovipositing in flowering stems until about mid-August to complete the life cycle. The ten dissected females (reared and field-collected) had egg loads ranging from 6–30, with an average of 18.2 ( $SE = 2.4$ ).

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*Description of immature stages.* EGG (Fig. 4a). Length 1.50–1.60 mm, greatest width 0.22–0.28 mm; color and structure as described for *Coquillettia insignis* (see McIver and Stonedahl, 1987, fig. 5a), except slightly larger with shorter, broader and apically truncated opercular process and chorionic rim collar.

*NYMPHS* (Fig. 4b–f). Nymphal descriptions and illustrations are based on alcohol-preserved specimens displaying normal growth and orientation of the various body regions and appendages. Only 3rd–5th instars are treated, as younger stages (1st and 2nd instars) were not encountered in high enough numbers to allow for an adequate sample of specimens. Third through fifth instar nymphs are most easily differentiated by overall length, size of the head capsule, length of the rostrum and second antennal segment, and size of the wing pads. Sex can be determined by the greater development

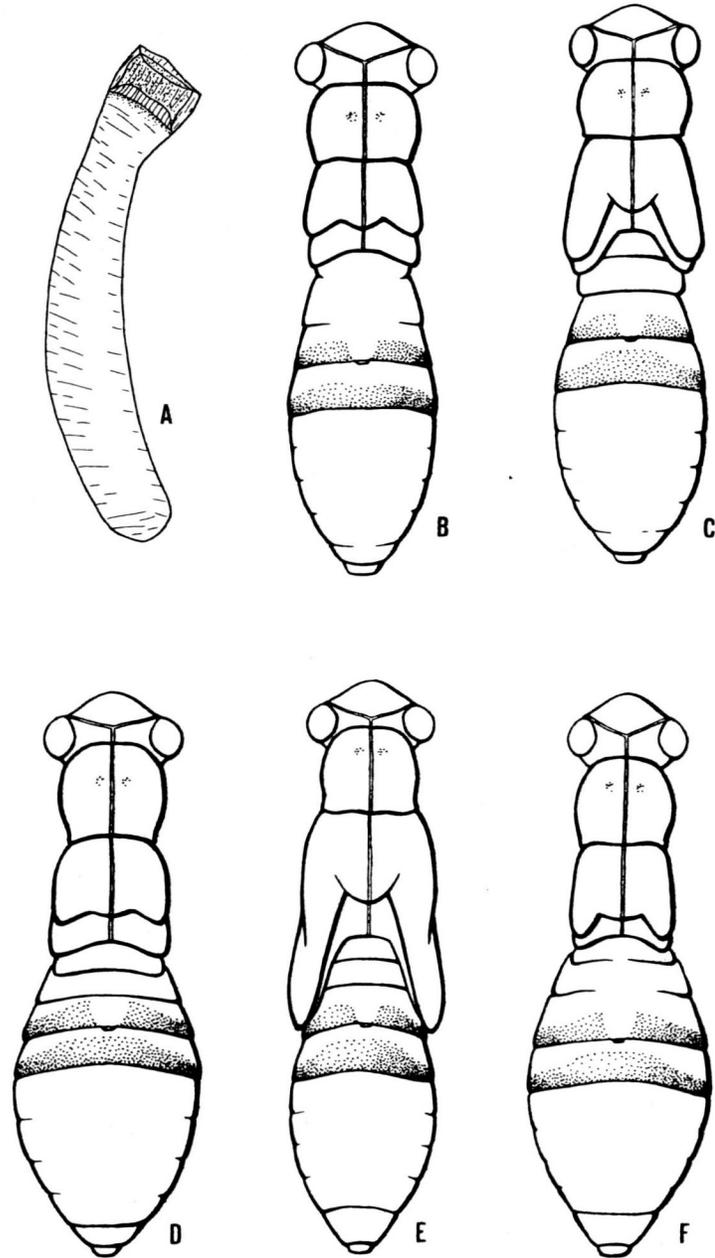


Fig. 4. Immature stages of *O. obliquus*. a. Egg. b. Third instar. c, d. Fourth instar. c. Male. d. Female. e, f. Fifth instar. e. Male. f. Female.

of wing pads in the male and by differences in the position of the sclerotized plates on the ninth abdominal sternite (see following descriptions for detail and fig. 5e, f in McIver and Stonedahl, 1987). All measurements are in millimeters.

**THIRD INSTAR (Fig. 4b).** Length 2.65–2.80; strongly myrmecomorphic; brown or dark brown general coloration; head and thorax, especially pronotal disk, shagreened or finely granulate, moderately shining; dorsum with sparsely distributed, black, bristle-like setae; antennae and legs, especially tibiae, with more densely distributed bristle-like setae. Head: large, subovate, strongly declivous; length 0.77–0.81 (measured from posterodorsal margin to apex of tylus), width across eyes 0.67–0.68, distinctly broader than pronotum, vertex 0.31–0.35; posterior margin rounded; frons broad, weakly convex, junction with tylus indistinct; antennal fossa large, situated well anterior of eye; tylus, jugum, and lorum short; buccula short, narrow; gena and gula well developed, gular region broadly produced. Rostrum: length 1.06–1.11, reaching between metacoxae. Antennae: linear, segment I slightly broader than II–V, narrowed basally; brown or yellowish brown, segment IV sometimes lightly tinged with red; length of antennal segment I 0.18; II, 0.61–0.62; III, 0.48–0.50; IV, 0.46–0.56. Thorax: uniformly brown or dark brown, sternites yellowish brown; pronotal disk broader than long (length 0.38–0.40; median width 0.51–0.59), broadest medially, anterior angles broadly rounded, posterior angles right-angulate, anterior margin slightly concave medially, posterior margin nearly straight, calli indistinct; wing pads short, mesothoracic pair not produced posteriorly in the female, slightly produced in the male, length 0.04 (measured from posterior margin of mesonotum to apex of wing pad). Abdomen: oblong-oval, somewhat bulbous, segments I and II constricted; translucent brownish yellow, except segments I and II opaque creamy white; weakly sclerotized, except tergites III, IV, and IX, and small subspherical lateral plates on tergites V–VIII more heavily sclerotized and dark brown; abdominal sternite IX of female with small sclerotized plate either side of midline, plates narrowly connected medially, male with pair of broadly separated plates on ninth sternite. Legs: uniformly brown, tibiae and tarsi sometimes lighter brown or brownish yellow; pretarsal pulvillus large, reaching beyond apex of claw.

**FOURTH INSTAR MALE (Fig. 4c).** Similar to third instar except larger, rostrum reaching only to apices of mesocoxae or slightly beyond, wing pads longer, and abdomen slightly more sclerotized, with lateral plates on tergites V–VIII and ventral plates on sternite IX slightly larger. Length 3.35–3.80. Head: length 0.88–0.94, width across eyes 0.82–0.85, vertex 0.42–0.45. Rostrum: length 1.41–1.59. Antennae: I, length 0.21–0.23; II, 0.91–0.96, slightly thicker distally; III, 0.64–0.71; IV, 0.60–0.65. Thorax: length of pronotal disk 0.54–0.55, median width 0.65–0.72; length of mesothoracic wing pad 0.32–0.35, reaching to anterior margin of second abdominal tergite.

**FOURTH INSTAR FEMALE (Fig. 4d).** Similar to male, except body usually slightly smaller, and wing pads much shorter. Distinguished from third instar female by larger size, broader head, much longer rostrum and second antennal segment, and mesothoracic wing pads slightly produced posteriorly. Length 3.20–3.25. Head: length 0.92–0.95, width across eyes 0.79–0.84, vertex 0.44. Rostrum: length 1.37–1.51, reaching between metacoxae or nearly so. Antennae: I, length 0.22; II, 0.87–0.88; III, 0.65–0.66; IV, 0.51. Thorax: length of pronotal disk 0.51, median width 0.62–

0.65; length of mesothoracic wing pad 0.06–0.08. Abdomen: eighth sternite with small sclerotized plate on ventroposterior margin.

**FIFTH INSTAR MALE** (Fig. 4e). Similar to fourth instar except body size larger, head broader, and with rostrum, antennal segment II, and wing pads much longer. Length 4.35–4.65. Head: length 1.04–1.11, width across eyes 0.96–1.05, vertex 0.48–0.50. Rostrum: length 2.00–2.15, reaching between mesocoxae or slightly beyond. Antennae: I, length 0.25–0.28; II, 1.26–1.57; III, 0.91–1.06; IV, 0.75–0.88. Thorax: length of pronotal disk 0.65–0.72, median width 0.75–0.90; length of mesothoracic wing pad 0.98–1.25, reaching to posterior margin of third, or sometimes onto fourth abdominal tergite. Abdomen: lateral sclerotized plates on tergites V–VIII and ventral plates on sternite IX much larger than in fourth instar, those on ninth sternite only narrowly separated medially.

**FIFTH INSTAR FEMALE** (Fig. 4f). Similar to male except body usually slightly smaller with much shorter wing pads and second antennal segment more abruptly expanded distally. Distinguished from fourth instar female by larger size, broader head, and longer rostrum, second antennal segment, and wing pads. Length 3.90–4.65. Head: length 1.04–1.19, width across eyes 0.90–1.06, vertex 0.49–0.54. Rostrum: length 1.90–2.17, reaching between metacoxae or slightly beyond. Antennae: I, 0.24–0.31; II, 1.28–1.39, distal third distinctly expanded, more so than in male; III, 0.86–0.94; IV, 0.72–0.76. Thorax: length of pronotal disk 0.62–0.75, median width 0.79–0.90; length of mesothoracic wing pad 0.21–0.25. Abdomen: sternites VIII and IX with large ventral sclerotized plates.

**Behavior.** A total of 14 individuals of *O. obliquus* (2nd instar to adult) were observed continuously on *P. p. brachycanthus* for 894 minutes in July and August 1984. Behavior varied little among life history stages, and so all observations are pooled in this analysis. In general, *O. obliquus* is an active, diurnal plant bug that feeds primarily on the plant juices of *P. p. brachycanthus*. Individuals do not interact with ants or other insects in any way, and until mating, lead completely solitary lives. These visually-oriented herbivores divide their time into five fairly distinct behavioral categories: 'rest,' feed, groom, run, and probe.

The 'rest' phase is defined as complete inactivity and occurred 34.5% of the time. While resting, the insect was responsive to outside visual stimuli, but remained immobile with the proboscis tucked in. Bugs usually rested on the lower portions of the plant, and on the underside of penstemon leaves. Interspersed with periods of rest were extended bouts of feeding, during which the proboscis was inserted into a leaf, stem, or flower and plant juices extracted. Over half of the total amount of feeding time was spent sampling flowers or chlorotic areas of leaf tissue. The average duration of a feeding bout was 164 seconds, during which time the antennae were gently waved and the insect was relatively unresponsive to external visual stimuli. About 30% of the time budget consisted of plant-feeding, suggesting that *O. obliquus* is primarily an herbivore—only two individuals were observed feeding on other insects (both aphids) in the 894 minutes of observation.

Grooming behavior was observed at fairly regular intervals, usually just after feeding. *Orectoderus* individuals spent a total of 3.6% of their time grooming the face, eyes, antennae, proboscis, and all three pairs of legs. Tarsi of the first pair of legs were used to groom all head-associated parts, while the 2nd and 3rd pairs of

legs were rubbed against one another. The amount of time spent grooming is similar to that observed for two other mirid species, the myrmecomorph *Coquillettia insignis* Uhler and the non-mimetic orthotyline *Lopidea rolfsi* Knight (McIver and Stonedahl, 1987), suggesting that this activity is essential to basic body maintenance in plant bugs.

*Orectoderus* is a very active plant bug, spending a significant amount of time (19%) running rapidly from one point to another on its host plant or between host plant patches. During the run mode, the antennae are waved about and the proboscis is tucked in. Very often, an individual will slow down and insert the proboscis into plant tissue for a brief period of time (probing, 12.6%). Presumably, this behavior serves to assess the quality of the resource, since probing periods are very often followed by feeding. Individual bugs tended to remain on a single plant for long periods of time, but were commonly observed running along the ground between host plants. The amount of observed interplant movement suggests that individual bugs can disperse significant distances by running. This observation is supported by the fact that adults of both sexes were collected on a variety of plant species in habitats adjacent to the rocky meadows where *P. p. brachycanthus* grows. Clearly, both macropterous males and brachypterous females move among meadows, at least on a local scale.

*Possible models and operators.* A total of eleven species of ants were collected on and around *P. p. brachycanthus* from June through August 1983 and 1984, of which six were particularly common (Fig. 5). The common species vary considerably in size, shape, color, and behavior, and so the overall correspondence between these species and *O. obliquus* varies accordingly. With respect to morphology and behavior, *O. obliquus* (as well as other hemimetabolous myrmecomorphs) potentially belongs to a 'transformational' mimetic complex (Reiskind, 1972), where at least two genera and six species of ants may serve as models for the various instars.

There are no ant models of appropriate size for the first and second instars of *O. obliquus*. Third instar nymphs correspond in size to the myrmecine *Leptothorax muscorum* (Nylander) and to the dolichoderine *Tapinoma sessile* (Say) (Fig. 5). Because of the lighter color, strongly constricted body, and relatively slow, non-stopping running behavior, *L. muscorum* is unlikely to be an effective model for third instar nymphs which are darker, less constricted, and quicker afoot. A much closer correspondence in morphology and behavior is observed between *T. sessile* and third instar *O. obliquus*, because this ant species is dark brown, has a less constricted body and is very active. Fourth instar nymphs correspond in size to only one common ant species, *Formica lasioides* Emery. The dark color and close match in size and shape make 4th instar *O. obliquus* convincing mimics of *F. lasioides*. Three other *Formica* species may serve as models for fifth instar nymphs: *F. altipetens* Wheeler, *F. fusca* Linnaeus, and *F. neorufibarbis* Emery. Because of caste and morph variability, individuals of these three species also are similar in size to adult females of *O. obliquus*. Since *Formica* species are similar in shape to *O. obliquus* and are also very active, these correspondences in size, shape and behavior between mimics and presumed models are convincing. However, both *F. altipetens* and *F. neorufibarbis* are 'red' ants and hence, are easily distinguished from darker *O. obliquus*. It is interesting that color variation in the adults of *Orectoderus* species and within species

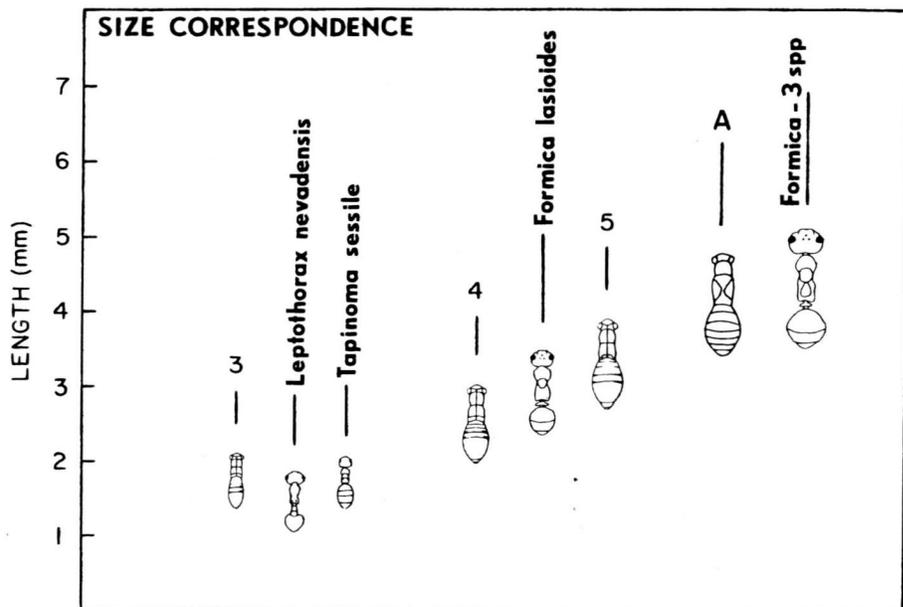


Fig. 5. Correspondence in size and shape between female *Orectoderus obliquus* (3rd instar to adult) and the six most common co-occurring ant species; Carpenter Mt., H. J. Andrews Exp. Forest, Oregon.

of other ant-like mirids (e.g., *Paradacerta* Carvalho and Usinger, *Coquillettia*) tend to be expressed as a dimorphism of red versus brown phenotypes, with the distribution of color among body parts closely paralleling color distribution in various *Formica* species. It is not known if these color patterns are relevant to the mimicry systems within which these species presumably interact.

Although there is evidence that some myrmecomorphic insects derive benefit from their appearance by gaining access to or preying on ants (Oliveira and Sazima, 1984), most myrmecomorphs are probably Batesian mimics (Reiskind, 1977; McIver, 1987). Most ants defend themselves with some combination of mandibles, stings or noxious chemicals (Wilson, 1971), and it is likely that many visual predators learn to associate these characters with ant morphology and/or behavior, subsequently avoiding not only ants, but other arthropods that resemble them (Wickler, 1968). Although it is difficult to identify the operators that may actually maintain a mimetic system in *O. obliquus*, it is likely that predators such as small birds and visual arthropods are involved. We identified several species of ground-foraging birds on our study sites, including dark-eyed juncos, varied thrushes, American robins, and cedar waxwings. The arthropod predator fauna is potentially more diverse. We collected seven very common species of visual predators on *P. p. brachycanthus*, including five species of salticid spiders (*Eris margineta* (Walck.), *Phidippus johnsoni* G. & E. Peckham, *Habronattus viridipes* (Hentz), *Sassacus* sp., and *Metaphidippus* sp.), an oxyopid

spider (*Oxyopes scalaris* Hentz), and a very common damsel bug (*Nabis alternatus uniformis* Harris). Traditionally, arthropods have been excluded from the list of important operators in Batesian mimicry systems, because of their small size, and limited perceptive and learning skills. But there is evidence that at least some arthropods are capable of discrimination among prey types and can learn from their experiences (Gelperin, 1968; McIver, 1987). Since ants are well within the acceptable size range preferred by many arthropod predators, it is worthwhile to investigate the possibility that visual arthropods may be important operator species. Both *Orectoderus* and the related genus *Coquillettia* offer excellent opportunities for the study of perception and learning in arthropod predators. Understanding how these predators perceive and learn is critical to identifying their role in the regulation of Batesian mimicry systems.

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