BIOLOGY OF *OBEZA FLORIDANA* (ASHMEAD) AND *PSEUDOCHALCURA GIBBOSA* (PROVANCHER) (HYMENOPTERA: EUCHARITIDAE)

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Abstract.—Brief descriptions of life history are given for *Obeza floridana* (Ashmead) and *Pseudochalcura gibbosa* (Provancher) from Florida and northern Ontario, respectively. *Obeza floridana* oviposits into fruits of *Cyanococcus simulatus* Small and *P. gibbosa* into overwintering floral buds of *Ledum groenlandicum* Oeder. and leaf buds of *Arbutus menziesi* Pursh. Descriptions of eggs and first-instar larvae of each species are provided and compared to other Eucharitidae. *Pseudochalcura gibbosa* was reared from *Camponotus herculeanus* (L.) and details of complete life history and descriptions of all larval stages are supplied. Comparisons are made with the Old World genus *Stilbula* and their taxonomic interrelationships discussed.

Key Words: life history, larval stages

Obeza floridana (Ashmead) and *Pseudochalcura gibbosa* (Provancher) belong to the family Eucharitidae (Hymenoptera: Chalcidoidea). The genus *Obeza* Heraty was recently erected to hold the New World species that were previously considered to be members of the widespread Old World genus *Stilbula* Spinola (Heraty 1985). The genus *Stilbula,* and the genera *Obeza, Lophyrocera* Cameron (considered here to include *Tetramelia* Kirby) and *Pseudochalcura* Ashmead comprise a monophyletic group (Heraty 1985, 1986).

Systematic relationships within this clade have already been discussed (Heraty 1985, 1986) and are summarized as follows. *Obeza* has been regarded as the sister group to *Lophyrocera* + *Pseudochalcura* while *Stilbula* was considered the sister taxon to these three New World genera (Heraty 1985). *Lophyrocera* was again recognized as a sister group to *Pseudochalcura* by Heraty (1986) although this was questioned at the time. Exact placement of the genus *Pseudochalcura* is problematic since it is the only member lacking lateral propodeal processes and short, bifurcating spines issuing from the frenum. Close taxonomic relationship between *Pseudochalcura* and *Obeza* or *Stilbula* is supported by synapomorphies which include similar structure of the pronotal-prepectal area and musculature of the mesosoma (Heraty 1989). A recent discovery of two undescribed species of *Pseudochalcura* from the Orient suggest a closer relationship to the Old World genus *Stilbula* and to the recently described genus *Stilbuloidea* Bouček. Exact systematic relationships of these taxa have yet to be assessed but the monophyly of the group is certain (Heraty 1986).

As with other members of the Eucharitidae, the above-mentioned genera are specialized parasites of mature larvae and pupae of ants. Adult females deposit their eggs

away from the host into plant tissue. The active first-instar larva, termed a planidium, must make its way back to the ant nest, usually phoretically on an adult ant, where it can attack the brood (Clausen 1940a, b, 1941). Morphology of the immature stages, and in particular, the well-sclerotized planidium, is highly conservative and can be useful in positing relationships at the higher taxonomic levels (Heraty and Darling 1984). Such an approach can serve to test, supplement, and refine hypotheses derived from studies of adult morphology.

Lophyrocera (including *Tetramelia*) includes six described Neotropical species and *L. apicalis* Ashmead in the western United States (Heraty 1985). Nothing is known of the biology or immature stages of any of these seven species.

The genus *Obeza* is widespread in South America with two species represented in North America: *Obeza septentrionalis* (Brues) in Arizona and New Mexico and *O. floridana* in Florida and Georgia (Heraty 1985). The biology and immature stages of *Obeza* have remained completely unknown until this time.

Pseudochalcura is also widely distributed in the Neotropics (ten species) with three other species occurring in the Nearctic (Heraty 1986). *Pseudochalcura gibbosa* is widespread in North America and has a typical Boreal distribution to the north and occurs throughout the Rocky Mountains in the west (Heraty 1986). Adults of *P. gibbosa* have been recorded as ovipositing into flower buds of *Gossypium* (Malvaceae) in Arizona (Pierce and Morrill 1914) and *Arbutus* (Ericaceae) in California, along with collecting associations made with various other plants (Heraty 1986). *Pseudochalcura gibbosa* has been reared from *Camponotus novaeboracensis* (Fitch) in Michigan (Wheeler 1907), *Camponotus laevigatus* (F. Smith) and *Camponotus* sp. possibly *vicinus* Mayr in California (Heraty 1986). The only description of immature stages of *P. gibbosa* was by Wheeler (1907) for the female pupa and

position of two pupae in a cocoon of *C. novaeboracensis.*

In contrast to the paucity of information on the biology of the New World genera discussed here, there are detailed life history documentations and descriptions of immature stages for *Stilbula cyniformis* Rossi (Parker 1932, 1937, Parker and Thompson 1925), *Stilbula manipurensis* (Clausen) (Clausen 1928, 1940a, b), and *Stilbula tenuicornis* (Ashmead) (Clausen 1923, 1940b, 1941). Some peculiar features in the life histories of *Stilbula* species are useful in distinguishing this group from other Eucharitidae and for comparison to the two species in this paper. Females deposit their large egg masses of more than one thousand eggs in a single oviposition, and in *S. tenuicornis* and *S. cyniformis,* the eggs have the ability to overwinter (Clausen 1928, 1940b, Parker 1937). As in other eucharitids, planidia are mobile and attach themselves externally to mature ant larvae. The first-instar larvae are unique in their ability to complete development on the mature larva within the cocoon, and in *S. tenuicornis,* are cast off with the host's larval exuvium. The second-instar larvae then relocates to the mid-section of the pupa to resume feeding (Clausen 1923, Parker 1928). Finally, the third-instar larva has a distinctive morphology with respect to other known genera of Eucharitidae, and more than one eucharitid can develop on a single host pupa (Clausen 1923, 1940a, Parker 1932). The recorded ant hosts include *Camponotus herculeanus japonicus* Mayr and *Camponotus herculeanus obscuripes* Mayr for *S. tenuicornis* (Clausen 1923, 1941), *Camponotus* sp. for *S. manipurensis* (Clausen 1928), and *Camponotus aethiops* (Latr.) for *S. cyniformis* (Parker 1932, 1937).

The discovery of populations of *O. floridana* and *P. gibbosa* allowed us to gather information on the oviposition habits and life histories of these species. It also provides an opportunity to make comparisons between the New World genera and the pro-

posed outgroup genus, *Stilbula,* and to reflect upon the phylogenetic relationships of these taxa.

Obeza floridana (Ashmead)
(Figs. 2, 4, 8)

Location and habitat.—The collection site was located just outside of the Apalachicola National Forest, 3.0 kilometres south of Sopchoppy, Wakulla Co., Florida. The host plant was located within a narrow windrow of *Pinus* sp. that paralleled the highway and bordered a large tree-less bog. Within the windrow, the sandy soil was covered by a thick mat of pine litter and scrub vegetation that consisted of sporadic clumps of *Cyanococcus simulatus* Small. (Ericaceae), *Diaspyros* sp. (Sapotaceae), *Cyrilla racemiflora* L. (Anacardiaceae) and *Sabal glabra* (Mill.) Sarg. (Palmae).

General observations and collections.—Collections of adult *O. floridana, Cyanococcus* fruits, and ants were made on two separate occasions in 1987—25–26 May and 4–5 June. Adult *O. floridana* were localized in their distribution and although some males were collected in a broader area, most males and all of the females except one were collected from one isolated *C. simulatus* bush. All but one of the females were devoid of eggs. Most adults were collected 4–5 June while no females and only two males were collected 25–26 May after a similar collecting effort. No copulating pairs were observed.

Cyanococcus simulatus fruits were collected and returned to the laboratory. Egg masses were maintained at 75% RH over a saturated salt solution, either within intact berries or isolated in cotton stoppered glass vials, for a one month period. Although they remained viable over this period, no hatch of mature planidia occurred. Eggs retained for a longer period succumbed to desiccation and/or fungus.

Strays of *Camponotus abdominalis floridanus* (Buckley) were found but no association could be made. Therefore, no additional immature stages of *O. floridana* became available for study. *Obeza floridana* has been reared from the pupae of *C. abdominalis floridanus* near Gainesville, Florida (Lloyd Davis, Insects Affecting Man and Animals Research Laboratory, Gainesville, FL, personal communication).

Life history.—Adult females oviposit into developing fruits of *C. simulatus* in May and June. Adults were observed hovering around the edges of the *Cyanococcus* or settled on the fruits themselves. The single gravid female readily oviposited into green berries and later dissection showed the ovaries to contain about 3500 fully developed eggs. Egg masses in the fruits consist of small clusters of 25–180 eggs (mean = 100.9, SD = 47.3, n = 15) that are deposited in pockets within the epidermal layer of the fruit (Fig. 2). They can be seen through the skin of the fruit and are associated with a minute oviposition scar. A sample of 20 berries yielded 15 egg masses with 1–5 egg masses per fruit. The eggs were found in varying states of development within a single berry from pure white (recently deposited) to a darkened coloration owing to the mature planidium inside. These observations indicate multiple ovipositions in individual fruits by different females.

No information is available on how planidia escape the fruit or enter the host ant nest. Adults of *Camponotus femoratus* Fabr. are known to collect independently the pulp and seeds of berries from a number of plants (Davidson 1988). The berries may be direct attractants to the host with planidia collected along with the fruit pulp. Deposition of eggs into a perishable fruit, as early as June, indicate that planidia complete development within the season, even though egg hatch could not be stimulated in the laboratory.

Description of the immatures.—Egg (Fig. 4): Undeveloped eggs white with a smooth chorion. Length of egg body about 0.13 mm (SD = 0.01, n = 10); of caudal stalk 0.15 mm (SD = 0.02). Mature eggs with well-

sclerotized first-instar larva occupying almost entire egg body; head oriented toward stalk and small yellowish yolk mass attached to abdominal apex (Fig. 4). Except for the more rounded appearance of the egg body, the egg is similar to those of other Eucharitidae as described in Heraty and Darling (1984).

First instar (as dissected from egg; Figs. 8, 10, 12): As described for other Eucharitinae (Heraty and Darling 1984) but distinguished as follows. Length 0.14 mm (SD = 0.01, n = 10); maximum width 0.06 mm, widest medially and circular in cross-section. Cranium with labial plates present, including hatchet-shaped posterior labial plate; two pairs of dorsal sensilla; large, paired, weakly sclerotized cranial processes arising dorsally from an unsclerotized region. Tergite I + II separated ventrally, fused dorsally; tergopleural line absent. Tergite I + II with two dorsal and one ventral pair of setae; lacking one pair of ventral setae along ventral margin of tergite III; ventral margins of tergites V–VI extended posteriorly as long narrow processes; posterior-ventral margins of tergites V–XI strongly scalloped.

Additional information.—A second, undescribed species of *Obeza* was collected on 21 July 1987, in a dry cactus/scrub woodland habitat, 39.1 kilometres southeast of Teotitlan del Camino, Oaxaca, Mexico. Adults were observed ovipositing into the green berries of *Tragia volubilis* L. (Euphorbiaceae) which are similar in size and texture to the fruits of *C. simulatus*. The manner of egg deposition, relative size of the egg mass, and morphology of the first-instar larva were identical to those of *O. floridana*.
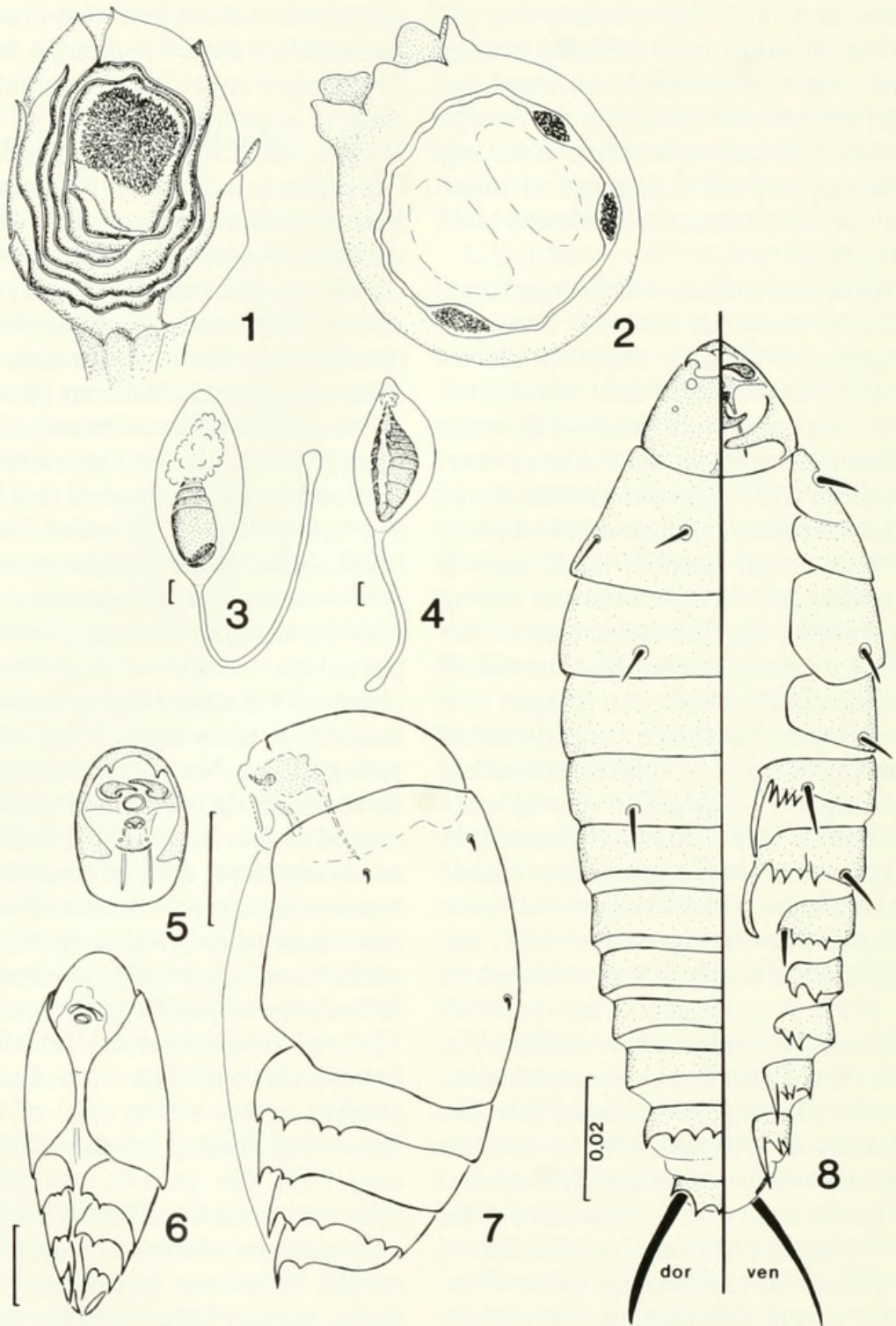
Pseudochalcura gibbosa (Provancher)
(Figs. 1, 3, 5–7, 9–15)

Location and habitat.—The collection site was located northeast of Sault Ste. Marie, Ontario approximately 18 kilometres northeast of Searchmont, at about mile 15 on Whitman Dam Road. The habitat is a disturbed, cutover area strewn with considerable fallen dead wood, slash, and stumps. The ground cover is predominated by *Vaccinium angustifolium* Ait., *V. myrtilloides* Michx., and *Ledum groenlandicum* Oeder. Other plants include *Polytrichum commune* Hedw. (Polytrichaceae), *Sphagnum angustifolium* (Russ.) C. Jens. (Sphagnaceae), *Gaultheria hispidula* (L.) Muhl., *Epigaea repens* L. (Ericaceae), *Cornus canadensis* L. (Cornaceae), *Clintonia borealis* (Ait.) Ras. (Convallariaceae), *Rubus* sp. (Rosaceae), and *Ribes glandulosum* Grauer. (Grossulariaceae) with scattered individuals of *Pinus strobus* L., *Abies balsamea* (L.) Mill., *Picea mariana* (Mill.) B.S.P., and *Larix laricina* (DuRoi) K. Koch (Pinaceae) and *Prunus pensylvanica* L. f. (Rosaceae).

General observations, collections, and phenology.—Adults of *P. gibbosa* were first observed 1 August 1986 as occasional males in sweep nets, in flight, or on branch tips of young spruce. No copulating pairs were observed. Female oviposition activity was localized on the floral buds of *Ledum groenlandicum* in an area of roughly 10 metres square and directed a concentration of future observations and collections here. In addition, occasional observations were made of females ovipositing in a wider area. In 1987, a Malaise trap was installed approximately 150 metres from this focus on another aspect of the edge of the cutover forest edge. Trap catches were accumulated over 7–14 day periods and those with *P. gibbosa* are summarized in Table I.

From these collections a minimum flight period of adults, particularly gravid females, occurred from 15 July to 12 August. Oviposition presumably occurs throughout this period and was supplemented by direct observation on 22 July and 11 August. The female-biased sex ratio (50:4) probably reflects differential behaviour of the sexes with concentration of activity and abundance of males in the vicinity of parasitized ant colonies where they might wait for emerging females. The lower number of spent females

Figs. 1–8. 1, Sub-sagittal section of floral bud of *Ledum groenlandicum* with single egg mass of *Pseudochalcura gibbosa*. 2, Sub-saggital section of fruit of *Cyanococcus simulatus* with three egg masses of *Obeza floridana* in different stages of development. 3, Egg of *P. gibbosa*. 4, Egg of *O. floridana*. 5–7, Planidium of *P. gibbosa*: 5, Ventral view of head; 6, Ventral habitus; 7, Lateral habitus. 8, Planidium of *O. floridana* (dor = dorsal, ven = ventral). All scale bars 0.02 mm.

Table 1. Occurrence of adult *P. gibbosa* in a Malaise trap, 1987.

Trapping Period	Days	Females		Males
		Gravid	Spent	
7–15.vii	9	1	0	0
16–22.vii	7	5	2	0
23–30.vii	8	15	7	2
31.vii–11.viii	12	4	2	2
12–25.viii	14	8	6	0
Totals	50	33	17	4

relative to gravid females (17:33) is likely due to reduced vigour and probability of flight interception after oviposition. Several *Ledum* buds were observed to have a dead spent female with its ovipositor still embedded.

Ledum buds were collected in August of 1986 and 1987 in order to obtain eggs and to attempt rearings of planidia. Eggs were held under a variety of conditions including cold storage at 2°C for four months, but even though the masses darkened relatively quickly after initial deposition (larvae matured internally), the eggs never hatched. A small sample of egg masses adhering to the dehiscing bracts of blooming *Ledum* on 29 May 1987 also failed to hatch.

Eight separate sample collections were made of *Camponotus* colonies (larvae, pupae, and adults) from 24 June to 22 July 1987. Two colonies of *C. novaeboracensis* about 20 metres from the *P. gibbosa* oviposition focus were found on 24 June not to be parasitized by *P. gibbosa*. The six collections of *C. herculeanus* (L.), on the other hand, were made within 3–5 metres of the focus. In total, four of these were eventually found to be parasitized. Ant larvae with planidia were evident in collections made on 24 June and 15 July while late-pupal or preadult *P. gibbosa* were found on 22 July.

Life history.—Adult females oviposit into the floral buds of *Ledum groenlandicum* (Ericaceae) in July and August. The ovipositor is used to penetrate directly through the bracts on the apical half of the buds. Some females are known to maintain this position on the bud for over one hour while others are found dead and devoid of eggs. These buds enclose an undeveloped inflorescence which overwinters and blooms in May–June the following season. Small, darkened, rose-brown spots visible on the external surface of the bracts could represent ovipositional scars but this was not evaluated.

Eggs are laid in the extrafloral cavities of the bud and not within plant tissue per se. One to five masses were found near the centre of the bud (not necessarily from the same female as evidenced by differential development) under several layers of bracts. The caudal stalks of the eggs were all joined at the centre of the egg mass by the apical swelling. The number of eggs in a single mass ranged from 400–1800 eggs with a mean of 943 (SD = 442, n = 10). Dissection of ovaries in unemerged females of *P. gibbosa* yielded 2000–2500 fully developed eggs. These relatively large egg masses suggest that no more than two or three ovipositions are made per female on average. It is possible that only a single oviposition is modal and some of the smaller egg masses may have been the result of interrupted oviposition during collection.

Eggs overwinter within the overwintering floral buds of *Ledum* and become exposed the following spring as the inflorescences expand. The failure of spring-collected eggs to hatch may have been because they were already dead, representing those egg masses left after dispersal of the successful planidia. The overwintering of eggs is well documented for *S. tenuicornis*. Clausen (1923) presented several ideas, which can be equally applied to *P. gibbosa*, on how the planidia eventually gain access to the *Camponotus* nest. Larvae dissected from the eggs of *P. gibbosa* after four months cold storage were viable and capable of limited (voluntary) movement of the head region. If representative of the condition of a normally eclosed

planidium, then this sharply contrasts with other members of the Eucharitidae whose planidia must actively search for their respective hosts. The means by which *P. gibbosa* enters the nest of *C. herculeanus* is unknown.

In June 1988, buds of *Ledum groenlandicum* were collected that were swollen to the point that egg masses could be observed protruding between the bracts. Egg hatch was observed shortly thereafter and the ruptured eggs produced copious amounts of liquid. The planidia were observed to undulate through the liquid and were able to occasionally lift the anterior region of the body. *Camponotus* adults were confined with the hatched egg masses and were observed to palpate the liquid mass resulting in the transfer of several larvae to the mouthparts of the ant. In one case, dead mosquitoes were also provided and the following day, macerated tissue was found with several active planidia attached. It is postulated that the egg fluid liberated by the hatch of the first instar serves to attract foraging ants which results in the transfer of several larvae to the ant. Further foraging for food or eventual tending of ant brood likely results in the transfer of several planidia to the host larva, possibly along with a food bolus. This method appears more likely than the transfer of an entire egg mass as suggested for *S. manipurensis* which should result in a tremendous number of planidia within a single colony (Clausen 1928).

In colonies of ants that were parasitized, mature larvae had an average of 3.35 planidia (SD = 1.56, n = 20). This sample represented a total of 67 planidia primarily concentrated along the creases between segments II–IV (Fig. 9). Planidia remain attached externally to the ant larva and do not burrow into the cuticle as observed for some eucharitids. They did not show any signs of feeding (as expansion of body segments) while on the ant larva until the cocoon was formed and pupation of the host initiated (Fig. 10). Clausen (1923) believed that it

may be the early stages of hystolysis that trigger development of the eucharitid. Engorged first-instar larvae (Fig. 12) were found attached to the exuvium of an ant pupa within the cocoon and are presumed to be initially "cast off" and then either the first- or second-instar larvae migrate to the ventral midsection of the ant pupa (Fig. 11) where they resume feeding. No first-instar larvae were found feeding on the ant pupa. In *S. tenuicornis,* the engorged first-instar larvae were shed in a similar manner and Clausen (1923) reported that larvae moulted to a second instar before assuming the new position.

The second-instar larva was found attached to the posterior ventral portion of the thoracic region on the host pupae (Fig. 11) while the feeding position of the third instar was usually shifted dorsolaterally to the pleural region of the host. A maximum of four second-instar larvae were observed feeding on one host pupa, and as many as four pupae were found in a single cocoon although one or two were more common. Wheeler (1907) also found one cocoon with four pupae.

One engorged first instar was seen feeding upon a second-instar of *P. gibbosa*. Remains of second- or third-instar eucharitid larvae were found in some cocoons along with mature pupae of *P. gibbosa*. This suggests a cannibalistic mechanism of limiting superparasitism although the mean number of planidia per host (3.35) would generally not suggest this.

The psithergate pupae of the ants were not as strongly deformed as found in some ants attacked by eucharitids (Wheeler 1907), but did show some fusion and enlargement of the thoracic segments and poor definition of the leg segments (Fig. 11). Especially where only one *P. gibbosa* was found in a cocoon, remains of the ant host were not always devoured and one callow adult exhibited a strong resemblance to a deformed psithergate.

Description of the immatures.—Egg (Fig.

3): Undeveloped eggs white with smooth chorion. Mean length of egg body 0.17 mm (SD = 0.01, n = 10); of caudal stalk 0.24 mm (SD = 0.02). Mature eggs with well-sclerotized (black) planidial larva occupying less than half of overall volume with head oriented toward stalk; yellowish yolk mass attached to abdominal apex, filling other half of egg body.

The small size of the planidium with regard to the size of the egg body and large yolk mass may be adaptations to maintaining energy stores for an overwintering egg or act as an attractant to the ant host with the simultaneous emergence of an egg mass in the spring. A similar difference in size was not found in either *S. tenuicornis* or *S. cyniformis* which were both suspected to overwinter in the egg stage (Clausen 1923, Parker 1937).

First instar (Figs. 5–7, 12): Mean length of planidial stage, 0.08 mm (SD = 0.06, n = 10), maximum width 0.05 mm; laterally compressed, oval in cross section. Cranial sensilla absent; hatchet-shaped posterior labial plate (found in all other Eucharitinae) either absent or reduced to a barely discernible sclerite below anterior labial sclerite; pleurostomal spines and circular labial sclerite present. Reduction in number of tergites to five (Fig. 7) (12 in other Eucharitidae); tergopleural line absent. Tergites II–V (numbering not indicative of homology with same tergites in other Eucharitidae) scalloped along posterior ventral margin; strong ventral extensions of terga absent. Tergite I with three pairs of setae; all other tergal setae and enlarged caudal setae absent. The morphology of the first-instar larva of *P. gibbosa* is markedly different from any other described eucharitid.

Second instar (Figs. 11, 13): More typically hymenopteriform, white, very weakly sclerotized, with a single pair of mesothoracic spiracles (propneustic). First-instar exuvium remaining attached to ventral surface (Fig. 13). Head region weakly delineated; containing a pair of small, pincer-like mandibles. This stage is virtually identical to that of *S. cynipiformis* Rossi (Parker 1932) and *Kapala terminalis* Ashmead (as figured in Clausen 1940a) which is the only other described second instar within the Eucharitinae. *Kapala* is distantly related indicating a general conservatism of morphology in the second instar.
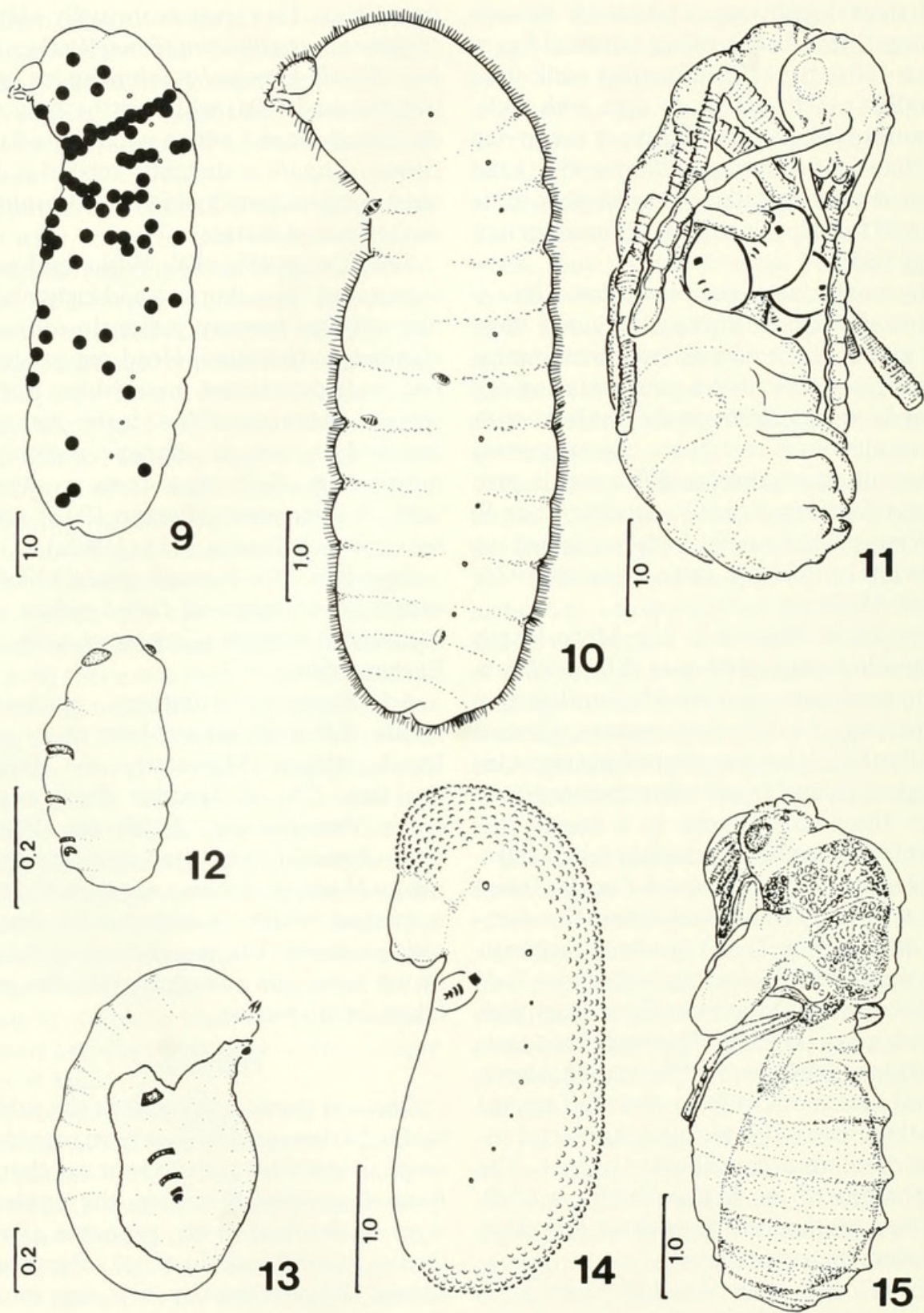
Third instar (Fig. 14): White and poorly sclerotized. Two thoracic and eight abdominal sclerites present; entire dorsal surface minutely tuberculate. Head region defined but well-developed mandibles not observed. Exuvium of first instar remaining attached to ventral thoracic region. The morphology of the third instar is identical with *S. cyniformis* (Parker 1932) and *S. tenuicornis* (Clausen 1923, 1940a).

Pupa (Fig. 15): Typically chalcid-like with exception of series of raised ridges along metasomal tergites in common with other Eucharitidae.

Additional information.—oviposition habits of *P. gibbosa* have been observed by Dr. K. Hagen (University of California, Berkeley, CA) at Amador Pines and Pioneer, Amador Co., California. Females were observed oviposited into overwintering leaf buds of *Arbutus menziesi* Pursh. in a manner which is identical to that described above. The morphology of the first-instar larva was identical with the larvae taken from Ontario.

DISCUSSION

Obeza is the first member of the subfamily Eucharitinae which has been recorded to oviposit into fruit and have the egg chamber formed completely within the epidermal layer of the fruit as the egg mass expands during oviposition. In most other Eucharitinae, females deposit their eggs into existing cavities in plant tissue such as between the scales of an overwintering flower bud by *S. manipurensis* and *S. tenuicornis* (Clausen 1923, 1928) or into flower heads of *Picris* among the bracts or achenes as in *S. cyniformis* (Parker 1937). In contrast

Figs. 9–15. *Pseudochalcura gibbosa*: 9, Cumulative distribution of planidia on 20 mature ant larvae; 10, Early feeding stages of planidia on ant host in preparation for pupation (cocoon removed); 11, Second instars feeding on ant pupa; 12, Engorged first instar; 13, Second instar; 14, Third instar; 15, Pupa of male. Scale bars in mm.

to both *Stilbula* and *Pseudochalcura*, *O. floridana* and the undescribed species from Mexico deposit relatively few eggs in each egg mass with each female undertaking many separate ovipositions. Morphologically, adults of *Obeza* are very similar to *Stilbula* and generic differentiation is based on the possession of lateral propodeal processes and posterior extension of the genae in *Obeza* (Heraty 1985). If other species of *Obeza* share similar oviposition habits, this biological distinction serves to support recognition of the two genera.

The planidium of *Obeza* shows a number of distinctive features that provide recognition at the generic level but otherwise it is fairly typical of most Eucharitinae (see Heraty and Darling 1984). The pair of large hook-like cranial processes is similar to the anterior cranial spines found in *Perilampus* of the Perilampidae (Heraty and Darling 1984). However, the processes are unsclerotized and therefore regarded as of different derivation (not homologous) from those of *Perilampus*.

The planidium of *P. gibbosa* is highly derived within the Eucharitidae. In a family where conservatism of first-instar larvae is extreme, the reduced number of terga and lateral compression of body segments are anomalous. The reduction of segmentation of this planidium would be expected to allow very limited mobility in comparison with other eucharitids including *Stilbula* and *Obeza*. In contrast to the derived condition of the planidium, life history information and morphology of the other larval stages is virtually identical to *S. tenuicornis* (the reader is referred to Clausen (1923) for a full description) and again suggests a close relationship within the lineage regardless of their very different adult morphology.

Poor descriptions for planidia of *Stilbula* render them as generally uninformative for comparison with *Obeza* or *Pseudochalcura*. However, it is notable that the tergopleural line (a desclerotized line that runs laterally across the tergites and found in some form in all other Eucharitidae) was absent in *Obeza* and *Pseudochalcura*, and not figured in any drawings of *Stilbula* planidia. Clausen (1940a) was the first author to illustrate the tergopleural line in three other genera of Eucharitinae. In that paper, he referred to the absence of a line in *S. cyniformis* as probably due to an oversight by Parker (1932) but neglected to mention the absence in his own earlier illustrations of *S. manipurensis* and *S. tenuicornis*. Heraty and Darling (1984) similarly considered the tergopleural line as a synapomorphy of the Eucharitidae. It is now apparent that the absence of a tergopleural line may be a common feature of a clade including *Stilbula*, *Obeza*, and *Pseudochalcura*. The position of this group with respect to other Eucharitidae will need to be determined to assign correct polarity to this state.

With few exceptions, the immature stages of the Eucharitidae have proven to be very conservative in the amount of morphological change and behavioural adaptation. This allows the immature stages to provide useful evidence of higher level relationships. *Stilbula* and *Obeza* share similar adult morphology but dissimilar oviposition habits; *Stilbula* and *Pseudochalcura* share similar life histories and morphology of immatures but dissimilar adult morphology. Some of the larval and ecological characters described and compared here could represent synapomorphies or ground-plan characters of the clade discussed (e.g. general similarity of morphology of larval stages including absence of tergopleural line in planidium), thus supporting the monophyly of the clade but not providing any resolution of the relationships among the four genera. In the absence of data for other taxa, particularly *Lophyrocera*, other characters appear to be autapomorphies (e.g. cranial processes, oviposition into plant tissue in *Obeza*; reduction of segmentation in planidia in *Pseudochalcura*) that furnish no insight into inter-generic relationships. Information on the within-nest biology of *Obeza*, *Lophyrocera*, and other species of *Pseudochalcura* as well as oviposition habits and ant host

selection of these taxa throughout their geographical ranges will provide invaluable in further resolving the relationships of these taxa.

The description of the life history of *P. gibbosa,* though more extensive than that of *O. floridana,* is not exhaustive. A number of key questions still remain unanswered and certain suggestions or speculations require verification. How does the planidium travel from the *Ledum* buds to the ant nest and when is this accomplished? Reader (1977) listed only flies and bees visiting *Ledum* flowers and made no mention of ants. Do the planidia discriminate between young ant larvae (maturing in the following season) and mature larvae (pupating in same year) (Sanders 1964, 1972)? If not, how do the non-feeding planidia survive if they must remain on the host for at least a full year? These are likely to be answered only with additional observation and possibly experimentation.

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