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The ethology of the wasp, Pseudomasaris Edwardsii (Cresson), and a description of its immature forms (Hymenoptera: Vespoidea, Masaridae)

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CONTRIBUTIONS IN SCIENCE

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THOLOGY OF THE WASP, *PSEUDOMASARIS EDWARDSII* (CRESSON), AND A DESCRIPTION OF ITS IMMATURE FORMS (HYMENOPTERA: VESPOIDEA, MASARIDAE)

By PHILIP F. TORCHIO

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THE ETHOLOGY OF THE WASP, *PSEUDOMASARIS EDWARDSII* (CRESSON), AND A DESCRIPTION OF ITS IMMATURE FORMS (HYMENOPTERA: VESPOIDEA, MASARIDAE)[1]

By PHILIP F. TORCHIO[2]

ABSTRACT: In a greenhouse, each nest of *Pseudomasaris edwardsii* (Cresson) was constructed of nectar-moistened soil, was solitary and was placed in open but concealed niches attached to a variety of substrates. The wasp anchored her egg by its posterior tip to the bottom of the cell, deposited a jellylike cylindrical provision composed of *Phacelia* pollen and nectar and constructed a cell cap. Soil carried to the nest was attached to the postgenal surfaces of the female's head, and the pollen and nectar were transported in her honey stomach. Cells were clustered and attached to each other and to the substrate along their lateral margins. Most nests were covered with separate layers of soil (surface ornamented in various ways) that camouflaged the nest against natural enemies and protected it against extreme temperatures.

The larva, after consuming its provision, spun a cocoon which closely adhered to the inner surface of the cell, and then voided its feces across the bottom of the cell. The post-defecated larva subsequently migrated to the anterior limit of the cell where it firmly appressed against the cocoon as it assumed a strongly decurved, overwintering, prepupal position. Rearings in the laboratory indicated that the species is univoltine and nonproterandrous.

The immature forms of *P. edwardsii* and *Euparagia scutellaris* Cresson are described and represent the first descriptions of the immatures within the family Masaridae. Relationship of these immatures is discussed and both are compared with the immature forms of other known vespoids.

INTRODUCTION

Pseudomasaris is one of 19 genera comprising the vespoid family Masaridae. Except for the predatory genus *Euparagia*, all masarid genera thus far studied provision their nests with pollen and nectar. This behavior is similar to the provisioning habits of bees, but it is not found in other wasp families and has, as a consequence, attracted attention from biologists and systematists alike.

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The family Masaridae is also distinctive morphologically. All its members possess clavate antennae, and, unlike other vespids, their wings (except in the *Quartinia* group) are not folded longitudinally when they are at rest. In 1962, O. W. Richards published a world revision of masarid wasps in which he summarized the literature pertaining to the nesting habits of 4 species of *Pseudomasaris: vespoides* (Cresson) (as reported by Ashmead, 1902, Davidson, 1913, Cockerell, 1913, and Hicks, 1927, 1929, 1931); *edwardsii* (Cresson) (by Hicks, 1931); *occidentalis* (Cresson) (by Hungerford, 1937); and *texanus* (Cresson) (by Bequaert, 1940). Richards (1963) published a revision of the genus *Pseudomasaris* in which he added biological notes on a fifth species, *P. coquilletti* Rohwer. Parker (1967) published notes on the nests of 3 additional species: *P. maculifrons* (Fox), *P. phaseliae* Rohwer and *P. zonalis* (Cresson). Thus, there is now at least limited published information about the biology of 8 of the 15 species recognized by Richards' revision.

Although Richards firmly established the systematics of the Masaridae and revised the genus *Pseudomasaris*, the biology of the genus remains imperfectly known because the species have limited distribution and the nests are difficult to locate. The literature does, however, indicate that the biology of *Pseudomasaris* is nearly as uniform as it is unique. All species construct nests of mud attached to open but partially concealed niches, provision their cells with pollen and nectar, attach one egg to the bottom of each cell before provisioning, and attach cells to the substrate or to each other along the long axis of each cell.

In late May, 1966, a large population of *P. edwardsii* associated with bloom of *Phacelia leucophylla* Torr. was discovered on a grassy hillside 7 miles south of Logan, Cache County, Utah, at an elevation of 1,525 meters. I transferred 25 females to a greenhouse provided with *Phacelia tanacetifolia* Benth. to determine whether they would nest in confinement. Three survived and nested, but only two cells were provisioned and capped. In one cell, the egg died before the larva hatched; in the second cell, the larva developed to the prepupal stage. Then, in early June, 1967, 70 freshly emerged *P. edwardsii* were captured from the same hillside and introduced into the same greenhouse. All the wasps died within 96 hours of their introduction. Later, it was discovered that inadequate ventilation along the greenhouse "ridgepole" allowed the temperatures at the upper levels to rise well above the survival tolerance of most flying Hymenoptera. This condition was corrected, and in late May, 1968, 54 female and 15 male *P. edwardsii* were introduced into the greenhouse. By the end of the nesting season in late August, 41 nests were found. The observations of the nesting wasps, their nests and the developing progeny are reported here.

NEST STRUCTURE

The soil nest of *P. edwardsii* is normally attached to a flat surface in an open but somewhat concealed niche, and each nest is composed of one

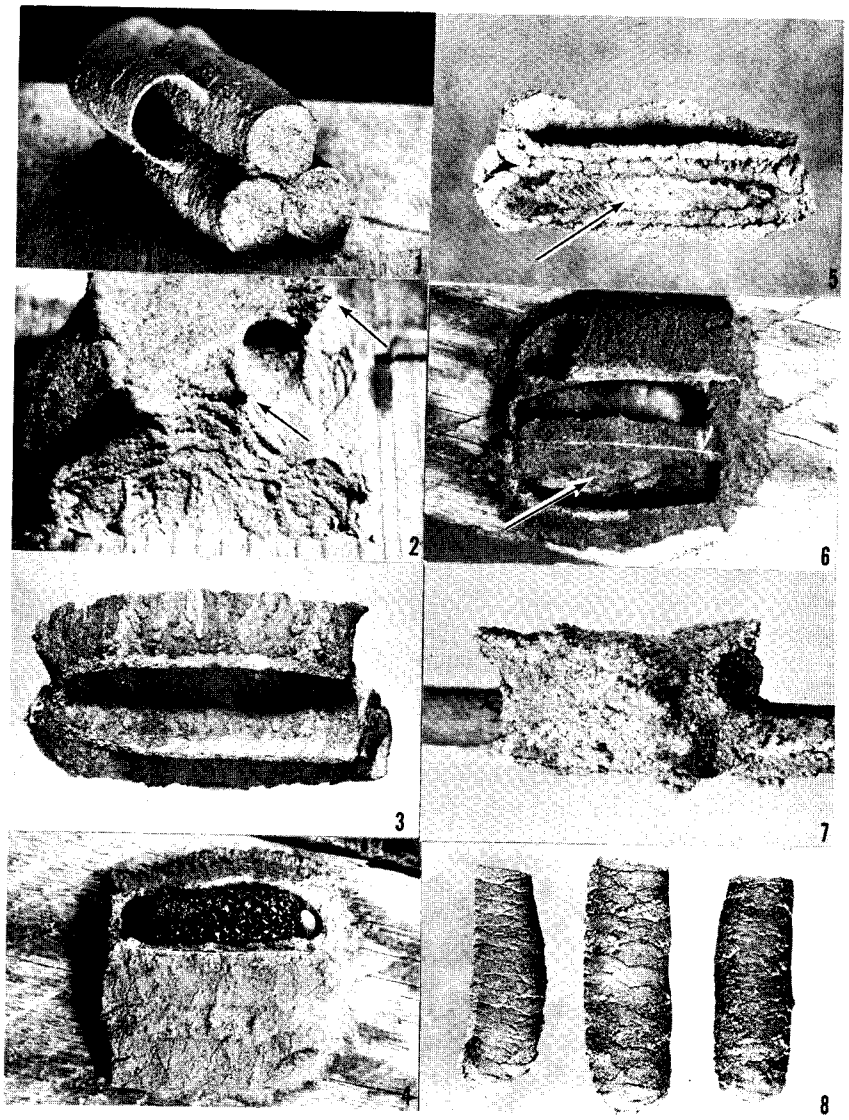
or more elongate, parallel-sided cells joined to the substrate or to other cells along the lateral margin. However, cells attached to the substrate are incomplete in that a small area of the substrate surface is not covered with soil but is used as part of the cell (figs. 5, 6). After the cells are constructed, additional soil is often placed over them as a complete covering. Orientation of the nests with respect to gravity appears to be random.

The examination of over 40 nests of *P. edwardsii* revealed that details of the nest architecture were highly variable although certain features remained constant. The major variations included the number of cells and their arrangement and the presence and degree of development of nest covering. The architectural features that remained constant were: (1) the shape and form of each cell; (2) the manner in which the cells were attached to each other and/or to the substrate; (3) the use of soil for all components of the nest; and (4) the fact that cells made up the greatest volume of each nest.

After the first cell was constructed, the wasp normally initiated construction of a second cell which she attached to the first. However, a few wasps did not construct more than one cell per nest, and of these, some did not provide nest covers, but others constructed complete covers of various shapes. Most nests were composed of two or more cells, and all but one of these nests contained cells joined to each other along the lateral margin. When many cells were constructed within a nest, they were clustered and attached strongly to each other and/or to the substrate (fig. 1). However, in one nest, the cells were placed in a long narrow groove, arranged in a linear series, and separated from each other. Most nests (including those arranged in linear-series) were each covered by an additional layer of soil. However, several multicelled nests were abandoned immediately after the last cell was capped and others were only partially covered in various ways before they were abandoned. Some covers possessed spinelike projections and roughened surfaces (figs. 2, 7) which probably served to protect and camouflage the cells. Those nests that were provided with hemispherically shaped, smooth covers (fig. 17) were always exposed to the heat of the afternoon sun. All nests were fastened to one side of the substrate (figs. 2, 7), even if the substrate was slender and cylindrical, as a stem or a bamboo stake (fig. 7).

CELL DESCRIPTION

The most diagnostic feature in the nest architecture of *Pseudomasaris* is the soil cell. It is a parallel-sided structure whose outer dimensions range between 14 and 21 mm in length and 5 to 6 mm in width. The variation in cell wall thickness is between 0.25 and 1.0 mm; however, the wall thickness of any particular cell is constant. The inner surface is smooth, unlined and nonreflective. The cell cap is a plug of soil with a flat, unlined inner surface that usually possesses two concentric rings (fig. 16). Its outer surface is normally flat, smooth and flush with the anterior margin of the cell (fig. 1). The thickness of the cell cap varies between 0.75 and 1.80 mm.



FIGURES 1-8. *Pseudomasaris edwardsii*. Fig. 1. Cluster of cells. Fig. 2. Completed nest with spinelike projections produced from soil covering. Fig. 3. Nest cover represented as a ridge of soil deposited across the surface of each cell. Fig. 4. Nest with cells parallel and nest cover a continuous, smooth surface. Fig 5. Cocoon visible where cell was attached to substrate. Fig. 6. Nest with lower cell dissected to expose area of cell attachment not covered with soil or a cocoon. The upper cell contains a last-stage larva consuming its provision. Fig. 7. Completed nest attached to bamboo stake. Nest covering produced into spinelike projections. Fig. 8. Outer surface of cells with scars demarking each soil deposition.

Figures 1 and 7 demonstrate how the cells are attached to each other and to the substrate. Those attached to each other are complete and cylindrical in cross section. Those cells attached to the substrate are incomplete and asymmetrical in cross section because the area of attachment is not coated with soil (figs. 5, 6).

A total of 87 completed cells were constructed in the 41 nests examined; the number of cells found in each nest ranged from 1 to 7, or a mean of 2.46 cells per nest. Twenty-four cells contained dead immature forms: 16 had collapsed eggs; 2 had growing larvae; 2 had prepupae; 2 had pupae; 1 had an egg destroyed by dermestid beetles; and 1 prepupa was parasitized by the chalcid wasp, *Monodontomerus obscurus* Westwood. Of the 41 nests examined, 4 were attached to bamboo stakes, 7 were fastened to flat-surfaced lumber and 30 were found on metal.

NESTING

Preliminary activities

The first three days after wasps were introduced in the greenhouse were utilized to complete orientation, mating, selection of nest sites and selection of soil collecting sites. Each wasp was fastidious in its selection of soil. All but two individuals which nested in the greenhouse selected one soil type (high in silt-particle size) from a wide variety of soils available. Apparently, only soils with proper texture, particle size and wetting capacity were selected. Each wasp, however, usually restricted its collecting to a small portion of the total area where the proper soil type was found. The wasps were gregarious in their collection of soil, but each wasp invariably returned to the same microniche of the soil site for additional soil loads. Some used one microniche throughout their nesting activities; others established new soil-collecting sites for each cell constructed; and a few used two soil sites during the construction of a single cell. However, competition for any particular soil collection site was never observed.

Nest sites were always established in open but concealed niches available throughout the greenhouse. As a result, the nests were solitary and widely dispersed.

Cell construction

Cell construction was initiated after the wasp selected a nesting site and a soil-collecting site. The manner of attaching the first layer of mud as a cornerstone of the first cell was characteristic. First, she attached a small quantity of soil to each side of the postgenal surface of her head and carried it to the nesting niche. There, she tried unsuccessfully to apply the soil directly to the substrate by dragging the underside of her head across the site. After several attempts, she returned to the soil-collecting site and added more soil to the original deposit. She then returned to the nesting site where she again

dragged the underside of her head across the surface. She sometimes made as many as 12 trips of this type before she acquired a load large enough to deposit on the nesting surface. This behavior may help the female establish a strong orientation between the nesting site and the soil-collecting site.

P. edwardsii used only one method of collecting and carrying soil. Each time a wasp returned to her soil site, she hovered 10 to 60 cm above it while she intermittently bobbed up and down a maximum distance of 3.75 cm in either direction. This hovering activity continued for 8 to 49 seconds, whereupon the wasp landed and immediately proceeded to collect soil. Little variation was expressed in the method of soil collecting; the female first moved her mouthparts forward 20 to 40° from their normal perpendicular position, embedded the tips of the mandibles nearly a millimeter into the loose-textured, slightly damp or dry soil surface and then began to spread and close her mandibles while flexing her head downward and toward her thoracic venter. As the wasp repeatedly scraped the soil surface with her mandibles, she periodically kicked soil from beneath her head region with rapid, flicking motions of her front legs. These activities made it possible for her to scrape up particles of soil with her mandibles that were subsequently pulled in the direction of her postgenal area by a combination of events initiated with the flexing of her head. This flexing caused her mandibles to scoop into the soil until her head reached its normal perpendicular position. As her head continued to flex, her mandibles were pulled posterodorsally until the collected soil particles were deposited under her head. She continued to carve into the same excavation until a mound of soil eventually appressed against her mouthparts which, when folded, lay well below the postgenal surfaces. At this juncture, her front legs periodically excavated the central area of the mound to clear the area directly below her mouthparts. This activity divided the mound into two portions, and each was sufficiently large to appress against the stipites and postgenal surfaces of the head capsule. Nectar (method by which this liquid was determined to be nectar will be discussed in section on foraging) was then exuded through her folded mouthparts where it was rapidly absorbed into the soil mounds until the surface of each mound was moistened and adhered to the postgenal surfaces of her head. Additional nectar was exuded periodically as the size of the mound increased. Eventually, the complete load of soil was represented by two large, moist, nearly spherical balls that filled a space delimited by the wasp's stipites and the mesepisternal and postgenal surfaces.

After the wasp gathered a load of soil, she flew back to her nest where she quickly fashioned each load into the particular structure she was building. During cell construction, the returning wasp landed on the brim of the cell and curved her body until the posterior two or three abdominal sterna touched the outer surface of the cell immediately below the brim. At the same time, she thrust her head into the cell cavity until her mandibles, which appressed against the inner cell surface, were opposite the posterior abdominal sterna.

She then pulled her mandibles apart as soil flowed from her postgenal areas, across the dorsal faces of her mandibles and onto the cell brim. As soil was deposited, she moved her mandibles to shape the deposit while she simultaneously tamped the outer surface of the fresh deposit vigorously with her posterior abdominal sterna. During each deposition of soil, she periodically jerked her front legs across both faces of her postgenal areas, presumably to clear them of soil. She also moved her large labial palpi across the load in an oarlike fashion to aid in the deposition.

During the latter phases of cell construction (prior to provisioning and following cell cap construction) the wasp periodically added soil to areas of the outer surface of the cell. Apparently, these additional deposits reinforced the structure. The method by which she transferred this soil from her head to the substrate was similar to the second method described. However, she first examined the surface by rapidly pacing about and tapping the substrate continuously with her apical antennal segments. Then she applied one or more soil deposits from one load by using her mandibles and labrum to smear the material over a relatively large area. This method of deposition was also practiced during the construction of the nest cover.

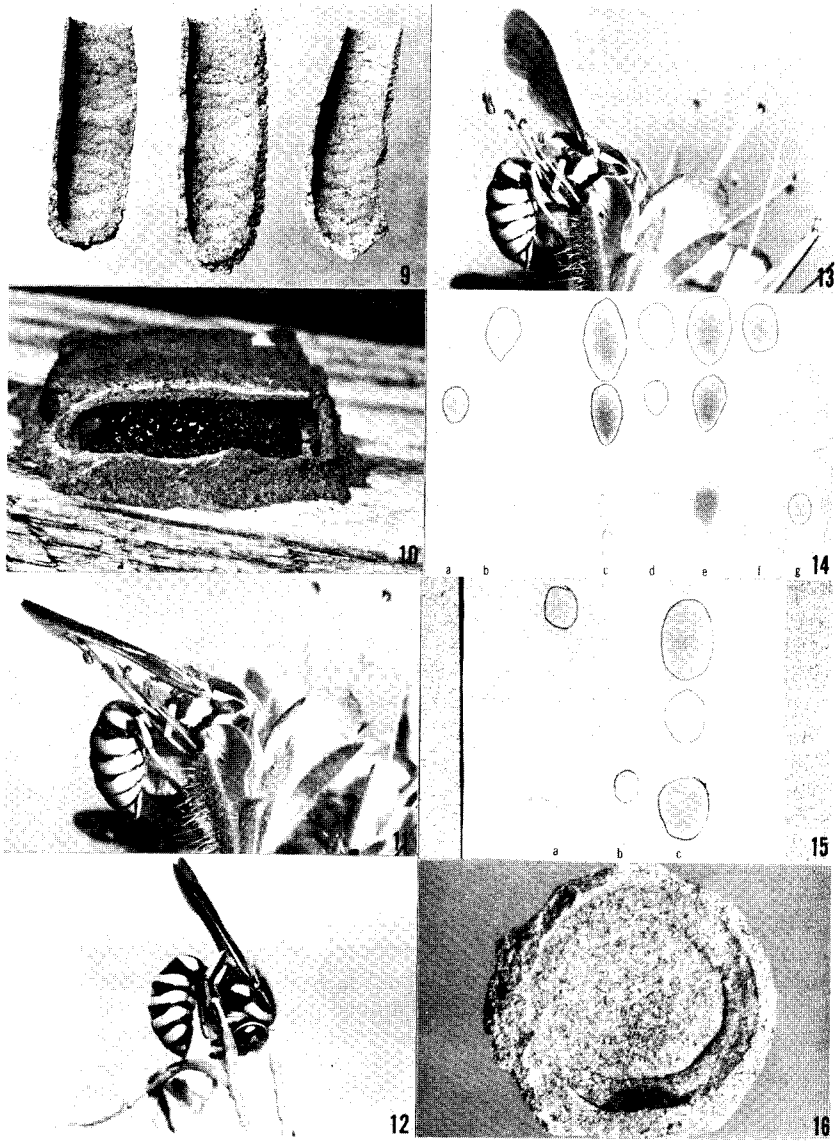
Each deposit added to the cell during its construction left an outline scar (fig. 8) which roughened the inner and outer surfaces of the cell wall. As construction neared completion, the wasp deposited the last few loads of soil within the cell (fig. 25) and smeared it as evenly as possible to smooth the inner surface (fig. 9). The smoothing was accomplished as follows: the returning wasp landed in front of the cell opening, crawled head first into the cell until only her posterior abdominal segments were visible above the cell, and then began to crawl backward and forward within the cell as she deposited and smeared the moistened soil over the surface. Deposition of the final load of soil therefore required a lengthy period (9 minutes, 30 seconds) as the wasp slowly rotated within her cell.

The method of soil deposition practiced during the construction of the cell cap is described in that section.

Egg deposition

Although actual oviposition was not observed, one wasp was watched during the period of egg laying (fig. 25). This wasp, after depositing and smearing her last load of soil across the inner face of the cell, backed out, turned, and backed into the cell until her head was 1 mm below the cell orifice. Then she remained motionless for 3 minutes, 30 seconds while her egg was deposited, whereupon she crawled out of the cell head first, turned, and re-entered it head first to deposit the first load of the provision. Subsequently, this particular cell, as well as other capped cells, was dissected to study details of the egg and its placement.

Each egg examined was white, 2.1 to 2.8 mm long, 0.955 to 1.0 mm wide medially, and slightly curved; the surface was minutely reticulated. Normally, it was anchored by its narrowed (0.15 mm wide) posterior tip to



FIGURES 9-16. *Pseudomasaris edwardsii*. Fig. 9. Inner surface of cells with a layer of soil coated over scars. Fig. 10. Position of egg and provision within cell. Fig. 11. Sleeping position of female on a *Phacelia* flower. Fig. 12. Sleeping position of female on *Brassica*. Fig. 13. Female awakened from sleep (wings raised). Fig. 14. Paper chromatograph of glucose (A), fructose (B), water solution of pollen from cell (C), water solution of cell walls (D), contents from honey stomachs (E), fructose (F), and sucrose (G). Fig. 15. Paper chromatograph of fructose (A), sucrose (B), and nectar of *Phacelia tanacetifolia* flowers (C). Fig. 16. Inner face of cell cap.

the cell wall near its base. The curvature of the egg closely paralleled the convex posterior face of the provision (see description of provisioning), and its unattached anterior tip (0.31 mm wide) faced the cell cap and terminated less than a millimeter below the provision (fig. 10). As the egg matured, its posterior area gradually cleared. The first stage larva emerged 46 hours after egg deposition.

In some cells, the egg was found attached to the provision rather than to the cell, and its ventral surface was appressed against the inner face of the provision medially with both unattached tips facing the cell walls. Since the egg was always deposited before the cell was provisioned, this aberrant position probably resulted when the wasp pressed her first load of pollen and nectar against the ventral surface of the egg. Subsequently, the strong surface tension of the provision pulled the egg from its attachment to the cell wall and straightened it until only the tips of the egg remained detached from the provision.

Provisioning

The provision of *P. edwardsii* is a tacky, homogeneous mass of *Phacelia* pollen bound with *Phacelia* nectar (fig. 10), shaped into a solid cylinder, 12.5 to 12.7 mm long and 3.5 mm in diameter. The anterior and posterior surfaces are normally smooth and slightly convex, while the remaining lateral surface is covered with numerous tightly appressed, cone-shaped, papillalike projections (fig. 10). Each projection is broad basally, as much as 0.75 mm wide, and narrows apically for nearly 0.75 mm until the diameter approaches 0.10 mm. The remainder of the projection is composed of a parallel-sided, spinelike, apical extension which varies in length from 0.20 to 0.75 mm; the terminus is either blunted or pointed. The longer projections touch the inner face of the cell wall while those which are shorter remain free apically. The posterior surface of the provision normally lies 2.5 to 3.0 mm above the base of the cell, and the anterior surface is positioned 2.0 to 2.5 mm below the cell cap. The provision, therefore, touches the cell walls only by the apical tips of its longer projections.

Notes on provisioning habits were taken from 7 cells, but the observations were so similar that the following description of the only complete provisioning observed could serve as a general description (fig. 25). However, the time spent gathering pollen and nectar was obviously affected by the abundance, proximity and species of *Phacelia* bloom available.

The wasp provisioned her cell in 4 hours, 25 minutes; 24 minutes was spent within the cell depositing the provision, and the remaining time was spent foraging. Eight pollen and nectar trips ranging from 21 to 34 minutes (a mean of 30 minutes) were made to complete provisioning of one cell. The minimum time required to deposit one load was 1 minute, 30 seconds, and the maximum period was 5 minutes, 40 seconds (a mean of 2 minutes, 55 seconds). The vertical distance in the cell displaced by each consecutive load of pollen was 2.45, 2.23, 0.77, 1.40, 0.95, 1.90, 1.50 and 1.50 mm.

On the last foraging trip prior to egg deposition, the wasp collected her first load of pollen and nectar, stored it in her honey stomach, and then collected a load of soil. As noted, once she deposited the soil on the inner walls of the cell and deposited her egg near the bottom of the cell, the wasp crawled from the cell, turned, and re-entered it head first until only the tip of her abdomen was visible above the cell orifice. The provision was deposited immediately above the egg as the abdomen pulsated rapidly while the body rotated intermittently within the cell (clockwise 180°, clockwise 90°, counterclockwise 360°, clockwise 45°, and counterclockwise 280°). Thus, in one trip, the wasp collected a load of pollen, a load of soil, deposited the soil, laid its egg and deposited the first load of pollen. Periodic examination of the cell during the period of provisioning revealed that each deposit of pollen, including the first, was a moist mass spanning the inner diameter of the cell. The anterior surface of each deposit remained smooth and strongly convex. The papillalike projections covering the outer wall of the provision were molded during the deposition of each load of pollen and nectar.

The wasp scarcely deviated in her method of depositing the eight loads of pollen. However, during the third and subsequent deposits the wasp rotated her body intermittently counterclockwise through at least one revolution, and during the deposition of the last two loads she made four and five complete revolutions respectively. The method by which she added pollen could be observed only during the final deposition when the surface of the provision was immediately below the cell orifice. This elevated position prevented her from inserting and concealing her head within the cell. As she touched her mouthparts to the provision, she regurgitated the mixture of pollen and nectar from her honey stomach for a short period and then slowly lifted her head above the provision for a maximum distance of 2 mm. When her head was fully lifted, she stopped depositing pollen, rotated a short distance clockwise within the cell, and repeated the procedure of laying down the provision and adding the papillalike projections to its surface. She often used her front legs to complete transfer of pollen from her mouth to the provision as follows: the front legs were pulled together with the femora paralleling the underside of the head while the tibiae were held perpendicular to her head. Then, with these legs held rigidly in this position, she jerked them rapidly forward and backward. These leg movements not only increased the rapidity of pollen transfer but also aided in the compaction of pollen into the provision. Each time that the wasp stopped rotating to deposit pollen, she turned the tip of her abdomen ventrally until it touched the outer cell surface, whereupon, she began to pulsate it rapidly and vigorously.

Sleeping

The female wasp slept within its nearly completed cell, within a corolla tube of a host plant flower, *Phacelia* spp. (fig. 11), or attached to a non-flowering structure of mustard, *Brassica* spp. (fig. 12). The sleeping position differed for each niche. When a wasp slept in her cell, she crawled into it head first 1 to 2 hours before sunset, crossed her wings, and remained motionless until 9:00-9:30 AM (M.D.T.) the following day. She always slept with her sterna facing in the direction of the cell attachment, regardless of its relation to gravity.

Phacelia bloom provided a favorite sleeping station. In late afternoon, the wasp entered the corolla tube head first, pressed her thoracic sterna against the style, and positioned her propodeum above the stigma. She subsequently clasped the pistil firmly between her mandibles while using her front legs to encompass some anther filaments. Her flexed midlegs, which were pressed against the thoracic pleura, also clasped a few filaments at the tibiotarsal joint. Her partially flexed hind legs did not normally encompass filaments, but rather grasped the margin of a lower petal with the hind tarsal claws. Her wings were held flat and partially crossed apically, and her metasoma was bent ventrally 90° where the posterior segment normally touched a petal (fig. 11). She normally slept with her head, front legs and the anterior area of her thorax embedded within the corolla tube.

Although a number of males were introduced into the greenhouse, none was observed in the sleeping position.

All wasps sleeping on mustard were found clinging to green seed pods in a completely exposed environment. Their sleeping position was assumed in late afternoon when each wasp grasped a seed pod with her mandibles and the tarsal claws of her flexed midlegs and hind legs (fig. 12). The thoracic sterna were pressed against the seed pod which terminated apically under her propodeum. The antennae were positioned downward in front of the mandibles and the metasoma was turned ventrally 90° or more until it touched the opposite face of the seed pod. The wings were held flat and partially crossed apically and the front legs were folded and held against the postgenal surfaces.

Termination of sleep was apparently dependent on rising temperatures. Each morning as 21°C was approached, the wasp began to palpitate her abdomen at a rate that was slowly increased until it reached 150 palpitations per minute. She then lifted and spread her wings above her body (fig. 13), released her grasp of the plant and straightened her abdomen. After a short preening period, she flew directly to a host plant and began to collect nectar.

Pseudomasaris edwardsii, unlike many aculeate Hymenotpera, is solitary in both its nesting and sleeping behavior. It never clusters or is attracted to other wasps during the search for a sleeping station, nor does it sleep night after night at a particular station. The species, however, is highly adaptable, as demonstrated by almost every facet of its biology including its sleeping habits. Therefore, it was not surprising to learn that each female could and did sleep in most niches and assumed every position of sleep described at least once during her nesting life.

Foraging

In the greenhouse, *Pseudomasaris edwardsii* practiced two methods of collecting *Phacelia* pollen: (1) A wasp would land on the sexual organs of

the flower, grasp a few stamens and the style with her midlegs and hind legs, and then remove the pollen from each anther with her mandibles while her prothoracic legs clasped the supporting filament; or, (2) after hovering above a flower for 2 to 8 seconds, the wasp would drop closer to the flower until her extended legs bounced on the anthers once or twice. Then, still hovering, she would remove pollen from the anthers with her mouthparts while using her forelegs, and sometimes her midlegs, to grasp and steady each filament.

Both methods of collecting pollen were used during any one foraging trip. However, the first method was observed more frequently within the first hour of flight activity or whenever the greenhouse became cooler. The second method was observed more frequently during cell provisioning or when bloom was in poor condition. Females collected pollen periodically whenever they were foraging, but the rate of pollen consumption increased markedly during cell provisioning.

The wasp collected *Phacelia* nectar during each foraging trip throughout her adult life by using techniques much like those she used to collect pollen. During the morning, she usually landed on the inner face of the corolla or on the sexual organs and extended her proboscis to the base of the corolla tube where she imbibed nectar. In the afternoon, she normally hovered immediately above a flower with her legs sometimes grasping the anthers and/or filaments while she extended her proboscis to reach the layer of nectar at the base of the corolla. However, both methods of collecting nectar were used on any one foraging trip throughout each day's activities.

Extensive observations of foraging indicated that the methods by which the wasp collected *Phacelia* pollen and nectar were influenced by: (1) the quantity and condition of available bloom (when either or both were reduced, the hovering method was used more often); (2) the response to light and temperature (if either or both were reduced, the landing technique was employed more frequently); and (3) the particular phase of nest construction (the hovering technique was generally used during cell provisioning).

Cooper (1952) reviewed the flower records of masarid wasps and discussed the oligolectic tendencies expressed within the genus *Pseudomasaris*. He concluded that *Pseudomasaris* collects pollen and nectar primarily from 3 host genera: *Phacelia, Eriodictyon* (Hydrophyllaceae) and *Penstemon* (Scrophulariaceae). Some wasps, such as *P. vespoides,* are monolectic on *Penstemon,* but most of the smaller wasp species such as *P. phaceliae, zonalis* and *maculifrons* have a predilection for *Phacelia* and less often for *Eriodictyon.* One species, *P. wheeleri* Bequaert, is found on both *Eriodictyon* and *Penstemon.* Interestingly, none of the 15 species of *Pseudomasaris* collects from both *Penstemon* and *Phacelia,* but several species utilize *Eriodictyon* and either *Phacelia* (*P. edwardsii*) or *Penstemon* (*P. wheeleri*). Apparently, *Eriodictyon* represents a host whose size of flower falls between the size offered by *Phacelia* and *Penstemon* and is, therefore, periodically used by either *Phacelia* or *Penstemon*-collecting *Pseudomasaris* species. It would be

interesting to compare the tongue length of *Pseudomasaris* species with the length of the corolla tubes of their respective host plants.

The greenhouse studies therefore tended to support Cooper's conclusions regarding the oligolectic tendencies expressed by *Pseudomasaris.* Both sexes of *P. edwardsii* collected only from flowers of *Phacelia leucophylla* in the field, and when they were introduced to a variety of flowers in the greenhouse (*Melilotus* spp., *Baileya multiradiata* Harv. and Gray, *Cosmos* sp., *Borago* sp., *Medicago* spp., *Brassica* spp., *Clarkia unguiculata* (Lindl.), *Phacelia tanacetifolia, Lycopersicon* spp. and *Helianthus* sp.), only *Phacelia tanacetifolia* was visited. When the supply of *P. tanacetifolia* dwindled, bouquets of *P. leucophylla* were introduced into the greenhouse from the field, and the wasps freely collected pollen and nectar from both *Phacelia* species during any foraging trip.

The supplying of bloom to *P. edwardsii* in the greenhouse revealed several interesting aspects of the wasp's biology that normally would have been overlooked. First, the collection of pollen and nectar is apparently characteristic at the generic rather than the specific level because this habit is not peculiar to *P. edwardsii* and is widespread in the genus. Secondly, there was a direct correlation between time required to construct and provision a nest of *P. edwardsii* in the greenhouse and the quality and quantity of available bloom. Figure 25 outlines the time required to construct and provision a cell when bloom was in excellent condition and its quantity was sufficient to support the wasp population. Third, wasps nesting in the greenhouse lived nearly twice as long as individual wasps in the field population from which they were collected. Apparently, the continual addition of *Phacelia* bloom in the greenhouse allowed the wasps to express their life potential more fully. Conversely, the field population quickly pollinated its *Phacelia* host plant and then disappeared as the bloom turned to seed.

A number of wasps were observed throughout the entire periods of cell and nest construction and cell provisioning. At no time did they gather liquids other than nectar, but they always added liquids to soil collected for cell building. Indeed, it was only during the cell construction period that the honey stomach was full. Also, when samples taken from the honey stomachs of cell building and provisioning wasps were compared (by using a paper chromatography method) with samples of (1) a solution derived from an unprovisioned cell; (2) nectar from *Phacelia* blossoms; (3) cell provisions; and (4) known concentrations of glucose, fructose and sucrose in water (figs. 14, 15), it was apparent that the liquid added to the soil and the liquid added to the cell provisions was regurgitated *Phacelia* nectar stored in the honey stomach where it had been subjected to minimum enzymatic action. The large quantities of *Phacelia* pollen found in the midgut and hindgut of all dissected wasps indicated that they always consumed enough pollen to satisfy their nutritional needs.

Cell capping

The cell cap was composed of a soil plug, 4.5 mm in diameter, 0.75 to 1.8 mm thick centrally, and 1.3 to 2.0 mm thick laterally. The inner face (fig. 16) was divided into a thickened, peripheral ring 0.7 mm wide and 1.3 to 2.0 mm thick which surrounded a flattened inner surface (inner cell cap) 3.0 mm in diameter and 0.25 to 1.0 mm thick. In some cells, the inner cell cap was also divided into a peripheral soil ring surrounding a central core of soil 1.0 mm in diameter. The outer surface of the cell cap was normally flat, devoid of annulatiions and did not extend above the anterior edge of the cell wall. Sometimes, however, the cell walls were extended for several millimeters above the cell caps during construction of the nest cover so that some cell caps looked as if they were placed well below the anterior margin of the cells.

Construction of cell caps was observed on three occasions each of which occurred immediately after cell provisioning. The soil-laden wasp returned to the cell, placed her head into the cell orifice, and applied soil to the inner face of the cell immediately below its anterior edge as the rapid pushing motion of her front legs transferred soil from her postgenal areas to her mandibles. She slowly circled the lip of the cell as the soil was deposited until a complete peripheral cell cap ring was formed (fig. 16). In one of the three cells observed, one load of soil was required to complete construction of the ring; in the other two cells two loads were required for each. One or 2 additional loads of soil were deposited to complete closure of the cell cap. During the deposition of these loads of soil, the wasp moved clockwise and counterclockwise as she filled the lateral edges of the inner cap with a thin layer of soil until only a small, circular area at the center of the cap remained uncovered. She then rotated in one direction while she plugged this central area of the inner cell cap. This operation required 30 to 40 seconds. At this juncture, she began to spread the moist soil by brushing the dorsal face of her clubbed flagellum across the freshly deposited material (the flagellum was lifted upward and outward on each brush stroke). The brushing continued for 15 to 23 seconds until the central soil was smooth and thoroughly incorporated into the dry surrounding soil of the inner cell cap. Whenever a wasp failed to brush the lateral edges of the central deposit thoroughly, the inner cell cap appeared subdivided into a peripheral ring (first deposit) and a central core (second deposit).

Additional loads of soil, which varied in number, were added to the outer surface of the cell cap until it was flush with the anterior edge of the cell walls. Each of these loads was deposited as a single mound that was thoroughly tamped into the cell cap. The wasp used her labrum and the apical tips of her antennae to tamp as she jerked her head up and down very rapidly for short periods.

Nest covering

Figures 2, 3, 4 and 17 show the variability of the nest coverings. Structural similarities include: (1) each covering was attached to the cells (figs. 3, 4); (2) each layer of the nest cover was 1 mm or less thick (figs. 3, 5); (3) in nests where cells were not completely covered, soil was laid down as a thin perpendicular layer on the long axis of each cell (fig. 3); (4) in nests where cells were completely covered, the layers were deposited horizontally on top of the cells (fig. 4); (5) the nest covering extended well beyond both the anterior and posterior margins of the cells (fig. 18); (6) air spaces were present between the covering and the anterior-posterior margins of the cells (fig. 18); (7) the cell walls of each cell were extended beyond the cell cap and reached the nest covering (fig. 18).

Nests devoid of soil coverings generally had one partially constructed cell attached to one or more completed cells (fig. 1). In others, the area between the attached cells was filled or partially filled with soil. One nest was composed of a single, naked cell, while in another nest the single cell was completely covered. These features indicate that some females apparently died or abandoned their nests before or during construction of the nest covering. Conversely, I was not able to ascertain if all completed nests possessed soil coverings.

LARVAL DEVELOPMENT

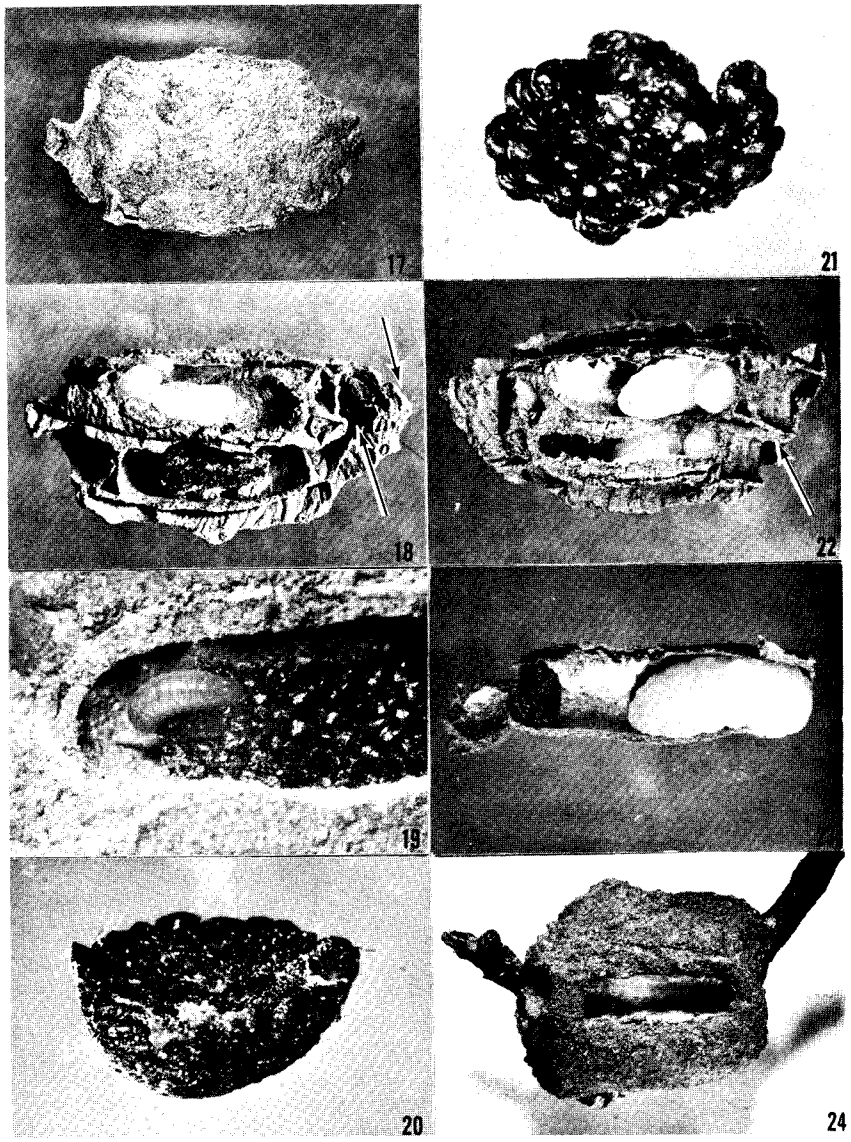
Feeding

The first-stage larva began to feed after freeing itself from the anterior tip of the egg and crawling onto the basolateral surface of the provision. Eventually, only its posterior abdominal sterna rested on the anterodorsal area of the collapsed egg chorion (fig. 19). The second-stage larva completely abandoned the egg chorion which remained attached to the cell wall by its posterior tip. As the larva migrated anteriorly, it either began to drill a central core through the provision or to consume the surface of the provision, including the papillalike projections. The "drillers" were usually found in cells oriented perpendicular to gravity. The "nondrillers" were found in cells attached to horizontal surfaces. After the larva had cut a core through the provision, it began feeding on its periphery until it was consumed.

Regardless of whether the cells were placed on the top surface or the under surface of horizontal structures, the larvae always placed themselves so their sterna faced gravity as they fed. Invariably, each larva rested its sternum on a thin layer of the provision, which was consumed last.

The feeding larva normally buried its head capsule completely in the provision. Then, as the mandibles were pulled apart, the head was retracted slightly, and conversely, as the mandibles were closed, the head was protracted slightly. In this way the mandibles procured a quantity of pollen that was forced into the mouth by rapid protractions and retractions of the labium.

The postfeeding, precocoon spinning larva was active, turgid and always oriented to face the cell cap. It was long and narrow (2.75 mm in diameter); its posterior abdominal segment rested on the bottom of the cell and its head nearly reached the cell cap. The cuticle, though highly reflective, was sufficiently translucent where the gut and the major tracheae were visible through it.



FIGURES 17-24. *Pseudomasaris edwardsii*. Fig. 17. Smooth-surfaced nest covering. Fig. 18. Dissected nest exposing air spaces, and extensions of the nest cover. Fig. 19. First instar larva crawling onto provision. Fig. 20. A normal fecal cake. Fig. 21. A fecal mass consisting of appressed fecal pellets. Fig. 22. Dissected nest exposing extensions of cell walls beyond the cell caps, and the position and shape of overwintering larvae. Fig. 23. A dissected cell containing the fecal cake, cocoon, and overwintering larva. Fig. 24. *Pseudomasaris vespoides*. Nest attached to limb with a cell dissected to expose the cocoon lining.

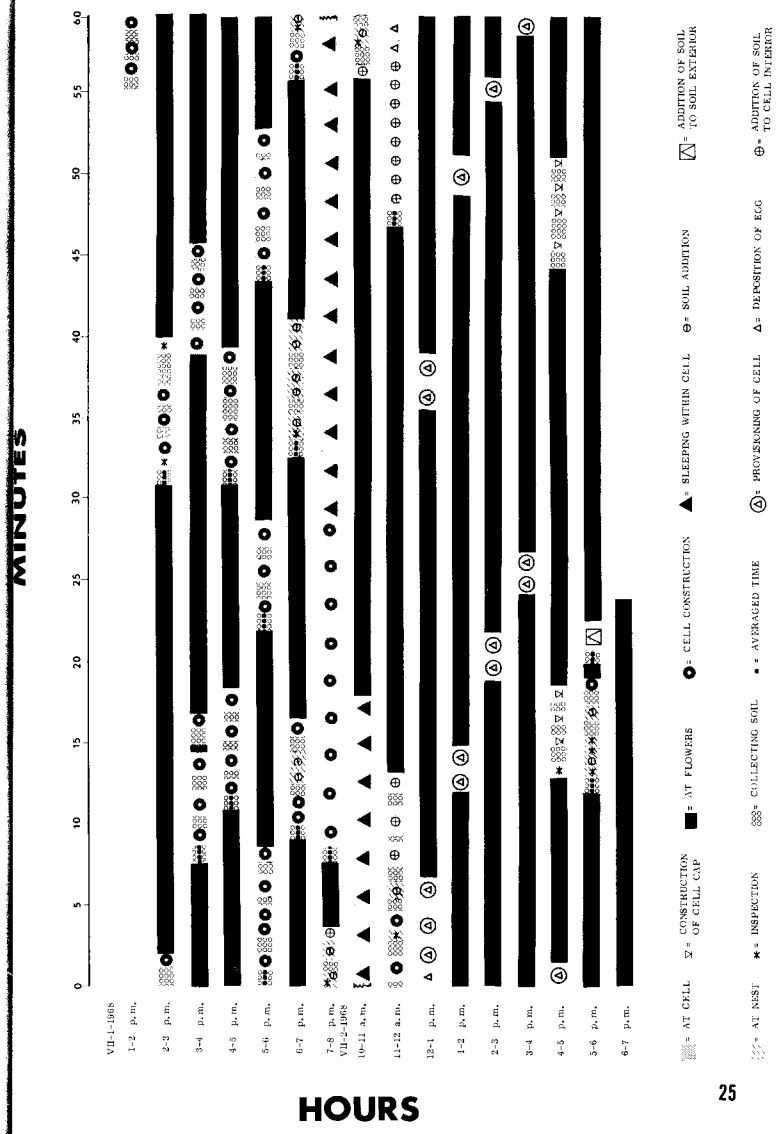


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FIGURE 25. *Pseudomasaris edwardsii*. Activities of a single female throughout the period of constructing one cell.

Cocoon construction

The cocoon was a single-layered structure closely adhering to the inner soil surface of the cell wall and cap. It was pliable, less than 0.01 mm thick and composed of salivary secretion laid down as a translucent matrix interspersed with numerous silk strands.

The larva started to spin its cocoon almost as soon as it had consumed its provision. It laid down two forms of salivary secretion (strands and matrix) intermittently. When depositing the matrix, the larva pressed the apical area of its prementum firmly against the cell wall and secreted a quantity of salivary material that it spread across the surface of the cell wall with its transverse salivary lips. During the few minutes that the matrix remained moist, it was incorporated slightly into the cell wall, thereby attaching the two surfaces firmly together. Each silk strand was formed when the larva attached a spot of salivary material to the cell surface through its salivary lips. When it pulled its head away from this point of attachment, a strand of salivary material was drawn through the salivarium. Invariably, the larva dragged its salivary lips across the surface of the cell as each strand was emitted, thus guaranteeing complete attachment of each strand to the cell surface. At times, deposition of these strands appeared organized; the larva deposited 20 to 30 subequal lengths closely parallel to each other and less than 0.06 mm apart. Then, for no apparent reason, it would abruptly change position and deposit strands more randomly. As each strand was deposited, the transverse salivary lips and mandibles opened and closed, and the labium palpitated rapidly. Sometimes, the movement of the mouthparts caused the strands to be emitted at varying speeds, which resulted in strands of unequal thickness.

Cocoon spinning was usually completed within three days. During this time, the larva frequently interrupted its spinning for various periods, straightened its body, and moved its anterior segments in random directions. Cocoon spinning continued after the larva completely encased itself, but the additional spinning was restricted to attachment of silk to the inner cocoon surface near its anterior margin. Thus, the larva always terminated cocoon spinning activities before a second cocoon layer was formed.

Defecation

After the larva completed construction of the cocoon, it straightened its body until its head nearly touched the cap. If the free surface of the cell faced gravity, the larva positioned itself with its terga touching that side of the cell facing gravity and then began to slowly protrude and retract its head slightly. These movements initiated a persistalsis which continued for nearly an hour. The larva then assumed a C-shaped position, with its head touching or nearly touching its 4th to 6th abdominal sterna and maintained this position for variable periods (4 minutes, 3 seconds to 18 minutes, 52 seconds). Within the first minute, while it remained motionless, a fecal particle was extruded that remained attached to the anus by a thin strand of translucent, rapidly drying, anal secretion. During the remaining time it maintained the C-shaped position, the larva periodically, but rapidly, moved its mouthparts, except its mandibles, and pulsated its body slowly. Eventually the larva uncurled and moved its terminal body segments in circles and figure eights for nearly 2 minutes, 30 seconds. Then it again assumed the C-shaped position and deposited another fecal particle. This behavioral pattern was repeated with little variation until defecation was completed (54 to 76 hours).

Before defecation, the larval body was distended, fat bodies were visible beneath the cuticle and the cuticular surface was highly reflective. As defecation neared completion, the cuticle turned opaque white, and the body became semiflaccid.

The fecal cake was deposited on top of the inner surface of the cocoon at the bottom of the cell. It was a compressed, flat-surfaced, brittle, dark purple cake about half as deep as wide and molded to (but not attached to) the cocoon (fig. 20). The surface of the cake was always perpendicular to the side walls of the cell regardless of the orientation of the cell to gravity. The surface sometimes contained discolored areas which probably represented malpighian excretion deposited after defecation.

Although the feces were deposited as individual pellets, the resultant fecal cake did not normally contain discernible pellets; it usually consisted of a uniform mass of pollen exines (attached to each other by a rectal secretion) which was formed after each pellet was smeared across the base of the cell by the terminal segments of the twisting and turning larva. However, in some cells each fecal cake was composed of dorsoventrally compressed pellets of various sizes that were strongly attached to each other (fig. 21).

When larvae were placed in a petri dish, the feces were observed to be extruded as moist, subcylindrical, brown pellets normally narrowed at both tips. They were 0.2 mm wide centrally and 0.1 mm wide at their narrowed tips and their lengths varied from 1.2 to 1.8 mm. When not disturbed, these pellets remained attached to each other by a thin, translucent strand of anal secretion. When a freshly extruded fecal particle was slowly teased away from its anal attachment, a long strand of clear anal secretion, 0.2 to 0.5 cm long attached to the posterior tip of the fecal particle, was emitted through the anus. Possibly, then, the anal strand was a continuous secretion that traversed the long axis of all the fecal particles rather than a discontinuous secretion that merely attached the fecal pellets to the anus.

As each fecal particle dried in the petri dish, its color changed from medium brown to nearly black and its shape changed from nearly straight to slightly arched. Most, but not all, fecal pellets extruded from any particular larva possessesd a lateral groove that traversed the length of each side of each particle and measured 0.025 mm deep and 0.05 mm wide. In addition, the surface of a few pellets in each fecal cake appeared to be covered with a smooth, thin varnish, which possibly represented secretions of the peritrophic membrane.

During the relatively long defecation period, an average of 2.04 pellets per hour were extruded. If they had been deposited loosely in the cell, they would have nearly filled it. Obviously, compression of the pellets into a solid cake was necessary to conserve space.

Postdefecation activities

The larva moved to the area of the cell cap immediately after depositing the last fecal particle and curved the anterior area of its body posteroventrally. Eventually, the slightly retracted head and the anterior margin of the prothoracic segment were appressed against the first two abdominal sterna, and the metathoracic tergum and abdonimal terga I (or I and II) were pressed against the cell cap and the anterior margin of the cell wall. The slightly protuberant ventrolateral tubercles of the mid- and posterior body segments and the ventral area of the last two abdominal segments also touched the cocoon. Although the larva became flaccid as it established this decurved position, it continued to remain firmly appressed against the anterior area of the cell. This position separated it from its fecal cake by approximately a third of the cell's length (figs. 18, 22, 23).

Four prepupae were placed in a cool room (constant 10°C) on July 30, 1968. By January 6, 1969, these larvae straightened and became semiturgid. They remained motionless until they transformed into pupae (10 males, 3 females) between January 11 and 12, 1969. The pupae were active and cream white when they were first formed and pigmentation of the adult cuticle developed gradually. The eyes darkened within 60 hours after pupation, well before others parts of the body began to darken. Subsequently, the head, and then the thorax, gradually became pigmented. The abdomen, legs and antennae were the last to darken. Adults emerged on January 25 and 26, 14 to 15 days after they entered the pupal stage. When 8 additional larvae were subsequently reared together, 3 male and 5 female pupae transformed into the adult forms within a 36-hour period. These data indicate that the species does not practice proterandry in the greenhouse.

ASSOCIATES

Hicks (1929) reported three parasites attacking *P. edwardsii*: a mutillid, *Photopsis* sp., a chrysidid, cited as *Chrysura densa (Cresson)* (= *Chrysis*) *densa* Cresson, and an unidentified chalcid wasp (considered as possibly a hyperparasite). In the same paper, Hicks reported *C. densa* and a new species (near *Chrysura tota* Aaron) attacking *P. vespoides*. Parker (1967) reported *C. densa* as a parasite of *P. zonalis* and Hungerford (1937) reported it on *Pseudomasaris occidentalis*. Some chrysidids parasitize megachilid bees, and others are parasites mostly of wasps. The parasitism of *Chrysura densa* on *Pseudomasaris* may result from the similarity of provisions between megachilids and *Pseudomasaris*.

In the present study, one *P. edwardsii* cell was attacked by *Monodontomerus obscurus* Westwood (family Torymidae). Inasmuch as *M. obscurus* was already established in the greenhouse as a parasite of *Megachile rotundata* (Fab.) and other osmiine bees, its association with *Pseudomasaris* is not clear, especially when only one cell was parasitized.

NESTS OF OTHER MASARID WASPS

In addition to *P. edwardsii*, cells of *P. vespoides*, *P. phaceliae*, and *Euparagia scutellaris* were examined. They are described and compared with cells of *P. edwardsii*.

Nest of *Pseudomasaris vespoides*

The one nest of *P. vespoides* examined (fig. 24) was collected in an orchard in Box Elder County, Utah. It consisted of a cluster of nine parallel cells attached to a twig of a peach tree. The cluster was covered laterally and ventrally by the same soil mixture used to construct the cells. The smooth nest covering was attached directly to the cells and filled the areas between them which caused the nest to be nearly spherical. The area of the nest anteriad of the cell caps was not covered so that each cell cap was exposed. However, extensions of the cell walls were sometimes constructed above the cell caps and their lengths varied between 3 and 9 mm.

The large parallel-sided cell measured 20 to 23 mm long and 7 mm wide at its widest point centrallly. A single-layered cocoon covered the entire inner surface of the cell and it was tightly pressed against the unlined inner cell wall and cap. Its composition of a clear matrix interspersed with many silk strands was very similar to the cocoon of *P. edwardsii* although it was thicker and shinier. Also, the cell cap of *P. vespoides*, even though thicker (4.5 mm) than those of other *Pseudomasaris* species examined, was very similar to that of *P. edwardsii* in shape and in form. In addition, the shape, color, form and placement of the feces was nearly identical with *P. edwardsii*. The provision of *P. vespoides*, as well as the position of the prepupa as described by Hicks (1927), were nearly identical to those of *P. edwardsii*.

Cell of *Pseudomasaris phaceliae*

One broken cell of *P. phaceliae* and its dried provision were examined. The cell differed from those of *P. edwardsii* and *P. vespoides* in only that it was more delicately constructed and the inner face of the cell cap was not differentiated into a distinguishable sequence of rings. The provision was similar to that of *P. edwardsii* except that the anterior surface possessed a central spine of pollen, 0.675 mm long, 0.450 mm wide basally and 0.100 mm wide apically.

Cells of *Euparagia scutellaris*

The 4 cells of *E. scutellaris* were examined and compared with cells of *Pseudomasaris* spp. Several distinct similarities were noted: (1) cells of both taxa were constructed of soil; (2) cells were nearly identical in shape and form; and (3) the inner faces of the cell walls were unlined. The shape of the overwintering larvae of the two taxa were also similar. However, the larvae of

TABLE I.

A comparison of *Pseudomasaris* and *Euparagia* immature forms with other vespoid immature forms as figured and described by Reid (1942) but utilizing characters exclusive of those used by Reid

Characteristics	*Pseudomasaris edwardsii*	*Euparagia scutellaris*	Eumeninae	Polistinae	Polybiinae	Vespinae
1. Cleavage line complete	−	−	−	±	−	−
2. Salivary opening a transverse slit surrounded by sclerotized lips	+	+	+	+	+	±
3. Mandibles with three teeth	−	+	+	−	−	+
4. Mandibles broadened	−	+	+	−	−	+
5. Antennae positioned low on head	−	+	+	−	−	±
6. Spiracular atria with spines	−	−	−	−	−	+
7. Mandibles crossed apically	+	−	−	−	−	±
8. Labrum emarginate medially	+	+	±	+	+	+
9. Labrum spinulate	−	+	+	±	+	±
10. Vertex strongly indented	+	−	−	±	±	±
11. Antennae with sensilla apically	+	+	+	±	+	+

Euparagia were much less flaccid and were positioned at the base of the cell with their ventrolateral tubercles not appressed against the lateral walls of the cell. Because *Euparagia* and *Pseudomasaris* are members of different subfamilies and, since *Euparagia* represents the only known predatory masarid, it is not surprising that their cocoons and fecal cakes have many differences.

The cocoon of *Euparagia* was a brownish, paper-textured structure that lined the inner walls of the cell. It was opaque and pressed against the cell wall but not strongly attached to it. Also, it was very thin (less than 0.01 mm thick) and composed of a homogeneous matrix lightly interspersed with silk strands. The outer surface was dull brown, and the inner surface was highly reflective. The anterior covering was perfectly flat, traversed the cell at least 2 mm below the position of the cell cap (cells examined were without cell caps) and was composed of two complete layers separated by as much as 0.75 mm. The area between the layers was filled with a mixture of soil, feces and a few sclerites of the weevil prey. The cell walls between the flattened anterior end of the cocoon and the cell cap were lined with cocoon silk. Most of the weevil prey, represented by unconsumed head capsules and other structures, were deposited at the base of the cell and appressed between the cocoon and the cell wall. Some feces were intermixed with these weevil parts but most fecal particles were deposited on the inner surface of the cocoon over most of the lower fifth of the cell. The fecal cake was dark grey, brittle, 0.1 mm thick and strongly attached to the cocoon surface.

DESCRIPTION OF IMMATURE FORMS

Pseudomasaris edwardsii (prepupa)

Head: Integument sclerotized; with mandibular apices, anterior tentorial pits, apices of maxillae including palpi and galeae, hypopharynx, labial palpi, salivary lips and hypostomal area darkened; few setae scattered on head capsule; numerous sensoria on head capsule; epicranial suture narrow, incomplete, terminating above clypeus; epicranial area limited dorsally by large indentation of vertex and terminating ventrally above the anterior tentorial pits; antennae represented by large circular convexities, each with three sensoria; parietal bands distinct, narrow, but moderately long; posterior thickening of head capsule well developed laterally and moderately developed dorsally; hypostomal thickening well developed; pleurostomal thickening broad, well developed; anterior tentorial pits distinct, at lateral margin of clypeus; epistomal suture strong laterally, distinct centrally; clypeus moderately protuberant; labroclypeal suture slightly emarginate, distinct; labrum with distal margin emarginate centrally, tuberculate laterally; lateral margin of labrum curved; labral tubercles moderately protuberant; mandibles elongate, bidentate, narrowed and pigmented apically; outer tooth larger, inner tooth ending subapically, more sharply tapered; teeth minutely serrate on inner edges; inner apical surface with concavity traversing length of pigmented area; concavity surrounded by carinalike lateral edges of mandibular teeth;

maxillae with scattered sensoria; larger than postmentum from which it is separated; hypopharynx flattened anteriorly, with flattened area strongly rugose; salivarium surrounded by transverse salivary lips positioned apically on prementum; salivary lips serrate apically, traverse width of prementum, and extend well above its surface; labial palpi subapical, broader than long, with two apical sensoria; labial palpi less developed than maxillary palpi; prementum plicate dorsally.

Body: Overwintering form strongly decurved; head hidden; strongly appressed against abdominal sterna; body subcylindrical, semiflaccid; integument with sensoria; intersegmental lines complete; dorsolateral and ventrolateral tubercles absent; spiracle not elevated above cuticle; peritreme flat, atrium slightly sclerotized, grapefruit-shaped, with walls smooth, lacking spines or denticles, 0.033 mm in diameter; primary tracheal opening with collar, without spines; subatrium convoluted; anus a transverse apical slit on terminal segment.

Pupa: The pupa, except for its color and delicacy, is very similar to the adult form. It is, therefore, necessary to describe only those structures and positions of structures peculiar to this stage; clypeus with tubercle on apical margin positioned medially; abdominal terga spinulate, spinulae not in a band but positioned randomly; male with antennae having tubercle on inner margin of flagellar segments 2 and 3; club normal; antennae bent posteroventrally; first flagellar segments rest on tarsi of front legs and antennal clubs rest on tarsi of middle legs; mouthparts extended posteriorly with glossa resting on antennal clubs where clubs touch along innerapical margins; *female* with antennal clubs resting on basitarsi of front legs; glossa free.

Euparagia scutellaris (prepupa)

Head: Integument sclerotized with mandibular apices and articulation, maxillary and labial palpi, salivary lips, and anterior tentorial pits heavily pigmented, antennae lightly pigmented; pleurostomal and hypostomal thickenings, and posterior thickening of head capsule pigmented; head capsule, clypeus, labrum and labium with few small setae, maxillae with few long hairs; clypeus spinulate apically; labrum heavily spinulate along apical edge; epicranial suture strong, incomplete, represented by a deep narrow furrow ending at frons; vertex of the head capsule round, not indented; frons represented as a flattened, triangular, indistinct area limited anteriorly by the epicranial suture and laterally by the anterior tentorial pit; pair of large shallow indentations on frons above epistomal ridge; small deep pit superimposed on each large indentation basally; epistomal ridge very broad and sinuate dorsomedially; epistomal suture distinct; parietal bands distinct, narrow, slightly produced, straight but converge dorsally; antennae slightly produced, positioned low on head capsule, each with three sensoria; a pair of circular, deep pits located above antennae and adjacent to frons; clypeus produced; labroclypeal suture distinct, tuberculate; labrum large, truncate apically with narrow central area deeply emarginate; posterior thickening of head capsule

narrow but well developed and equally developed around head; dorsal margin of posterior head capsule thickening positioned below vertex of the head; hypostomal thickening strongly developed; pleurostomal thickening well developed, but not as well developed as hypostomal thickening; tentorial pits distinct; mandibles robust, sclerotized, nearly truncate apically, apical margin interrupted by three short teeth, inner apical surface concave and limited basally by transverse carina; abductor and adductor apodemes shorter than mandible, mandibular apex and area surrounding concavity deeply pigmented; maxillae distinct with galea and palpus positioned subapically, palpus with three sensoria; labium produced, prementum and postmentum distinct; salivary opening a transverse slit surrounded by sclerotized lips which project very little above prementum; labial palpi subapical, large, but not strongly produced, each with three sensoria.

Body: Postdefecating form strongly decurved with head touching second abdominal sternum; body not flaccid; intersegmental lines complete; intrasegmental lines indistinct; dorsolateral and ventrolateral tubercles developed, without sensoria; cuticle plicate; spiracle not elevated above cuticle; peritreme flat; atrium 0.066 mm in diameter, "donut"-shaped, with walls lightly sclerotized, reticulated; primary tracheal opening without spines and without developed collar; subatrium with walls smooth, expanded, diameter greater than atrium, posteriorly narrowed into primary trachea; surface of subatrium and trachea without denticles; anus a transverse slit positioned subapically on terminal segment.

DISCUSSION

Nest architecture and biology

The family Masaridae, with 19 genera and 228 species, is a relatively large taxon, but the biology of most of its species and the morphology of the immature forms of almost all of them are unknown (see appendix). Therefore, a discussion of the phylogeny of the family based on a biological comparison between *Pseudomasaris* and other masarid genera is premature at this time. Conversely, particular aspects in the biology of *Pseudomasaris* should be compared and discussed for a number of reasons: (1) the degree of ethological variability expressed within the genus can be demonstrated; (2) some questions proposed in the literature can now be answered; and (3) some of the earlier literature included faulty observations and unwarranted assumptions and conclusions that require correction.

During the course of this study numerous nests of *P. edwardsii* were examined and compared with those of two other *Pseudomasaris* species and with nests figured and described in the literature. These comparisons indicate that little variation in nest construction is shown among individuals of the same species (*P. edwardsii*) and not a great deal more variation is expressed between species. In the section on nest structure, there is a list of nest architectural features that are similar in all nests of *P. edwardsii*. Most of these are

also features in nests of other *Pseudomasaris* species studied. Additional nest similarities between species studied include: nests constructed in open but concealed niches; nest covers, when present, attached to cells; and cell walls with inner surfaces not lined.

Other ethological patterns discernible in the nests of *Pseudomasaris* also have relative constancy within the genus (cocoons, fecal deposits, and position of the overwintering larvae). The vespoid characteristic of depositing the egg before provisioning the cell is retained in *Pseudomasaris,* but an exception to this habit within the superfamily Vespoidea is apparently practiced by *Euparagia.* According to Clement and Grissell (1968), *E. scutellaris* provisions its cell with weevil larvae before depositing its egg.

Descriptions of the provisions of four *Pseudomasaris* species [*P. maculifrons* and *P. phaceliae* (Parker, 1967), *P. vespoides* (Hicks, 1927), and *P. edwardsii* (Hicks, 1929, and the present paper)] indicate that only the size of the provision and the shape of the surface projections vary interspecifically. Hicks (1931) believed that each projection on the provision represented one load of pollen, whereas the present study demonstrates that a few papilla-like projections were constructed during each deposit of pollen and nectar. Because *Pseudomasaris* retains the vespoid characteristic of laying its egg before provisioning its cell, the shape and form of the provision may represent the method by which the wasp has resolved the problems of airing the egg and larva, maintaining a constant humidity in the cell, protecting the provision and larva against temporary but excessive heat, and reducing the surface area of the provision in contact with the moisture-absorbing cell wall. If the genus has, in fact, evolved in this direction, it should not be surprising that little variation is found in the provisions of those species studied.

Richards (1962) pointed out that the labrum of the Masarini is sclerotized and suggested that this feature is in some way related to the extension and retraction ability of the glossa. In my studies, the labrum was used extensively for tamping and spreading wet soil during nest construction, and the sclerotized labrum aided the wasp in this use of the structure for tamping.

Richards (1962) also reported that one female specimen of *P. occidentalis* collected from Texas had a large lump of clay stored beneath the head and supported on the tips of the labial palpi. Two similar observations were made for *P. edwardsii* during two soil collections, but in the majority of cases, two separate balls of soil were found on the postgenal surfaces. On three different occasions, I observed a different individual carrying a single, dry, soil particle between its mandibles as it returned to its nest. Evans (1966), in quoting Bequaert (1940), mentioned that *Pseudomasaris* also carried pollen pellets between the mandibles. However, Bequaert states, ". . . the female wasp merely gathers with the mandibles and carries in pellets in the mouth." *P. zonalis* was studied in the greenhouse during 1969, and this species carried soil between its mandibles in pellet form. Possibly, the method of soil carriage is interspecifically variable in *Pseudomasaris.*

The question of whether the female consumes pollen that will be deposited in the cell was posed by Richards (1963). Direct observations of pollen and nectar collections by *P. edwardsii,* dissections and paper chromatographic analyses proved that the pollen and nectar collected for provisions are stored in the honey stomach. Further, little if any enzymatic action takes place in the nectar or pollen during this short period. The nectar serves a multiple function since it is also used as a wetting agent for soil collected during nest construction. When this soil dries, the incorporated nectar acts as a hardening agent.

Immature forms

Reid (1942) treated the vespoid immatures taxonomically and demonstrated that the subfamilies Eumeninae, Vespinae, Polistinae and Polybiinae, established on the basis of adult characters, could also be distinguished on the basis of larval characters. He also discussed the relationships of these subfamilies from the evidence of the larval characters. Accordingly, he separated Eumeninae and Vespinae from Polistinae and Polybiinae on a characteristic of the clypeus: Eumeninae and Vespinae have the entire lower margin of the clypeus ventral to a line drawn between the insertion of the mandibles; Polistinae and Polybiinae have all or most of the lower clypeal margin above this line. He distinguished Eumeninae from Vespinae on the basis of two characters: in Eumeninae, the width of the labrum is as great as, or greater than, the width of the clypeus where the two join, and the distance from the antenna to the nearest mandible is less than the distance from the midpoint on the anterior margin of the labrum to a line drawn between the dorsal mandibular articulations; in Vespinae, the width of the labrum is less than the width of its clypeus, and comparisons of the measurements are opposite the typical measurements for Eumeninae. The Polistinae and Polybiinae were separated by a single characteristic: in Polistinae, several sensory bristles were found behind each labial palpus; only one sensory bristle was found in Polybiinae. Reid also examined one species of *Zethus* and concluded that Zethinae was closely related to Eumeninae. Thus, Reid's classification of vespid immatures nearly paralleled Richards' 1962 classification of the adults.

Because of the differences in food habits and the morphological diversity expressed by adults, it was not surprising that the immature forms of *Pseudomasaris edwardsii* and *Euparagia scutellaris* did not demonstrate a close relationship (figs. 26-33). It was, however, surprising to learn that these two masarids did not demonstrate a closer affinity to each other by Reid's system of classification. In *Pseudomasaris,* the clypeus lies above a line drawn between the mandibular insertion to the head capsule. By Reid's classification, this character should lead *Pseudomasaris* directly to the Polistinae-Polybiinae complex. Conversely, the apical margin of the clypeus in *Euparagia* lies well below the area of mandibular insertion, a character that should relate this genus to the Eumeninae-Vespinae complex. In Reid's separation of Eumeninae from Ves-

pinae, several characteristics were compared, and, in each case, *Euparagia* associated better with Eumeninae. Conversely, it was impossible to compare *Pseudomasaris* by Reid's separation of Polistinae and Polybiinae because this masarid lacks the only character he found to distinguish the two taxa, the sensory bristles behind the labial palpi.

When I compared larvae of *P. edwardsii* and *E. scutellaris* with Reid's description and figures of Eumeninae, Vespinae, Polistinae and Polybiinae by using characters exclusive of those applied by Reid but important in the discrimination of bee larvae, I observed the results presented in table I. This table indicates an affinity between *Euparagia* and Eumeninae, and between *Pseudomasaris* and the Polistinae-Polybiinae complex. It also demonstrates that the Vespinae do not fit neatly into the characters. Thus, the results gained from the study of additional characters are similar to those procured when both masarid groups are studied by Reid's classification.

It is apparent that a second revision of vespid immatures is required. However, before another attempt is made, much more material should be collected and described.

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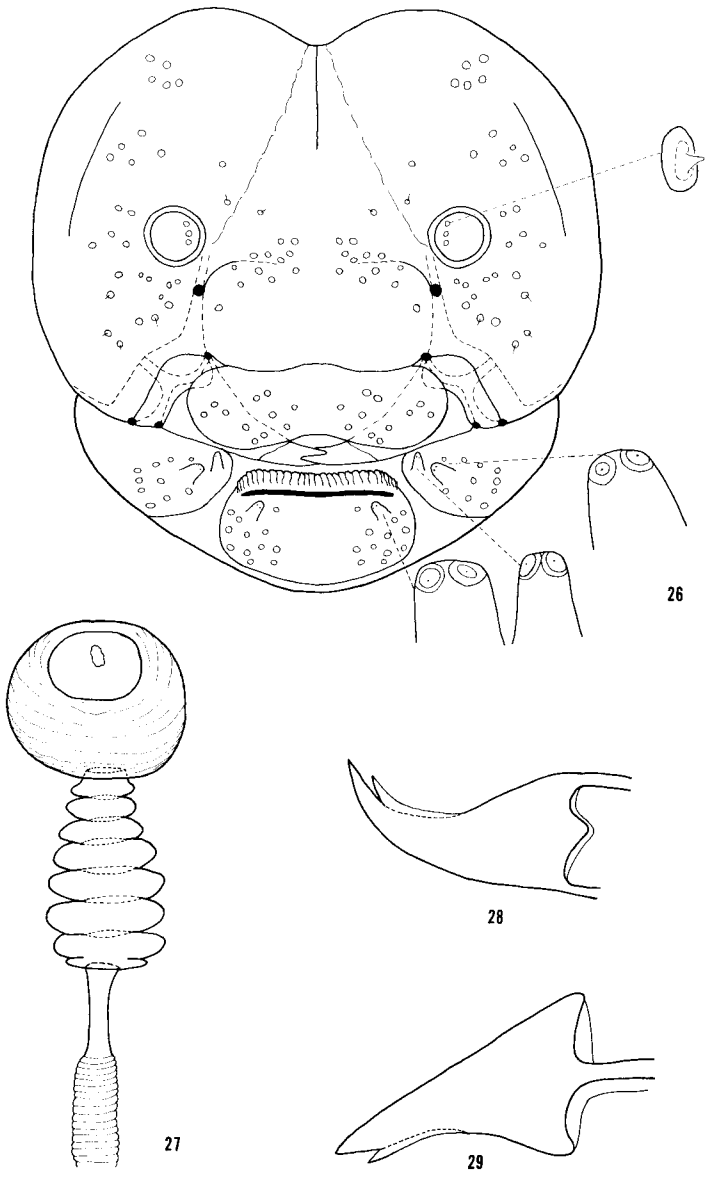
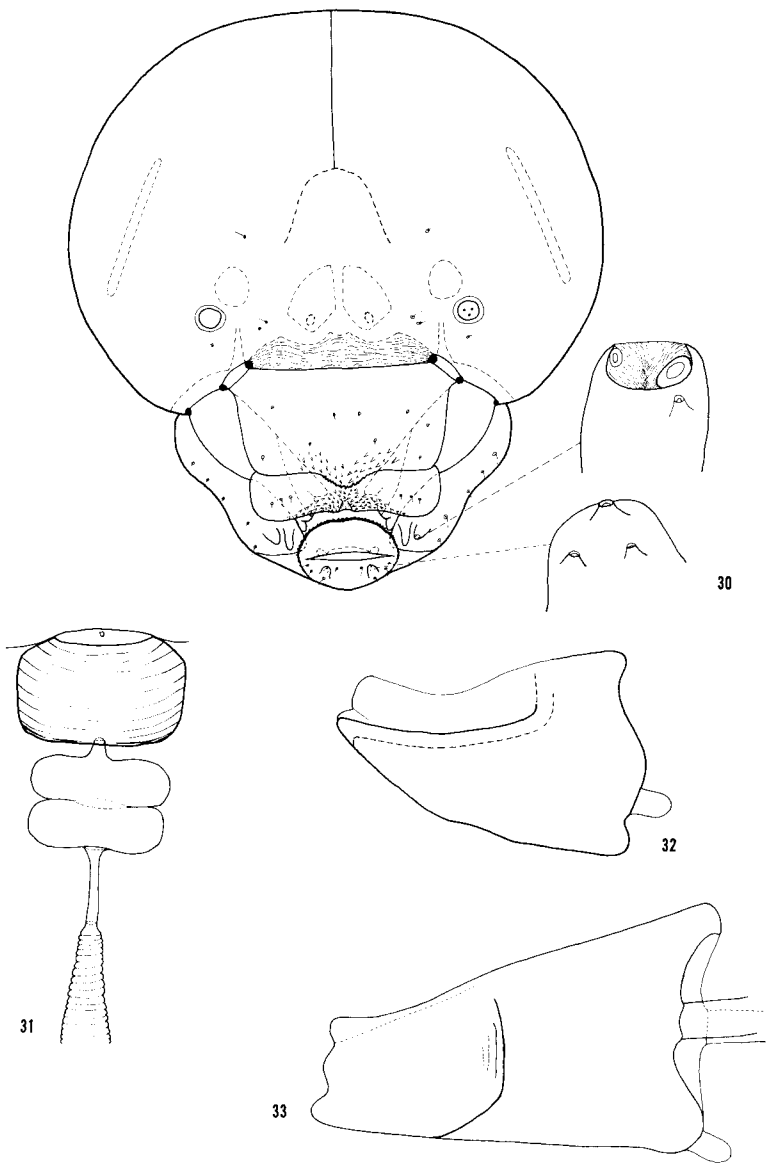


FIGURES 26-29. *Pseudomasaris edwardsii* (prepupa). Fig. 26. Frontal view of head. Fig. 27. Spiracle. Fig. 28. Ventral view of mandible. Fig. 29. Inner view of mandible.



FIGURES 30-33. *Euparagia scutellaris* (prepupa). Fig. 30. Frontal view of head. Fig. 31. Spiracle. Fig. 32. Ventral view of mandible. Fig. 33. Inner view of mandible.

APPENDIX

A generic list of the Masaridae according to Richards (1962); it includes some biological features of the family, (+ = yes; − = no; ? = not known)

	No. of species	Distribution	Nest location	Turrets	Cells in clusters	Progressive provisioning
Masaridae						
Euparagiinae						
Euparagia	7	Western North Amer.	in soil	+	−	−
Gayellinae						
Gayella	4	Chile, Argentina	exposed	−	+	−
Paramasaris	1	Central America	?	?	?	?
Masarinae						
Paragiini						
Paragia	14	Australia	in soil	+	?	−
Metaparagia	2	Australia	?	?	?	?
Rolandia	1	Australia	?	?	?	?
Riekia	1	Australia	?	?	?	?
Ceramiopsis	1	South America	in soil	+	?	?
Ceramius (includes *Paraceramius* and *Ceramioides*)	26	Africa, Eurasia	in soil	+	+	+
Masarini						
Trimeria	7	South America	?	?	?	?
Microtrimeria	1	South America	?	?	?	?
Quartinia	40	Africa	?	?	?	?
Quartiniella	5	Africa	?	?	?	?
Quartinoides	38	Africa	?	?	?	?
Masaris	2	Middle East	exposed	−	+	?
Masarina	3	Africa	?	?	?	?
Jugurtia	20	Africa	?	?	?	?
Pseudomasaris	15	No. Amer., Africa	exposed	−	+	−
Celonites	37	Africa, Middle East	exposed	−	+	−

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A REVIEW OF THE EXTINCT AVIAN GENUS, *MANCALLA*

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