Developmental Morphology of Larvae and Eggs of the Imported Fire Ant, *Solenopsis invicta*[1]

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ABSTRACT

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The egg of the imported fire ant, *Solenopsis invicta* Buren, becomes embryo-like before the larva emerges. Hatching is described. First instars are hairless. Second instars have only a few small, simple hairs. Third instars have moderately numerous short hairs, either simple, branched or bifid. Fourth instars have long, straight, simple hairs on the head and anteroventral body region; all other body hairs and some posterior head hairs are strongly bifid. The mandibles of only the 4th instar are sclerotized.

Both eggs and larvae stick together in clumps in the colony by means in eggs and 1st and 2nd instars of an adhesive coating, and in 3rd and 4th instars by hooked hairs which interlock on adjacent larvae.

A simple method for determining the developmental stage of live larvae of the imported fire ant is provided.

We know little about the developmental biology of ants despite their ecological, sociobiological, and economic importance. The general morphology of larvae of the genus *Solenopsis* was described by Wheeler and Wheeler (1955, 1960), who, however, did not determine the number of larval instars for any species of *Solenopsis*, and described only "mature" or "young" larvae of undetermined age. Either 3, 4, or 5 instars occur in species of other ant genera (reviewed by Delage-Darchen 1972). Delage-Darchen (1972) described 3 instars for *Crematogaster* (*Nematocrema*), distinguished by mandible size and, to a lesser extent, chaetotaxy. O'Neal and Markin (1975) described 4 larval instars in the imported fire ant, *Solenopsis invicta* Buren, differentiating them by the morphology of the mouthparts, and by Dyar's principle (1890). However, the 1st instars of *S. invicta* were found to have a larger number and variety of setae than the youngest larvae of *S. molesta* (Say) as described by Wheeler and Wheeler (1955). Thus, the morphological variation within the genus seemed ususually large. We investigated the developmental morphology of *S. invicta* with the view of clarifying these discrepancies, and to discover a means to identify the developmental stage of fire ant larvae.

Materials and Methods

Mature colonies of *S. invicta* were maintained according to Petralia and Vinson (1978). Examination of individual larvae and eggs was made on moist tissue paper in small plastic petri dishes. The relationships between brood and adult worker ants were observed with 1–100 workers in a petri dish provisioned with moist filter paper and a small amount of peanut butter. Most studies, including the descriptions of minor worker larvae, were conducted with colonies producing only minor workers.

Most specimens for light microscopy were mounted alive in Hoyer's medium or Hoyer's modified with iodine and potassium iodide (Schuster and Pritchard 1963). Mature reproductive larvae (either unmounted or whole mounted as above) were fixed in Kahle's fixative (Vinson 1969) and stored in 80% ethanol. Other specimens were examined alive. For most scanning electron microscope (SEM) studies, larvae were mounted on stubs with either silver paint or "Tube-Coat"™ and examined alive. "Tube-Coat" allowed fire ant larvae to survive longer exposures to the electron beam than silver paint. Some SEM studies were conducted using larvae metal-coated alive or fixed in 2–3% glutaraldehyde or Kahle's fixative. Following fixation, specimens were dehydrated in an ethanol series and critical-point dried. Specimens were examined in a Jeol JSM-U3 or 35 SEM at 20-25 kV for metal coated specimens and 15 kV for live specimens.

The morphological terminology of Wheeler and Wheeler (1976) was followed in most cases. The term "microsetae" denotes protuberances in early instars, which are probably precursors of hairs found in equivalent positions in succeeding instars. Bifid hairs were measured from the base to the intersection of the branches, because measuring the length of the branches was too difficult.

Details of molting were studied to provide evidence for the number of instars. A larva was considered ready to molt when the hairs of the succeeding instar became visible under the transparent cuticle (Fig. 17, 24). Usually the hairs of the body's anteroventer and of the head became visible first. Newly molted larvae and larvae ready to molt were compared for each instar. We examined all hairs, microsetae, spinules, the antennae, mandibles, maxillary palps and galea, labial palps, labial spinules, and the opening of the sericteries. Newly formed larvae (Fig. 5), experimentally removed from the egg shell within 12–14 h after the egg took the shape of the fully formed embryo, were compared with 1st instars in which 1 or 2 hairs of the 2nd instar were visible in the lateral region of the head (i.e., 1st instar preparing to molt). Larvae which had just molted to the 2nd instar (Fig. 9) (< 3 h after molting) were compared with larvae ready to molt to the 3rd instar. Third instars similarly were studied (Fig. 14, 17) (new molted larvae examined

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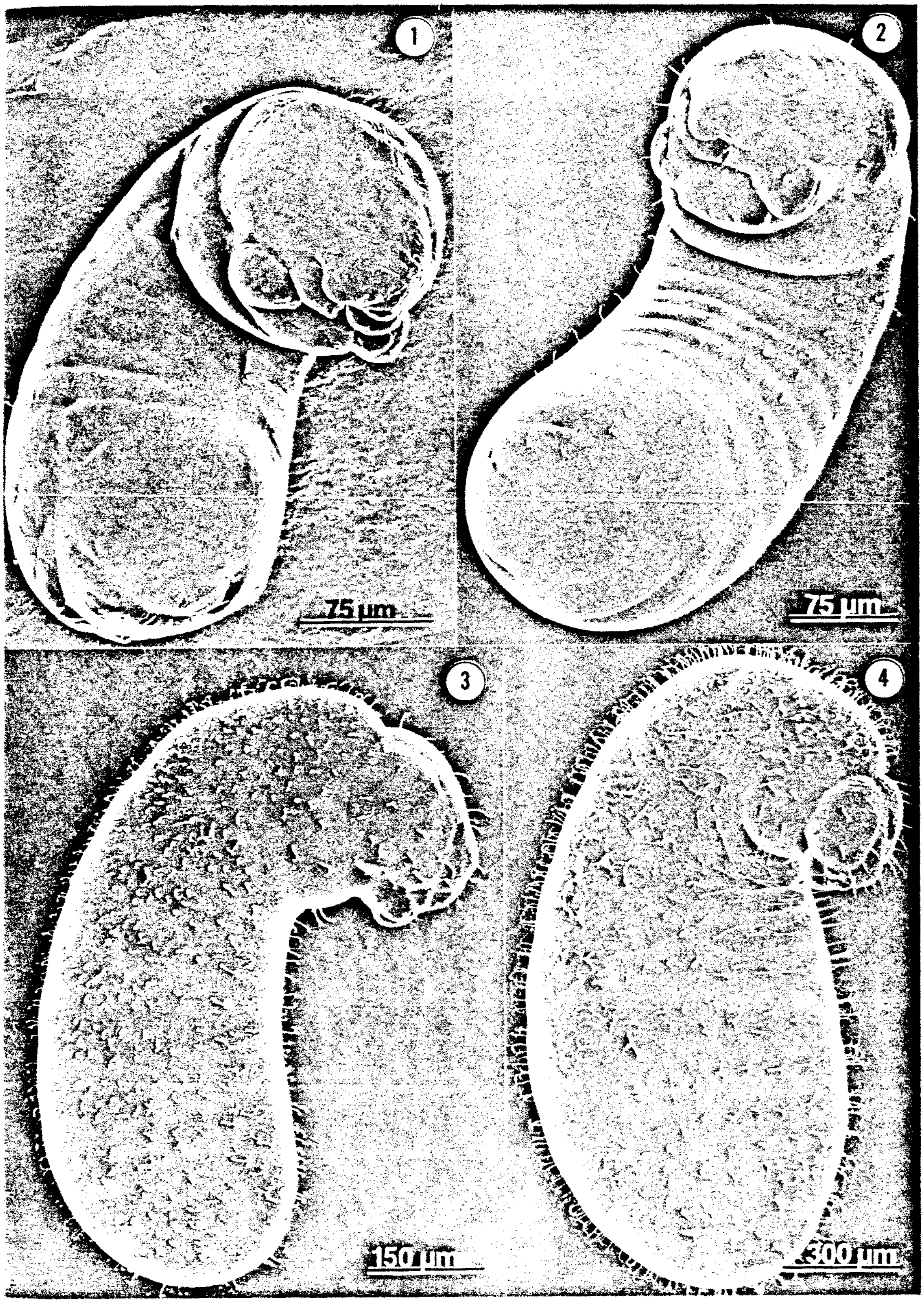

FIG. 1–4.—1. First instar (All specimens in figures examined alive, mounted with Tube-Coat™, unless otherwise indicated); 2. Second instar; 3. Third instar; 4. Fourth instar.

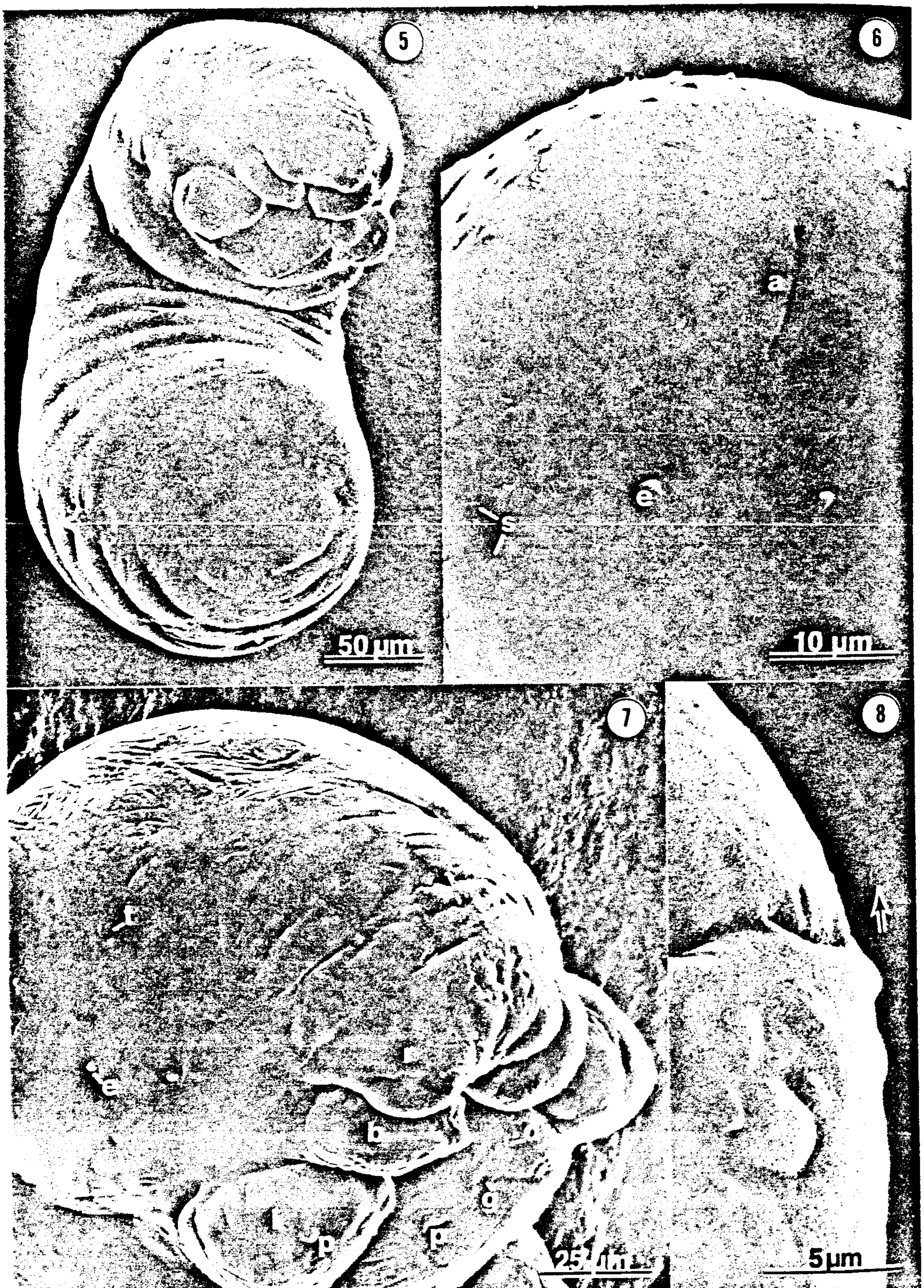

FIG. 5–8.—5. First instar experimentally removed from egg membranes; 6. Posterior body region of 1st instar showing anus (a), microsetae (e), and posterior spinules (s); 7. Head of 1st instar. Note microsetae (e). Antenna (t); labrum (r); mandibles (b); maxilla (l) with palps (p); labium with labial spinules (d), palps (p), and opening of sericteries (g); 8. Left maxillary palp of 1st instar. Arrow points laterally.

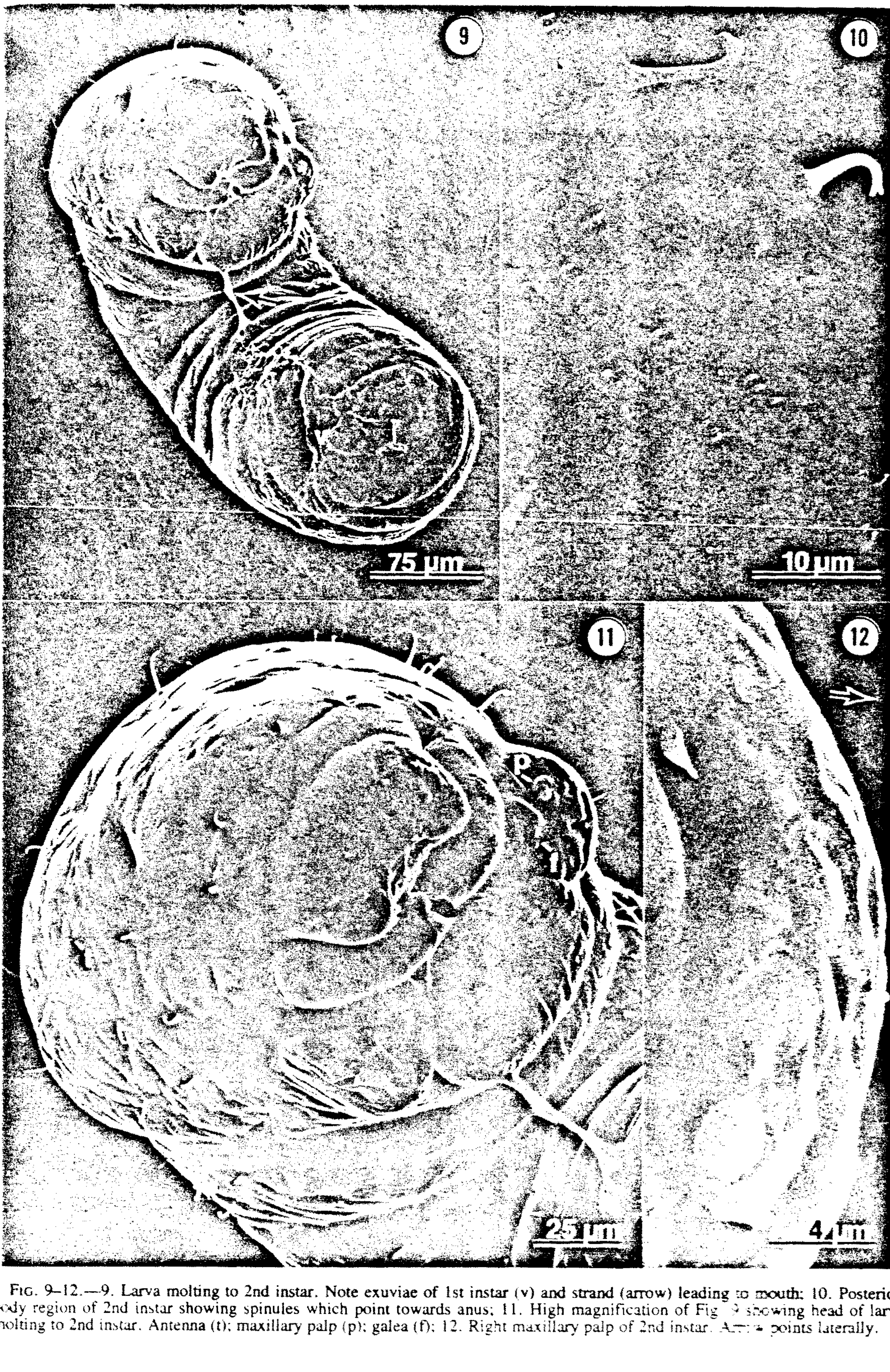

FIG. 9–12.—9. Larva molting to 2nd instar. Note exuviae of 1st instar (v) and strand (arrow) leading to mouth; 10. Posterior body region of 2nd instar showing spinules which point towards anus; 11. High magnification of Fig. 9 showing head of larva molting to 2nd instar. Antenna (t); maxillary palp (p); galea (f); 12. Right maxillary palp of 2nd instar. Arrow points laterally.

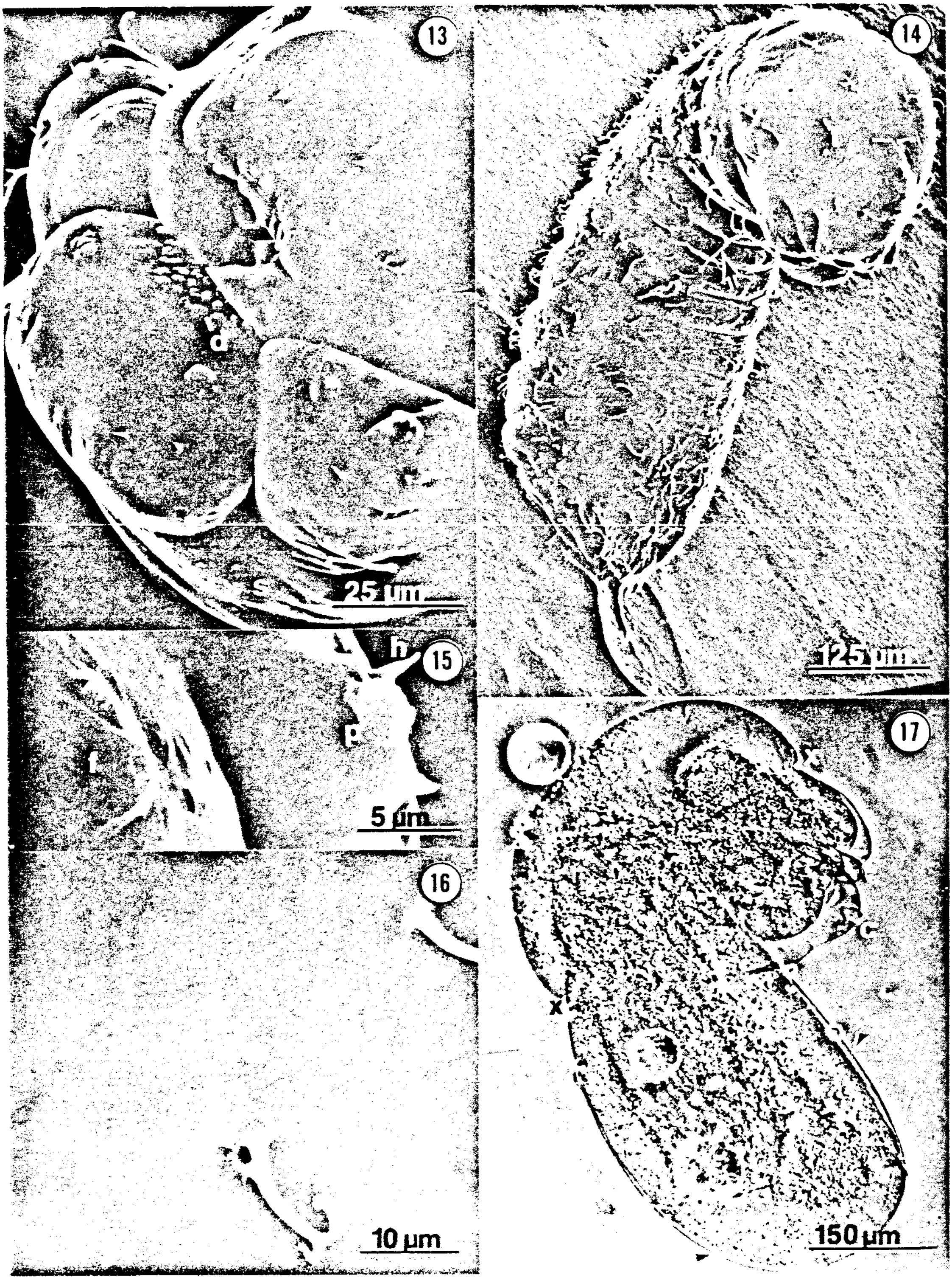

FIG. 13–17.—13. Head of 3rd instar. Note spinules on body. Labial spinules (d); 14. Larva molting to 3rd instar. Note exuviac (v) of 2nd instar and strand leading to mouth (arrow). Antenna (t); 15. Maxillary palp (p) and galea (f) of 3rd instar. Note separat maxillary seta (h) behind the palp; 16. Posterior body region of 3rd instar showing spinules which point towards anus. Note smal bifid hair; 17. Larva molting to 3rd instar. The 3rd instar head and body is bulging out anterodorsally (between x's). Mouthpart have pulled away and the old lining of labial gland common duct (c) has been expelled. Posterior part of the body still bears doubl cuticle. Note 3rd instar hairs visible on inner cuticle (arrow). Whole-mounted in Hoyer's modified with iodine and potassiur iodide and examined with light microscopy (phase contrast).

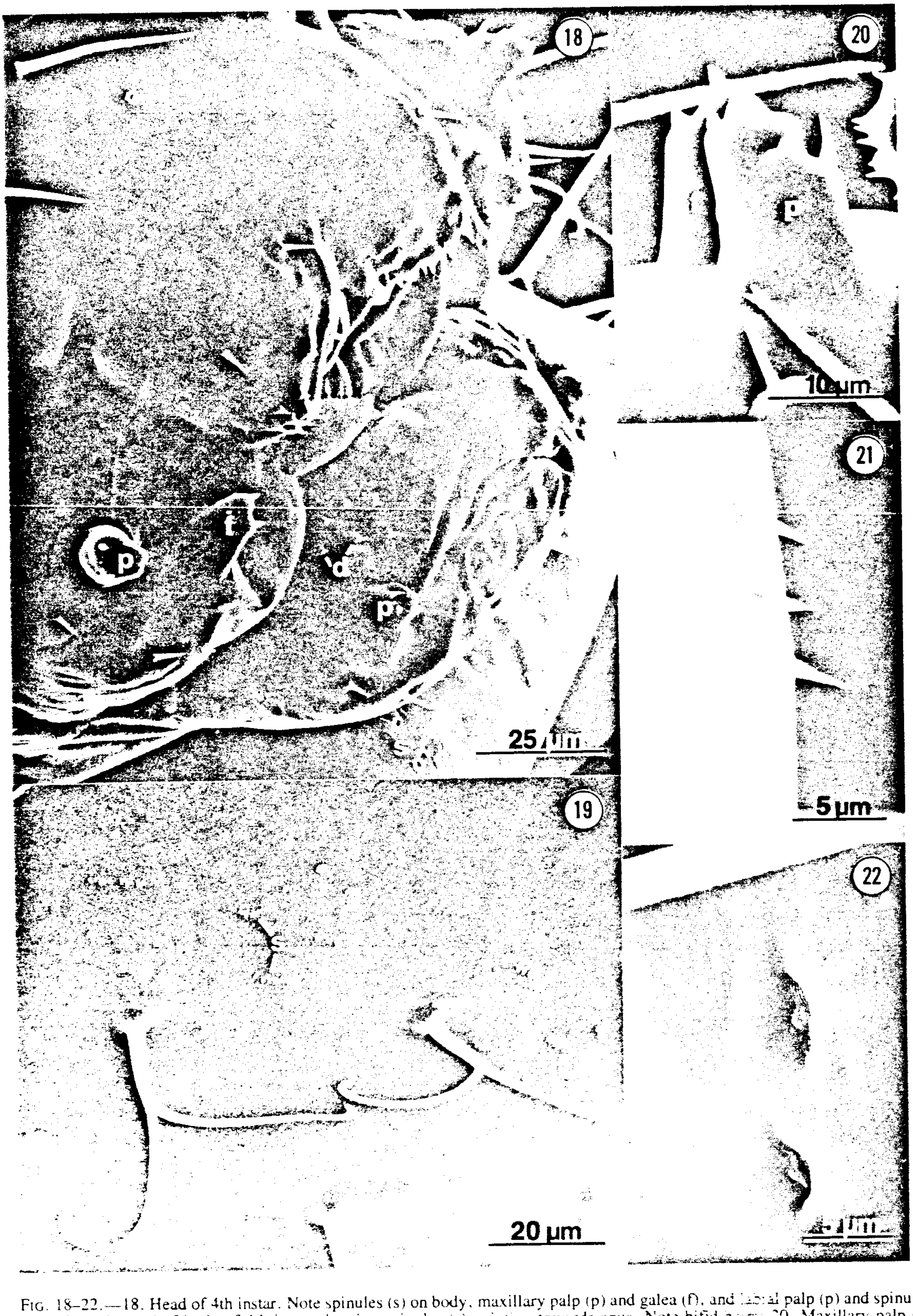

FIG. 18–22.—18. Head of 4th instar. Note spinules (s) on body, maxillary palp (p) and galea (f), and labial palp (p) and spinules (d); 19. Posterior end of body of 4th instar showing spinules (s) pointing towards anus. Note bifid hairs; 20. Maxillary palp (p) and galea (f) of 4th instar; 21. Antennal setae of 4th instar; 22. Facial sensilla on 4th instar.

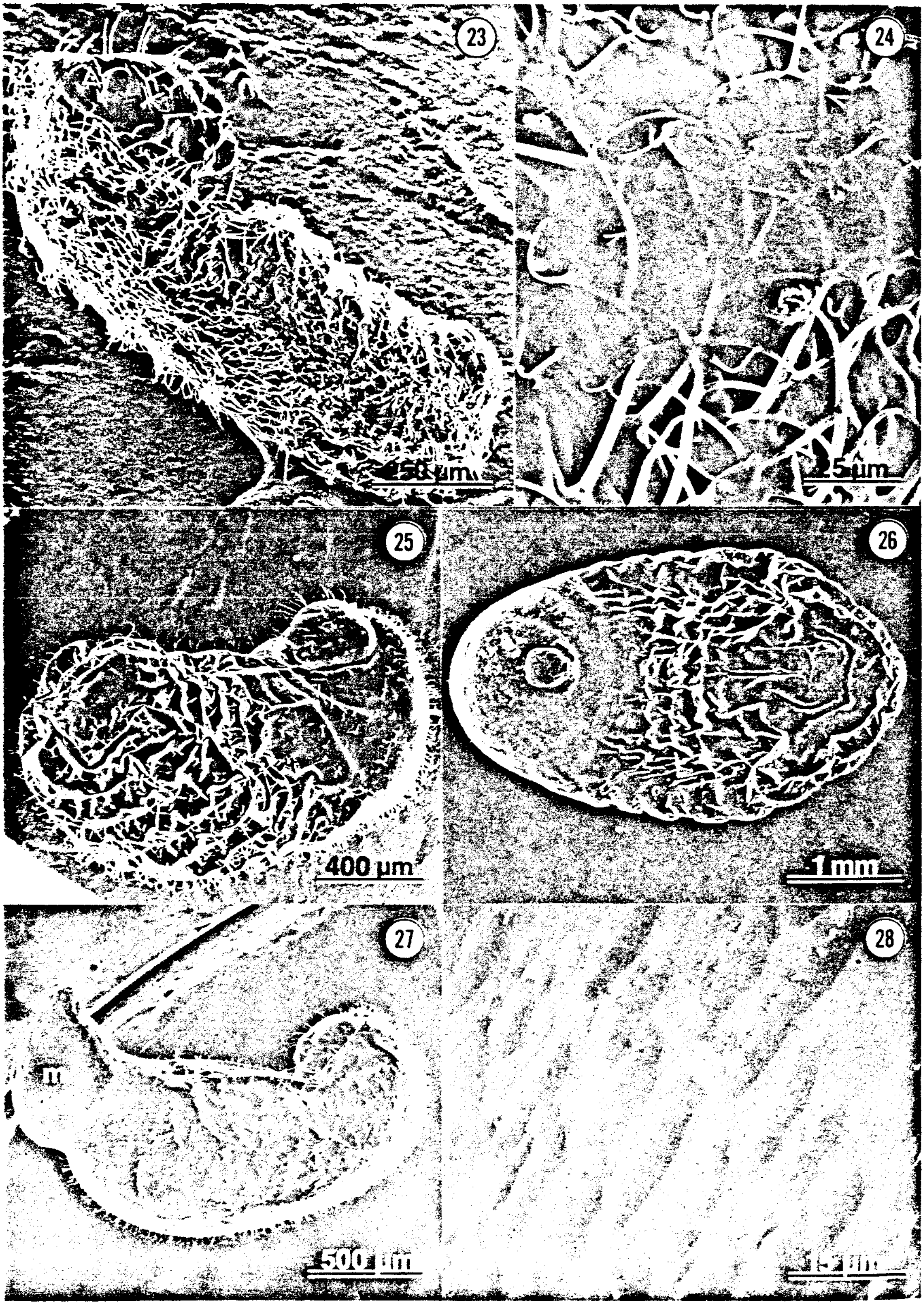

FIG. 23–28.—23. Larva molting to 4th instar. Note exuviae of 3rd instar (between x's); 24. High magnification of Fig. 23 showing interface between 3rd instar cuticle (above) and new 4th instar cuticle (below). Large bifid hairs of 4th instar also visible under 3rd instar cuticle (arrows); 25. Prepupa of worker; 26. Prepupa of male reproductive; 27. Larva passing the meconium (m) 28. High magnification of spines of anteroventral region of male prepupa (Fig. 26).

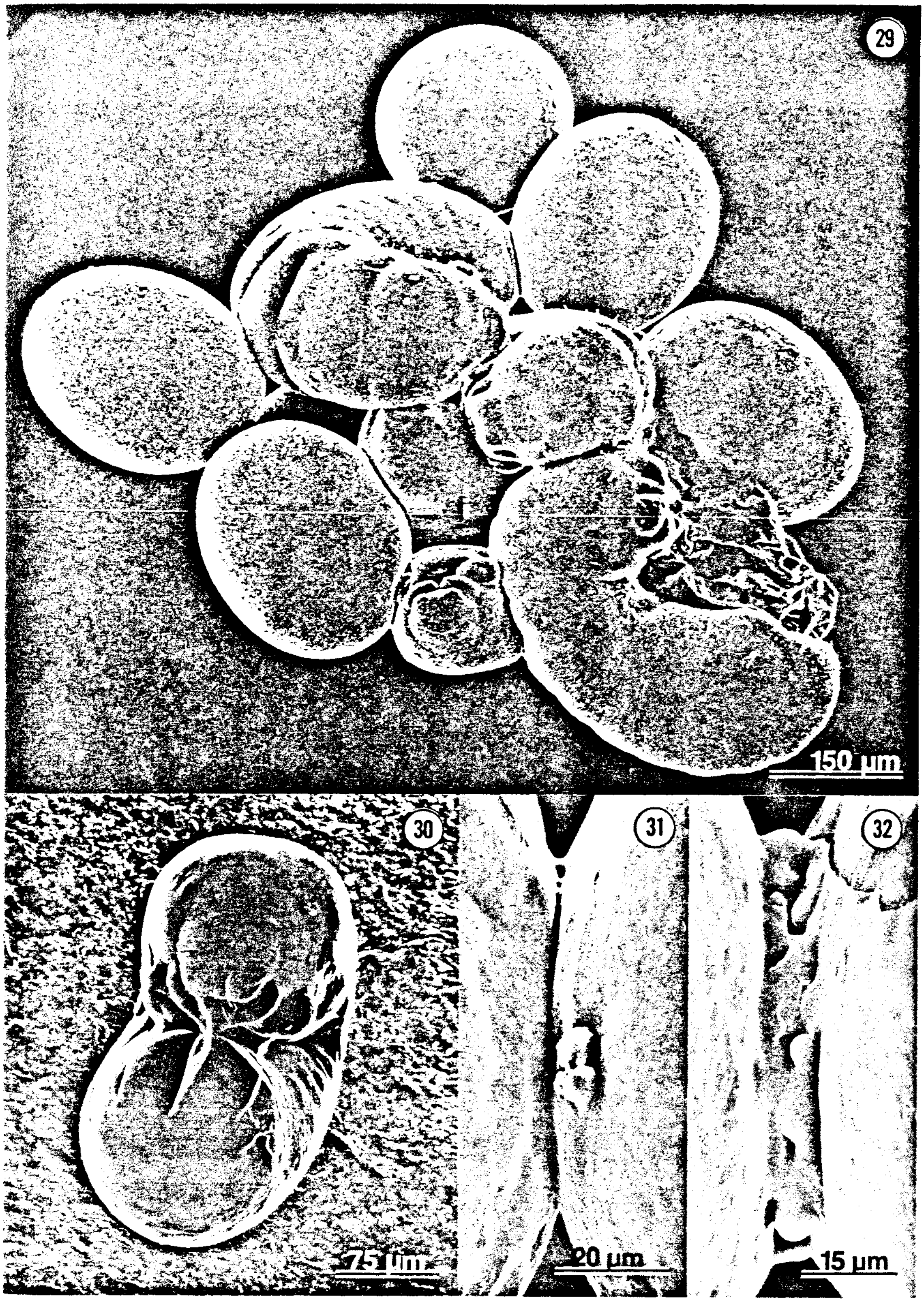

FIG. 29–32.—29. Small brood pile including 5 eggs, three 2nd-instar larvae, and one 1st-instar larva (i). Note bridges of adhesive material connecting them; 30. Hatching egg. Head of larva is partially free of egg membranes. Examined alive on silver paint; 31. Bridge of adhesive material between 2 eggs; 32. Bridge of adhesive material between 2 eggs. Fixed in glutaraldehyde, critical point dried, and metal coated.

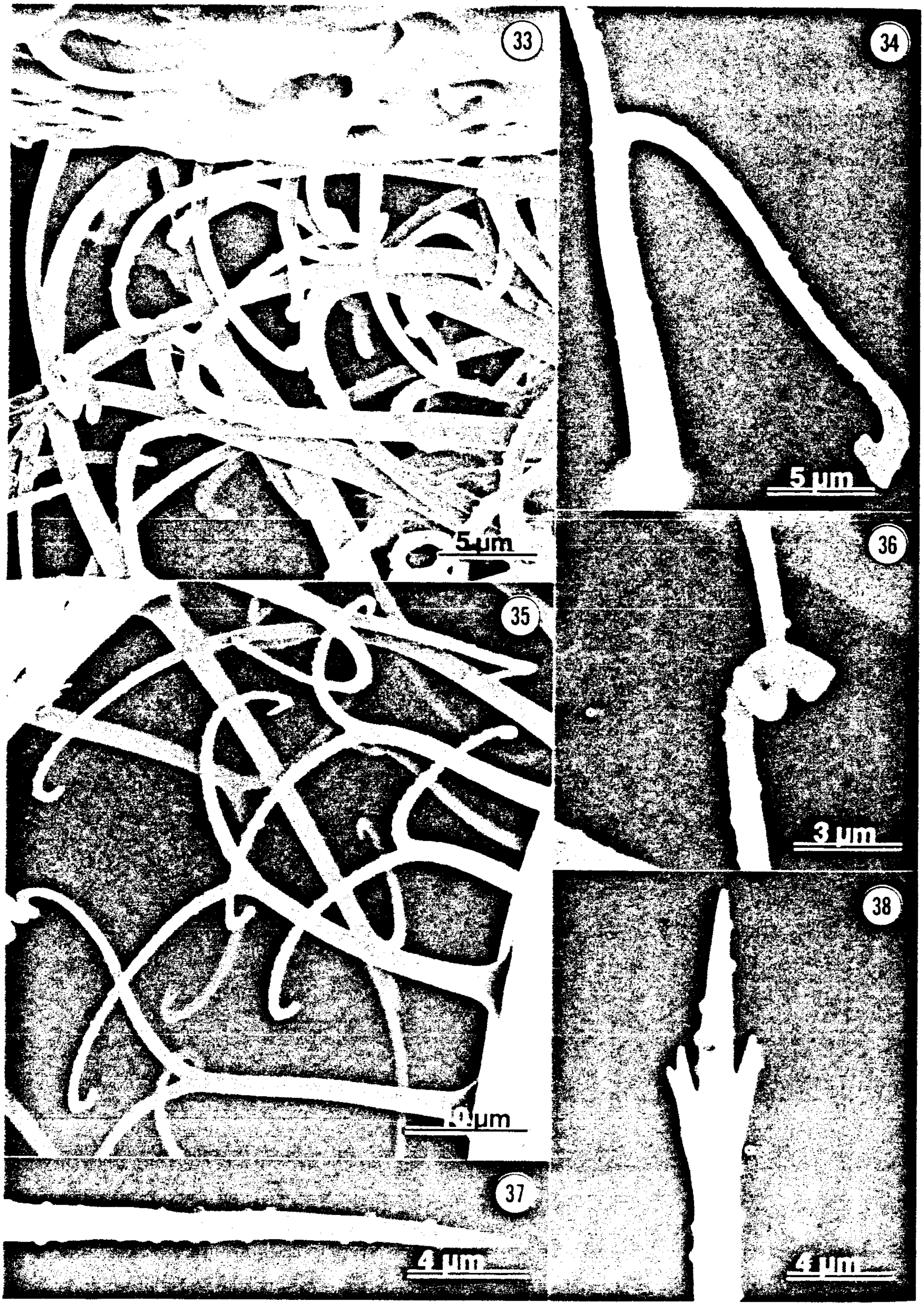

FIG. 33–38.—33. Interlocking hairs between 3rd (upper) and 4th (lower) instar. Note smooth hairs of 3rd instar and papillose hairs of 4th instar; 34. Bifid hair of 4th instar; 35. Interlocking hairs of two 4th instars; 36. Apical ends of 2 interlocking bifid hairs between two 4th instars; 37. Apex of a straight, simple hair from anteroventral region of 4th instar; 38. Apex of a straight simple hair from anteroventral region of 4th instar showing apical branching.

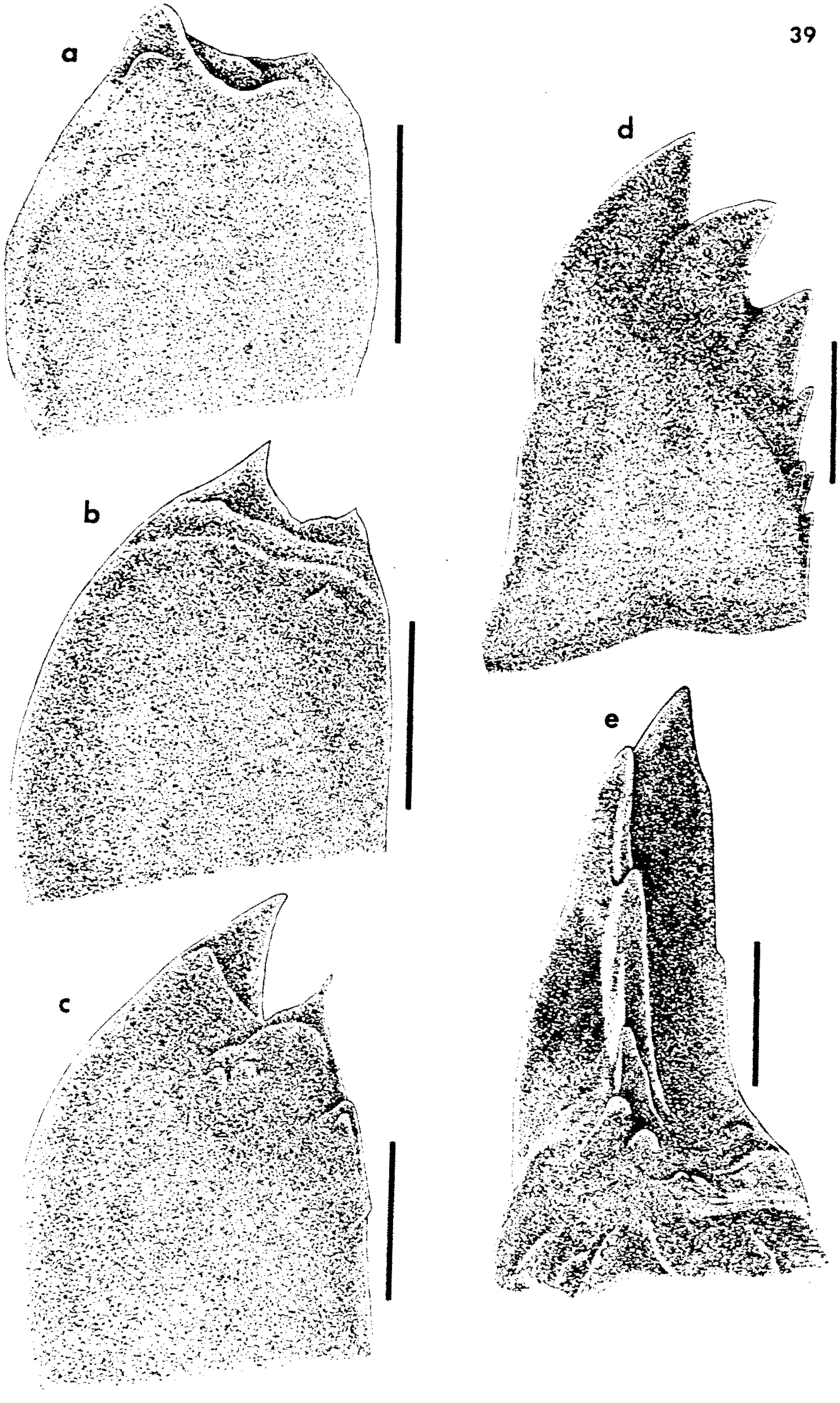

FIG. 39.—Drawings of left mandibles, based on observations with SEM and CM. Line scales are ca. 20 μm: a) 1st instar—dorsal view; b) 2nd instar—dorsal view; c) 3rd instar—dorsal view; d) 4th instar—dorsal view; e) 4th instar—medial view.

within 4 h). Newly molted 4th instars (Fig. 23) (within 8 h) were compared with prepupae (Fig. 25, 26). Head widths of newly molted 3rd instars were compared with those of larvae ready to molt to the 4th instar. Head widths of newly molted 4th instars were compared with head widths of prepupae.

Results

Description of Larval Instars–Minor Workers

Four larval instars were determined on the basis of morphological characters.

First Instar.—Straight length 0.27–0.42 mm. Hair absent, but small, blunt microsetae (Fig. 1, 5, 6, 7) on mouthparts and head, in rows along anteroventral body region, and in perianal region. Rows of spinules in groups of 1 or 2 just posterior to anus, on ventral surface, continuing around posterior end of body and onto dorsal surface, always pointing anteriorly (Fig. 6). Head width 0.14–0.16 mm ($\bar{x}$ = 0.15 mm, N = 15). Antenna represented by 3 indistinct sensilla (Fig. 7). Mouthparts unsclerotized (Fig. 7). Labrum with 2 prominent, dorsomedial microsetae and 6 smaller anteromedial microsetae. Mandible slightly longer than wide, bearing distinct apical tooth and poorly defined subapical tooth (Fig. 39). Maxillary palp (Fig. 8) poorly developed; appearing to consist of 3 sensilla, of which 2 bear a single spinule each and one with possibly 2 spinules. Galea not evident. Labium with a few minute spinules just posterior to indistinct opening of sericteries; palps like maxillary palps, each consisting of 3 or 4 sensilla with a minute spinule.

Second Instar.—Straight length 0.42 mm (newly molted) to 0.57 mm (ready to molt to 3rd instar). Hairs of body and head small, simple, smooth (Fig. 2, 9, 10) (6.1–15.2 mm); apical end enlarged and curved (Fig. 10); body hairs in rows along ventral and perianal region; rows of microsetae medial to ventral rows of hairs. Posterior rows of spinules as in 1st instar, but spinules slightly longer, more numerous, and usually found in groups of 2 or 3 (Fig. 10). Head width 0.16–0.19 mm ($\bar{x}$ = 0.17 mm, N = 33). Antennae distinct, each bearing 3 sensilla with a spinule (Fig. 11). Mouthparts unsclerotized (Fig. 11). Labrum with 4 small dorsal hairs and 6 anterior sensilla. Mandible like that of 1st instar but with both apical and subapical teeth more distinct; at least 2 small papillae also visible (Fig. 39). Maxilla bearing 2 large microsetae; palp poorly developed but distinct, each with 5 (2 encapsulated and 3 bearing a spinule each) sensilla (Fig. 12); galea indistinct, represented by 2 sensilla each bearing a spinule. Labium with 2 large lateral, 2 large anteromedial, and 2 small medial microsetae just lateral to opening of sericteries; labial spinules more prominent than those of 1st instar, many in short rows; labial palps like maxillary palps (Fig. 11).

Third Instar.—Straight length 0.59–0.76 mm newly molted to 0.79–0.91 mm (ready to molt to 4th instar). Hairs of head and body short, smooth, numerous, and very variable (9.1–25.8 μm) (Fig. 3, 14, 16); apical ends simple, branched or bifid, and usually strongly hooked; pattern of head hairs like that of 2nd instar; ventral body hairs in rows extending from head to anus. Posterior spinules similar to those of 2nd instar, but longer and usually in groups of 3–5 (Fig. 16). Anteroventral body region with a few spinules. Head width 0.20–0.25 mm ($\bar{x}$= 0.21 mm, N = 17 [newly molted]) to 0.21–0.25 mm ($\bar{x}$ = 0.23 mm, N = 41 [ready to molt to 4th instar]). Antennae as in 2nd instar, but the 3 spinules longer (Fig. 14). Mouthparts unsclerotized (Fig. 13). Labrum with 4 small dorsal hairs and 6 anterior sensilla as in 2nd instar; a few pointed spinules anterolaterally. Apical and subapical mandibular teeth sharper and longer than those of 2nd instar; at least 2–3 small papillae present (Fig. 39). Maxilla with 2 lateral hairs homologous to the 2 microsetae of 2nd instar; palp and galea well developed, bearing same pattern of sensilla as on maxillary palp and galea of 2nd instar, but better developed (Fig. 15). Labium bearing short hairs homologous to the 6 microsetae of 2nd instar; palps similar to maxillary palps but less prominent; spinules similar to those of 2nd instar. Anteroventral body region bearing a few spinules (Fig. 13).

Fourth Instar.—Straight length 0.79–1.20 mm (newly molted) to 1.50–1.82 mm (prepupae). Body hairs papillose (Fig. 33–38) those of anteroventral body straight, simple (51.7–85.1 μm) (Fig. 4, 23, 37), and sometimes possessing minute apical branches (Fig. 38); all other hairs bifid (15.2–54.7 μm) (Fig. 4), usually with strongly hooked apical ends (Fig. 34). Head hairs similar to body hairs of 4th instar, and with pattern like that of 3rd instar; most straight, simple (54.7–97.3 μm), some posterior hairs simple or bifid, even within same pairs. Food basket (Petralia and Vinson 1978)[3] consisting of anteroventral body region, whose hairs flank laterally a medial hairless area bearing rows of spinules, spinules of posterior segments pointing anteriorly, spinules of anterior segments pointing posteriorly or laterally (Fig. 18); chunks of solid food often anchored in this region. Posterior spinules (Fig. 19) similar to those of 3rd instar. Head width 0.26–0.33 mm ($\bar{x}$ = 0.29 mm, N = 82 [new molted]) to 0.28–0.32 mm ($\bar{x}$ = 0.30 mm, N = 51 [prepupae]). Antennae as in 3rd instar, but spinules more tapered (Fig. 21). Mouthparts (Fig. 18) partially sclerotized. Labrum with same hair pattern as in 3rd instar, but longer; anterolateral spinules abundant. Mandible with 2 prominent apical teeth, one prominent subapical tooth, and up to 4 small basal teeth or prominences, latter not always easily seen; sclerotization increasing with age (Fig. 39). Two (perhaps 3) sensilla on head near base of mandible, each with a central protuberance (Fig. 22). Maxillae, maxillary palp, and galea (Fig. 20), labium, and labial palp with sensilla and hair patterns as in 3rd instar, but larger; palp and galea at least as long as wide; labial spinules more laterally located on labium than in previous 3 instars; opening of sericteries well developed.

Description of Larval Instars–Reproductives and Majors

Except for size, minor, major, and reproductive larvae are morphologically indistinguishable. Head width and mandibles of very large 4th instars are larger tha[n] those of minor worker prepupae. Head widths of matur[e] larvae and prepupae of major workers were 0.30–0.3

[3] Wheeler and Wheeler believe this is not a true food basket (1976, and pers. comm.)

ım, while those of reproductive larvae and prepupae ᷉ig. 26) from another colony were 0.42–0.49 mm. ꞉eproductive larvae are very robust when mature, the ıtegument is greatly expanded, and structures such as ıe anteroventral body spinules tend to thrust almost ‾traight out (Fig. 28). One 3rd instar from a colony pro-lucing only males was larger (1.28 mm) and had a vider head (0.27 mm) than 3rd instars of workers. Al-hough male and female reproductive larvae lack any ignificant external morphological differences, there are nternal gonopodal imaginal discs just anterior to the ınus which differ in males and females, and which be-꞉ome visible through the cuticle after the larvae are fixed n Kahle's (Petralia and Vinson, unpubl. data).

Ɔescription of Hatching and Molting

The newly deposited egg is oval and remains un-꞉hanged in size for ca. a week (Fig. 29). The egg then assumes the shape of the fully formed embryo (Fig. 30). If the egg shell is experimentally removed, a fully formed larva is exposed (Fig. 5). When placed with adult workers, newly formed larvae remain at least partially covered with shell membranes for one to several days. Larvae can usually free the mouthparts from the shell by a series of body movements but appear unable to complete hatching without the aid of adult workers. The molting process of this species was previously described by O'Neal and Markin (1973) but is illustrated in more detail in Fig. 17. At the end of the molt, a strand of undetermined material usually connects the mouth to the exuviae (Fig. 9, 11, 14), which remains on larvae if they are isolated from adult workers. Expulsion of the meconium (Fig. 27) (formation of prepupa) and formation of pupa is possible without the aid of adult workers.

Evidence for Number of Instars

Four distinct instars were delineated according to morphology, as described above, and by observations of molting. No molting within any one of the 4 instars was observed. Many structures, especially hairs, varied much in size but this variation was in the same range for both the newly molted instar and the instar preparing to molt. There are no significant morphological differences within any one of the 4 instars. In 3rd and 4th instars, the head is slightly less wide in new molted larvae than in larvae ready to molt.

The hairs of newly molted 2nd, 3rd, or 4th instars are close together and the cuticle is wrinkled (Fig. 9, 14, 23). The head of these larvae is large relative to the body. Late in the instar the body is greatly expanded, the head relatively small (Fig. 2, 3, 4), the cuticle unwrinkled, and the hairs farther apart.

Brood Piles

Eggs and larvae cling to each other, and are stored in clumps in the colony (Fig. 29). Adult worker ants often groom brood, apparently over their entire surface. Eggs and 1st and 2nd instars usually had a bridge of material where they were in contact with each other (Fig. 29). This bridge was evident in live eggs (Fig. 31), but was most prominent in fixed eggs (Fig. 32). When 3rd and 4th instars were placed in contact with other larvae of similar age, the bifid hairs were seen to interlock, via the apical hooks, with each other (Fig. 33, 35, 36). A bridge of material may also be seen between two 3rd instars. Third and 4th instars fixed and stored in alcohol retained their ability to cling to each other.

Discussion

O'Neal and Markin (1975) described 4 larval instars for the imported fire ant. However, the figures and descriptions of larvae in their paper correspond only to our 3rd and 4th instars (Table 1). Their observed changes in mouthparts may be attributed to the use of light microscopy for discerning morphological details. Very minute details of mouthparts are difficult to resolve with the compound microscope and may be badly distorted in whole mounts for light microscopy. Scanning electron microscopy permits higher resolution, greater depth of field and examination of live larvae at higher magnifications. We could examine larval structures undistorted in their natural shape and position on the body.

O'Neal and Markin (1975) relied upon an application of Dyar's Rule when they determined the imported fire ant has 4 instars. However, this Rule may not apply to many insects (Schmidt et al. 1977). We found larval head-width increases vary considerably. As the larva grows, an increase of the body's volume just behind the head may cause the unsclerotized head itself to become wider. In addition, adult major-workers and reproductives have larger heads than minor workers, and their larvae too—even of the same instar—will differ.

Our studies of eclosion and the 3 larval molts support the morphological evidence for the 4 instars we describe. Female reproductive larvae probably differentiate from worker larvae before the 3rd instar, as 3rd-instar reproductives were larger than workers in the same instar.

Most morphological changes during the development of fire ant larvae are not radical; a basic pattern of body structures becomes more complex. This is evident in the development of the ventral rows of hairs and the position of head hairs, as well as the development of the labral hairs and sensilla, maxillary hairs, palps, and galea, labial hairs, palps, spinules, and the opening of the sericteries. We infer from this that there is a basic arrangement of epidermal cells laid down in the embryo and maintained throughout larval development. The most evident distinguishing characteristics for larval instars are the changes in chaetotaxy and mandible structure. Other important characteristics include changes in the size and position of labial spinules and the development of other spinules.

These morphological changes in larval development can be related to changes in function. Thus the development of sclerotized, well developed mandibles, and the specialization of hairs and spines on the anteroventral body region of the 4th instar, facilitate feeding on the solid chunks of food placed on the larvae by adult workers (O'Neal and Markin 1973, Petralia and Vinson 1978). The function of the posterior body spinules is not known.

Eggs and larvae have adaptations which facilitate the transport, handling, and storage of brood by adults. It appears that eggs stick together by means of an adhesive coating. First and 2nd instars are usually found mixed

Table 1.—Comparison of descriptions of instars of minor workers.

Petralia and Vinson (this report)			O'Neal and Markin (1975)		
Instar	Mandible	Hairs	Instar	Mandible	Hairs
1st	Unsclerotized; only apical tooth prominent	Absent; a few microsetae present	—	—	—
2nd	Same as 1st	Few simple hairs, curved at apex	—	—	—
3rd	Same as 1st	Most head and ventral body hairs simple, curved at apex; bifid hairs numerous on body	1st	Partially sclerotized; apical tooth	Head and part of anteroventral body with simple, curved hairs; other hairs numerous
			2nd	Degree of sclerotization not described; apical tooth	Same as 1st
4th	Sclerotized; 3 large distal teeth and up to 4 smaller proximal teeth	Most head and antero-ventral body hairs simple, straight; other hairs strongly bifid	3rd	Sclerotized; 3 distal teeth	Same as 1st
			4th	Sclerotized; 3 large distal teeth and 3 small proximal teeth	Same as 1st

with the eggs and also have an adhesive coating. Because adult workers constantly groom the eggs and young larvae, the adhesive coating is probably either applied or at least kept moist by the adults. This has been suggested for other ants by Wheeler (1910). Third and 4th instars may be too massive to cling together by means of an adhesive coating on the cuticle; moreover, alcohol fixation which nullified the adhesive properties of eggs, 1st and 2nd instars, did not hinder 3rd and 4th instars from clinging to each other. From SEM studies, it appears that these larvae cling together by means of their hooked hairs. This function has been described in other ants (Wheeler 1910, Wheeler and Wheeler 1973). The function of the papillae on the hairs of 4th instars is not yet known. These papillae are solid parts of the hair (revealed by transmission electron microscopy).

In summary, the 4 larval instars of *S. invicta* are clearly distinguishable by changes in vestiture and mouthparts. These changes are correlated with changes in feeding and handling of larvae by workers.

Finally, we hope that the information presented in this paper will be useful to other researchers, for identifying the developmental stage of live larvae of the imported fire ant. This is most easily accomplished by placing larvae on thin, moist paper on a slide, examining them with a compound microscope at high magnification (> 100×), and comparing numbers and types of hairs observed with the figures in this paper. Also, sclerotization of mandibles is a definite indication of 4th instars, but one should note that the sclerotized apical ends of the mandibles of 4th instars are usually visible internally in 3rd instars preparing to molt. With practice, 3rd and 4th instars may be quickly and efficiently distinguished from each other, and from younger larvae, with a stereomicroscope.

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