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POSTEMBRYONIC DEVELOPMENT OF *WOHLFAHRTIA MAGNIFICA* (SCHINER, 1862) (DIPTERA: SARCOPHAGIDAE)

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ABSTRACT: A description of the larval development of *Wohlfahrtia magnifica* (Schiner, 1862) is given. An interpretation of the morphological development correlated with functional and adaptive aspects of myiasis-causing flies is also included.

A detailed analysis of morphological changes that occurred in *W. magnifica* larvae during postembryonic development is carried out. These changes happen in 2 larval interinstars, I–II and II–III, in which several structures such as anterior and posterior peritremes and cephalopharyngeal skeleton play an important role. The possible functions of these structures are considered.

We also describe the first instar in *W. magnifica* to differentiate it from that belonging to *Sarcophaga* species, paying special attention to disposition of the cephalopharyngeal skeleton, anterior peritremes, and spinulation on the last 3 segments.

Several structures, not described previously in Sarcophagidae, were observed: modified spines of the buccal and peritremal cavities, peritremal tubercles, and modified spines on the ventral surface. Changes occurring in these structures during larval development are described. Their probable role in the taxonomy of the genus *Wohlfahrtia* and their application to Nearctic species belonging to this genus, *Wohlfahrtia vigil* and *Wohlfahrtia opaca,* are also discussed.

Wohlfahrtia magnifica Schiner, 1862, is a Palearctic species (Rohdendorf, 1956) causing severe myiasis in domestic animals from the Mediterranean region (Hadani et al., 1971; Ruíz-Martínez et al., 1987) to the U.S.S.R. (Ternovoi, 1961; Valentyuk, 1971; Isimbekov and Zhumabekov, 1983) and Mongolia (Yasuda, 1940; Schumann et al., 1976). Other myiasigenic species such as *Wohlfahrtia vigil* (Walker, 1937) and *Wohlfahrtia opaca* (James and Gassner, 1947) have a Nearctic distribution (Teskey, 1981).

The third instar of *W. magnifica* is the most frequently studied stage (Portchinsky, 1884; Yasuda, 1940; Seguy, 1941; Zumpt, 1965). Descriptions of the first instar are rare possibly owing to the difficulty in obtaining species in this stage (Valentyuk, 1971; Schumann et al., 1976). Recently, some aspects of larval development in this species were surveyed (Lehrer and Fromuda, 1986). There are remarkable differences between *Wohlfahrtia* and *Sarcophaga* in the last instar (Draber-Monko, 1973). In the first 2 instars, however, differentiation between the genera can be problematic, although the arrangement of the cephalopharyngeal skeleton, distribution of spines on the 3 terminal segments of body, and structure of the anterior peritremes are characteristic for each genus.

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According to the latest trends in Calliphoridae taxonomy (Erzinclioglu, 1985, 1987), in which the presence of "fine hairs" in the peritremal cavity, as well as the distribution of the peritremal tubercles have taxonomic value, we describe these structures that have not been described before in Sarcophagidae. Other morphological features found in *Wohlfahrtia* that can be applied to Nearctic species belonging to this genus and, generally, to Sarcophagidae are also described.

Changes during *W. magnifica* development also are described, with special reference to structures defining phases of ontogeny.

MATERIALS AND METHODS

More than 150 specimens of each larval instar and interinstar (collected from 300 cases of sheep myiasis in southern Spain) were used for this study. These specimens were compared with others from a culture of *W. magnifica* in our laboratory.

The samples were prepared according to the technique described by Soler-Cruz et al. (1979) with some modifications aimed to a correct visualization of the material. At first it was classified according to instar or interinstar. Then, the material was manually cleaned with bidistilled water and 0.9% saline solution (9 g NaCl in water 1,000 ml) to eliminate the numerous particles adhered to the body spines. Later, larvae were placed into a solution of 50% alcohol and 85% lactic acid during 2–5 days at room temperature. After this period, the material was treated with 85% lactic acid solution and stored 15–35 days at 20–30 C. The modification consisted of the treatment of the samples with KOH (Erzinclioglu, 1985) and heating to accelerate the clearing of larvae belonging to instar III. Then, the

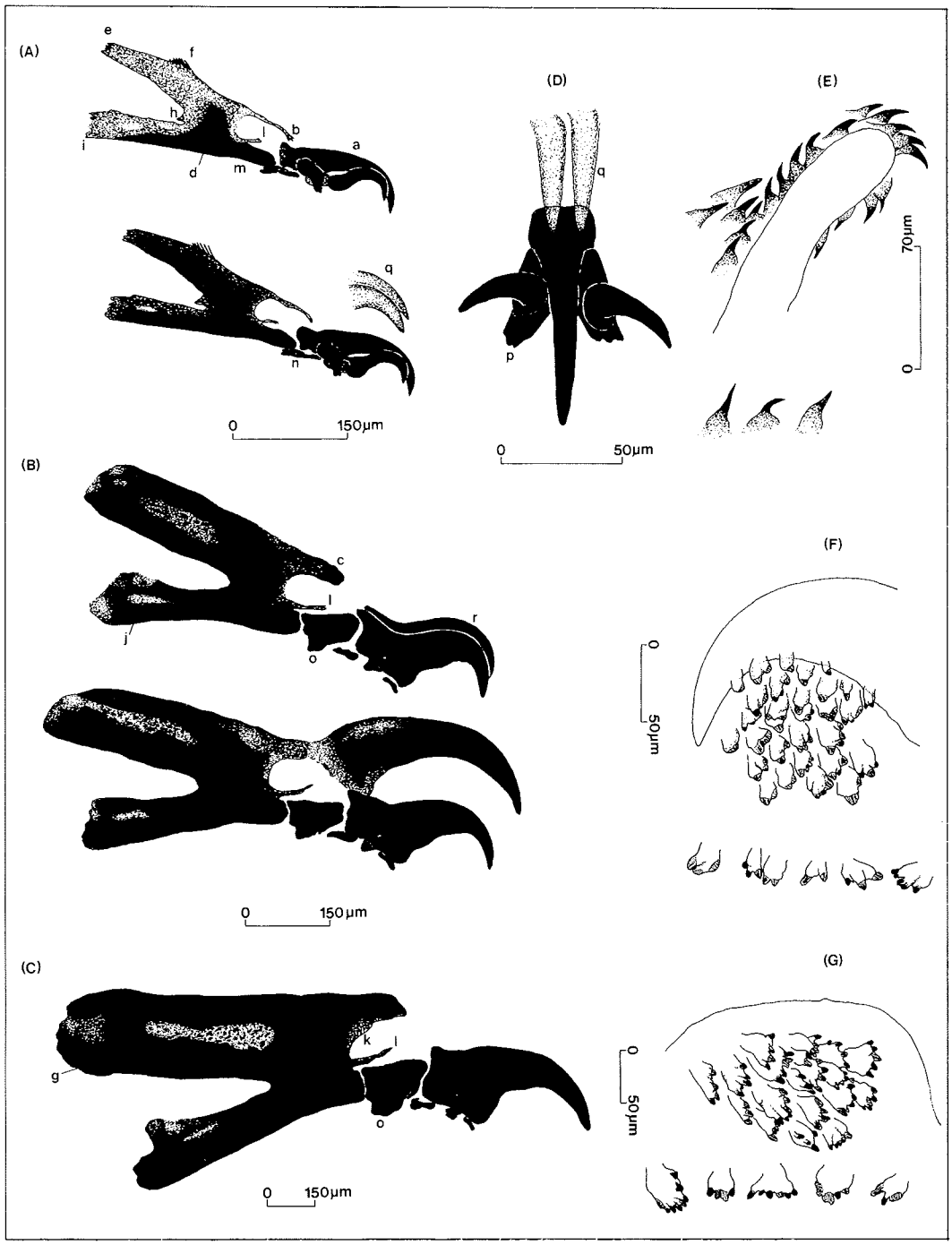


FIGURE 1. Development of the cephalopharyngeal skeleton and buccal modified spines of *Wohlfahrtia magnifica*. **A.** Lateral view of the cephalopharyngeal skeleton of instar I (above) and the first phase of interinstar I–II (below). a: mouth-hooks; b: anterior prolongations of the pharyngeal skeleton; d: lateral plate of pharyngeal skeleton; e: dorsal cornu; f: dorsal projections of dorsal cornu; h: triangular plate of pharyngeal skeleton; i: ventral cornu; l: parastomal bar; m: parastomal sclerite; n: parastomal sclerite of interinstar I–II; q: hooks of instar II. **B.** Instar II and the last phase of interinstar II–III. In this figure the disposition of new hooks (corresponding to instar III) on those belonging to instar II can be observed. c: dorsal arc; j: pharyngeal window; l:

samples were mounted permanently on slides using Hoyer's liquid and sealed with DePex®.

The samples were examined by phase-contrast microscopy when the structures were poorly chitinized. Figures were drawn with a camera lucida.

RESULTS

Cephalopharyngeal skeleton (Fig. 1)

The cephalopharyngeal skeleton of instar I consists of an inner pharyngeal part, formed by a supporting complex of skeletal components, a cephalic part with 3 mouth-hooks (Fig. 1A: a), 2 lateral and 1 median, forming a tridentlike structure (Fig. 1D). The tridentlike structure is characteristic of this instar and absent in subsequent stages. In general, the pharyngeal skeleton is lightly chitinized.

The pharyngeal skeleton in the first instar consists of 2 slender prolongations in the anterior margin (Fig. 1A: b). These prolongations are frayed at the end although no dorsal arc is formed. This arc appears during interinstar I–II, and later, in the second instar it acquires consistency and definitive shape (Fig. 1B). However, the lateral plate (Fig. 1A: d) of the pharyngeal skeleton is maintained throughout larval development.

In the first instar, the dorsal cornu (Fig. 1A: e) is slender with a frayed end, bearing 6–8 regular chitinous dorsal projections where musculature is inserted (Fig. 1A: f). After molting, from interinstar I–II on, this arrangement is lost, giving rise to a dorsal cornu divided into 2 branches by an ample low neck that is seen clearly in instar II but disappears in instar III, forming a pharyngeal window (Fig. 1C: g). The union between the dorsal and ventral cornu presents a triangular chitinized plate (Fig. 1A: h) during instar I. The plate originates from the dorsal cornu and ends abruptly upon contact with the ventral one. This structure is lost in instar II and does not reappear in subsequent larval development.

In instar I the ventral cornu (Fig. 1A: i) has an elliptic pharyngeal window (Fig. 1B: j) near its posterior end that facilitates muscular insertion. This structure is in continuity with a homologous window throughout the pharyngeal ridge. Anteriorly, a low neck allows anteroposterior rotation of the system of mouth-hooks. Like the ventral cornua, the joint of the ocular depression (Fig. 1C: k) and the parastomal bar (Fig. 1A: l) are present invariably throughout development. The anterior part of the lateral plate of the pharyngeal skeleton gives rise to an elongated parastomal sclerite (Fig. 1A: m). This heavily chitinized structure (which subsequently forms the rotational axis of the mouth-hooks) is laterally connected to the mouth-hooks. In instar II this sclerite is replaced by an H-shaped hypostomal sclerite (Fig. 2) that was situated behind the parastomal sclerite in interinstar I–II (Fig. 1A: m), and now delimits the anterior low neck of the pharyngeal ridge. This ridge determines the maximum angle of retraction of the mouth-hooks. The hypostomal sclerite is trapezoid in shape, strongly sclerotized, and articulates by 2 protuberances with the lateral plate of the pharyngeal skeleton. Both hypostomal sclerites are joined by their inferior parts, conferring greater mobility to the retraction–extension movement of the oral pieces and mouth-hooks. This structure, although shed in each larval molt, is present to the end of development.

In instars II and III the subhypostomal sclerites (Fig. 1B: o) are behind the hypostomal sclerites. Their posterior section is flattened, favoring articulation with the hypostomal sclerites. Both subhypostomal sclerites are joined by a chitinized cross-shaped plate. Above this plate is a square-shaped hypostomal plate with 4 symmetrical perforations. This structure is definitive. The anterior parts of the subhypostomal sclerites are situated behind the mouth-hooks.

Mouth-hooks (Fig. 1)

The mouth-hooks system is formed in instar I (Fig. 1D) by 3 hooks: 2 lateral and 1 medial hook. The medial hook is 1.5–2 times longer and less curved. The hooks create the "trident-shaped" structure mentioned previously.

Two basal pieces (Fig. 1D: p) are joined to both flanks of the medial hook by 2 articular protuberances; their internal parts present 2 lightly sclerotized plates where the lateral hooks are articulated. In instar I the lateral hooks curve markedly away from the medial hook.

←

parastomal bar; o: subhypostomal sclerites. **C.** Instar III. g: pharyngeal window; k: ocular depression; l: parastomal bar; o: subhypostomal sclerites. **D.** Frontal view of mouth-hooks of interinstar I–II showing the tridentlike structure. p: basal pieces of lateral hooks of interinstar I–II; q: hooks of instar II. **E.** Modified buccal spines of instar I. **F.** Modified buccal spines of instar II. The number of lobes of each spine is greater than in instar I. In this instar the modified buccal spines are not simple. **G.** Modified buccal spines of instar III.

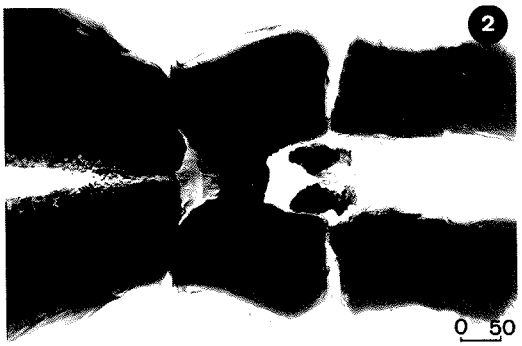


FIGURE 2. Hypostomal sclerite of *Wohlfahrtia magnifica* instar III, ventral view.

In specimens obtained from in vitro cultures, the mouth-hooks of instar I, when leaving the uterus, are arranged anteriorly and are closely joined. These larvae lack the capability of anchoring to the host. However, in the following 15–30 sec they begin to diverge, forming a marked angle with respect to the pharyngeal skeleton. This arrangement allows them to anchor into a potential host.

During interinstar I–II the anchoring of the definitive hooks of instar II appears (Fig. 1D: q). Development of these structures is very rapid. They gradually contact the parastomal sclerite, displacing the anterior ones. In the larval molt the hooks of instar I are detached with the pharyngeal skeleton. The definitive pharyngeal skeleton of instar II then appears as a neoformed structure. In instar II there are only 2 thicker, longer, and more markedly curved hooks (Fig. 1B: r). This arrangement is maintained until the end of larval development.

Modified spines of the buccal cavity (Fig. 1)

In the frontal and inner margins, a group of spines delimiting the buccal cavity surrounds each mouth-hook. Although in instar I (Fig. 1E) they present no substantial modification from those of the rest of the body except for their smaller size and increased density. During interinstar I–II a group of neoformed spines differs notably from the corporal ones.

The spines consist of a narrow proximal and an enlarged distal part. They acquire their definitive shape during instar II (Fig. 1F), in which the spines, grouped in 6–7 bands, become flattened and polyhedral. The apex of these spines may have from 1 to 4 (usually 2 or 3) lobes that are more strongly sclerotized than the rest of the spines. These spines are replaced during interinstar II–III by others corresponding to instar III (Fig. 1G). These are triangular in shape, with 2–7 lobes that can be arranged in several planes and 1–4 anteroposteriorly oriented rows.

Cephalic lobes (Fig. 3)

The antennal primordia (antennae) (Fig. 3I) are arranged frontally in the superior part of each cephalic lobe (Fig. 3H). The primordia are composed of an ovoid bud resting on a cylindrical base. A button with a small protecting capsule occurs at the base. The maxillary "palpi" (Fig. 3J) are arranged frontally to the cephalic lobe. They appear as a keg-shaped structure containing 11 buds organized in 2 groups: 1 with 6 buds and the other with 5 (Fig. 3J: s). In the margins of this structure are the supramaxillary papillae, grouped in 2 buttons (Fig. 3J: t). These buttons and buds are involved in sensory function.

In the frontal part of the cephalic lobe, 3 groups of buttons occur: 2 simple (consisting of 1 button) in the mid-anterior position (Fig. 3H: u) and 1 complex (formed by 2 small lateral and 1 larger central button) that constitute the oral papillae (Fig. 3H: v). During larval ontogeny a slight turn in the disposition of antenna, "palpi," supramaxillary papillae, and the oral papilla occurs (Fig. 3K).

Body spinulation

The larval body, from the second thoracic to the XIIth somatic segment, is densely covered with spines of a characteristic distribution. Their anteroposterior orientation could facilitate anchoring to the host. Thus, they are adapted to a parasitic way of life, as their density and size suggest. The spines increase in size and complexity during larval development. In larval interinstars, new spines belonging to the next instar form under the integument. They become definitive with the next larval molt. The spines are generally sharp and hooked in instars I and II. In instar III they are less sharp and several are bifid or trifid. The ventral spines are usually larger than the dorsal ones.

Ventrally, in the thoracic segments, zones lacking spines can be observed. A group of small trifid spines arranged transversely exist along with epidermal pores (Fig. 3M).

Anterior peritremes

Anterior peritremes are arranged laterally, on the base of the first thoracic segment. During

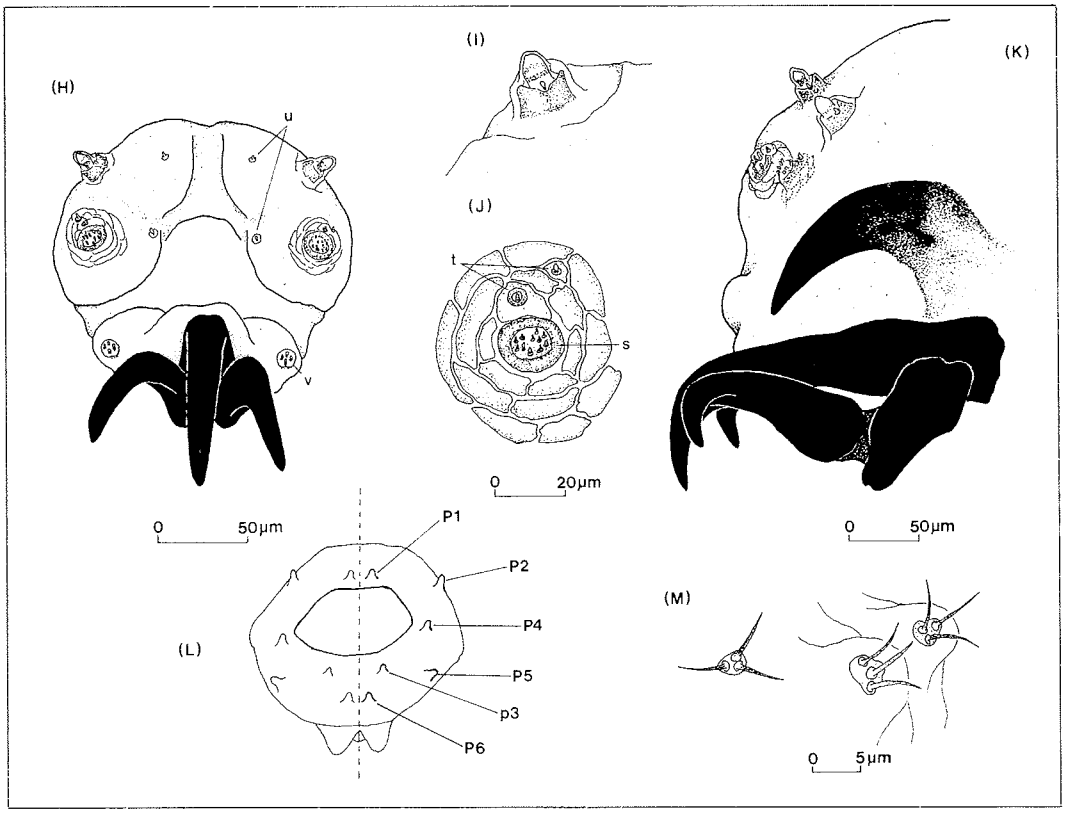


FIGURE 3. Larval structures of *Wohlfahrtia magnifica.* **H.** Frontal view of cephalic segment of first instar. u: button in the mid-anterior position of cephalic lobe; v: oral papillae. **I.** Detail of antennal primordia of instar I. **J.** Detail of "palpi" and situation of supramaxillary palps in instar I. s: supramaxillary papillae; t: keg-shaped structure of the maxillary "palpi." **K.** Lateral view of changes produced in mouth-hooks and palpi-antenna of interinstar I–II. **L.** Distribution of peritremal tubercles. P1: dorsal tubercle; P2: dorsolateral tubercle; p3: subterminal tubercle; P4: laterosubterminal tubercle; P5: ventrolateral complex terminal tubercle; P6: ventral complex terminal tubercle. **M.** Detail of modified body spines on ventral surface. This type of spine was found on the ventral surface of the 3 thoracic segments.

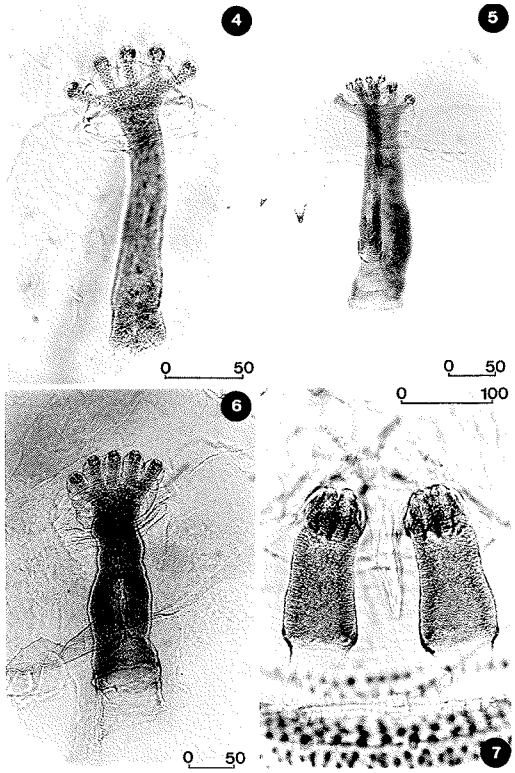
instar I in Calliphoridae and Sarcophagidae these peritremes are either absent or nonfunctional. Completely formed anlagen of the anterior peritremes were observed in instar I. Although they are weakly sclerotized and nonfunctional, the integument is interrupted at this level. During interinstar I–II the peritremes acquire their definitive conformation (Fig. 4) although they are shed in interinstar II–III (Fig. 5), to become larger in instar III. Peritremal digitations occur in each peritremal split. The digitation is characterized further by a superior opening on the dorsal surface of the split. The anterior peritremes are substituted during interinstar II–III. Those belonging to instar III (Fig. 6) then appear behind the existing ones.

Each peritreme has 4, 5, or 6 peritremal slits. In the same specimens a given peritreme may have 4 slits, whereas its homolog may have 5 or 6. The number of peritremal slits is more constant in instar III, in which 5–6 can be seen.

Peritremal cavity

In Sarcophagidae the peritremal cavity appears as a deep depression. Along the margin of this depression a group of peritremal tubercles (Fig. 3L) is symmetrically arranged. These peritremal tubercles can be complex (when the terminal button and the protecting capsule are surrounded by a group of epidermal scales, conferring mobility to these structures) or simple (when they are a raised area in the integument ending in an encapsulated immovable bud).

The peritremal tubercles are replaced in each larval molt. They are arranged in 2 rings: 1 terminal, composed of 6 complex tubercles, and the

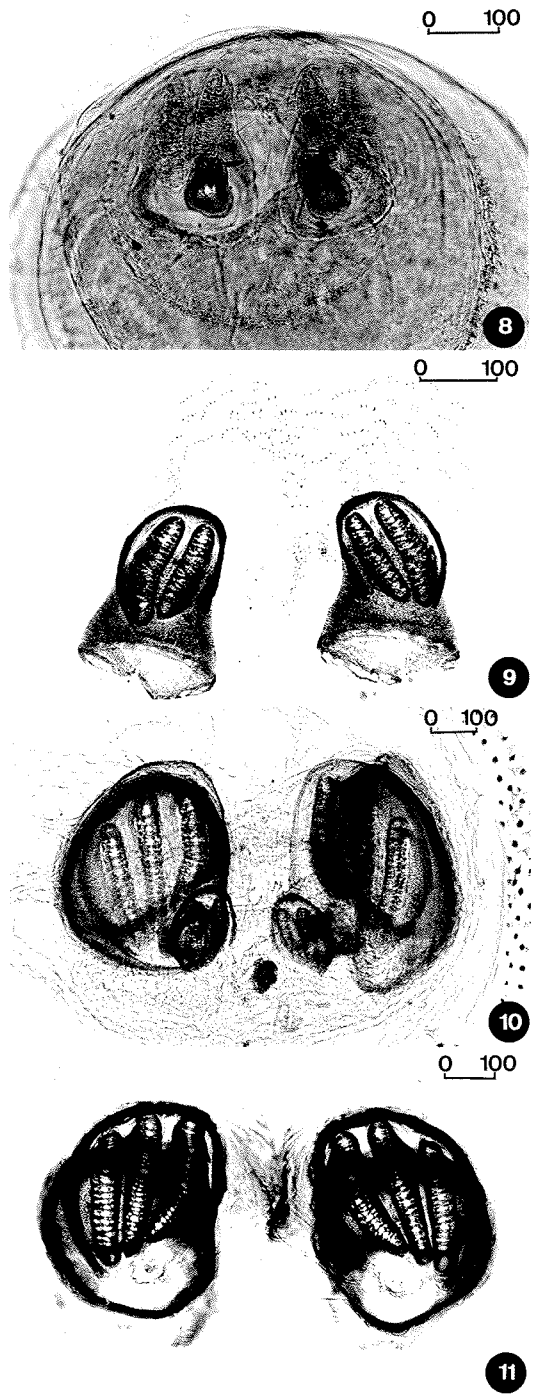


FIGURES 4–7. Peritremes of *Wohlfahrtia magnifica* instars. **4.** Anterior peritremes of instar II. **5.** Anterior peritremes of interinstar II–III. **6.** Anterior peritremes of instar III. **7.** Posterior peritremes of instar I.

other subterminal, composed of 4 complex and 2 simple tubercles. The 2 rings are usually arranged as follows: 2 pair of dorsal (1 dorsal [P1] and 1 dorsolateral [P2]) and 4 ventral tubercles (1 pair of subterminal simple tubercles [p3], 1 pair of lateral subterminal tubercles [P4], and 2 pairs of complex terminal ones [P5 and P6]) (Fig. 3L).

A group of modified spines, like "fine hairs," occurs both dorsally and ventrally around the inner margin of the peritremal cavity. The arrangement and structure of these "fine hairs" change throughout larval development. Thus, in interinstar I–II and in instar II, they are short, thick, rigid, and curved, grouped into clusters bearing 4, 5, or 6 "hairs," of greater density than those of instar I. In instar III the "hairs" are maintained, although they appear shorter and more strongly sclerotized, and are grouped in clusters of 3–8.

As in other Sarcophagidae, the posterior peritremes are elongated in the dorsal surface of the



FIGURES 8–11. Posterior peritremes of *Wohlfahrtia magnifica*. **8.** Interinstar I–II. **9.** Instar II. **10.** Interinstar II–III. **11.** Instar III.

XIth somatic segment. In instar I (Fig. 7) no peritremal wall surrounds them, and they present a short, rounded, and poorly sclerotized peritremal tube. Each of them is formed by 2 peritremal slits that are open superiorly. The inferior slit is crossed by numerous trabeculae that are organized during this instar.

During interstar I–II (Fig. 8) the peritremes of instar II are situated behind those of instar I, fusing with them basally. With the larval molt the peritremes of instar I are detached, leaving behind an orifice and interruption of the peritremal wall. This remains a constant feature during development. The second instar (Fig. 9) has 2 ellipsoid peritremal slits surrounded by a thick peritremal wall. The inner peritremal slit is shorter and less curved. The peritremal perforations (delimited by the crossing trabeculae) vary from 9 to 12 (generally 10) in the inner slit and from 12 to 13 in the outer one.

In interinstar II–III (Fig. 10) the peritremes of instar III form behind those of instar II. The peritremes III (Fig. 11) have 3 variably shaped peritremal slits: the inner one is curved, the median one is straight and long, and the outer one is curved and long. These slits contain from 14 to 22 perforations. The peritremal tube presents 4–7 dorsal and 3–5 ventral perforations in its connection with the tracheal tube.

DISCUSSION

Although instar I of *W. magnifica* has been studied in relative detail (Valentyuk, 1971; Schumann et al., 1976; Lehrer and Fromuda, 1986), structures such as the triangular sclerotized plate between the dorsal and ventral cornua, the superior margin of the dorsal cornua, and the inner chitinous structures attached to hypostomal sclerite have not been described previously. These structures should be considered useful taxonomic parameters in species belonging to the genus *Wohlfahrtia.*

The variability in the perforations of the posterior peritremes, including the number of anterior peritremal slits in an individual, means that these taxonomic features must be used with caution. Previous studies have described specific ranges of variability (Zakharova, 1969; Verves, 1979).

Our observations of the first instar of *W. magnifica* suggest that the arrangement of the cephalopharyngeal skeleton, the distribution of spines on the last 3 segments, and the structure of the anterior peritremes outlined under the larval integument allow *Sarcophaga carnaria* (Draber-Monko, 1973) to be separated clearly from the genus *Wohlfahrtia.* The readily visible spinulation and anterior peritremes cause no taxonomic problem in instars II and III.

Larval development of *W. magnifica* (Lehrer and Fromuda, 1986) is interpreted as a succession of 3 larval instars and 2 interinstar molts. The formation of the mouth-hooks during each interinstar occurs before the formation of the remaining pharyngeal skeleton. The high growth rate of these dipterans and the known competition for food make it important that structures like the buccal hooks for anchorage are functional immediately between instars. This could be an adaptation to the parasitic way of life such as proposed for other Diptera (Zdarek and Slama, 1972).

The pharyngeal skeleton in instar I is poorly sclerotized. This is due possibly to the brief duration of this stage (6–8 hr) in specimens maintained in our laboratory. The progressive sclerotization of the pharyngeal skeleton occurs during instars II and III. The changes during interinstars are mainly to fortify the mouth-hooks.

The hook system in instar I could represent an adaptation to a parasitic way of life, as this structure facilitates the anchorage of instar I to a plane and, furthermore, could be used in penetrating the host's body in primary invasion (Ruíz-Martínez et al., 1987). Larvipary may represent an initial adaptation to a parasitic existence. This notion should be considered with caution, given the existence of oviparous species causing myiasis (Oldroyd and Smith, 1973). In the genus *Wohlfahrtia,* the median sclerite of the mouth-hooks appears more fully developed in obligate myiasigenic species such as *W. vigil* (Walker, 1937) and *W. opaca* (James and Gassner, 1947; Teskey, 1981) than in primarily facultative or accidental myiasigenic species like *Wohlfahrtia pattoni* (Hilton, 1973). The observations of mouth-hooks of *W. magnifica* suggest that the middle sclerite in *W. vigil* and *W. opaca* should be termed a "middle hook."

The morphological structures described in *W. magnifica,* including modified spines of the buccal cavity, thin setae in the peritremal cavity ("fine hairs"), and modified spines in ventral zones, together with peritremal tubercles of Sarcophagidae (Lehrer and Fromuda, 1986) should be considered as preferred features in the taxonomy of the species belonging to the family Sarcophagidae. Their constancy and number are easily typ-

ifiable throughout larval development and lend themselves to taxonomic use. Several of these structures have been mentioned previously by Erzinclioglu (1985, 1987) in species of Calliphoridae.

These structures together with those described in the cephalopharyngeal skeleton could provide clues for the larval classification and phylogeny of *W. vigil* (Walker, 1937; Boonstra, 1977), *W. opaca* Coq. (James and Gassner, 1947), *Wohlfahrtia balassogloi* Port., *Wohlfahrtia meigeni* (Valentyuk, 1971), *Wohlfahrtia seguyi* Salem (Seguy, 1941), *W. pattoni* Salem (Hilton, 1972), and *Wohlfahrtia bella* (Gil Collado et al., 1974).

In addition to their possible taxonomic role these structures could be used, on the basis of their function, to discern saprophagic and myiasis-causing species (obligate as well as facultative ones) (Barnard, 1977; Boonstra, 1977; Teskey, 1981). This feature may be useful in species such as *W. bella* (Gil Collado et al., 1974), whose parasitic role is as yet unproved.

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