

The immature stages of European ichneumonid parasites of siricine woodwasps

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SYNOPSIS

The immature stages of *Rhyssa persuasoria*, *R. amoena*, *Megarhyssa emarginatoria*, *Pseudorhyssa sternata* and *Odontocolon geniculatus*, ichneumonid ectoparasites of European Siricidae, are described and a key based on the last larval instars of these species is included. Their relationships are discussed with reference to the morphology of the intermediate and final instars.

INTRODUCTION

DURING studies on the ecology of the siricid woodwasps infesting conifers and their natural enemies in Europe, it became desirable to distinguish the immature stages of the ichneumonid parasites *Rhyssa persuasoria* (L.), *R. amoena* Gravenhorst, *Megarhyssa emarginatoria* (Thunberg), *Odontocolon geniculatus* (Kriechbaumer), and *Pseudorhyssa sternata* Merrill as defined by Kerrich (1966).

The adults of these species emerge in late spring and early summer and, after a maturation period, search for their hosts, the larvae and pupae of siricids. *O. geniculatus* parasitises *Sirex juvencus* L. and *S. cyaneus* F. and also the melandryid beetle, *Serropalpus barbatus* (Schaller). The female primary parasite drills through the wood to reach the host and paralyzes it before oviposition. After about a month, the host is consumed, and the mature larva spins a cocoon in which it overwinters. The life-cycle is typically annual.

The descriptions and key for the last larval instars permit species determination of the larvae and their exuviae.

MATERIALS AND METHODS

Collections of siricid-infested timber were made in Britain, Norway, Sweden, Belgium, Holland, Germany, France, Switzerland, Italy, Yugoslavia, Bulgaria, Hungary, Czechoslovakia, Spain and Portugal. The material used for description was dissected from this infested timber and from laboratory cultures of parasites reared in logs, and was also reared artificially in cells (Spradbery, 1968).

Larvae were macerated for a day in 10 per cent. potassium hydroxide at room temperature. Head capsules, larval skins or entire larvae were then washed and mounted in lactophenol from 70 per cent. ethanol.

The terminology used is that of Finlayson (1960), and the classification is based on Townes & Townes (1960) and Finlayson (1967).

MORPHOLOGY OF IMMATURE STAGES

Pimplinae : *Ephialtini*

Subtribe *Rhyssina*

Rhyssa persuasoria (L.)

Rhyssa persuasoria was obtained from material collected in Scotland, England, Wales, Norway, Sweden, France, Germany, Switzerland, Spain, Czechoslovakia, Belgium and Holland.

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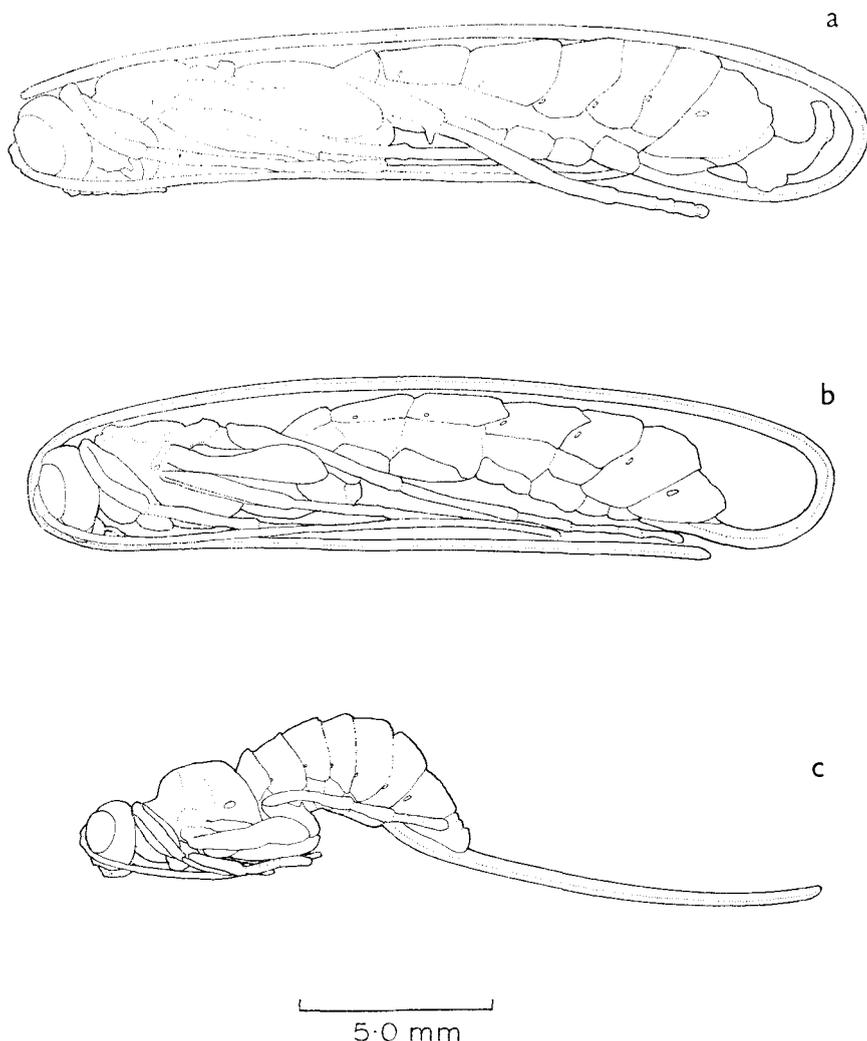


FIG. 1.—Female pupae: (a) *R. persuasoria*; (b) *M. emarginatoria*; (c) *O. geniculatus*.

Pupa (fig. 1a) and cocoon

Female pupa (length 15–36 mm.) with ovipositor curved over body dorsally, reaching vertex of head, ovipositor somewhat longer than body. Cocoon conforms to size and shape of host chamber, loosely spun, brownish, incorporating particles of frass, host remains and parasite exuviae from previous moults.

Male and female pupae are figured by van Vollenhoven (1860).

Fifth instar larva (fig. 2)

Fully-fed larvae: length, 6.3–23.0 mm. (mean 14.2); width, 2.0–7.5 mm. (mean 4.9) ($n = 10$). Consists of hypognathous head, 3 thoracic segments and 10 abdominal segments. Colour creamy white with marked sclerotisation of head-capsule. Shape fusiform, slightly arched dorsally; round in cross section with pair of pronounced pleural swellings. Spiracles (fig. 2b) on prothoracic segment and abdominal segments 1–8; atrium of spiracle large, funnel-shaped with sclerotised reticulations, about twice as long as wide, opening directly into closing apparatus. Larval cuticle (fig. 2c) covered with small, pointed papillae; setae short (0.026–0.045 mm.), lightly sclerotised, distributed in an irregular line around each thoracic and abdominal segment (40–50 setae on each segment), with cluster around anus on terminal segment. Head (fig. 2a) with well-sclerotised cephalic structures; epistomal arch more or less complete but not heavily sclerotised, pleurostoma very broad ventrally with well-developed superior mandibular process; hypostoma curved laterally, inferior mandibular processes each with 2 blunt struts; hypostomal spur broad at dorsal end; stipital sclerite broad at lateral end

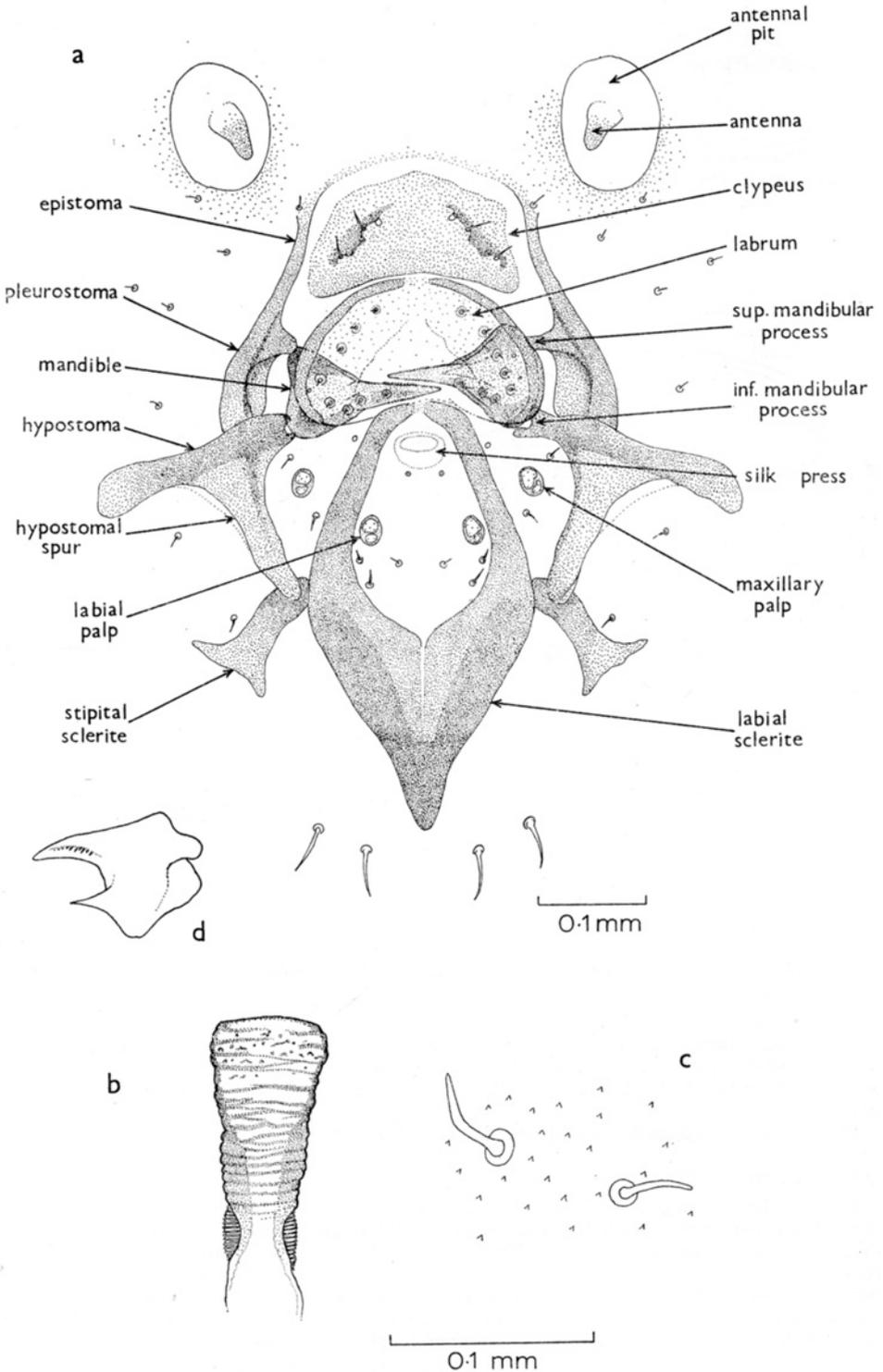


FIG. 2.—Fifth instar larva of *R. persuasoria*: (a) cephalic structures; (b) spiracle; (c) cuticle; (d) mandible.

which is free of hypostoma; labial sclerite heavily sclerotised, sharply pointed ventrally, inner ventral margin with well-defined cleft; labral sclerite well sclerotised laterally; maxillary and labial palps sclerotised each with 2 sensoria or occasionally with a third, small sensorium; sclerotised plate present on clypeus; mandibles with slender blade bearing 2 rows of small similarly-sized teeth and broad base, long sharp posteromedial tooth present (fig. 2*d*); antenna papilliform and sclerotised, antennal pit not sclerotised; silk press present, not sclerotised; labrum with 4–5 pairs of setae and 5–7 pairs of sensorial pits; clypeus with 2 moderately long pairs of setae and 1–2 pairs of sensorial pits; labium with 2–3 pairs of moderately long setae ventrally and 1 pair of sensorial pits dorsally.

The fifth-instar larva of *Rhyssa* sp. has been described by Beirne (1941) and Short (1959), and the larva of *R. persuasoria* was figured by van Vollenhoven (1860).

Fourth instar larva (fig. 3c and f)

Length, 6.2–10.5 mm. (mean 8.7); width, 1.2–2.5 mm. (mean 1.9) ($n = 5$). Similar in shape to fifth instar larva, with head capsule lightly but uniformly sclerotised (fig. 3*f*). Larval cuticle with small, pointed papillae in separate bands around dorsal and ventral surfaces and on paired pleural swellings of each segment, but continuous on first thoracic segments; 14–28 short setae (0.015–0.024 mm.) around each thoracic and abdominal segment, and a cluster around the anus. Spiracles on prothoracic and abdominal segments 1–8; atrium of spiracle small, cone-shaped, leading into long narrow stalk. Head (fig. 3*f*): epistomal arch complete and well sclerotised; pleurostoma sclerotised with well developed superior mandibular process; hypostoma curved laterally with long, narrow, curved hypostomal spur reaching labial sclerite; stipital sclerite lacking; labial sclerite well sclerotised laterally, less so ventrally and incomplete dorsally, not pointed ventrally; labral sclerite present, complete dorsally with very broad sclerotised margin; no sclerotised plate on clypeus; rudimentary maxillary and labial palps each with 1 large sensorium and 3 small sensoria; mandible with broad base, 2 rows of small equal-sized teeth on slender blade, posteromedial tooth present; antenna papilliform, sclerotised, antennal pit unsclerotised; clypeus with 2 pairs of setae and 1 pair of sensorial pits; labrum with 5 pairs of setae and 8 pairs of sensorial pits; labium with 2 pairs of setae ventrally and 1 pair of sensorial pits dorsally.

Third instar larva (fig. 3b and e)

Length, 3.5–5.9 mm. (mean 4.3); width, 0.8–1.6 mm. (mean 1.1) ($n = 5$). Similar to fourth instar except: head capsule not uniformly sclerotised; short setae (0.011–0.021 mm.) distributed in an irregular line around each thoracic and abdominal segment (14–30 setae on each) (fig. 3*b*). Head (fig. 3*e*): hypostoma long, narrow, curved laterally; hypostomal spur only lightly fused to hypostoma; labral sclerite with vacuoles dorsally; labial sclerite weakly sclerotised ventrally; maxillary and labial palps each with 1 large sensorium and 3–4 small sensoria; labrum with 4–5 pairs of setae and 4–7 pairs of sensorial pits; clypeus with 2 pairs of setae and 1 pair of sensorial pits.

Second instar larva (fig. 3a and d)

Length, 1.7–2.5 mm. (mean 1.94); width, 0.5–0.7 mm. (mean 0.6) ($n = 4$). Similar to fourth instar except: head capsule not uniformly sclerotised; short setae (0.015–0.022 mm.) around each thoracic and abdominal segment (12–16 setae on each segment); head: hypostomal spur more or less free from hypostoma; labial sclerite unsclerotised ventrally, very narrow laterally; maxillary and labial palps each with 4 small sensoria.

First instar larva (fig. 4a, c and e)

Length, 1.3–2.3 mm. (mean 1.8); width, 0.3–0.5 mm. (mean 0.4) ($n = 6$). Strongly mandibulate, prognathous head, fusiform body (fig. 4*a*). Colour creamy white with marked sclerotisation of head capsule. Spiracles on prothoracic and abdominal segments 1–8. Larval cuticle with small pointed papillae in broad dorsal and ventral bands; 8–16 short setae (0.011–0.015 mm.) distributed around each segment. Head capsule (fig. 4*c*): mandibles (fig. 4*e*) strong, heavily sclerotised, sickle-shaped, labial and maxillary palps each with 2–3 small sensoria; antenna large, papilliform, about twice as long as antenna of second instar larva.

Egg (fig. 5a)

Acuminate with hymenopteriform egg-body; length of egg-body, 1.8–2.3 mm. (mean 2.0); width, 0.4–0.5 mm. (mean 4.5); and long thin pedicel, 7.3–9.7 mm. (mean 8.8) ($n = 10$). Chorion smooth, milky white.

Rhyssa amoena Gravenhorst

Rhyssa amoena was obtained from material collected in Switzerland, Italy, Jugoslavia and Czechoslovakia.

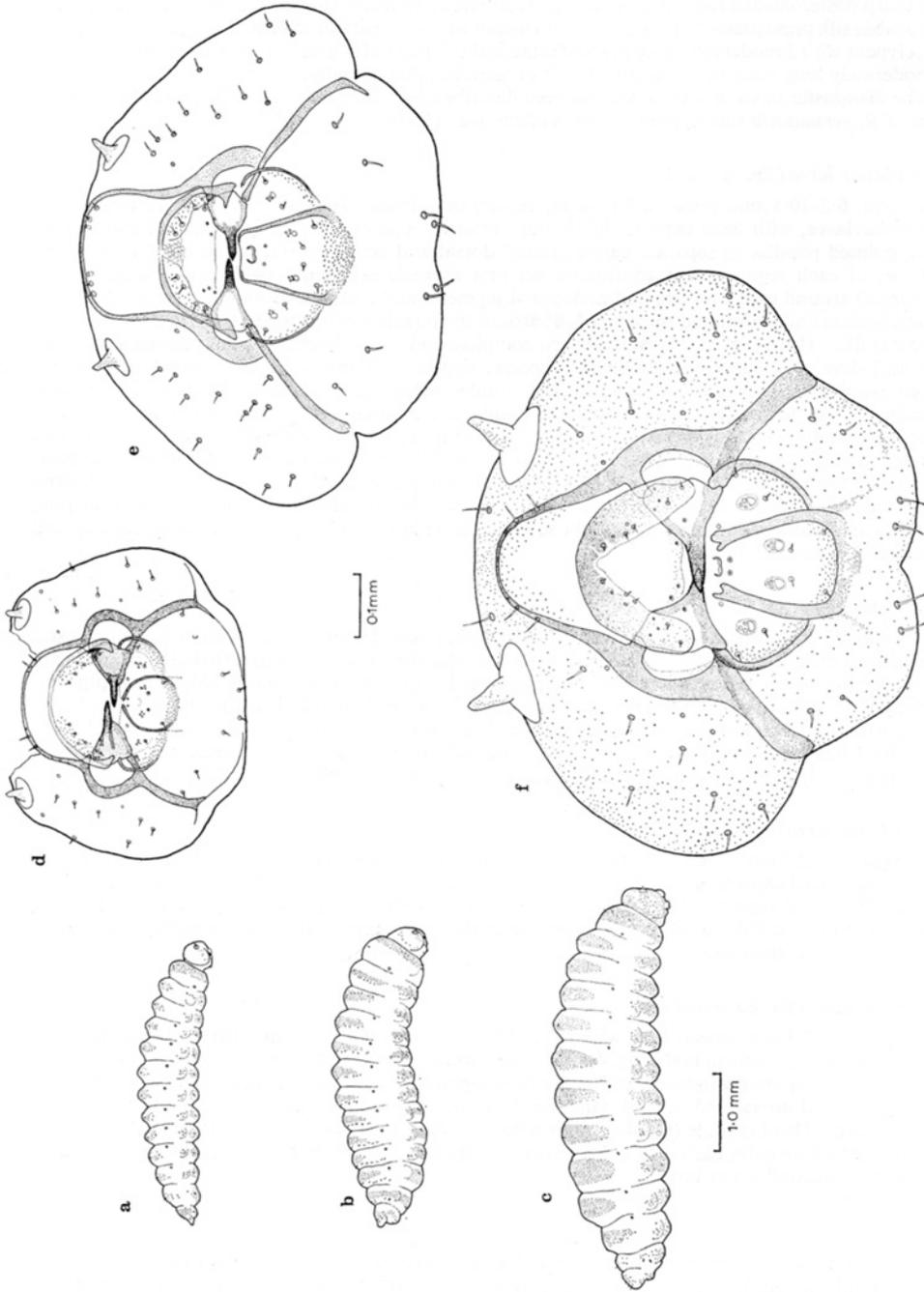


FIG. 3.—Intermediate larval instars of *R. persuasoria*: (a) second instar larva; (b) third instar larva; (c) fourth instar larva; (d) head capsule, second instar larva; (e) head capsule, third instar larva; (f) head capsule, fourth instar larva.

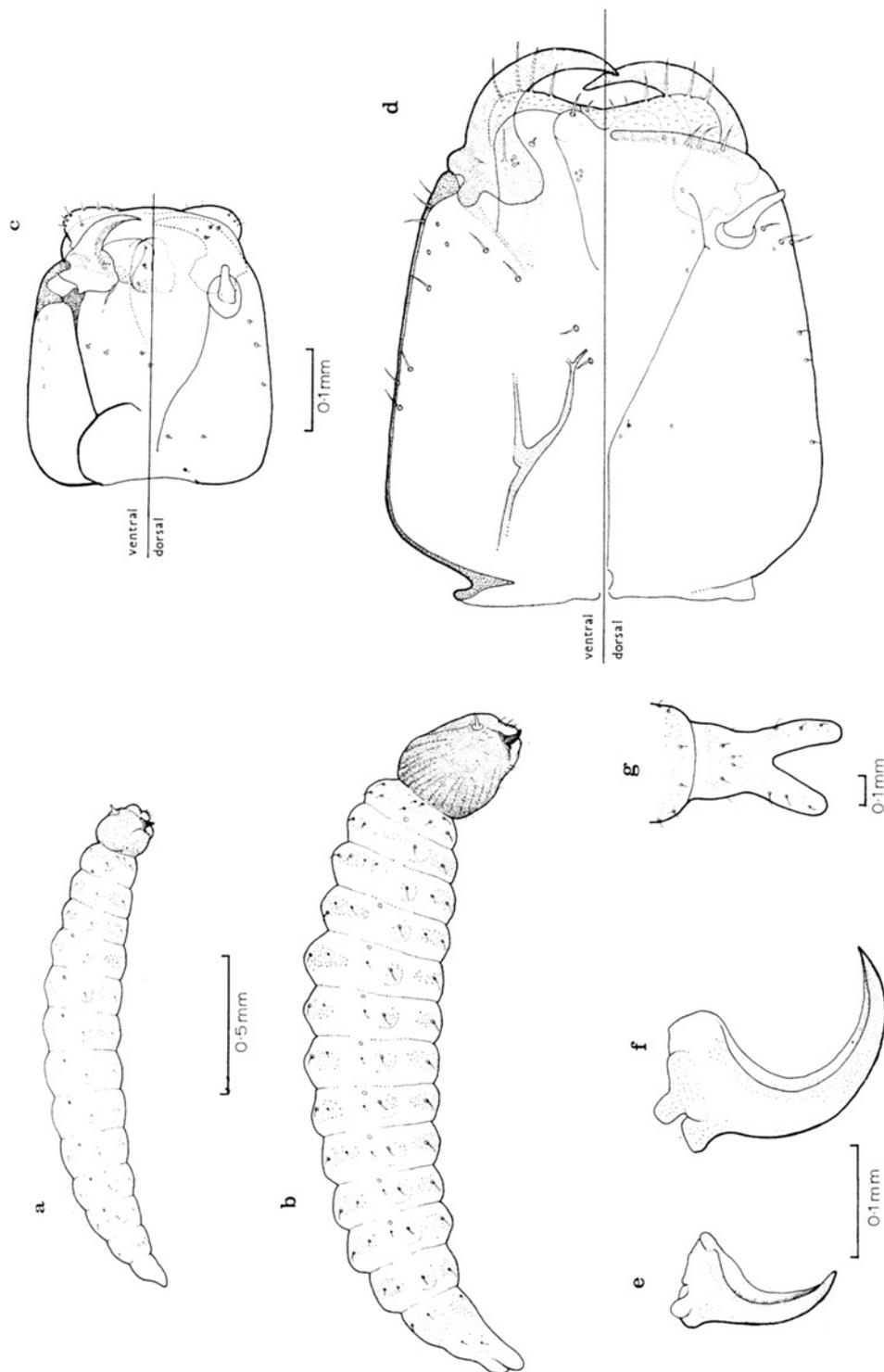


FIG. 4.—First instar larvae of *R. persuasoria* and *Ps. sternata*: (a) first instar larva, *R. persuasoria*; (b) first instar larva, *Ps. sternata*; (c) head capsule, *R. persuasoria*; (d) head capsule, *Ps. sternata*; (e) mandible, *R. persuasoria*; (f) mandible, *Ps. sternata*; (g) dorsal view of terminal segment, *Ps. sternata*.

Immature stages

There are no major differences between the eggs, larval instars and pupae of *R. amoena* and *R. persuasoria* except:

Fifth instar larva.—Cuticle sparsely covered with very small, pointed and cone-shaped papillae; labrum with 3–4 pairs of setae. Papillae on cuticle not always clear enough to use with certainty, but can give an indication of larval identity; papillae approximately half the size of those of *R. persuasoria*, the majority tending to be cone-shaped with a few pointed papillae.

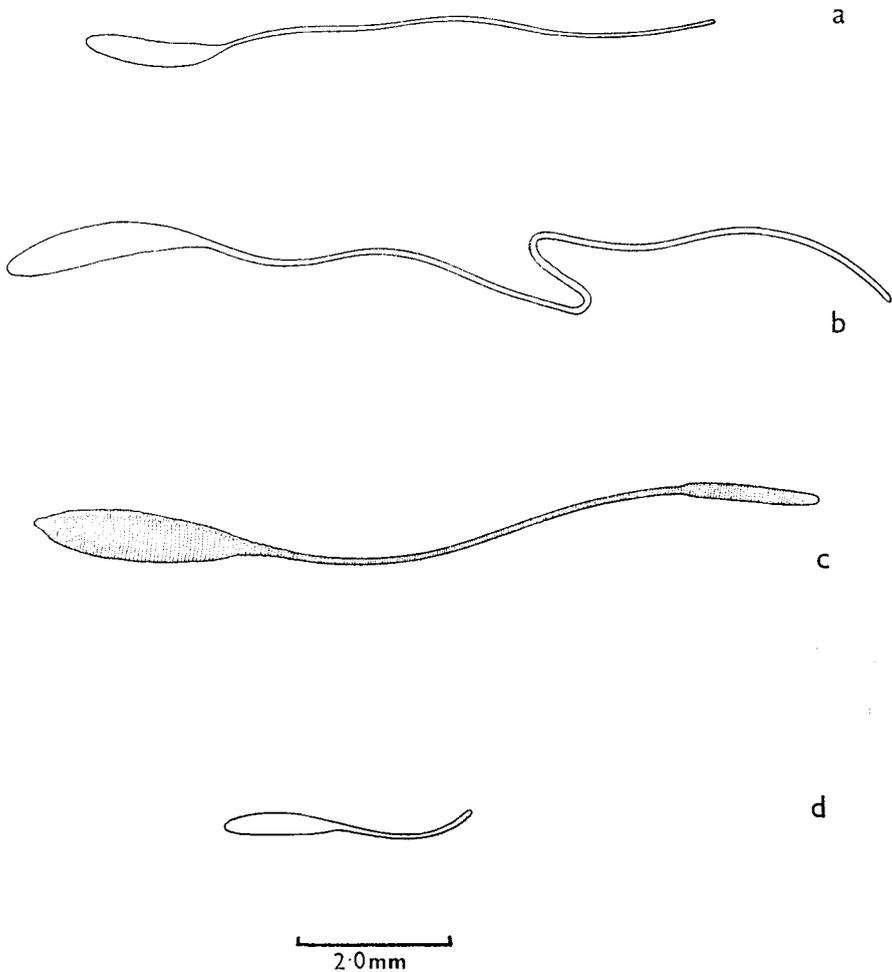


FIG. 5.—Eggs: (a) *R. persuasoria*; (b) *M. emarginatoria*; (c) *Ps. sternata*; (d) *O. geniculatus*.

Megarhyssa emarginatoria (Thunberg)

Megarhyssa emarginatoria was obtained from material collected in Sweden, France, Switzerland and Italy.

Pupa (fig. 1b) and cocoon

Female pupa (length, 21.0–39.0 mm.) with ovipositor curved over body dorsally, passing between antennae and continuing ventrally to base of ovipositor; ovipositor at least twice as long as body; abdominal tergites 4–6 strongly emarginate distally. Cocoon similar to that of *R. persuasoria*.

Fifth instar larva (fig. 6)

Fully-fed larvae: length 15.0–32.5 mm. (mean 23.7); width, 4.0–7.5 mm. (mean 5.5) ($n = 10$). Body similar to that of *R. persuasoria*. Spiracle (fig. 6*b*) with large, funnel-shaped atrium with narrow sclerotised reticulations, opening directly into closing apparatus. Larval cuticle (fig. 6*c*) densely covered with very small pointed papillae; setae short (0.019–0.038 mm.), lightly sclerotised. Head (fig. 6*a*): cephalic structures densely sclerotised; epistomal arch incomplete; pleurostoma very broad, especially ventrally, with robust superior mandibular process; hypostoma curved laterally, weakly sclerotised at lateral extremity; hypostomal spur broad, especially at dorsal end; stipital sclerite less heavily sclerotised, broad at lateral end which is free of hypostoma; labial sclerite sharply pointed ventrally, continuous dorsally, inner ventral margin ill-defined and corrugated; labral sclerite sclerotised throughout, forming well defined plate over mandibles; mandible with broad base and slender blade bearing 2 rows of moderately small and similarly sized teeth, and long, sharp posteromedial tooth present; well sclerotised plate on clypeus; maxillary and labial palps with 4–6 sensoria of unequal size and variable outline; antenna papilliform, sclerotised, about as long as diameter of unsclerotised antennal pit; clypeus with 2 pairs of moderately long setae, 2 pairs sensorial pits; labrum with 6–7 pairs of setae and 8–9 pairs of sensorial pits; silk press well defined, not sclerotised.

First, second, third and fourth instar larvae

Similar to those of *R. persuasoria* except: mandibular teeth of second, third and fourth instars more strongly developed; in fourth instar posteromedial tooth of mandible less pointed; rudimentary palps composed of 5–6 sensoria in all instars; third instar with 3–4 pairs of setae and 2 pairs of sensorial pits on clypeus, labrum with pronounced vacuoles dorsally; length of first, second, third and fourth instar larvae: 2.0–2.6 mm. (mean 2.3) ($n = 5$); 4.8 mm. ($n = 1$); 8.0 mm. ($n = 1$); 9.3 mm. ($n = 1$), respectively.

*Egg (fig. 5*b*)*

Similar to that of *R. persuasoria* except: egg body length, 2.4–2.7 mm. (mean 2.6), width, 0.50–0.55 mm. (mean 0.51); longer pedicel, length 10.8–12.8 mm. (mean 11.7) ($n = 4$).

Subtribe Theroniina

Pseudorhyssa sternata Merrill

Pseudorhyssa sternata was obtained from material collected in Sweden, France, Germany, Switzerland, Italy and Belgium.

This species utilises the oviposition drills made by *Rhyssa* species in order to gain access to hosts.

Pupa and cocoon

Pupa and cocoon similar to those of *R. persuasoria*.

Fifth instar larva (fig. 7)

Fully-fed larvae: length, 8.5–20.0 mm. (mean 14.4); width, 2.0–5.0 mm. (mean 3.5) ($n = 8$). Body similar to that of *R. persuasoria* except: abdominal segments 8–10 usually curved back over body; terminal segment with a pair of reduced, finger-like, caudal appendages. Atrium of spiracle large, funnel-shaped, length less than twice width, weakly reticulated orifice with annular sclerotisation below, opening directly into well defined closing apparatus (fig. 7*b*). Larval cuticle with wrinkled appearance and sparsely covered with small pointed papillae (fig. 7*c*); setae short (0.049–0.088 mm.), sclerotised, distributed in an irregular line around each thoracic and abdominal segment, with clusters on pleural swellings (20–56 on each segment). Head (fig. 7*a*): epistomal arch complete, well sclerotised; pleurostoma broad with large superior mandibular process; hypostoma curved latero-ventrally with simple inferior mandibular process; hypostomal spur heavily sclerotised; stipital sclerite curved laterally, reaching or nearly reaching hypostoma; labial sclerite incomplete dorsally, much thickened ventrally without point or lobes; labral sclerite with well sclerotised margins throughout and sclerotised area within; mandible (fig. 7*d*) with slender blade bearing 2 rows of fine, similarly-sized teeth on each margin of blade, pointed posteromedial tooth present; antenna short, cone-shaped, well sclerotised, antennal pit sclerotised; clypeus without sclerotised plate; silk press lightly sclerotised; labrum with 4–5 pairs of setae and 4 pairs of sensorial pits; clypeus with 4 pairs of strong setae and 3 pairs of sensorial pits; labium with 2 pairs of setae, 1 pair of sensorial pits.

Fourth instar larva

Similar to that of *R. persuasoria* except: terminal segment with pair of reduced caudal appendages; setae of larval cuticle moderately long (0.026–0.038 mm.); pleurostoma broad, with ill-defined margin; labrum with 2 pairs of setae and 2 pairs of sensorial pits.

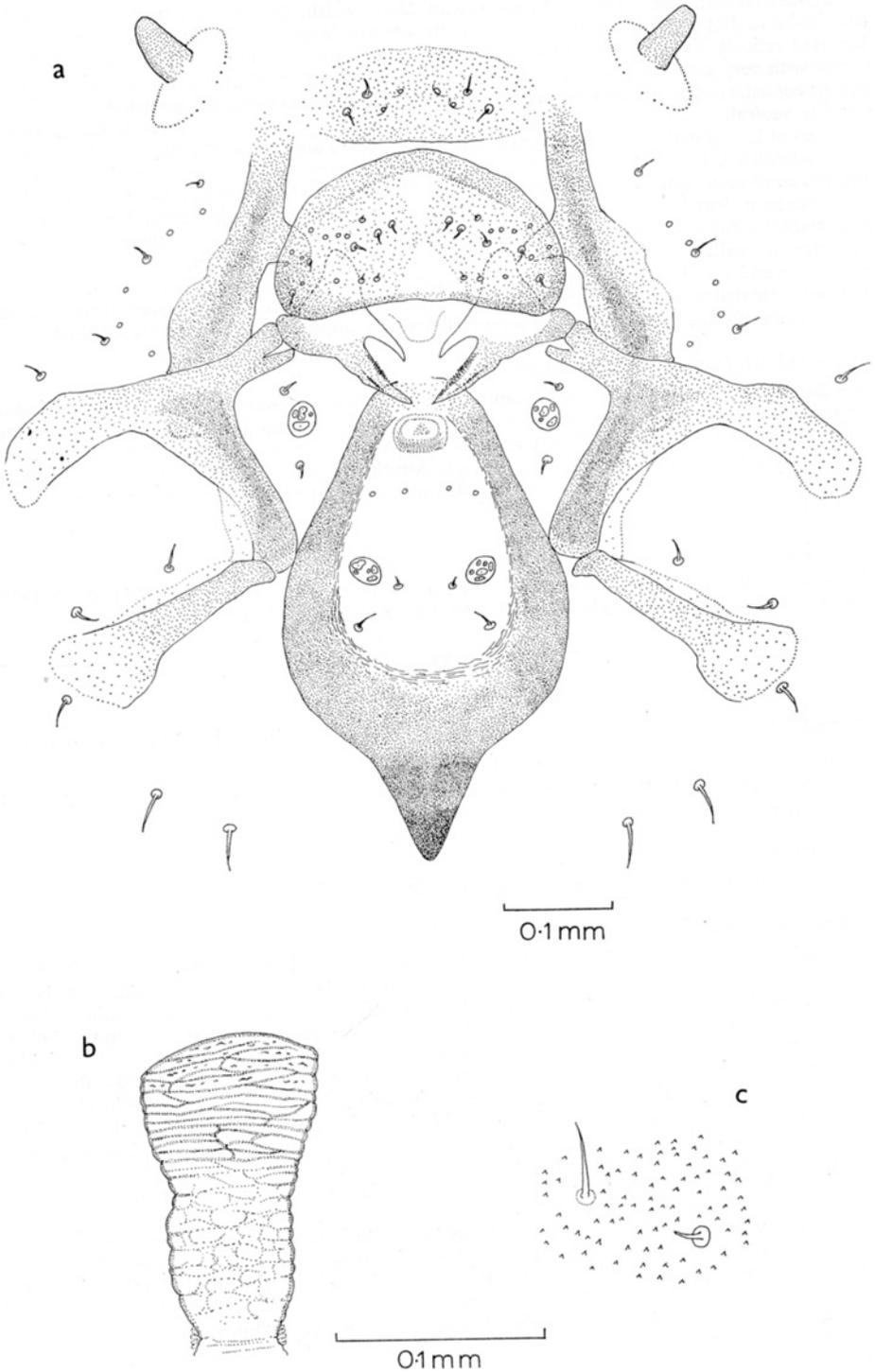


FIG. 6.—Fifth instar larva of *M. emarginatoria*: (a) cephalic structures; (b) spiracle; (c) cuticle.

Third instar larva

Similar to that of *R. persuasoria* except: terminal segment with pair of reduced caudal appendages; labrum with 5 pairs of setae.

Second instar larva

Similar to that of *R. persuasoria* except: terminal segment with pair of caudal appendages; mandibles moderately exposed, not fully covered by labrum.

First instar larva (fig. 4b, d, f and g)

Body (fig. 4b): length, 2.1–2.4 mm. (mean 2.3); width 0.56–0.62 mm. (mean 0.58) ($n = 5$). Very strongly mandibulate; terminal segment with pair of well developed caudal appendages (fig. 4g). Colour creamy white with very heavily sclerotised head. Spiracles on prothoracic segment and abdominal segments 1–8. Larval cuticle with small pointed papillae in broad dorsal and ventral bands and on pleural swelling of each segment; 8–18 setae (length 0.029–0.045 mm.) distributed around each segment. Mandible (fig. 4f) very large, heavily sclerotised, sickle-shaped; labrum with 4 pairs of long setae; rudimentary labial and maxillary palps each with 4 sensoria; antenna very large, papilliform (fig. 4d).

Egg (fig. 5c)

Similar to those of *R. persuasoria* except: egg-body length, 2.3–3.0 mm. (mean 2.4); width, 0.55–0.65 mm. (mean 0.60); pedicel, 4.2–7.5 mm. (mean 5.8) ($n = 6$) with slight dilation at distal end; basal end of egg-body with pronounced conical protuberance; chorion with transverse striae, milky white.

Xoridinae : Xoridini

Odontocolon geniculatus (Kriechbaumer)

Odontocolon geniculatus was obtained from material collected in France, Switzerland and Belgium.

Pupa (fig. 1c) and cocoon

Female pupa (length, 9.0–19.0 mm.) with ovipositor not curved over body, ovipositor as long as body. Cocoon (length, 11.0–32.0 mm.) conforming to maximum length of host chamber; densely spun, fibrous; colour ranges from white to brown with characteristic dark brown area at one end produced by larval faeces.

Fourth instar (fig. 8)

Fully-fed larvae: length, 8.0–19.0 mm. (mean 13.5); width, 2.5–4.5 mm. (mean 3.5) ($n = 10$). Atrium of spiracle (fig. 8b) globose with pronounced reticulations, stalk with annular sclerotisation, without well-defined closing apparatus. Larval cuticle (fig. 8c) densely covered with large, pointed papillae; setae short (0.026–0.045 mm.), lightly sclerotised, distributed around each segment (14–18 setae on each segment). Head (fig. 8a): epistomal arch complete, moderately sclerotised with indefinite margin; pleurostoma moderately sclerotised, broad throughout with small, narrow superior mandibular process; hypostoma moderately sclerotised, curved laterally, inferior mandibular process extends as bar beneath the mandible; hypostomal spur well developed, moderately sclerotised, resting close to medial end of stipital sclerite where it touches the labial sclerite; stipital sclerite moderately sclerotised medially, less so laterally where it curves dorsally towards hypostoma; labial sclerite heavily sclerotised, pointed ventrally with a densely sclerotised "shoulder", lateral arms twisted in relation to ventral portion; mandible stout with a row of large, unequal-sized teeth on upper edge of blade and with or without a row of rudimentary teeth on the lower edge; antenna papilliform, lightly sclerotised with unsclerotised antennal pit; maxillary and labial palps with 2 sensoria, 1 generally somewhat crescentic in outline, rarely with a third, small sensorium; clypeus with 3 moderately long setae; labrum with 4–5 pairs of setae, 4–5 pairs of sensorial pits; labium with 2 pairs of setae, 1 pair of sensoria; silk press well defined, sclerotised.

Third instar larva

Length, 5.0 mm. Larval cuticle densely covered with large, pointed papillae; setae short (0.013–0.026 mm.), distributed irregularly around each thoracic and abdominal segment. Head: epistomal arch complete; pleurostoma broad; hypostoma with long, inferior mandibular process; hypostomal spur narrow, lightly sclerotised, fused dorsally to hypostoma; stipital sclerite present; labial sclerite sclerotised laterally, incomplete dorsally, ventral portion broad but not pointed; labral sclerite present, complete dorsally; mandible similar to that of fourth instar; antenna sclerotised, papilliform with broad unsclerotised base; clypeus with 2 pairs of setae, 1 pair of sensorial pits; labrum with

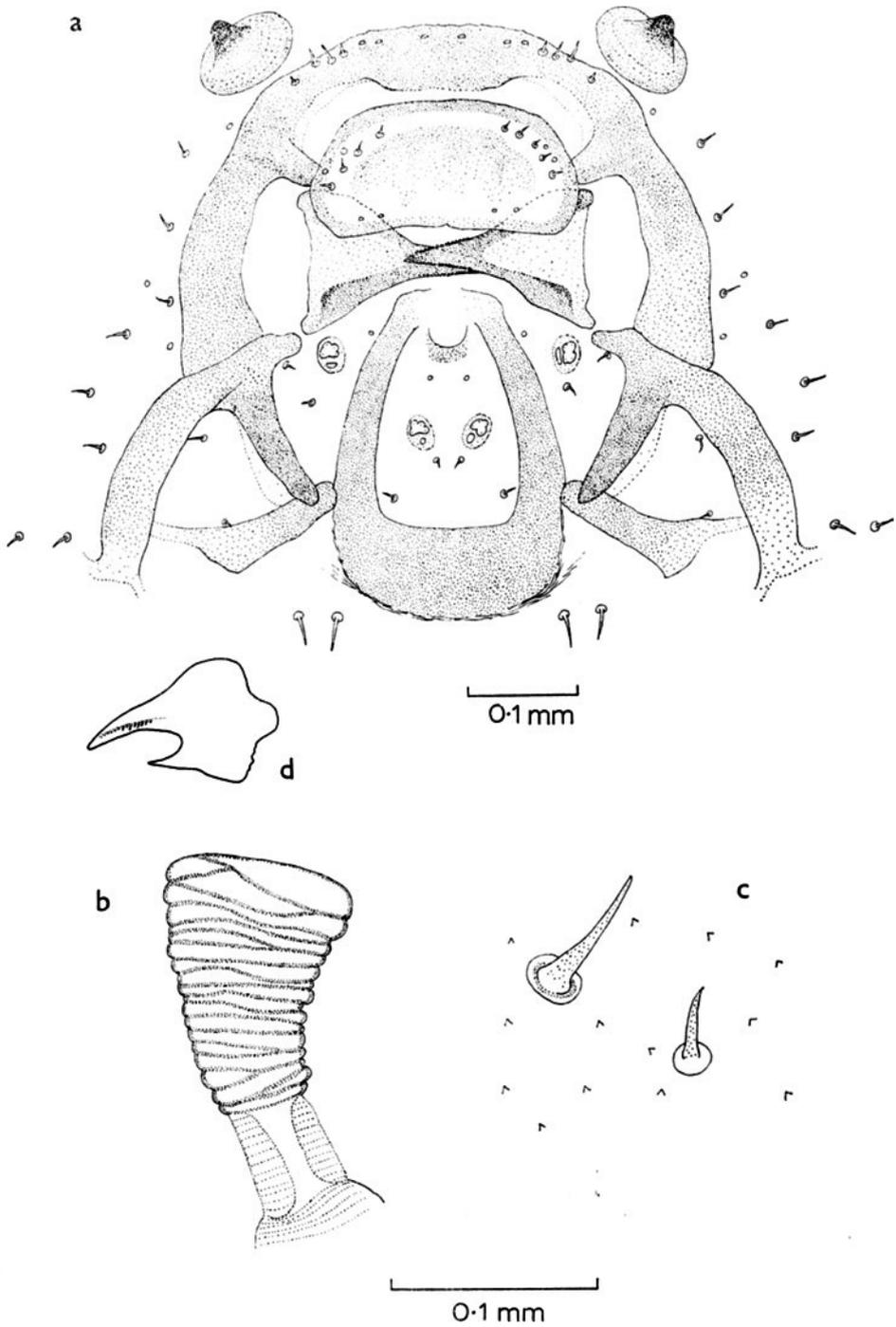


FIG. 7.—Fifth instar larva of *Ps. sternata*: (a) cephalic structures; (b) spiracle; (c) cuticle; (d) mandible.

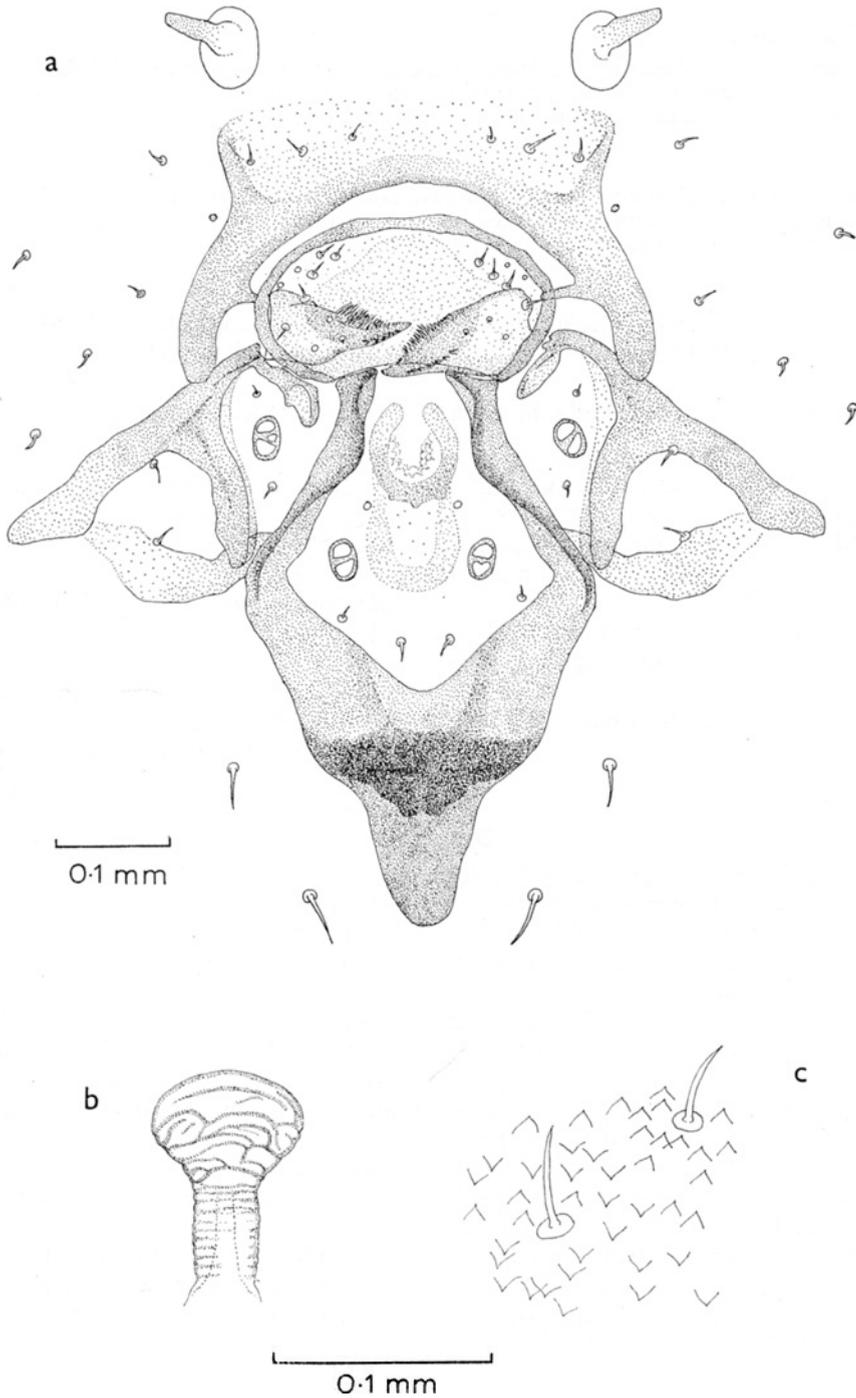


FIG. 8.—Fourth (final) instar larva of *O. geniculatus*: (a) cephalic structures; (b) spiracle; (c) cuticle.

4 pairs of setae and 7-8 pairs of sensorial pits; atrium of spiracle globose, long narrow stalk with annular rings, opening directly into closing apparatus.

Second instar larva

Length, 3.0 mm. Similar to third instar larva except: hypostomal spur curved, lightly fused to inferior mandibular process of hypostoma; stipital sclerite present but much reduced; labial sclerite less broad ventrally; labrum with 4 pairs of setae, 5-6 pairs of sensorial pits.

First instar larva

Length, 2.1 mm. Similar to second instar larva except: mandibles not covered by labrum and without teeth; only lateral arms of labial sclerite present; hypostomal spur rudimentary, faintly sclerotised; stipital sclerite lacking.

Egg (fig. 5d)

Similar to that of *R. persuasoria* but with much reduced pedicel. Length of egg body, 1.3-2.4 mm. (mean 1.9); width, 0.30 mm.; length of pedicel, 1.3-4.0 mm. (mean 2.7) (n = 5).

Key to parasites associated with siricine woodwasps, based on final instar larvae

- | | | |
|---|--|---|
| 1 | Labial sclerite pointed ventrally | 2 |
| - | Labial sclerite not pointed ventrally (fig. 7) | <i>Pseudorhyssa sternata</i> Merrill |
| 2 | Mandibles each with two rows of similarly-sized teeth, clypeal plate present | 3 |
| - | Mandibles with one row of large teeth and with or without one row of rudimentary teeth, clypeal plate lacking (fig. 8) | |
| | | <i>Odontocolon geniculatus</i> (Kriechbaumer) |
| 3 | Labial and maxillary palps moderately sclerotised, each with two or at most three sensoria (fig. 2) | |
| | | <i>Rhyssa persuasoria</i> (L.) and <i>R. amoena</i> Gravenhorst |
| - | Labial and maxillary palps only lightly sclerotised, each with four or more sensoria (fig. 6). | <i>Megarhyssa emarginatoria</i> (Thunberg) |

DISCUSSION

The eggs are similar among the ichneumonid species studied, and reflect the similarities in their oviposition habits. The eggs are adapted for passage down long narrow ovipositors, and are of the acuminate type (DeBach, 1964). The length of the pedicel is correlated with the length of the ovipositor, being greatest in *M. emarginatoria*, and least in *O. geniculatus*.

The first instar larvae of all species, except *O. geniculatus*, are typically mandibulate, with large mandibles for piercing the host cuticle, and killing supernumerary larvae in superparasitism or multiple parasitism. The first instar larva of the cleptoparasite, *Ps. sternata*, has the most highly developed head, and also a paired caudal process that is used for locomotion during its search for the primary parasite larva and for balancing during the ensuing fight. The setae of *Ps. sternata*, particularly those of the head capsule, are relatively longer than those of the primary larvae, and possibly function more advantageously as sensory organs.

The intermediate larval instars, which are morphologically similar to the final instar, are pertinent to taxonomic studies based on final instar characters. In *R. persuasoria*, the epistomal arch of the intermediate instars is complete and well sclerotised, but is lacking or only lightly sclerotised in the fifth instar. There is a general increase in the relative size of the pleurostoma and hypostoma, and an increase in the sclerotisation of the maxillary and labial palps with successive moults. The study of the intermediate instars confirms that the inferior mandibular process is part of the hypostoma (fig. 3e) and not a pleurostomal structure (Beirne, 1941). The hypostomal spur in second instar larvae of *R. persuasoria*, *R. amoena*, *M. emarginatoria* and *Ps. sternata* appears as a separate sclerite, and it becomes progressively more fused

to the hypostoma in succeeding instars. The stipital sclerite, which is an important taxonomic character, is wholly lacking in pre-final instars, but in some fourth instar *R. persuasoria* there is slight sclerotisation at the lateral margin of the labial sclerite, corresponding to the position in the final instar. In *O. geniculatus*, the stipital sclerite is only absent in the first instar. The labial sclerite of *R. persuasoria* is much reduced in the first and second instars, and the only indication of the pointed ventral portion of the final instar is a small area of sclerotisation in the fourth instar (fig. 3f). The mandibles of the intermediate and final instar larvae are very similar in each species, but differ markedly from the mandibles of the first instar. The mandibles of second to fifth instars are more or less covered by the labrum, but in the second instar of *Ps. sternata* the mandibles are considerably exposed. The first instar of *O. geniculatus* is very similar to succeeding instars, in strong contrast to the Ephialtini species.

The bodies of the larvae differ little between species or instars, except that *Ps. sternata* has a paired caudal process in all instars.

Ichneumonid taxonomy based on the cephalic structures of the final instar was studied by Beirne (1941) and Short (1959), who discussed the relationships between subfamilies and tribes. The larval taxonomy of Beirne (1941) and Short (1959) conforms to the adult taxonomy of Perkins (in Beirne), Townes & Townes (1951) and Walkley (1958). The species described in the present paper belong to the subfamily Cryptinae of Beirne (1941), in which *Rhyssa* species and *M. emarginatoria* would be placed in the Rhyssini, *Ps. sternata* in the Ephialtini and *O. geniculatus* in the Odontomerini, although specimens of *O. geniculatus* bearing a lower row of rudimentary mandibular teeth would key to the Sphecophagini. His description of *Ischnoceros rusticus* (Geoffroy) showed the inferior mandibular process extending as a bar below the mandible and is probably typical of the Odontomerini. Within the Pimplinae of Short (1959), *Ps. sternata* would be placed in the Theroniini, and *O. geniculatus* in the Xoridini, although the pointed labial sclerite of *O. geniculatus* invalidates the use of his key for this species.

Finlayson (1967) placed the subtribes Rhyssina and Theroniina within the Ephialtini, which with the Pimplini (= Ephialtini of Townes & Townes, 1960) are included in the Pimplinae. She states that the Pimplinae are characterised by having a hypostomal spur that "rests on the medial end of the stipital sclerite where it touches the labial sclerite". This characteristic places the previously described species of Xoridini (Chrystal & Skinner, 1931; Beirne, 1941; Ayyar, 1943; Short, 1959) outside the Pimplinae, because they possess a hypostomal spur that meets the stipital sclerite at its mid-point. However, the hypostomal spur and stipital sclerite relationship of *O. geniculatus* would place it in the Pimplinae of Finlayson (1967), although the mandible and submandibular bar of the hypostoma clearly show its affinities with the Xoridine, *I. rusticus*. Finlayson (1967) keys the Ephialtini from the Pimplini partly on the basis of an incomplete epistomal arch. This does not hold true for *Ps. sternata*, which has a complete and well sclerotised epistomal arch, in contrast to *Ps. alpestris* (Holmgren) (Thompson, 1958), but the presence of a labral sclerite and mandibular teeth exclude it from the Pimplini.

The present study indicates that within the Ichneumonidae phylogenetic relationships based on larval characters are somewhat confused. This situation will continue until a more representative range of species has been described.

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