

## The Biology and Morphology of *Entedon sylvestris* (Hymenoptera: Eulophidae), a Larval Endoparasitoid of *Ceutorhynchus sisymbrii* (Coleoptera: Curculionidae)

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**Abstract.**—The biology and morphology of preimaginal stages of *Entedon sylvestris* Szelenyi (Hymenoptera: Eulophidae), are described in detail for the first time. *Entedon sylvestris* is a larval endoparasitoid of the seed-feeding larvae of the weevil *Ceutorhynchus sisymbrii* Dieckmann on the small tumbleweed mustard, *Sisymbrium loeselii* L. (Brassicaceae). In the Ukraine, females of *E. sylvestris* begin ovipositing in late May and continue to lay eggs until the beginning of July. Females of *E. sylvestris* parasitize weevil larvae of various instars. The parasitoid larva remains within the body of the host weevil larva until the emergence of the latter from the dried host-plant pods. The morphology of each of the three larval instars is described in detail. The moult of the parasitoid larva into the final instar, as well as pupation, takes place underground. Adults of *E. sylvestris* must therefore penetrate a soil layer to emerge the following spring.

**Key words.**—Entedoninae, larval endoparasitoids, parasitoid-host relationships, preimaginal morphology, *Sisymbrium loeselii*

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Parasitic wasps of the genus *Entedon* Dalman (Eulophidae, Entedoninae) are endoparasitoids of immature stages of beetles. Curculionidae (including Scolytinae), Brentidae (including Apioninae), Anobiidae, Chrysomelidae (including Bruchinae), Buprestidae, Cerambycidae, Mordellidae, and Nitidulidae are recorded as hosts (Bouček and Askew 1968, Graham 1971, Askew and Kopelke 1989, Rasplus 1991). *Entedon ergias* Walker has been imported from Europe into North America for the biological control of the smaller European elm bark beetle, *Scolytus multistriatus* (Marsham) (Peck 1963). For some species, parasitism rates and/or general descriptions of the larval morphology are given (Ferrière 1939, Erdös 1944, Abedin and Quayum 1972, Tiwari 1976). However, these descriptions lack many morphological details, especially for the first instar larvae. Beaver (1966) and Fisher (1970) gave the most complete bioassays and reported egg-larval parasitism for *Entedon*

*ergias* Walker, *E. rumicis* Graham, *E. pharnus* Walker. Askew (1991) and Gumovsky (1997) provided some information on percentage parasitism, the biology of the final instar larva and pupation procedure of *E. cioni* Thomson, *E. cionobius* Thomson and *E. zanara* Walker.

In general, despite some thorough reviews (Parker 1924, Parker and Thomson 1925) and occasional detailed descriptions (e.g., Darling 1992, 1995) of the larvae of Chalcidoidea, our knowledge of morphology of preimaginal stages of chalcid wasps is incomplete. Most discussions on larval morphology and biology concern ectoparasitoids, whereas endoparasitoid larvae traditionally attract less attention, mainly due to the difficulties with their preparation and identification. The larvae of Eulophidae were classified by Parker (1924) in group II (the ectoparasitoid forms) and V (egg endoparasitoids), differing mostly in having spiracles (group II) or being apneustic (group V). Later, when



discussing the morphological peculiarities of the first instar larvae of *Anastatus* sp. (Eupelmidae) and *Miscogaster* sp. (Pteromalidae), Parker and Thomson (1925) stated that some endoparasitoid larvae represent a transitional type between the groups corresponding to groups V and VI sensu Parker (1924).

The larval morphology of *Entedon* species is even more vague. The papers of Beaver (1966) and Fisher (1970) are the only sources of comprehensive descriptions of preimaginal stages, but these concern mainly the size, body proportions and number of spiracles, and are illustrated mostly by diagrammatic figures. Many of the minute morphological structures (e.g. sensorial organs) remain obscure and undescribed.

Weevils of the subfamily Ceutorhynchinae have a wide range of host plants, but many are restricted to Brassicaceae. Some Ceutorhynchinae species have gained special attention as pests of economically important plants (e.g., *Ceutorhynchus napi* Gyllenhal, *C. pallidactylus* (Marsham) and *C. obstrictus* (Marsham) damaging cabbage and oilseed rape in North America). Other species (e.g. *C. merkli* Korotyaev, *C. cardariae* Korotyaev, *C. alliariae* Brisout, *C. roberti* Gyllenhal) are under investigation as potential biological control agents against some introduced weeds (i.e. whitetops *Cardaria* spp., garlic mustard *Alliaria petiolaria*: Hinz *et al.* 2004, Hinz and Gerber, 1998). The small tumbleweed mustard, *Sisymbrium loeselii* L., is a plant of European origin that was accidentally introduced into the New World, and is now recorded in 31 states of the USA, and is regarded as an invasive weed (Stubbendieck *et al.* 1994).

Some parasitoid species (e.g. *Tersilochus* spp., *Microctonus* spp.) have been released in North America to control *Ceutorhynchus* spp. (e.g. *C. obstrictus*) that are pests of economic plants (e.g. *Brassica* spp.). However, parasitoids—unless sufficiently host-specific—could hamper the effectiveness of the *Ceutorhynchus* spp. released as biolog-

ical control agents. It is therefore of vital importance to determine the parasitoid-host associations of Ceutorhynchinae and host plant preferences in various geographic regions.

This paper reports results obtained from and the methodological approaches used during the study of the parasitoid-host relationships between *Entedon sylvestris* Szelényi and its host, the weevil *Ceutorhynchus sysimbrii* Dieckmann on *Sisymbrium loeselii*, which is the first host record for the parasitoid.

## MATERIALS AND METHODS

Adults of *Entedon sylvestris* were collected in the field on plants of *Sisymbrium loeselii* during late June and early July in 1995, 1997, 2001, 2002, 2004 in Kiev (50°28'N; 30°32'E) and Kherson oblast of Ukraine (v. Lazurnoe) (46°04'N; 32°29'E). Collections were made by both sweeping and capture of individual adults in tubes. Females were kept in Petri dishes and fed with diluted honey.

Mature pods of *S. loeselii* infested by the larvae of *Ceutorhynchus sysimbrii* (living inside the pods and feeding on seeds) were exposed to females of *E. sylvestris* kept in various reservoirs (Petri dishes, sealed plastic bags or boxes). Infestation by the weevil was indicated by the presence of a distinct hole in the pod made by the female's rostrum before oviposition.

The sites where the parasitoid's oviposition took place were marked with black ink. To study the morphology of the different larval instars of *E. sylvestris*, weevil larvae were removed from the pods at regular intervals and dissected. Endoparasitoid larvae found were fixed in Bouin's fixing solution (15 cm<sup>3</sup> picric acid (saturated), 5 cm<sup>3</sup> formaldehyde solution, 1 cm<sup>3</sup> acetic acid) to keep their original shape, and further washed out in 96–98% ethanol.

Mature weevil larvae, leaving the pods of their host plant, were put into plastic tubes (50 × 16 mm) filled 3/4–4/5 with



soil taken from field sites of *S. loeselii*. The behavior of the mature weevil larvae was observed through the transparent walls of the tubes. In September/October, when the pupae of *E. sylvestris* were expected to be completely formed, all tubes were carefully searched for earthen cells or dead weevil larvae. Dead weevil larvae found, were put into 5–10% solution of lactic acid to regain their original shape and soften. The softened larvae were then dissected in order to find the parasitoid larvae, in particular, the final instar larvae. These were transferred into lactic acid solution of higher concentration (40–70%) to obtain maximum swelling. The parasitoid larvae were then put into Bouin's fixing solution in order to fix the regained shape and then washed out in 96–98% ethanol.

All fixed larvae were kept in 100% ethanol for one day and then in 100% molecular sieved ethanol for maximal dehydration. After absolute ethanol the specimens were Critical Point Dried. The minute parasitoid larvae were put into pipette tips of various diameters sealed on the sides with cotton wool plugs, to avoid their loss during drying. The dried parasitoid larvae were transferred to SEM stubs on metallic pins, using static electrical charges to avoid damaging their extremely soft integuments. Finally the specimens were coated with gold and observed using a Scanning Electronic Microscope LEO 1530VP in the Max-Planck Institute for Metal Research, Stuttgart (MPI).

Field and laboratory video recordings were made using either 8 mm VP-A800 Pal Samsung Video Camera or with digital imaging of Leica IC A Videomodule integrated in the Leica MZ 125 stereomicroscope, using the video grabbing option conducted in Adobe Photoshop 6.0 programme through the use of the Falcon\Eagle Frame Grabber. The alignment of the photos corresponding to different layers in focus was conducted using the Combine Z programme Version 3.9 (designed by Alan Hadley, <http://www.hadleyweb.pwp>).

[blueyonder.co.uk/CombineZ/CombineZ3.zip](http://blueyonder.co.uk/CombineZ/CombineZ3.zip)).

## RESULTS

### Taxonomy

*Entedon sylvestris* Szélenyi, 1981

*Entedon sylvestris* Szélenyi, 1981: 277; *Entedon sylvestris* Szélenyi; Askew, 1992: 119; *Entedon (Entedon) sylvestris* Szélenyi; Gumovsky, 1999: 142; *Entedon sylvestris*; Gumovsky, Boyadzhiev, 2003: 23.

*Material examined*.—Types: Holotype female, paratypes 10 females, 6 males, Hungary, Hortobagy National Park (Szélenyi) (Hungarian Museum of Natural History, Budapest); more than 2,000 specimens from Kiev (June 1995, 1997, 2003, 2002, 2004) and v. Lazurnoe (Kherson oblast), Ukraine, collected on plant shoots and fruits of *S. loeselii*; 7 females, 4 males, Kiev vicinity, Velyka Oleksandrivka, swept from *Berteroa incana* and *Capsella bursa-pastoris*, 31.V.2004, (Schmalhausen Institute of Zoology, Kiev); 54 females, 1 male, Kyiv, Trukhaniv Island, "Park Druzhby Narodiv", 24.VI.1995, swept from *Sisymbrium loeselii* (Natural History Museum, London); 1 female, 1 male, Gießen, ex *Capsella* seeds V.1995 (Weiffenbach) (Zoologische Staatssammlung Munchen).

*Recent literature*.—*Entedon sylvestris* has gained little attention since its description (Szélenyi, 1981). This species belongs to the assemblage of the *cyanellus* and *costalis* species groups in having the anterior margin of the clypeus produced (Figs 1A, C, E, cly; 2C).

Askew (1992) reported it for Great Britain, presented a short corrected diagnosis and reported the possession of traces of pale strips on the fore tibiae. He also proposed to locate this species in the *cyanellus* species group of *Entedon* based on the presence of these hardly discernible foretibial strips and the 3-segmented funicle of the male. Gumovsky (1999), when revising the *cyanellus* group of the genus, argued against Askew's placement of *E. sylvestris* based on that only about 20% of specimens in a population possess



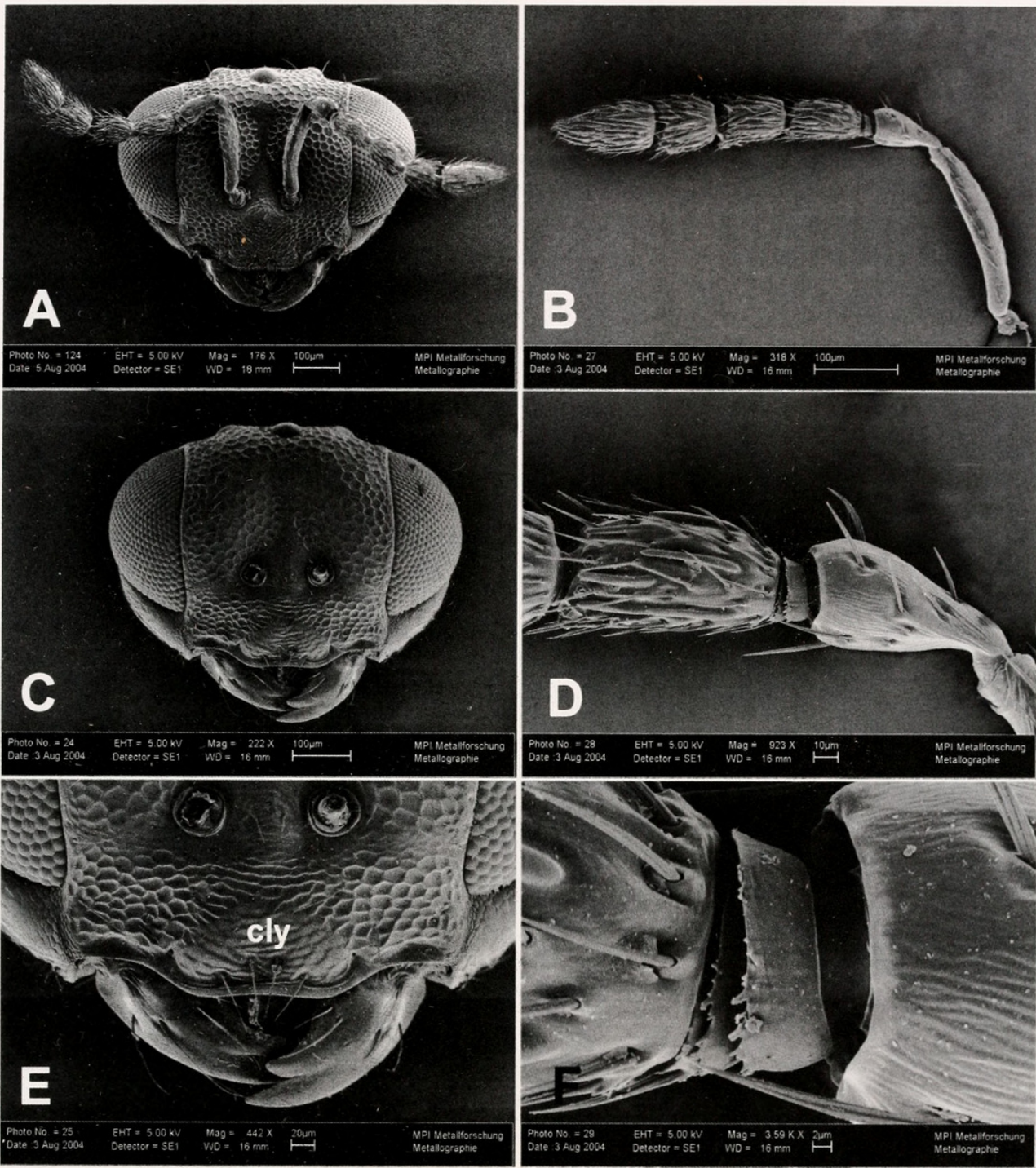


Fig. 1. *Entedon sylvestris*, female, details of morphology: A, C, head in frontal view; B, antenna; D, pedicel and 1st funicular segment; E, lower face; F, anelli; cly, clypeus.

the dim foretibial stripes, whereas the majority of the specimens have fore tibiae largely darkened, and proposed instead to accommodate *E. sylvestris* in the *costalis* species group (decreasing the value of the 3-segmented funicle of male as a species-group character). Gumovsky and Boyadzhiev (2003) reported this

species for Bulgaria and also provided its comparative diagnoses in their key to species.

*Comparative notes.*—Within the European fauna, *E. sylvestris* can easily be confused with *E. cyanellus* and *E. fufius*. From the former species, *E. sylvestris* is easily distinguishable as female has a shorter 1st



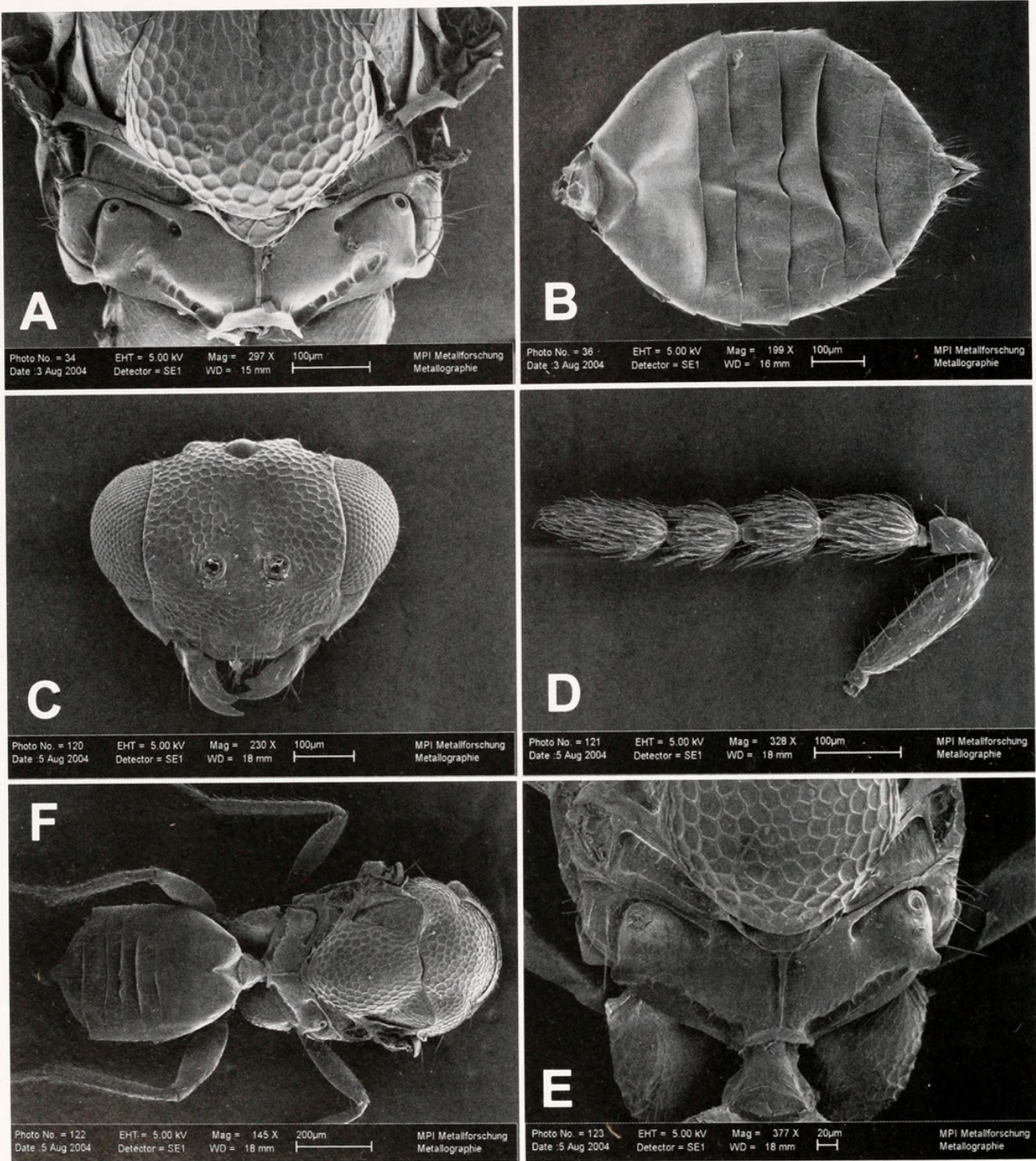


Fig. 2. *Entedon sylvestris*: A, B, female: A, posterior mesosoma; B, metasoma; C–F, male: C, head in frontal view; D, antenna; E, posterior mesosoma and anterior metasoma (petiole); F, body.

funicular segment (1.5–1.6 times as long as broad, Figs 1B, D, whereas in *E. cyanellus*—1.8–5.0 times) and by the narrower antennal scape of males (3.8 times as long as broad, Fig. 2D, about 3.0 times in *E. cyanellus*). Also, the foretibial stripes (when present) are much narrower and not terminated by a pale area on the distal

end of the tibia (the tibia is always with distal pale band in *E. cyanellus*). The distal pale bands on the tibiae also distinguish *E. sylvestris* from *E. fufius* in which all tibiae are completely dark. Also, the 1st funicular segment of females is about 2.2 times as long as broad and 1.4 times as long as the 2nd segment in *E. fufius*, whereas in *E.*



*sylvestris* the segment is 1.5–1.6 times as long as broad and just slightly (about 1.1 times) longer than the 2nd (Figs 1B, D). Moreover, all flagellar segments are free in males of *E. fufius* (the funicle is 4-segmented), whereas in *E. sylvestris* the funicle is 3-segmented and two last funicular segments are closely attached (forming the 2-segmented clava, Fig. 2D).

*Distribution*.—Hungary (Szelényi 1981), Britain (Askew 1992), Bulgaria (Gumovsky and Boyadzhiev 2003), Ukraine (Gumovsky 1999).

### Ecology

*The host, Ceutorhynchus sisymbrii Dieckmann*.—*Ceutorhynchus sisymbrii* is similar to *C. pulvinatus* Gyllenhal, 1837 in having dense coverage of dorsum and black rostrum, but differs from that species in that only the tibiae are red, not the entire legs (L. Behne, pers. comm.). Despite *C. sisymbrii* (Dieckmann 1966) being described nearly fifty years ago, its biology remained unknown. Dieckmann (1972) mentioned that studies on the life cycle of this species are of special value. Below I propose a brief synopsis of the field and laboratory observations on this species.

Adults of *Ceutorhynchus sisymbrii* (Figs 3A, B) feed on shoots, flowers and fresh seeds of *Sisymbrium loeselii*. Oviposition takes place in May–July. The female of the weevil lays its eggs into the pods of the host plant when the seeds are fully grown, but still soft and green (mature seeds are yellow to orange and hard). At first, the female makes an opening in the pod with her rostrum. It deeply penetrates the rostrum into the pod (up to the base of the rostrum) and eats the seed below the hole. Then the female turns back and presses its caudal end into the prepared opening, and begins oviposition. This behaviour is discernable by the rhythmic pulsing of her gaster. Occasionally, the female fails to aim into the prepared hole and lays an egg directly onto the

surface of the plant pod. She then eats the egg, as in other weevil species (Kozłowski 2003).

The larvae feed on the seeds and remain in pods until they are fully grown (Figs 3C, D, E; Figs 11A, B). The pods then split and the mature larvae fall to the ground (Fig. 11D). Larvae leave the host plant's pods at the end of June – beginning of July. They quickly bury themselves into the soil, where they prepare an earthen cell, in which they pupate (Fig. 11E). I have found adult beetles in the dissected earthen cells in October. However, I assume that adult weevils are already present before, but leave their soil/earthen cocoons only the following spring.

*Host searching and oviposition of the parasitoid, E. sylvestris*.—The females of *E. sylvestris* can be found in the field from late May until early July (Figs 4A–G). The parasitoid female searches along the pods of *S. loeselii* for weevil larvae, by drumming the pod surface with her antennae (Fig. 4A). Once she has located a host, she walks back and forth several times before starting to oviposit. She bends her gaster downwards and briefly hooks the ovipositor saw into the plant tissues. She then releases the gaster so that it strengthens in a position perpendicular to the ovipositor (Figs 4B, C). Thereafter she penetrates the pod wall with her ovipositor, and carries out rhythmic, twisting movements to find the weevil larva, as in other parasitoid species. Oviposition lasts about 30–90 seconds. Quite often the ovipositor penetration causes the host's haemolymph to exude, and then females of *E. sylvestris* feed on these excretions.

### Immature stages of *E. sylvestris*

*Egg*.—Elongate, white to transparent, without discernible sculpture. No stalks or terminal bulbous projections, reported by Beaver (1966) for *E. ergias*, were found. Size, about 260–300 µm long and about 80–100 µm wide.



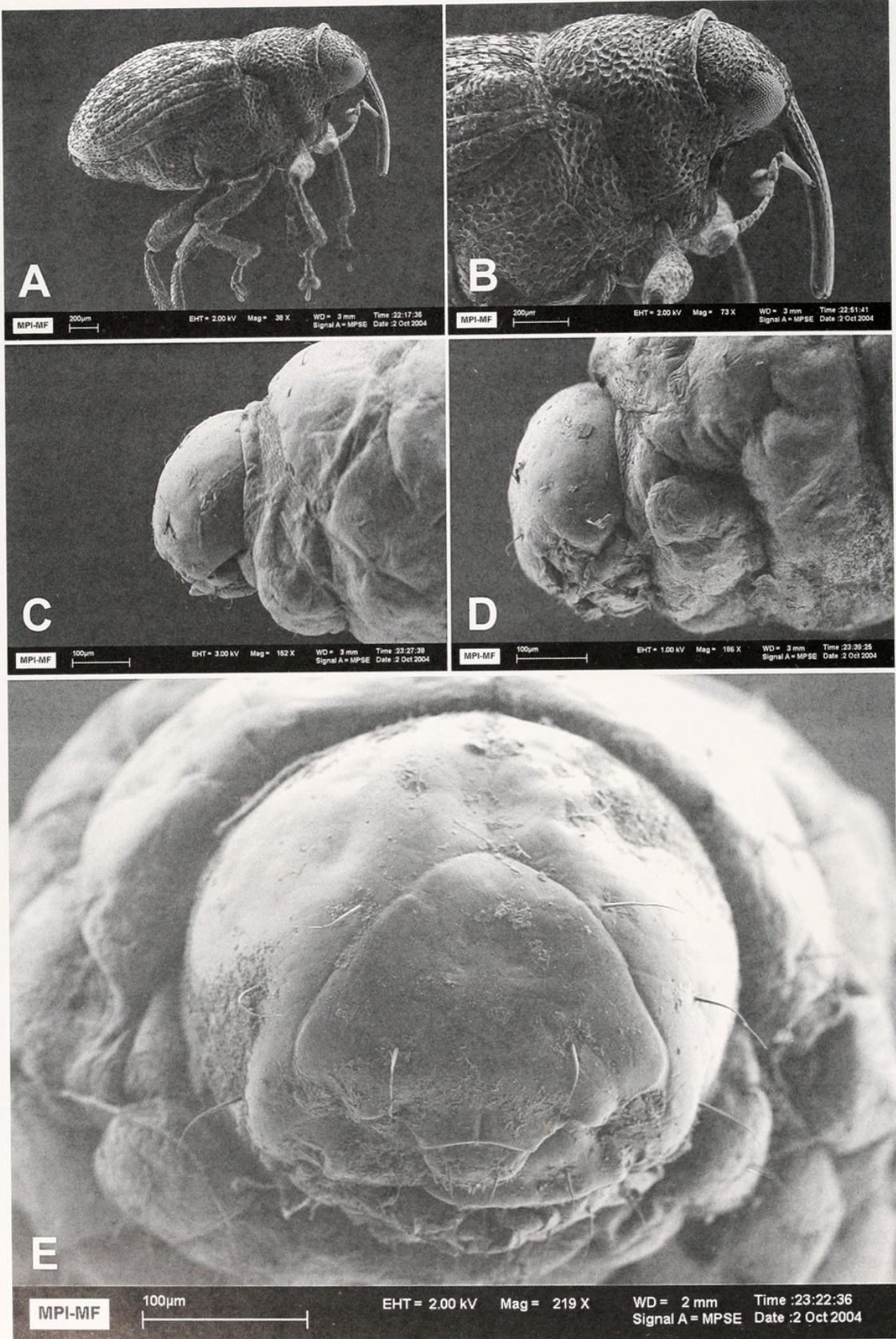


Fig. 3. A–E, *Ceutorhynchus sisymbrii*. A, B, female, C–E, mature larva.

*1st instar larva.*—Habitus. The first instar larva of *E. sylvestris* is hymenopteriform, pale (nearly transparent), has 13 body segments and a cranium. There are some

different forms, which were found during dissection of the host larvae. One is “slim” (Figs 5A, 6A), about 300 µm long and about 104 µm wide (max.), and another



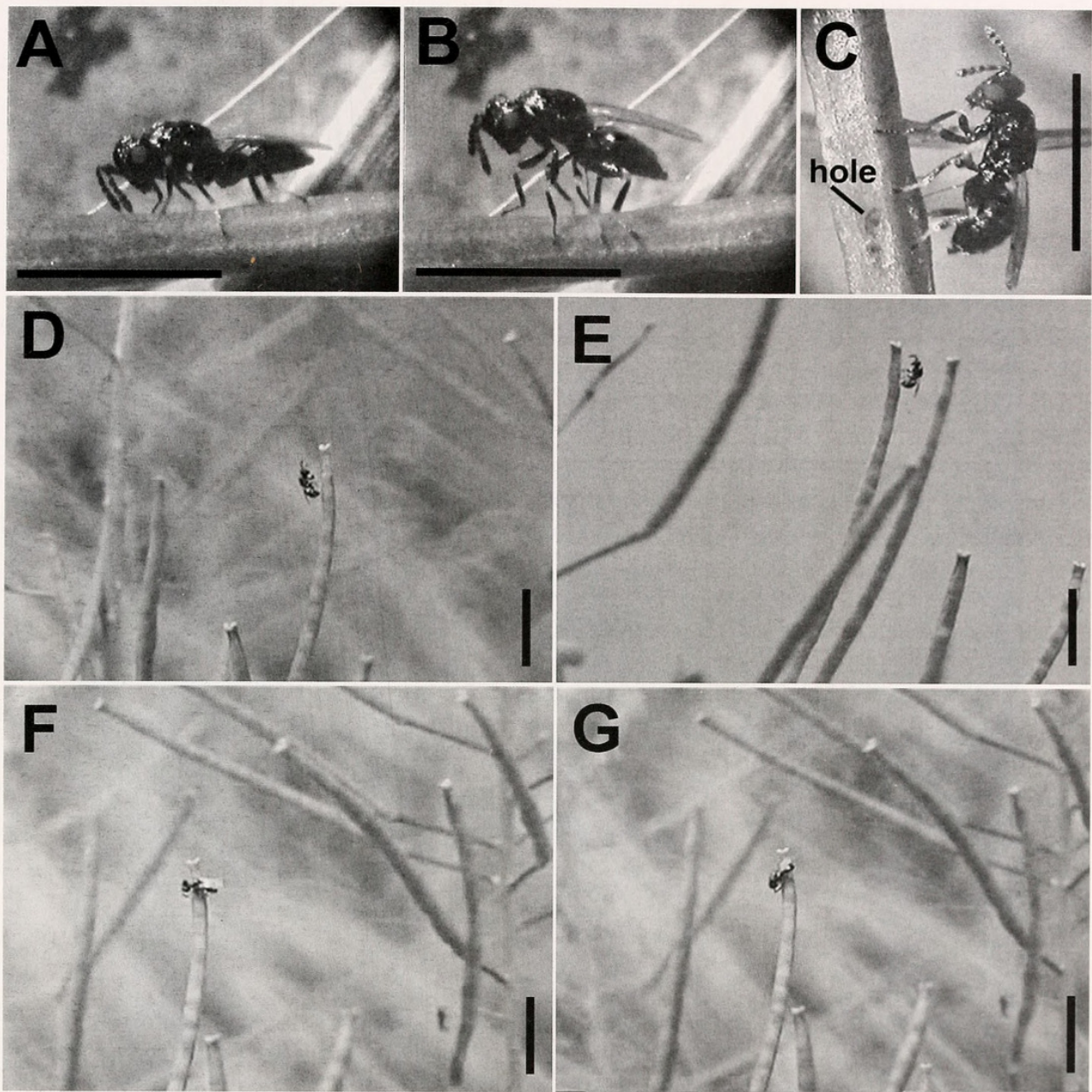


Fig. 4. A–G, the female of *Entedon sylvestris* oviposits into the larva of *Ceutorhynchus sisymbrii* in pods of *Sisymbrium loeselii*: A–C, in laboratory; D–G, in the field; hole, oviposition hole of weevil female. Scale bars: A–C, 2 mm; D–G, 5 mm.

form is “swollen” (Figs 6E, F), about 450  $\mu\text{m}$  long and about 206  $\mu\text{m}$  wide. Occasionally, specimens of an intermediate form were found (Fig. 6G), with a length of about 260  $\mu\text{m}$  and a maximum width of about 108  $\mu\text{m}$ . Despite the differences in size, I regard all three forms as belonging to the same larval instar, because of the possession of the peculiar shape of the head capsule (cranium) and body surface. The different body proportions are probably caused by different nutritional condi-

tions, and fixation and drying circumstances.

Body segments. The last, XIIIth, segment bears sharp triangular tubercles along its margin, arranged in two or three rows in the shape of a crown (Figs 6C, D). These tubercles are very distinct in freshly emerged larvae, but occasionally are coated with secretions (Fig. 6H). These rows of tubercles are also distinct in the “swollen” larvae (Fig. 6H), however, they are not so clearly distinguishable in these larvae due



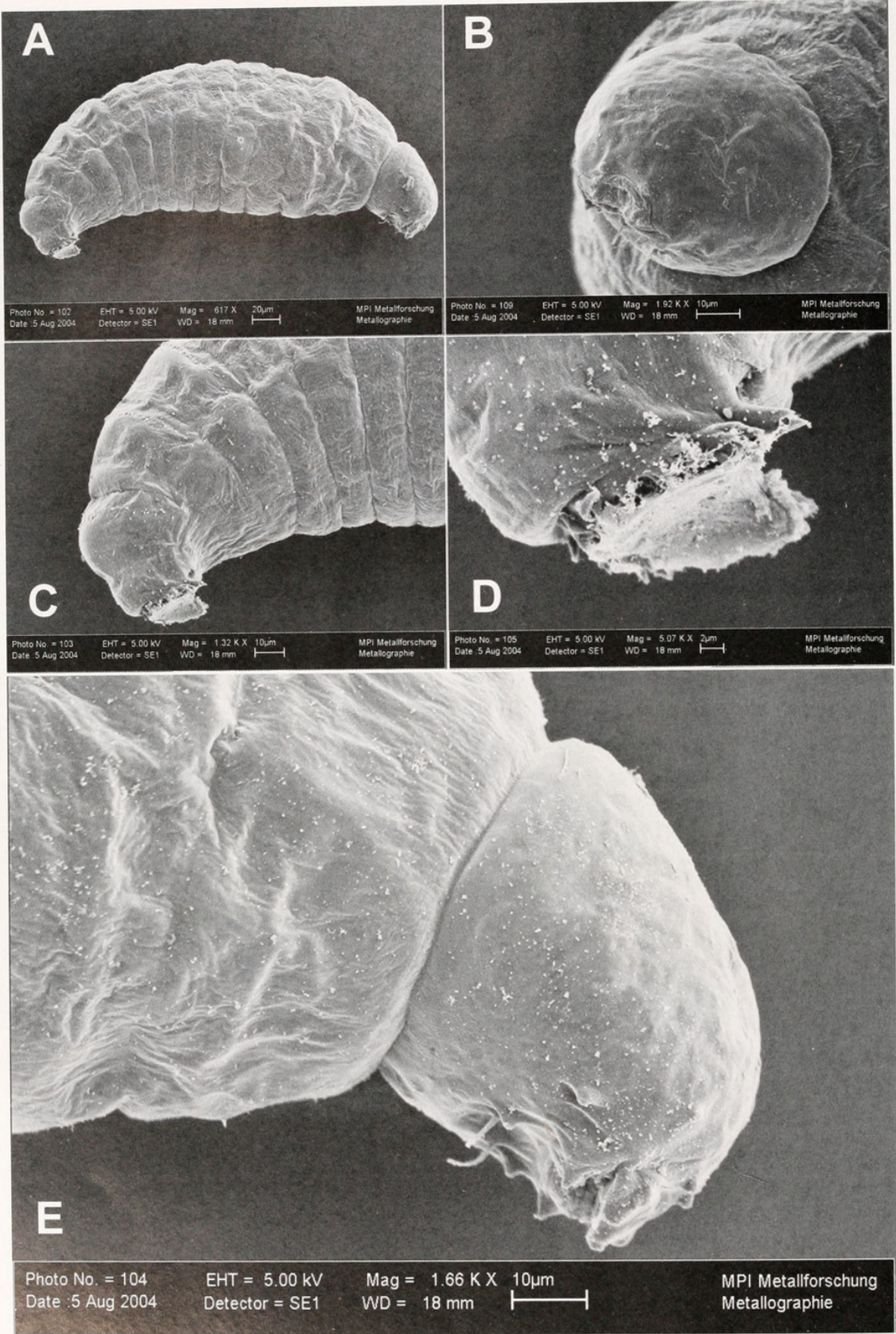


Fig. 5. *E. sylvestris*, first-instar larva: A, habitus; B, E, head close-up; C, D, cauda close-up.

to the thickness of the preceding segment (Figs 6E, F, H). Segments IV–XII bear distinct dorsal semicircular serrations (Fig. 6C, se) along their anterior margins,

which consist of small curved teeth. Segments I–III bear no distinguishable teeth or serration, which reflects the subdivision into thoracic (I–III) and abdominal (IV–



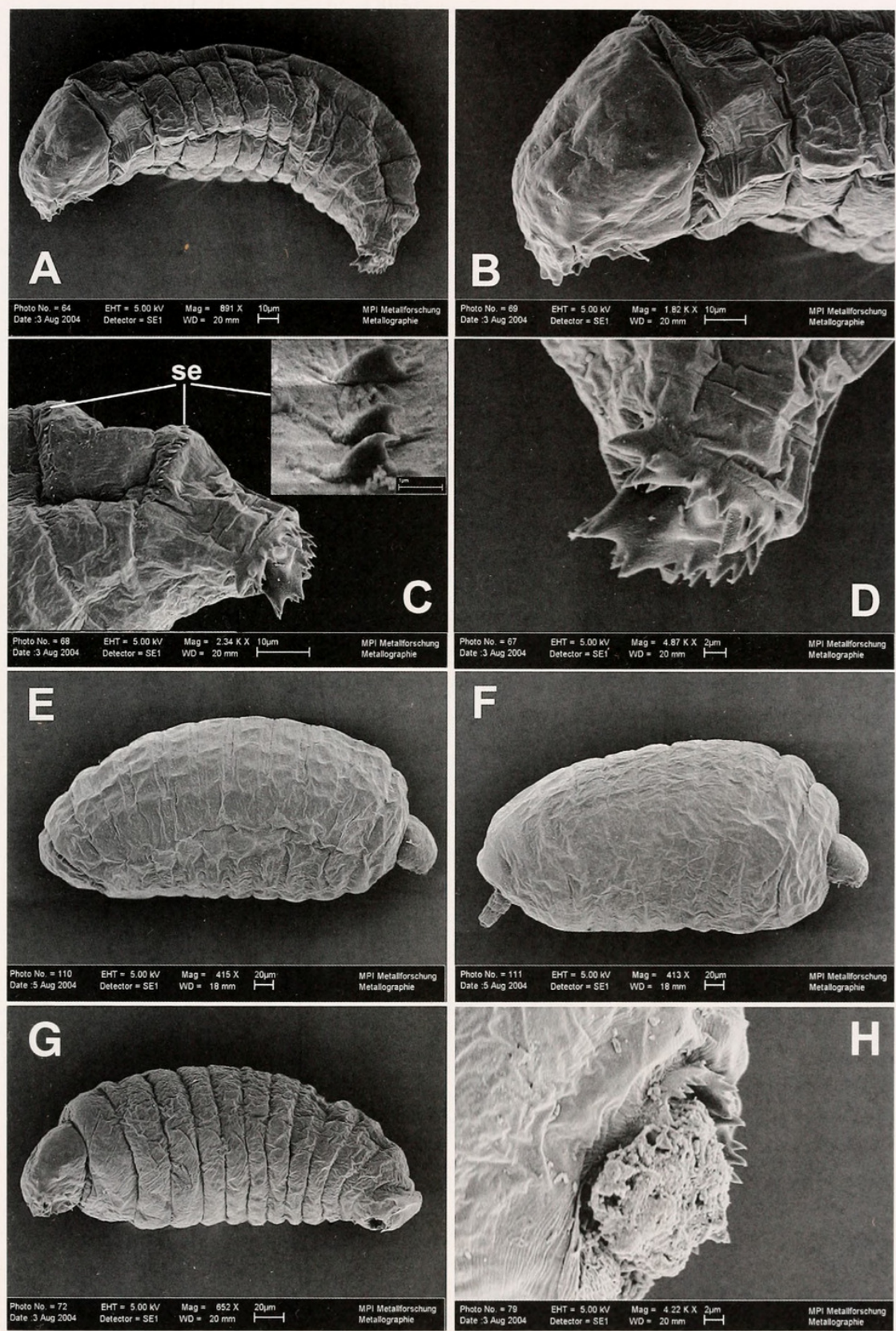


Fig. 6. *E. sylvestris*, first-instar larva: A, E–G, habitus; B, head; C, D, H, cauda; se, serration.

XIII) segments. No spiracles were found on the body of the larvae.

Head capsule (cranium). The head capsule is weakly sclerotized, narrowing ven-

trally, with a characteristic “beak”-shaped end, which is formed by the protruding palpi of the labrum. In light microscopy, the labrum adopts an active backward and



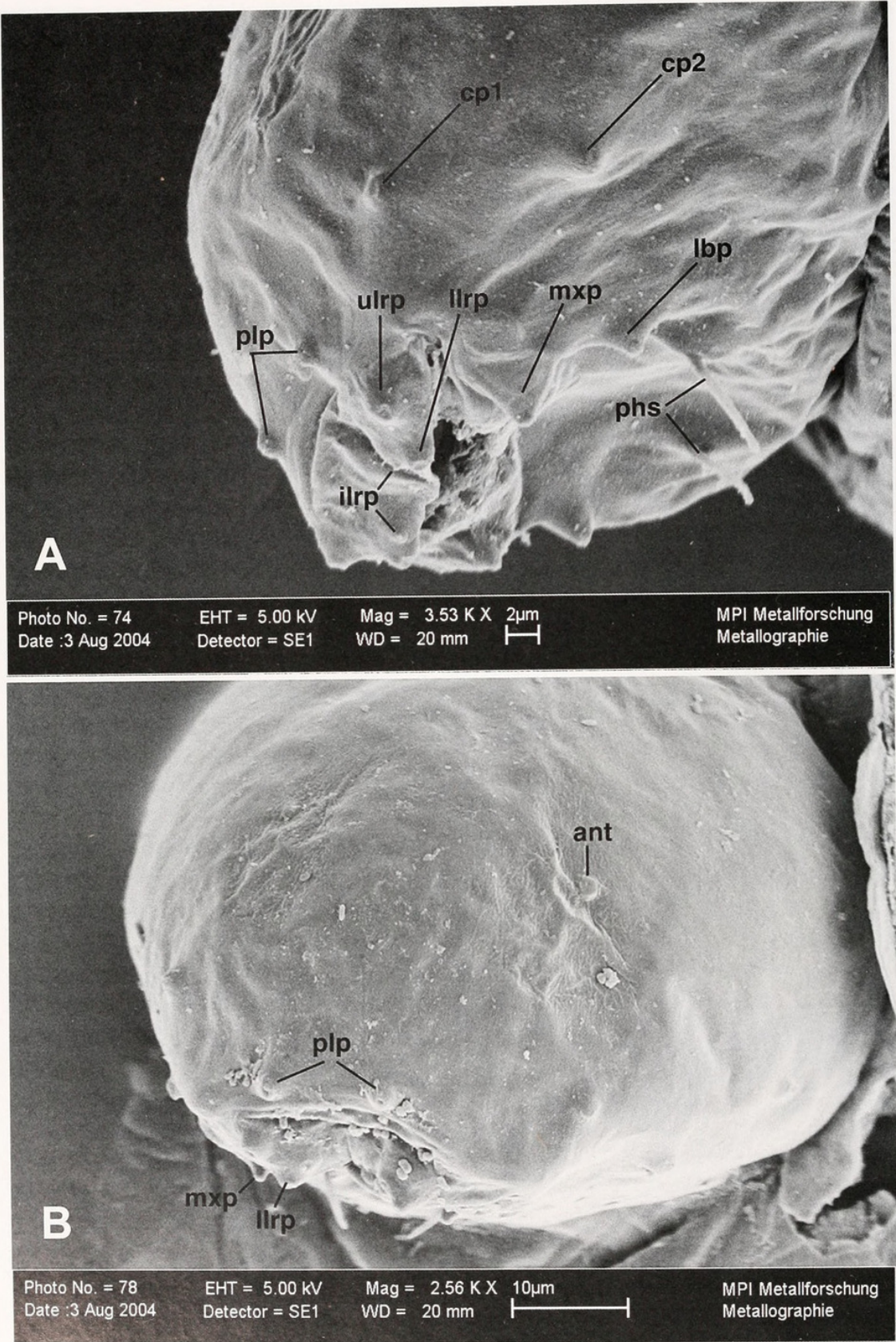


Fig. 7. *E. sylvestris*, first-instar larva, details of the head morphology (see text for abbreviations).

forward motion. Antennae are absent, indicated only as small swellings on the upper part of the head capsule. The sensorial structures of the head are well-

developed and arranged in a relatively fixed position (Figs 7, 8). The lateral area of the cranium bears three pairs of cranial palpi: the upper (cp1), the lower (cp2) and



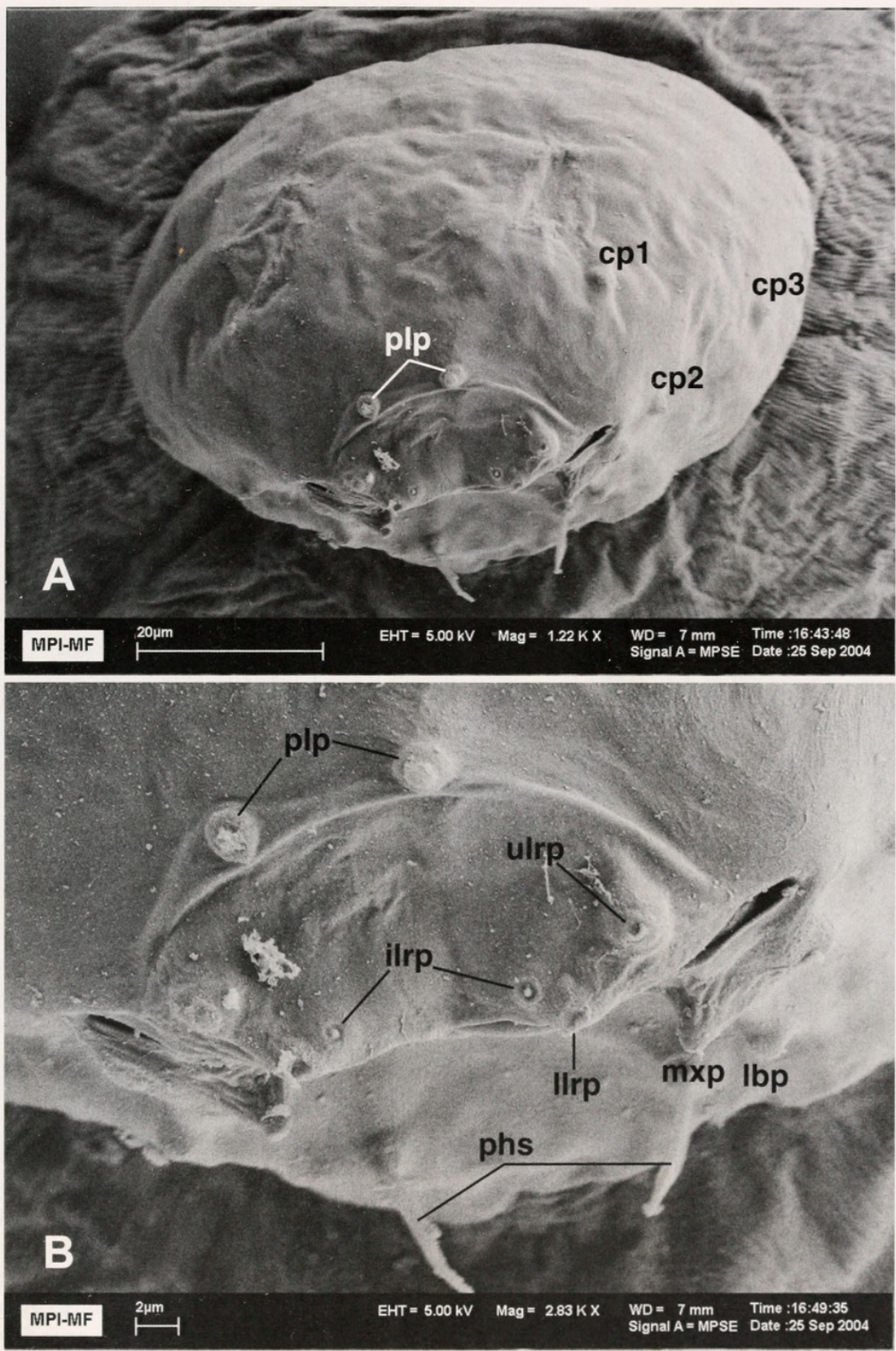


Fig. 8. *E. sylvestris*, first-instar larva, details of the head morphology (see text for abbreviations).

the posterior (cp3) palpi. There is a pair of enlarged pleurostomal palpi (plp) just above the labrum. The labrum bears 3 pairs of labral palpi (grouped by one from

each side): the upper lateral labral palpi (ulrp), the lower lateral labral palpi (llrp) and the inner labral palpi (ilrp). A large palpus is located near each maxilla (mxp)



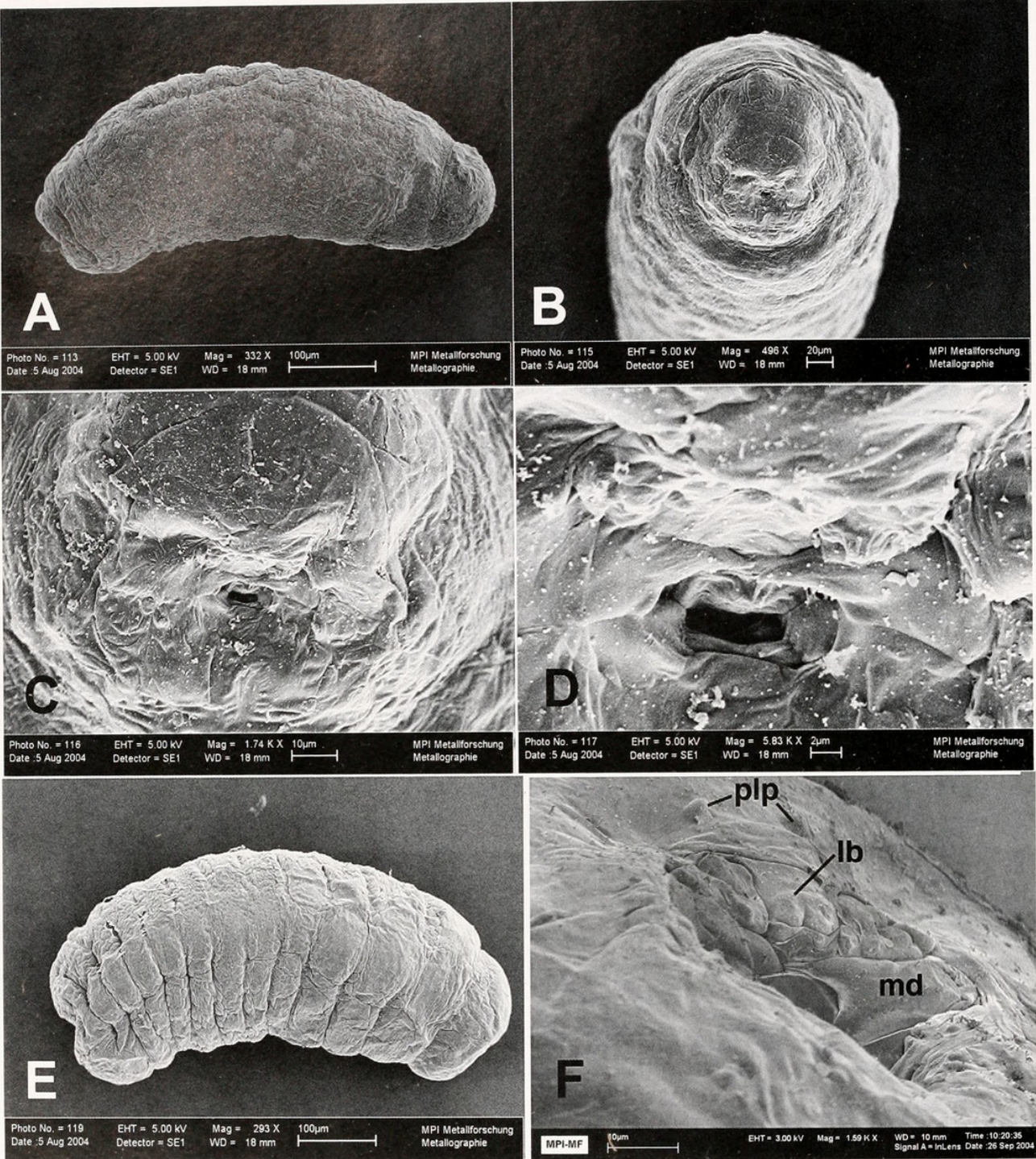


Fig. 9. *E. sylvestris*, second-instar larva, details of morphology: A, E, habitus; B, head in frontal view; C, head close-up; D, mouth area, close-up; F, mouth area, lateral view; plp, pleurostomal palpi; lb, labrum, md, mandible.

and behind them there is a pair of smaller labial palpi (lbp). A pair of comparatively long pharyngeal setae (phs) is situated behind the latter palpi.

*2nd instar larva.*—The second instar larva of *E. sylvestris* is also hymenopteriform and pale, with similar body segmentation (13 body segments and the head capsule), 500–

590  $\mu\text{m}$  long. However, the proportions and shape of the segments are different: the larva is more robust (Figs 9A, E) and none of the segments has serrations. The last segment bears no “caudal crown”. The head is more spherical and the sensorial structures of the head are less clear (Figs 9C, D). However, it is still possible



to discern the pleurostomal palpi, the delimited labrum and short mandibles (about 20  $\mu\text{m}$  long). No spiracles are recognizable.

*Final instar larva.*—Dissections of the dead host larvae revealed two forms of the parasitoid larvae, which differ from each other by their size and body shape. The smaller form fits the size range and morphological peculiarities of the second instar larva, described above. The larger form found within the body of the dead, buried host larvae, were 0.96–1.02 mm long (Fig. 10A), which is nearly twice as long as the second instar, but still nearly half of the average length of the pupa (1.8 mm). It has large (46  $\mu\text{m}$  long) and heavily sclerotized (dark brown in color) mandibles and discernible hypostome (Figs 10D, F). I regard these peculiarities to be specific to the final instar. The sensory structures of the head are hardly distinguishable, apart from large antennae situated on broad swellings (Figs 10B, C). Spiracles were difficult to distinguish because the skin of the larva was too shriveled. The large antennae are peculiar to the final instar larvae of Chalcidoidea (Parker 1924). Fisher (1970) also draws the large round areas (equivalent to the large antennae) on the upper part of the head of the final instar larva of *E. rumicis*, but does not mention them in the text. The possession of large antennae is one of the characters supporting the assumption that this is the final instar larva of *E. sylvestris*. The smaller body size of the larva is probably artificial and resulted from incomplete swelling of the dried, dead larvae.

*Pupa.*—Generally, pupation takes place in the host's earthen cell (Fig. 11F). Sometimes, pupae could be found directly in soil samples, which suggest that parasitoid pupation can also take place without the successful creation of an earthen cell by the host. In the laboratory, the host's earthen cells and the "free" pupae were found 2–3 centimeters from the upper soil level (the overall height of the soil level in tubes was

about 3 cm), and the host larvae can probably pupate even deeper.

The pupa is black, oblong, with distinct outlines of head, mesosoma, metasoma, wings, legs and antennae. The average length is 1.8–1.9 mm, the width of the head is about 0.6–0.7 mm, of mesosoma – 0.8 mm, of metasoma – 0.9 mm. The last larval skin, covered by soil particles, is often attached to the caudal end of the pupa.

*Parasitoid-host relations.*—Eggs of *E. sylvestris* were found singly in the host larvae. When the host larvae were dissected, the parasitoid eggs and first instar larvae were found free-floating anywhere in the host body cavity. No attempts to parasitize the host eggs were recorded. Parasitoid larvae hatch about one day after being laid. Females of *E. sylvestris* oviposited into weevil larvae of various instars, but only second instar larvae of the parasitoid were found within the mature host larvae. Only one parasitoid larva per host larva was found in all studied samples. Parasitoid larvae could sometimes be observed while inside the host.

The larvae of *E. sylvestris* never emerged from the host's body within the pods of *S. loeselli*. Behaviour and pupation of parasitized host weevil larvae did not differ from unparasitized.

## DISCUSSION

### Life history of *Entedon sylvestris*

Females of *Entedon sylvestris* attack their hosts, the weevils *Ceutorhynchus sisymbrii*, at their larval stage. The larvae of *C. sisymbrii* feed on the seeds of the small tumbleweed mustard, *Sisymbrium loeselii* L., and leave the host plant's pod when mature. Unlike most other parasitoids of seed-feeding weevils, which finish their ontogenesis and kill the hosts inside the host plant pods (e.g. *Trichomalus* spp., *Mesopolobus* spp., *Necremnus* spp.), the larva of *E. sylvestris* is in its second instar when the the host larva leaves the pod. The



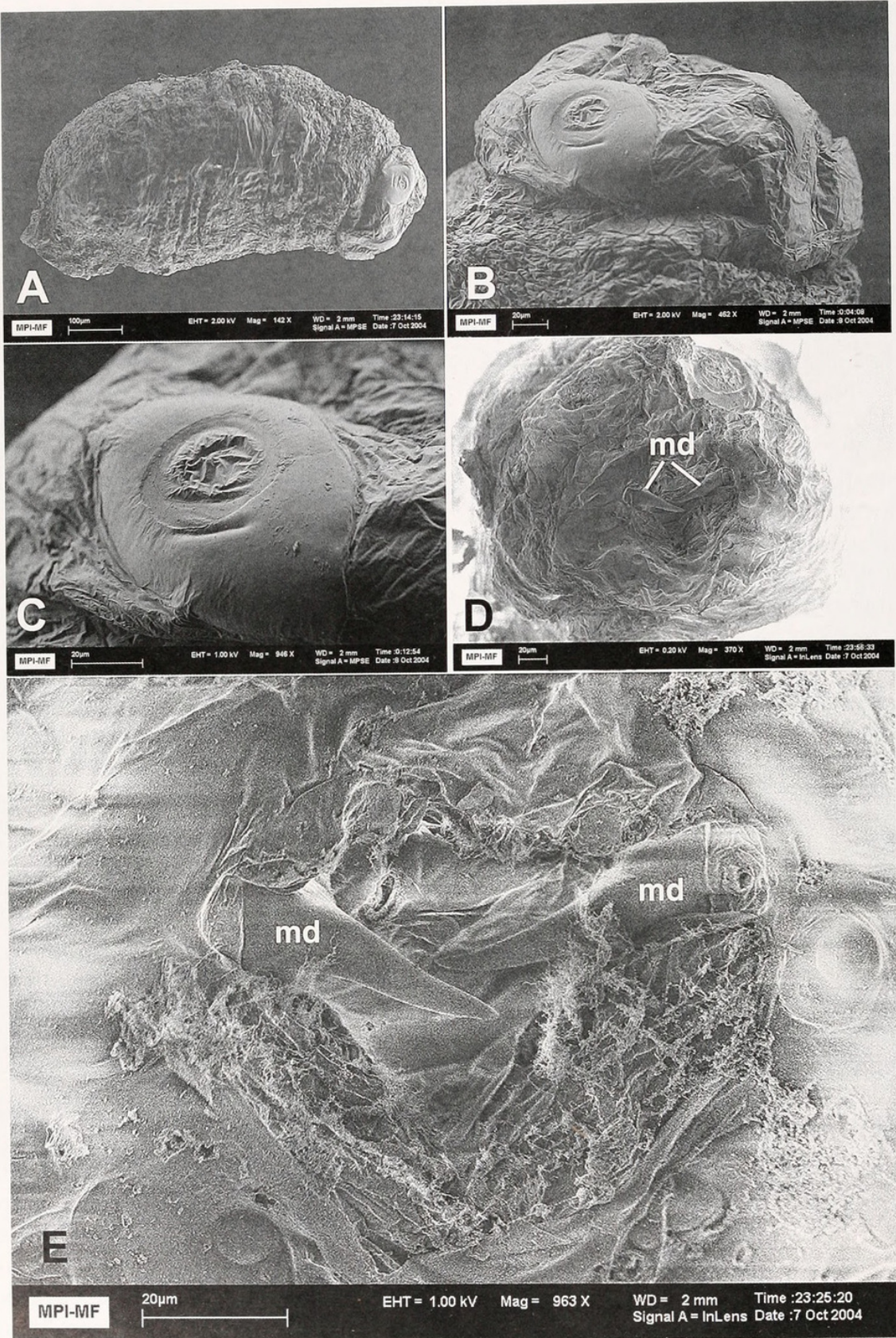


Fig. 10. A–E. *E. sylvestris*, final instar larva (isolated from the dead host larva): A, habitus, B, head, lateral view; C, antenna enlarged; D, head, frontal view; E, mandibles; ant, antenna; md, mandible.



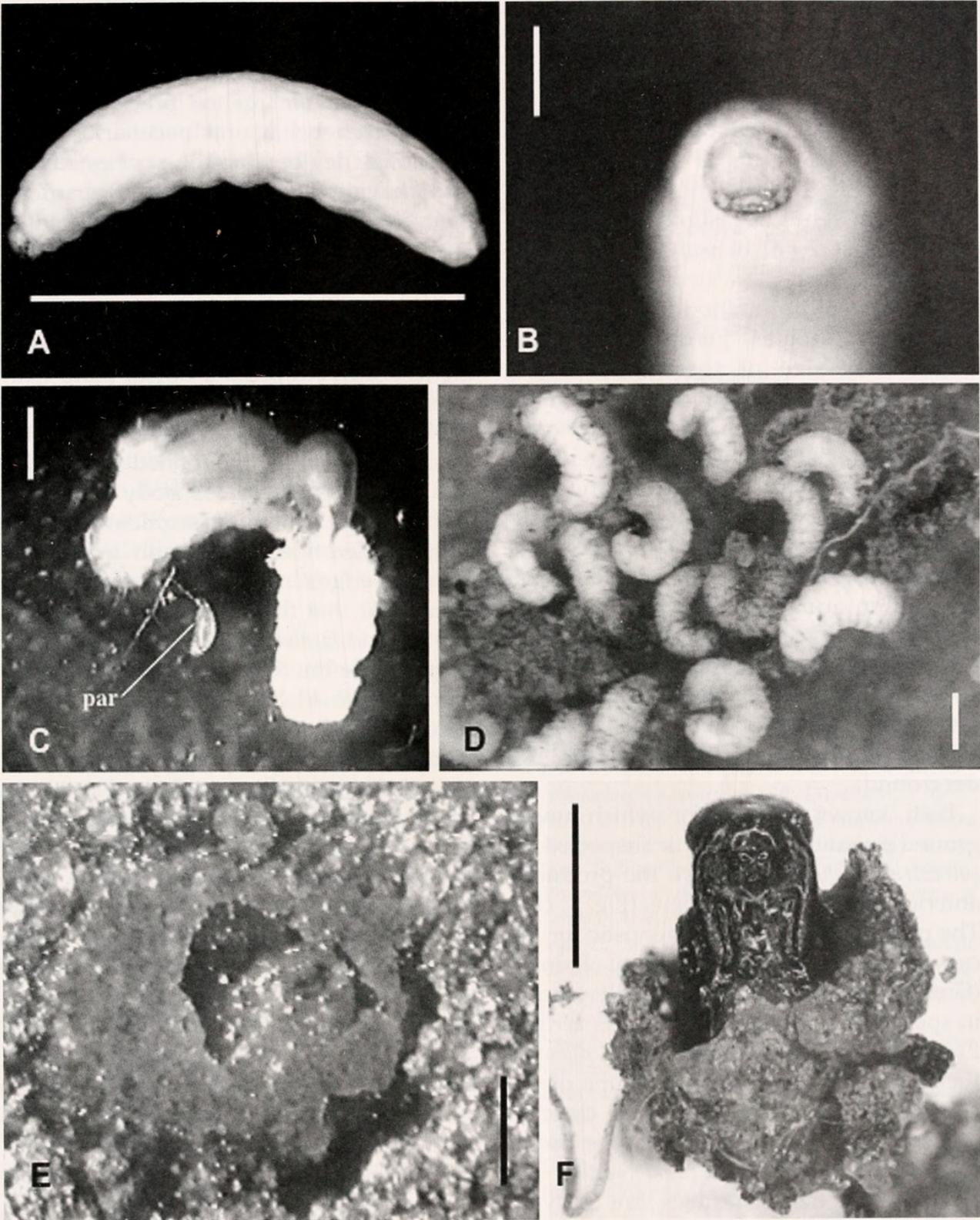


Fig. 11. A, B, the mature larva of *Ceutorhynchus sisymbrii*; C, first-instar larva of *E. sylvestris* isolated from the host's body; D, the dead weevil larvae isolated from the soil sample and treated by the lactic acid solution; E, the mature larva of *C. sisymbrii* creates an earthen cell (the larva is visible inside); F, the pupa of *E. sylvestris* in the host's earthen cell; par, parasitoid larva. Scale bars: A, 3 mm; B, 0.3 mm; C, 0.3 mm; D, E, F, 1 mm.



moult of the parasitoid larva into the final instar and final consumption of the host take place within the host's body, underground. Pupation takes place outside of the remnants of the host's body, also underground, at a depth of at least of 2–3 centimeters. The underground pupation means that adult parasitoids must penetrate at least 2 cm of soil to emerge the following spring.

Underground pupation is rather rare within Chalcidoidea, perhaps due to the small body size of these insects and corresponding problems with emergence from soil. Apart from *Entedon sylvestris*, the pupation and consequent emergence from the earthen cells of its host, is recorded for *E. cyanellus* Dalman, a parasitoid of *Tichius quinquepunctatus* (L.) (Gumovsky 1997). However, no detailed biological information is available for *E. cyanellus*, and records of its biology refer just to labels of museum specimens. So, *E. sylvestris* is the only chalcid species of known biology, which begins its ontogenesis above the ground and ends it underground.

Both known species for which underground pupation is known or suspected (*E. sylvestris*, *E. cyanellus*), have the produced anterior margin of the clypeus (Fig. 1, cly). The produced clypeus is diagnostic for the *cyanellus* and *costalis* groups of *Entedon* (Gumovsky 1997), and occasionally present in species of some other groups (*E. kerteszi* Erdős, *E. occidentalis* Girault, *E. diabolus* Rasplus). The function of the shape of the clypeus is unknown. The adult chalcids feed by sucking liquids through the use of their labio-maxillary complex. Neither the clypeus nor the mandibles are actively involved in this process. One of the possible functions of the produced clypeus may be associated with facilitating emergence from the ground. *Entedon rumicis*, *E. pharnus* and *E. philiscus* Walker also have the anterior margin of the clypeus produced, but their adults emerge from the host plant's stems, not soil (Fisher 1970).

The anterior margin of the clypeus is less produced in these species than in *E. sylvestris* and *E. cyanellus*. Further observations on the emergence procedure may reveal other behavioral peculiarities and functional devices for the species of *Entedon* having an "underground span" in their life cycles.

### Larval morphology

Beaver (1966) mentioned that the first-instar larva of *E. ergias* has 12 segments, but the last segment bears a dorsal plate with a series of sharp spines on its edge. Fisher (1970), when describing the first instar larva of *E. rumicis*, mentioned that it has the head capsule and 13 body segments, with "the last abdominal segment ventrally with a sclerotized plate with irregularly spinous edges". The same author also mentioned that the first-instar larvae of *E. pharnus* and *E. philiscus* have a similar body shape. Since the first-instar larvae of other species have 13 body segments, Beaver's statement of the possession of only 12 body segments by the first instar larva of *E. ergias* is likely erroneous.

The morphological peculiarities of the first-instar larva of *E. sylvestris* include the notable indentation on the XIII (last) body segment (Figs 6C, D, 8C, D). This indentation is likely equivalent to the plates with spinous edges reported for the first-instar larva of *E. ergias* (Beaver 1966) and *E. rumicis* (Fisher 1970), and also may be assumed for the larvae of *E. pharnus* and *E. philiscus* (mentioned as similar to the larva of *E. rumicis* by Fisher 1970). The tubercles of the indentation (the "caudal crown") is likely homologous to the small curved teeth of the dorsal semicircular serrations (Fig. 6C) along the anterior margins of the segments IV–XII. The function of the "caudal crown" for these larvae remains obscure, but there is no evidence of its usage for movement within the body cavity, since the parasitoid larvae observed within the host's body are generally passive.



The first-instar larva of *E. sylvestris* is, to some extent, similar to the larva of *Miscogaster* sp. described by Parker and Thomson (1925). Both larvae are apneustic, have the cuticular spines arranged in encircling lines (striations) on the body segments (IV–XII) and peculiar indentation of the last body segment (a semi-circular or bilobed “caudal crown”). However, the tubercles of the “caudal crown” are subequal in length in the larva of *E. sylvestris* (two inner spines are stouter than the surrounding spines of the “caudal crown” in *Miscogaster* sp.) and the sensorial structures of the head have a somewhat different arrangement.

Although data is available for only a few species, the “caudal crown” is likely inherent to all first instar larvae of *Entedon*. This character is quite remarkable and rare in Chalcidoidea (Parker and Thomson 1925), and thus may be used later to support monophyly of *Entedon*, if found in other species of the genus. Also, the combination of a nearly bare body and the “caudal crown” may facilitate separating the larvae of this genus from other endoparasitoid larvae. Furthermore, the proper affiliation of the first-instar larva of *E. sylvestris* to a peculiar larval type requires a revision of the current classification (Parker 1924) of these types in Chalcidoidea.

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