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Larvae of *Ataenius* (Coleoptera: Scarabaeidae: Aphodiinae): Generic characteristics and species descriptions

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Abstract. We compared the larval morphology of the genera *Ataenius* and *Aphodius*. The third larval instars of five *Ataenius* species: *Ataenius opatrinus* Harold, *A. picinus* Harold, *A. platensis* (Blanchard), *A. simulator* Harold and *A. strigicauda* Bates, are described or redescribed and illustrated. The most important morphological characteristics of the larvae of *Ataenius* are found in the respiratory plate of thoracic spiracle, the setation of venter of the last abdominal segment, the setation of the epicranial region and the morphology of the epipharynx. A key to larvae of the known species of *Ataenius* is included.

INTRODUCTION

The genus *Ataenius* Harold comprises 320 species, of which 228 species are found in America, 49 in Australia, 11 in Africa, 6 in East Asia, 2 in Madagascar, and single species in India, Sri Lanka, Turkestan, Japan, Hawaii and Sumatra, respectively (Dellacasa, 1987). Despite the richness of this genus and its worldwide distribution, the larval morphology of only 7 species is known at present (Jerath, 1960; Ritcher, 1966). The life histories of *Ataenius* species are not well known, but some records indicate that they are humus- and root-feeders in soil, with a few species attracted to decaying vegetation and animal dung (Wegner & Niemczyk, 1981; Ratcliffe, 1991). Some species have been captured in ant nests and animal burrows (Cartwright, 1974; Deloya, 1994). The trophic diversity, worldwide distribution, relative abundance [e.g., Cartwright (1974) collected about 275,000 specimens of *Ataenius simulator* Harold in a light trap in a single night] and the high level of fecundity (Cambefort & Hanski, 1991), could explain the potential of *Ataenius* species as a pest in areas recently transformed by man, such as the golf course fairways, greens and tees in the United States (Hoffman, 1935; Alm et al., 1992). It is very important to know both the larval stages of *Ataenius* and the biology of the species in order to pursue studies of the dynamics of their populations (Allsopp et al., 1995).

In this study we describe the third larval instars of five *Ataenius* species: *Ataenius opatrinus* Harold, *A. picinus* Harold, *A. platensis* (Blanchard), *A. simulator* Harold and *A. strigicauda* Bates. The larvae of the latter three species were described by Jerath (1960), but the lack of illustrations makes identification very difficult. In this paper, we give new descriptions and anatomical illustrations of the larvae studied. We also provide a key to the known larvae of *Ataenius*.

MATERIAL AND METHODS

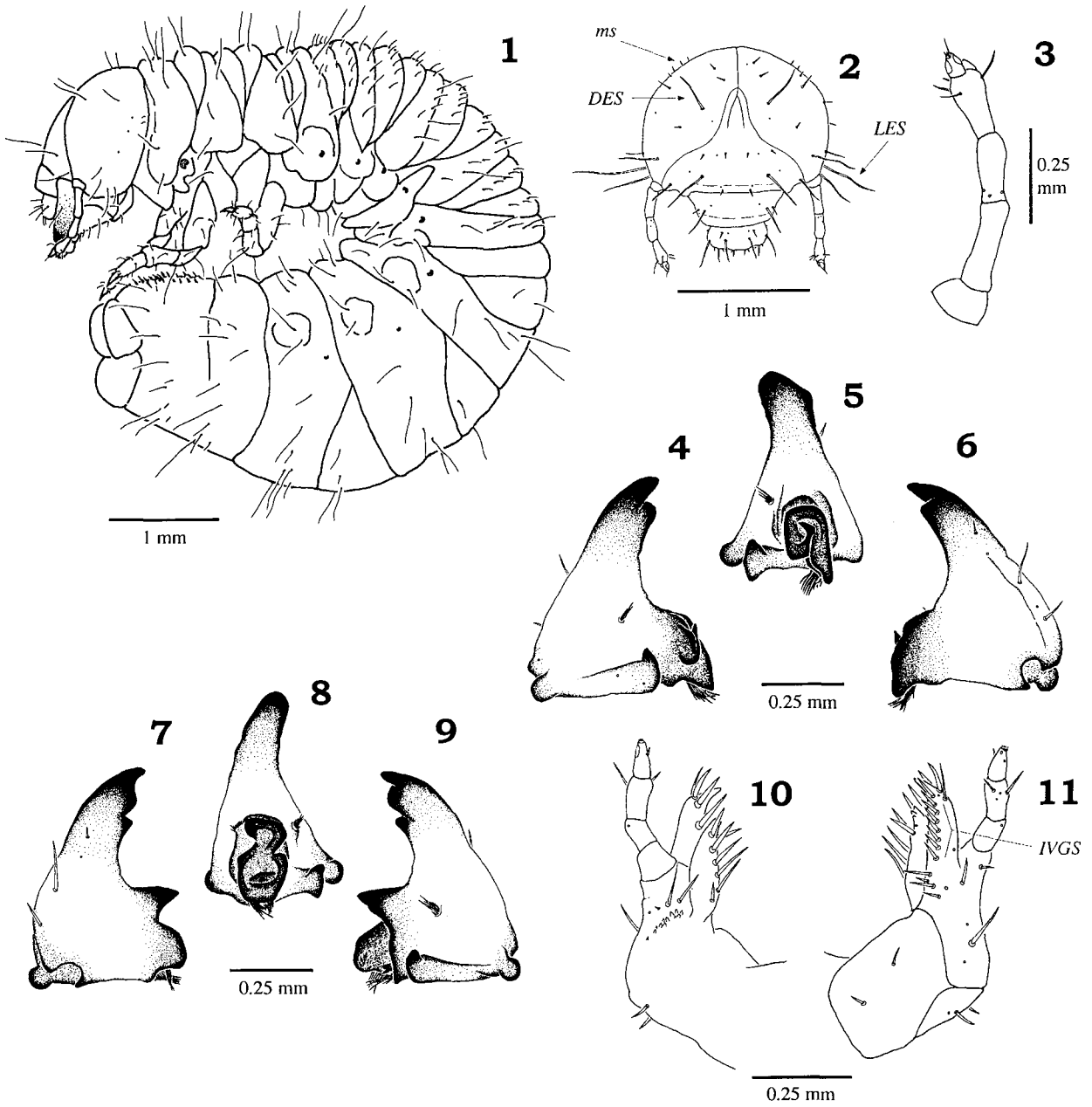
Breeding

Parental stock was collected in July, August and September 1995 from Castillos, Minas, San Miguel de Salinas, and Colonia del Sacramento (Uruguay). For the purpose of laboratory studies, a total of 10 to 20 adult specimens of each species were kept in cylindrical plastic breeding cages (20 cm high, 10 cm wide) with moist soil and dry cow dung from which they had been collected. The lid was an opening (6 cm diameter) covered with gauze screen. These breeding cages were maintained in an environmental chamber at 25 : 20°C (L : D), 80 ± 5% RH, with a photoperiod of 15 : 9 (L : D). The breeding cages were examined weekly and the results recorded. Throughout the study period, complementary data were obtained in the field. Voucher specimens are deposited in the Collection of Entomology of the Departamento de Ciencias Ambientales y Recursos Naturales, Universidad de Alicante, Spain (C.E.U.A.).

Laboratory studies

Larval specimens were fixed in KAAD solution (Carne, 1951) for 12 h and preserved in 70% ethanol. The head capsule was removed from the body and both parts were placed in warm potassium hydroxide for a few minutes. Finally, they were rinsed with distilled water and placed in glacial acetic acid for two minutes. Dissection took place under a binocular stereomicroscope (magnification up to 40 ×), separate parts were studied in temporary slides under a microscope using magnifications of 100 and 200 ×. Drawings were made using FSA 25 PE tube (Leica). The light micrographs of thoracic spiracles and tegilla of the last abdominal segment were recorded on Ektachrome 64T (Kodak) film with a photomicroscope Leitz DM-RB (Leica) using interference contrast.

Distinguishing characters that are readily seen using a binocular microscope (magnifications of 6 to 40 ×) and subject to the least variation were mostly selected for use in the diagnosis of species. Extremely minute characters were used only if necessary. Most diagnostic characteristics are found on the head and the mouthparts and on the ventral surface of the last abdominal segment (Ritcher, 1966; Edmonds & Halffter, 1972, 1978; Kim & Lumaret, 1988; Verdú & Galante, 1997). The morphology of larvae was described using anatomical terminology of Jerath (1960), Ritcher (1966), Kim & Lumaret (1988) and Verdú & Galante (1997). According to Ritcher (1966), when the distance between the two lobes of the respiratory plate of the thoracic spiracle ranges from 100 to 80% of the dorso-ventral diameter of the bulla, "equal to or slightly less than" has been used in describing the degree of constriction; "somewhat less than" is used when the distance is from less than 80 to 60%; "much less than"



Figs 1–11: *Ataenius opatrinus* Harold. 1 – third instar larva, left lateral view; 2 – head, frontal view; 3 – antenna; 4 – right mandible, ventral view; 5 – right mandible, molar view; 6 – right mandible, dorsal view; 7 – left mandible, dorsal view; 8 – left mandible, molar view; 9 – left mandible, ventral view; 10 – left maxilla, dorsal view; 11– left maxilla, ventral view. Abbreviations: DES – dorsoepicranial setae; IVGS – interior ventral galea setae; LES – lateral external epicranial setae; ms – microsetae.

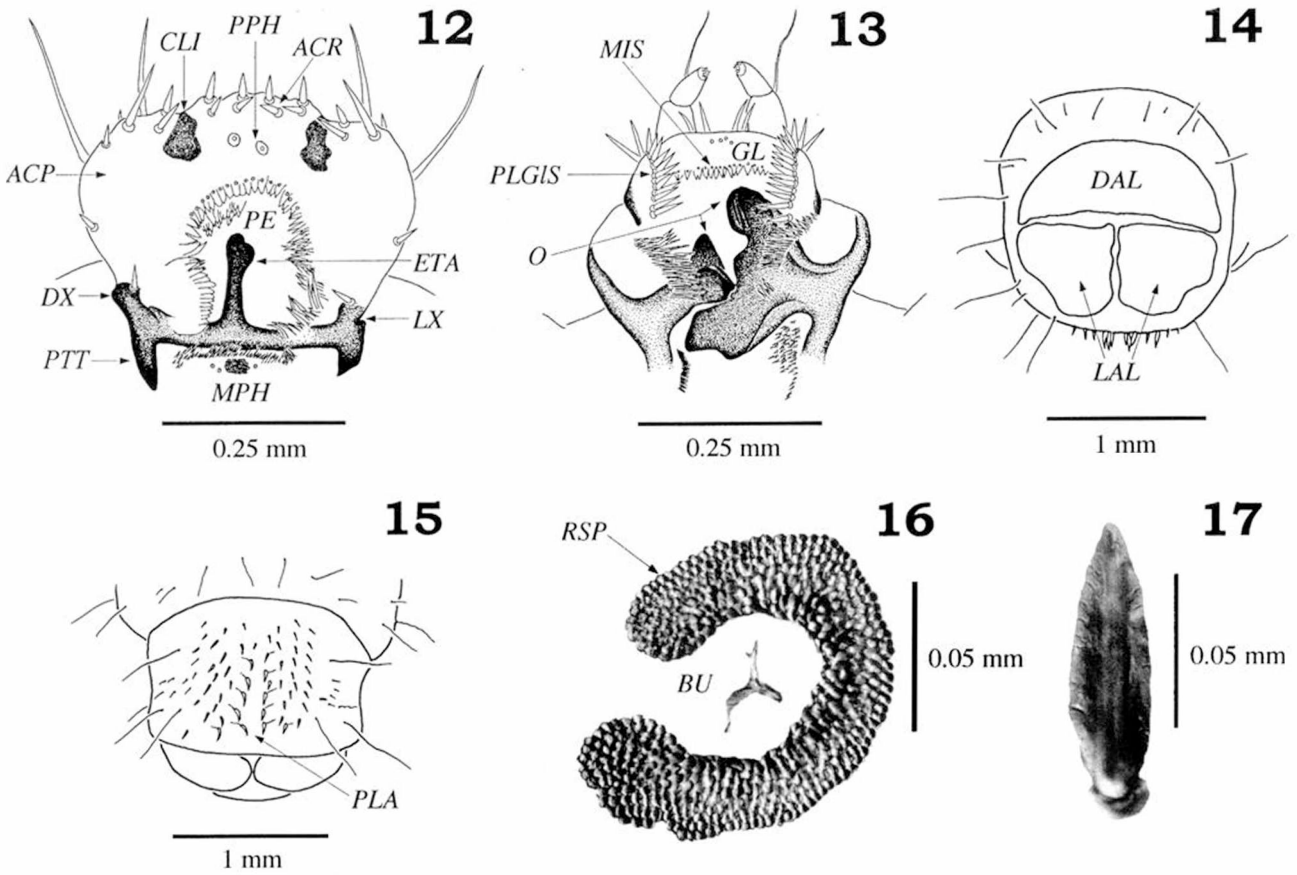
when it is from less than 60 to 20%; and "almost contiguous" when it is less than 20%.

RESULTS

Common morphological characteristics of *Ataenius* and *Aphodius* larvae

Body. Body arched (C-shaped) at the level of 4th or 5th abdominal segment (Fig. 1).

Head. Cranium transverse, bearing on each side: one long seta on anterior frontal angle, a similar one on the lateral frontal part, one seta on anterior frontal region; a posterior lateral seta on frontal region. Epicranial region: minimum of two dorsoepicranial setae, 5–9 lateral setae, 2–4 microsetae on posterior part. Coronal suture present, surpassing frontal suture. Clypeus transverse, on each side one short anterior seta and one lateral seta. Labrum trilobed; on each side: one internal seta and on posterior part one long lateral seta; lateral lobe of the labrum with one seta; middle lobe of labrum with two anterior setae and one posterior seta. Antennae 4-segmented. Third segment with one ring of 5 setae and one well-developed cone-shaped organ or one disc-like sensorial structure (Verdú & Galante, 1997). Fourth segment short, with an inner sensorial surface extended to dorsal and ventral parts; apical end with one ring of sensorial setae, one longer, whip-shaped. Mandibles: asymmetrical with two



Figs 12–17: *Ataenius opatrinus* Harold. 12 – epipharynx; 13 – hypopharynx; 14 – caudal view of last abdominal segment; 15 – raster; 16 – thoracic spiracle; 17 – palus. Abbreviations: ACP – acanthoparia; ACR – acroparia; BU – bulla; CLI – clithra; DAL – dorsal anal lobe; DX – dexiophoba; ETA – anterior epitorma; GL – glossa; LAL – lower anal lobe; LX – laeophoba; MIS – microsensillae; MPH – mesophoba; O – oncyli; PE – pedial area; PLA – palidium; PLGlS – posterior lateral glossae setae; PPH – protophoba; PTT – pternotormae; RSP – respiratory plate.

or three dorso-external setae and two microsensilla between setae. Maxilla: galea and lacinia separated. Galea with two dorsolateral setae and a variable number of internal setae; ventral portion with one longitudinal row of internal setae. Lacinia with trilobed uncus; a microseta at the base of each lobe; one row of setae situated dorsally, with short median seta on base; one basal seta on ventral portion; one basal seta on uncus. Stipes with a row of stridulatory teeth; one long lateral seta; two different sized fore setae and one small lateral microseta. Maxillary palpus 4-jointed; first joint (palpifer) with one ventral seta; third joint with two setae; fourth joint narrowed apically, with sensorial longitudinal area and distal ring of short microsetae. Epipharynx (Fig. 12) with anterior epitorma (ETA) situated in the central pedial area (PE), pternotormae (PTT) well-sclerotized. Mesophoba (MPH) with 3 pairs of macrosensilla covered by posterior expansions of tegument. Dexiophoba (DX) slightly more developed than laeophoba (LX). Protophoba (PPH) with expansions of integument and a transversal row of sensilla. Haptomerum with one pair of macrosensilla. Acroparia (ACR) with 4 short setae. Chaetoparia (CPA) with small setae on each side. Acanthoparia (ACP) with one short lateral seta. Clithra (CLI) well-developed. Hypopharynx (Fig. 13): asymmetrical oncyli (O) covered in part by tegumental expansion. Glossa (GL) with two pairs of macrosensilla and a transversal row of microsensilla on distal part of oncyli, proximal portion with a row of setae on each side; lateral lobe with 2 pairs of setae; central lobe with 4 setae and 4 macrosensilla.

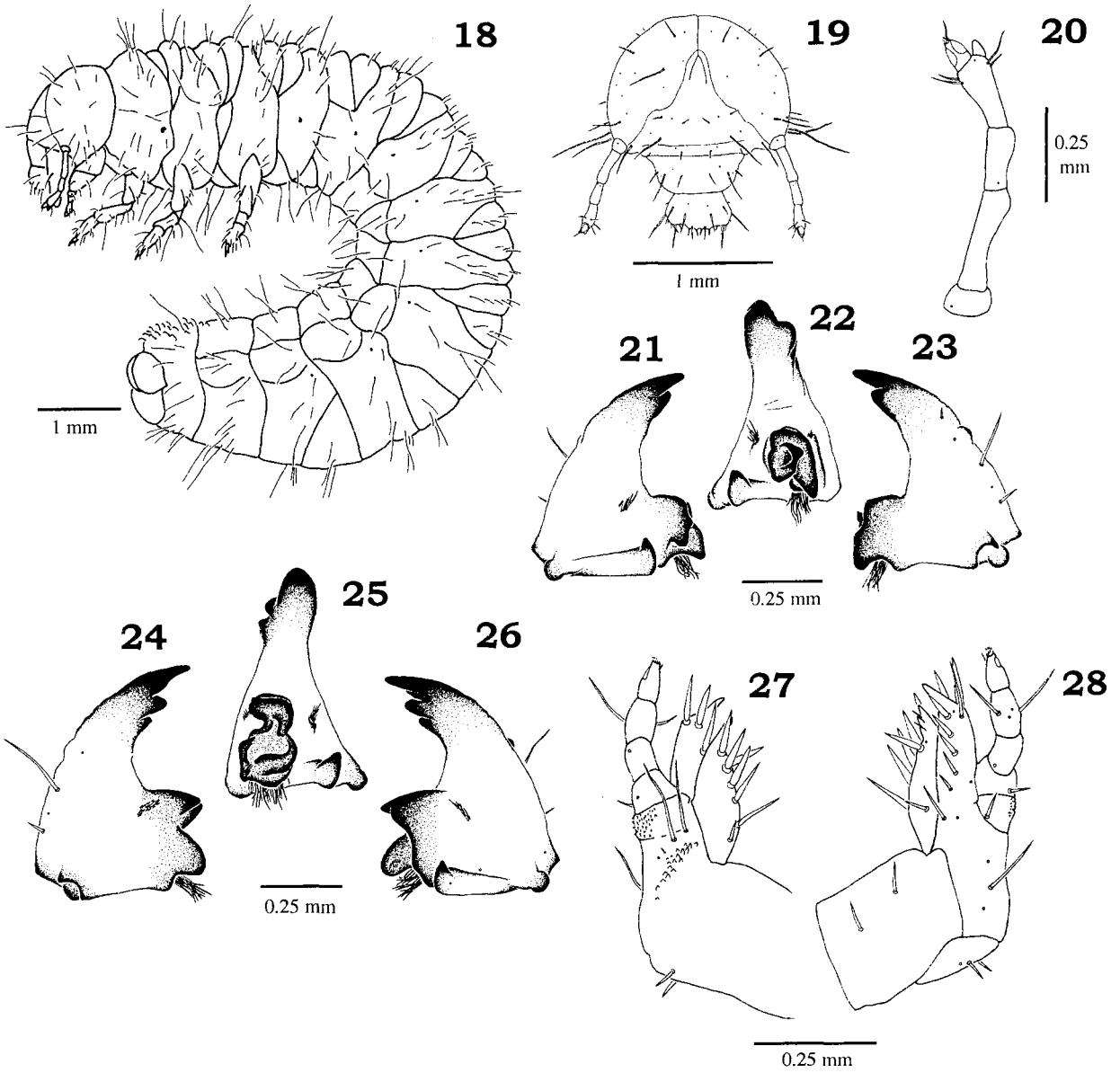
Thorax. Prothorax with a dorso-lateral plate lightly sclerotized, straw-coloured. Concavities of respiratory plates of thoracic spiracles facing posteriorly. Legs well-developed; distal portions of tarsal claws generally curved, with two ventral setae.

Abdomen. Concavities of respiratory plate of abdominal segments facing anteriorly. Raster with teges or with definite palidia.

Distinguishing morphological characteristics of *Ataenius* and *Aphodius* larvae

To the naked eye, *Aphodius* and *Ataenius* larvae appear nearly identical. Nevertheless, several characteristics differentiate the two genera.

Anal lobes. In *Aphodius* larvae, the lower anal lobe is emarginate or entire; *Ataenius* larvae show two lower anal lobes (LAL) (Fig. 14). The structure of the anal lobes allows the diagnosis of larvae in vivo using only a binocular stereo-microscope (magnification 20 to 40 ×). This characteristic has been previously used to identify closely related Aphodiinae species (Verdú et al., 1997).



Figs 18–28: *Ataenius picinus* Harold. 18 – third instar larva, left lateral view; 19 – head, frontal view; 20 – antenna; 21 – right mandible, ventral view; 22 – right mandible, molar view; 23 – right mandible, dorsal view; 24 – left mandible, dorsal view; 25 – left mandible, molar view; 26 – left mandible, ventral view; 27 – left maxilla, dorsal view; 28 – left maxilla, ventral view.

However, anal lobes are also good characteristics for the definition of higher taxa (Ritcher, 1966).

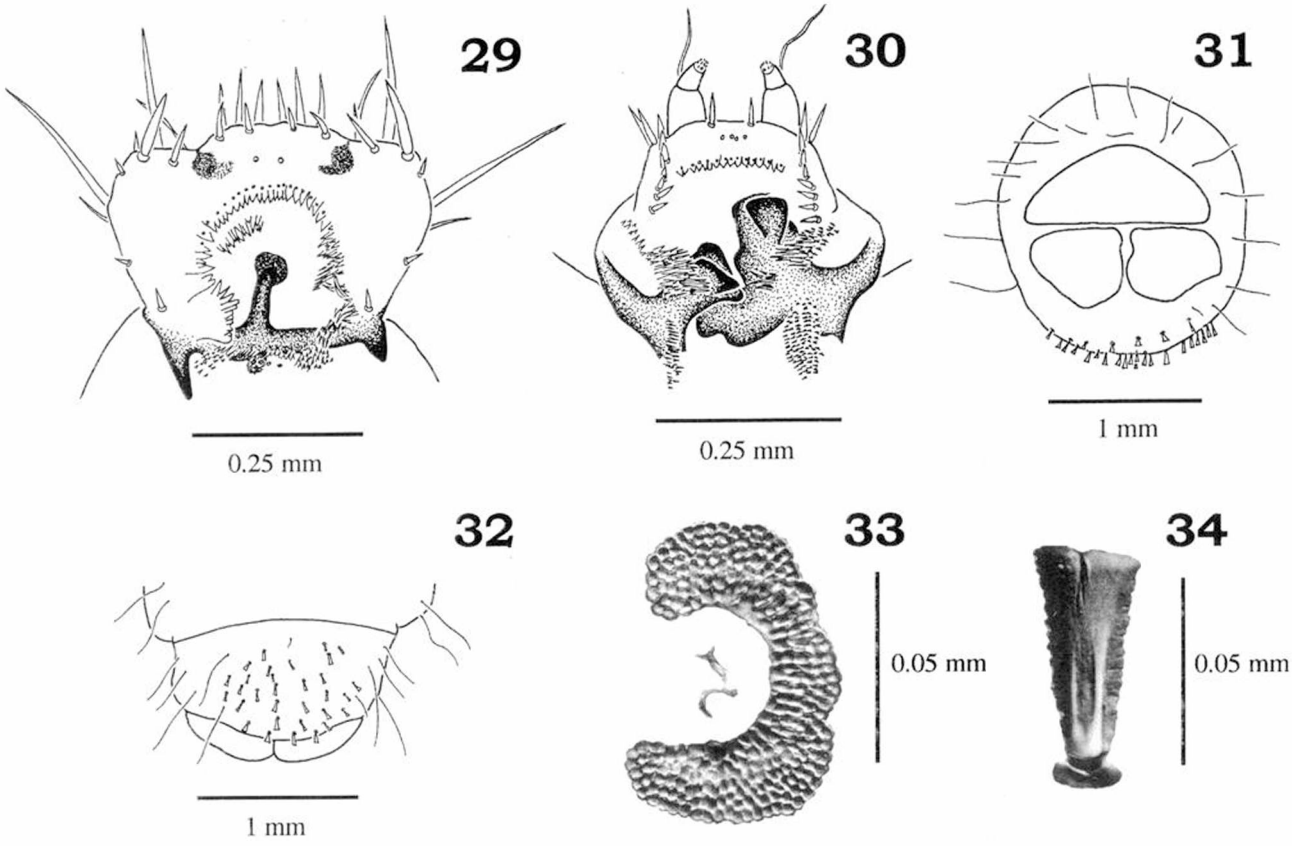
Thoracic spiracles. The relative size and the number of "holes" of the spiracular respiratory plates are good characteristics for identifying closely related species of the same subgenus (Verdú et al., 1997). Between the two genera, there are more differences related to the form of respiratory plates than the size or the number of holes on the plate. The respiratory plate in *Aphodius* is semicircular, not surrounding the spiracular slit completely; whereas, in *Ataenius*, the respiratory plate is longer and encircles the spiracular slit. In *Ataenius* species, there are usually fewer holes across the middle of the plate and more holes across the arms of the plate. In *Aphodius* species, there are more holes across the middle of the plate.

Chaetotaxy. Within the Scarabaeidae, the setation of the venter of the last abdominal segment and of the head has been used (Ritcher, 1966; Verdú et al., 1997). In *Aphodius* and *Ataenius* we have found one constant difference in setation. In *Aphodius*, the interior dorsal galea bears four setae while *Ataenius* has two setae (Fig. 10).

Ataenius opatrinus Harold, 1867

Medium size (Fig. 1). Length of body 9.0–9.7 mm; width of thorax 1.50–1.75 mm; maximum width of cranium 1.42 mm. The larva of *A. opatrinus* presents the aforementioned common characteristics and the following diagnostic characteristics.

Head. Epicranial region (Fig. 2) with 3–5 dorsoepicranial setae (DES), 4–7 (6) lateral setae (LES) and 4 microsetae (ms) on posterior part. Relation of lengths of the first, second and third segments of antenna is 1.4 : 1 : 1 (Fig. 3). Mandibles (Figs 4–9): Right mandible: S_1 and S_2 teeth fused; S_3 tooth isolated by one groove. Left mandi-



Figs 29–34: *Ataenius picinus* Harold. 29 – epipharynx; 30 – hypopharynx; 31 – caudal view of last abdominal segment; 32 – raster; 33 – thoracic spiracle; 34 – tegillum.

ble: S_1 and S_2 teeth separated by a very small incision; S_3 tooth separated by shallow groove. Stipes of maxillae with a row of 11–18 (13) stridulatory teeth (SD) (Fig. 10). Ventral portion of galea with one longitudinal row of 7–8 internal setae (IVGS) (Fig. 11). Epipharynx (Fig. 12): Protophoba (PPH) with expansions of integument and 16–19 (17) sensilla. Hypopharynx (Fig. 13): Glossa with 14–16 (16) microsensilla on distal part of oncyli (MIS), proximal portion with 11–15 (12) setae on each side (PLGlS).

Thorax. Diameter of the thoracic spiracle 0.10 mm; RSP (Fig. 16) with a maximum of 6–7 holes along any diameter. Distance of the two lobes of the respiratory plate much less than the dorsoventral diameter of the bulla.

Abdomen. Lower anal lobe divided into two separated sublobes (Fig. 14). Raster (Fig. 15) with palidia (PLA) nearly parallel, each palidium consisting of a rather sparsely set row of 5 to 10 plume-like setae (Fig. 17). Preseptular, hamate setae 36 to 47 in number (Fig. 15).

Material. 7 third instar larvae ex ovo, collected in Uruguay: Lavalleja, Minas-Cerro Arequita, 2.ix.1995, J.R. Verdú leg. Voucher specimens are deposited in the entomological collection of the Departamento de Ciencias Ambientales y Recursos Naturales, Universidad de Alicante (C.E.U.A.), Alicante, Spain.

Distribution. *Ataenius opatrinus* is known from Brazil, Argentina (Blackwelder, 1944) and Uruguay.

Bionomics. Laboratory and field observations showed that the oviposition period was in September and the immature instars occurred throughout the early spring. Larval development in laboratory lasted six weeks. Pupae were observed in October. *Ataenius opatrinus* was collected from dry cattle dung at a forest edge.

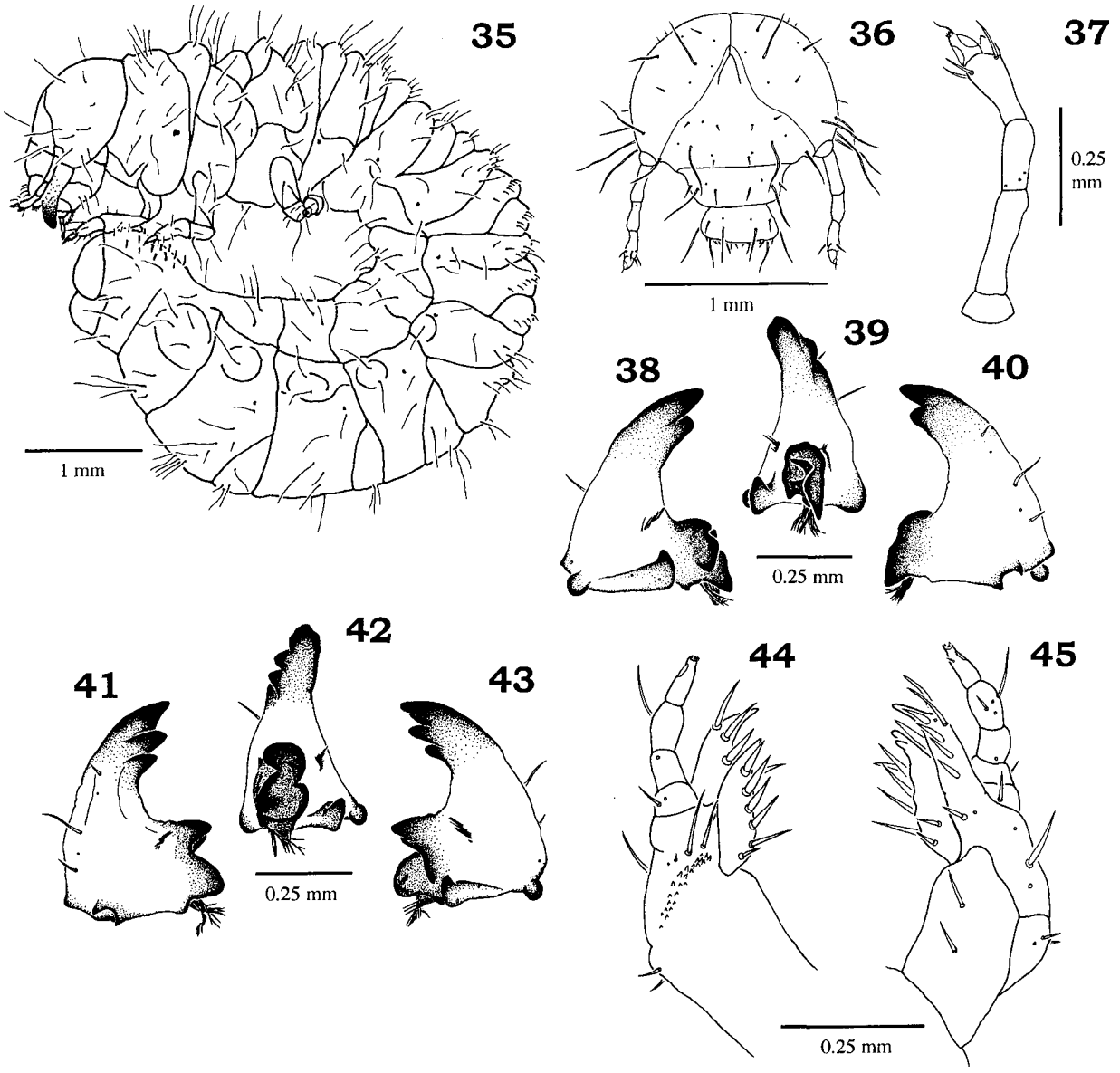
Ataenius picinus Harold, 1867

Small size (Fig. 18). Length of body 8.5–9.2 mm; width of thorax 1.5–1.7 mm; maximum width of cranium 1.30 mm.

Head. Epicranial region (Fig. 19) with 4 dorsoepicranial setae, 5–7 lateral setae and 2–3 microsetae on posterior part. Relation of the lengths of the first, second and third segments of antennae is 1.6 : 1 : 1.2 (Fig. 20). Mandibles (Figs 21–26): Right mandible: S_1 and S_2 teeth fused; S_3 tooth isolated by one groove. Left mandible: S_1 and S_2 teeth separated by small incision; S_3 tooth small and clearly separated by shallow groove. Stipes of maxillae (Fig. 27) with a row of 18–22 (19) stridulatory teeth. Ventral portion of galea with one longitudinal row of 5 internal setae (Fig. 28). Epipharynx (Fig. 29): Protophoba with 17–19 sensilla. Hypopharynx (Fig. 30): Glossa with 13–14 microsensilla on distal part of oncyli, proximal portion with 7–8 (8) setae on each side.

Thorax. Diameter of thoracic spiracle 0.08 mm; RSP (Fig. 33) with a maximum row of 7 holes. Distance between the two lobes of the respiratory plate slightly less than the dorsoventral diameter of the bulla.

Abdomen. Lower anal lobe (Fig. 31) divided into two separated sublobes. Venter of tenth abdominal segment



Figs 35–45: *Ataenius platensis* (Blanchard). 35 – third instar larva, left lateral view; 36 – head, frontal view; 37 – antenna; 38 – right mandible, ventral view; 39 – right mandible, molar view; 40 – right mandible, dorsal view; 41 – left mandible, dorsal view; 42 – left mandible, molar view; 43 – left mandible, ventral view; 44 – left maxilla, dorsal view; 45 – left maxilla, ventral view.

without palidia (Fig. 32). Teges consisting of a patch of 40–46 short spatulate setae (Fig. 34).

Material. 3 third instar larvae ex ovo, collected in Uruguay: Rocha, Castillos, 25.viii.1995, J.R. Verdú leg. Voucher specimens are deposited in the C.E.U.A.

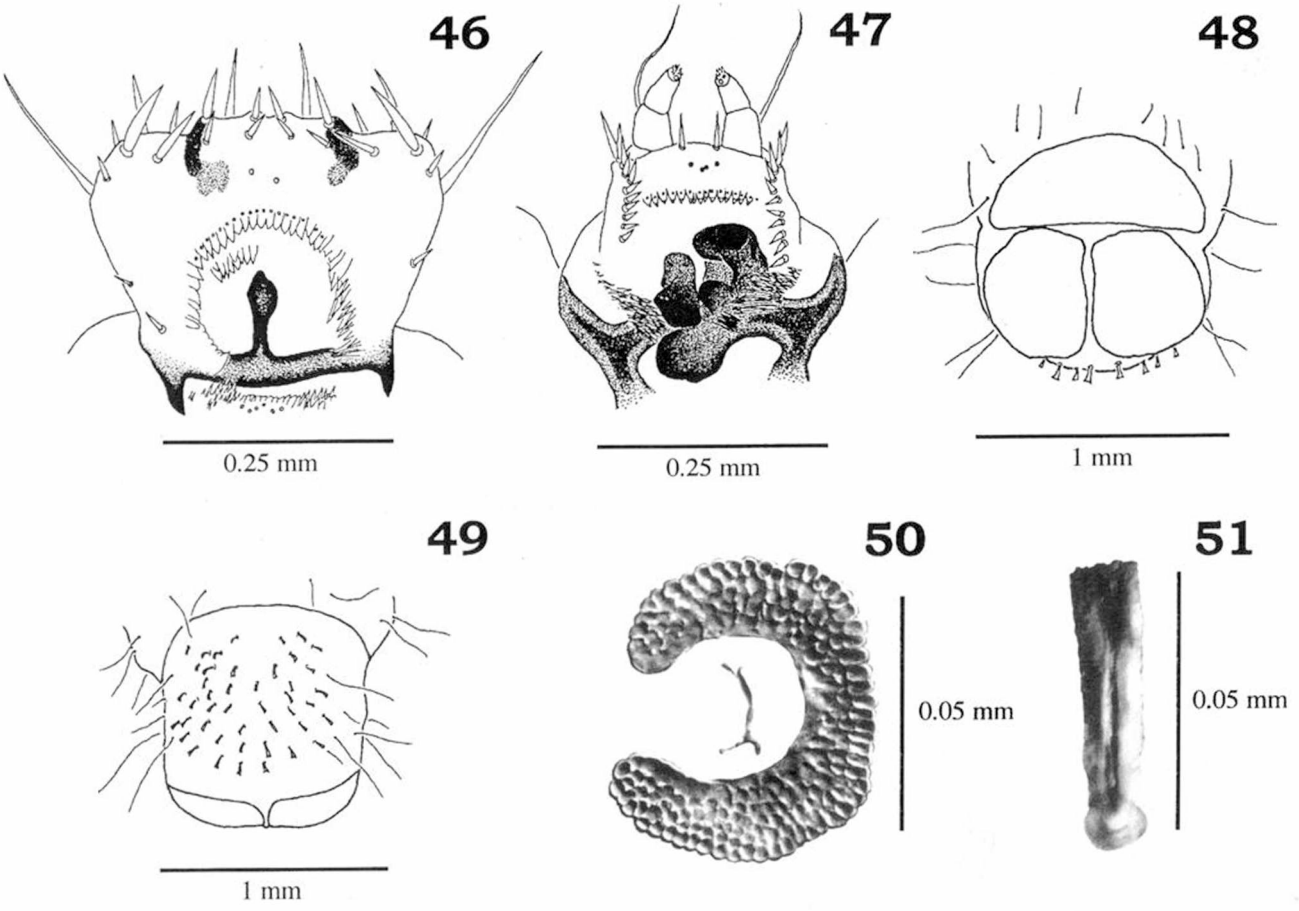
Distribution. *Ataenius picinus* is known from Argentina, Brazil, Uruguay (Blackwelder, 1944), the Antilles, New Zealand, Australia, Fiji Islands, New Caledonia (Chalumeau, 1983) and the USA (Cartwright, 1974).

Bionomics. Oviposition occurred during September and immature instars were found throughout early spring. Larval development lasted approximately 5–6 weeks. Pupae were observed in October. Adults were collected from dry cow dung, under carrion, associated with *A. platensis* and the trogid *Trox aeger* Guérin. This species is attracted to light, often in large numbers.

Ataenius platensis (Blanchard, 1846)

Small size (Fig. 35). Length of body 6.1–7.2 mm; width of thorax 1.0–1.3 mm; maximum width of cranium 1.15 mm.

Head. Epicranial region (Fig. 36) with 4 dorsoepicranial setae, 5–6 lateral setae and 2–3 microsetae on posterior part. Relation of the lengths of the first, second and third segments of antenna is 1.5 : 1 : 1 (Fig. 37). Mandibles (Figs 38–43): Right mandible: S_1 and S_2 teeth fused; S_3 tooth isolated by one groove. Left mandible: S_1 and S_2 teeth separated by small incision; S_3 tooth clearly separated by shallow groove. Stipes of maxillae with a row of 20–26 (23) stridulatory teeth (Fig. 44). Ventral portion of galea with one longitudinal row of 4–5 internal setae (Fig. 45). Epipharynx (Fig. 46): Protophoba with 18–19 sensilla. Hypopharynx (Fig. 47): Glossa with 12–15 micro-



Figs 46–51: *Ataenius platensis* (Blanchard). 46 – epipharynx; 47 – hypopharynx; 48 – caudal view of last abdominal segment; 49 – raster; 50 – thoracic spiracle; 51 – tegillum.

sensilla on distal part of oncyli, proximal portion with 7–10 (9) setae on each side.

Thorax. Diameter of thoracic spiracle 0.06 mm; RSP (Fig. 50) with a maximum row of 4–5 holes. Distance between the two lobes of the respiratory plate somewhat less than the dorsoventral diameter of the bulla.

Abdomen. Lower anal lobe (Fig. 48) divided into two large separated sublobes. Venter of the tenth abdominal segment without palidia (Fig. 49); teges consisting of a patch of 32–33 slender spatulate setae (Fig. 51).

Material. 5 third instar larvae ex ovo, collected in Uruguay: Colonia de Sacramento, La Estanzuela, 29.ix.1995, J.R. Verdú leg. Voucher specimens are deposited in C.E.U.A.

Distribution. *Ataenius platensis* is known from Brazil, Argentina, Uruguay (Blackwelder, 1944), Mexico, the Lesser Antilles (Deloya, 1994) and the USA (Cartwright, 1974).

Bionomics. Laboratory and field observations showed that the oviposition period was in September and immature instars occurred throughout early spring. Larval development in laboratory lasted six weeks. Pupae were observed in November. Adults were collected from dry or day-old cow dung in open pasture, under carrion, and attracted to lights. Deloya (1994) captured this species with a necro-trap.

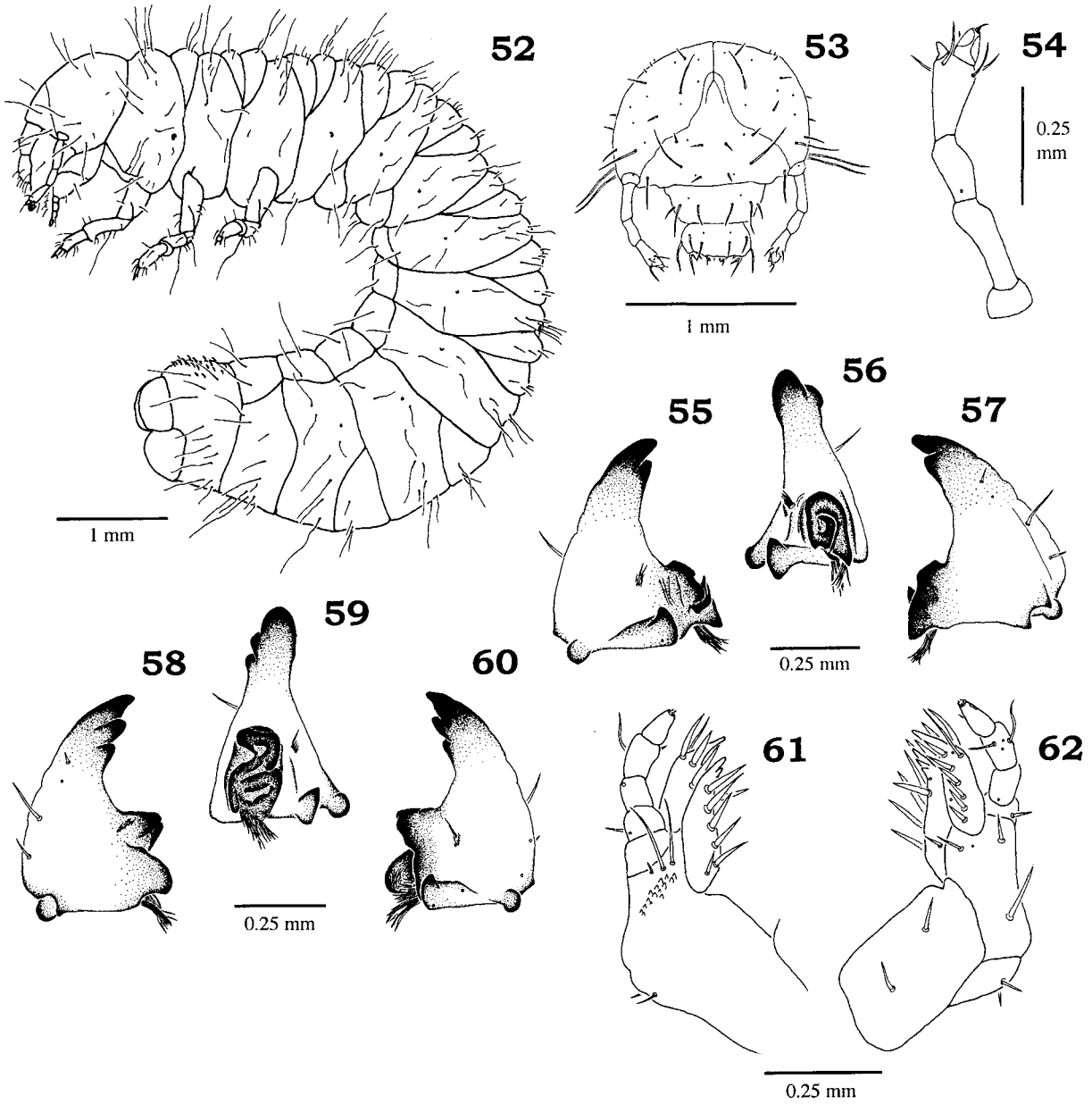
Ataenius simulator Harold, 1868

Small size (Fig. 52). Length of body 5.8–9.0 mm; width of thorax 1.1–1.5 mm; maximum width of cranium 1.16 mm.

Head. Epicranial region (Fig. 53) with 4 dorsoepicranial setae, 4–7 lateral setae and 2–3 microsetae on posterior part. Relation of the lengths of the first, second and third segments of antenna is 1.5 : 1 : 1.2 (Fig. 54). Mandibles (Figs 55–60): Right mandible: S_1 and S_2 teeth fused; S_3 tooth isolated by one groove. Left mandible: S_1 and S_2 teeth separated by small incision; S_3 tooth clearly separated by shallow groove. Stipes of maxillae with a row of 10–23 (16) stridulatory teeth (Fig. 61). Ventral portion of galea with one longitudinal row of 5–6 internal setae (Fig. 62). Epipharynx (Fig. 63): Protophoba with 16–17 sensilla. Hypopharynx (Fig. 64): Glossa with 14–16 microsensilla on distal part of oncyli, proximal portion with 8–9 (8) setae on each side.

Thorax. Diameter of thoracic spiracle 0.08 mm. RSP (Fig. 67) with a maximum row of 5–6 holes. Distance between the two lobes of the respiratory plate somewhat less than the dorsoventral diameter of the bulla.

Abdomen. Lower anal lobe (Fig. 65) divided into two big separated sublobes. Venter of tenth abdominal segment without palidia (Fig. 66). Teges consisting of a patch of 38–60 short spatulate setae (Fig. 68).



Figs 52–62: *Ataenius simulator* Harold. 52 – third instar larva, left lateral view; 53 – head, frontal view; 54 – antenna; 55 – right mandible, ventral view; 56 – right mandible, molar view; 57 – right mandible, dorsal view; 58 – left mandible, dorsal view; 59 – left mandible, molar view; 60 – left mandible, ventral view; 61 – left maxilla, dorsal view; 62 – left maxilla, ventral view.

Material. 4 third instar larvae ex ovo, collected in Uruguay: Rocha, Castillos, 25.viii.1995, J.R. Verdú leg. Voucher specimens are deposited in the C.E.U.A.

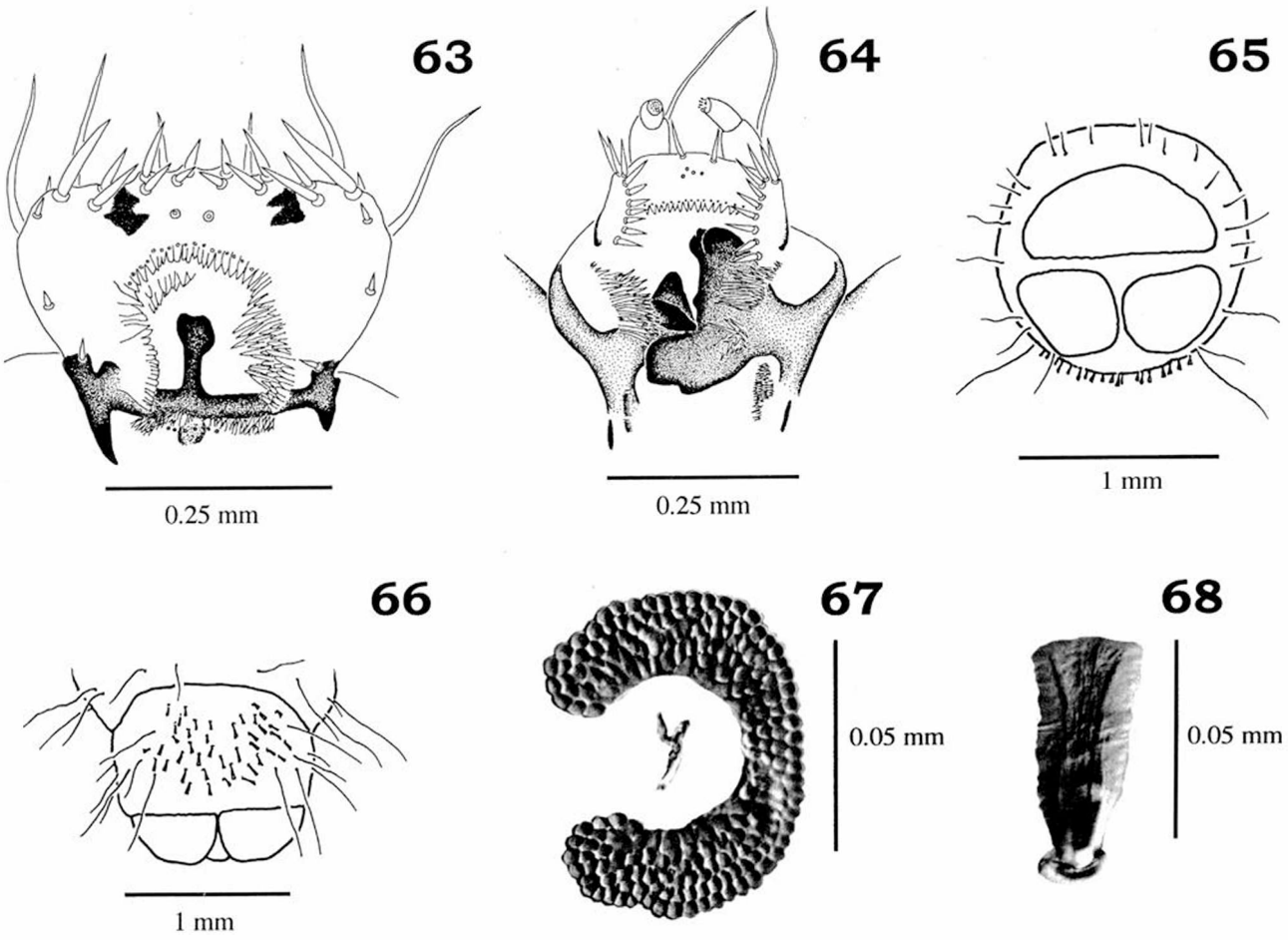
Distribution. *Ataenius simulator* occurs in Argentina (Blackwelder, 1944), Mexico (Deloya, 1994), the USA (Cartwright, 1974) and Uruguay, and has been introduced into Europe (Baraud, 1992).

Bionomics. Oviposition was in September; the immature instars occurred throughout the early spring. Larval development lasted approximately 7 weeks. Pupae were observed in October. Adults were collected from partly dry cow dung, but this species is rarely, if ever, a dung feeder; it is attracted to light, sometimes in enormous numbers (Cartwright, 1974).

Ataenius strigicauda Bates, 1887

Small size (Fig. 69). Length of body 7.0–8.7 mm; width of thorax 1.3–1.5 mm; maximum width of cranium 1.18 mm.

Head. Epicranial region (Fig. 70) with 5 dorsoepicranial setae, 5–8 lateral setae and 4 microsetae on posterior part. Relation of the lengths of the first, second and third segments of antenna is 1.6 : 1 : 1 (Fig. 71). Mandibles (Figs 72–77): Right mandible: S_1 and S_2 teeth fused; S_3 tooth isolated by one groove. Left mandible: S_1 and S_2 teeth separated by small incision; S_3 tooth clearly separated by shallow groove. Stipes of maxillae with a row of 19–28 (23) stridulatory teeth (Fig. 78). Ventral portion of galea with one longitudinal row of 4–5 internal setae (Fig. 79). Epipharynx (Fig. 80): Protophoba with 16–18 sen-



Figs 63–68: *Ataenius simulator* Harold. 63 – epipharynx; 64 – hypopharynx; 65 – caudal view of last abdominal segment; 66 – raster; 67 – thoracic spiracle; 68 – tegillum.

silla. Hypopharynx (Fig. 81): Glossa with 14–15 microsensilla on distal part of oncyli, proximal portion with 6–9 (8) setae on each side.

Thorax. Diameter of thoracic spiracle 0.06 mm. RSP (Fig. 84) with a maximum row of 6 holes. Distance between the two lobes of the respiratory plate slightly less than the dorsoventral diameter of the bulla.

Abdomen. Lower anal lobe (Fig. 82) divided into two large separated sublobes. Venter of tenth abdominal segment without palidia (Fig. 83); teges consisting of a patch of 34–45 fairly short spatulate setae (Fig. 85).

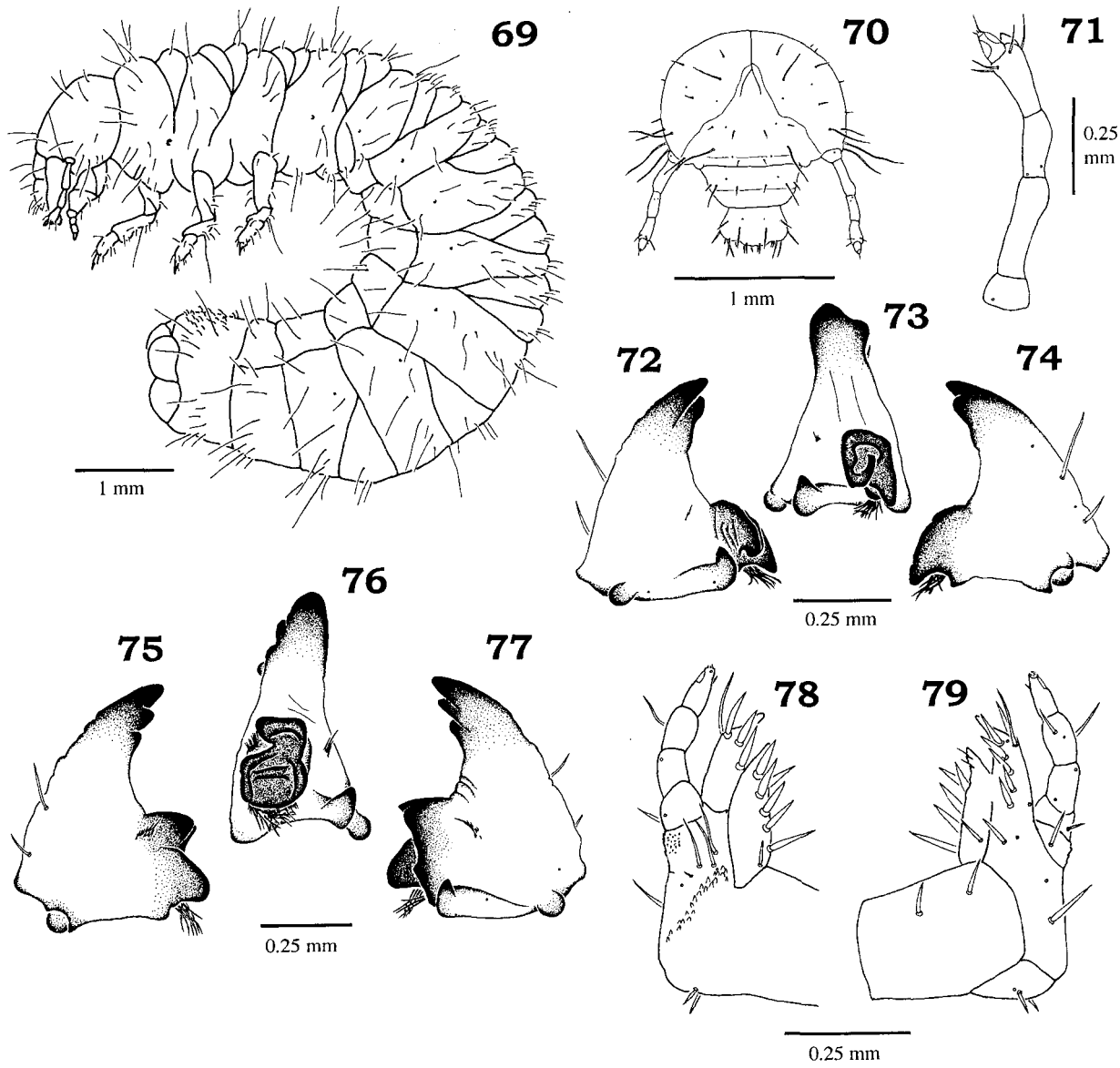
Material. 4 third instar larvae ex ovo, collected in Uruguay: Rocha, Los Ajos, 5.viii.1995, J.R. Verdú leg. Voucher specimens are deposited in the C.E.U.A.

Distribution. *Ataenius strigicauda* is known from Mexico, Guatemala, Honduras, Nicaragua, Panama, Trinidad, Brazil, Bolivia, Argentina, the Bahama Islands, Cuba, Jamaica, Hispaniola, Puerto Rico, St. Thomas (West Indies), St. Croix (Virgin Islands), Guadeloupe, Dominica, St. Lucia, Barbados, St. Vincent, Bequia (Grenadines), Grenada (Blackwelder, 1944), the USA (Jerath, 1960) and Uruguay.

Bionomics. The oviposition period was in September; the immature instars occurred throughout the early spring. Larval development lasted approximately four weeks. Pupae were observed in October. Adults were collected under decaying wood. This species was captured with a mosquito light trap (Deloya, 1994).

Key to known third-instar *Ataenius* larvae (after Jerath, 1960 and own results)

1 Raster with palidia ..... *A. opatrinus* Harold
— Raster without palidia 2
2 Epicranial region with 3 dorsoepicranial setae 3
— Epicranial region with more than 3 dorsoepicranial setae 6
3 Raster with teges of 28–35 setae; blunt stridulatory teeth on stipes 8–10 ..... *A. saxatilis* Cartwright
— Raster with teges of more than 34 setae; stipes with more than 10 stridulatory teeth 4
4 Maxillary stridulatory area with an irregular row of 13–19 conical teeth ..... *A. ovatulus* Horn
— Stridulatory teeth on stipes 20 or more 5
5 Raster with teges of 44–50 hamate setae. Width of head capsule 1.32–1.35 mm. Maxillary stridulatory area with an irregular row of 24–28 conical teeth ..... *A. erratus* Fall
— Raster with teges of 34–43 hamate setae. Width of head capsule 1.02–1.12 mm. Stridulatory teeth on stipes 21–24 .... *A. imbricatus* (Melsheimer)
6 Epicranial region with 4 dorsoepicranial setae 7
— Epicranial region with 5 dorsoepicranial setae 9
7 Distance between the two lobes of the respiratory plate slightly to much less than the dorsoventral diameter of the bulla. Respiratory plate with maximum row of 7 holes .... *A. picinus* Harold



Figs 69–79: *Ataenius strigicauda* Bates. 69 – third instar larva, left lateral view; 70 – head, frontal view; 71– antenna; 72 – right mandible, ventral view; 73 – right mandible, molar view; 74 – right mandible, dorsal view; 75 – left mandible, dorsal view; 76 – left mandible, molar view; 77 – left mandible, ventral view; 78 – left maxilla, dorsal view; 79 – left maxilla, ventral view.

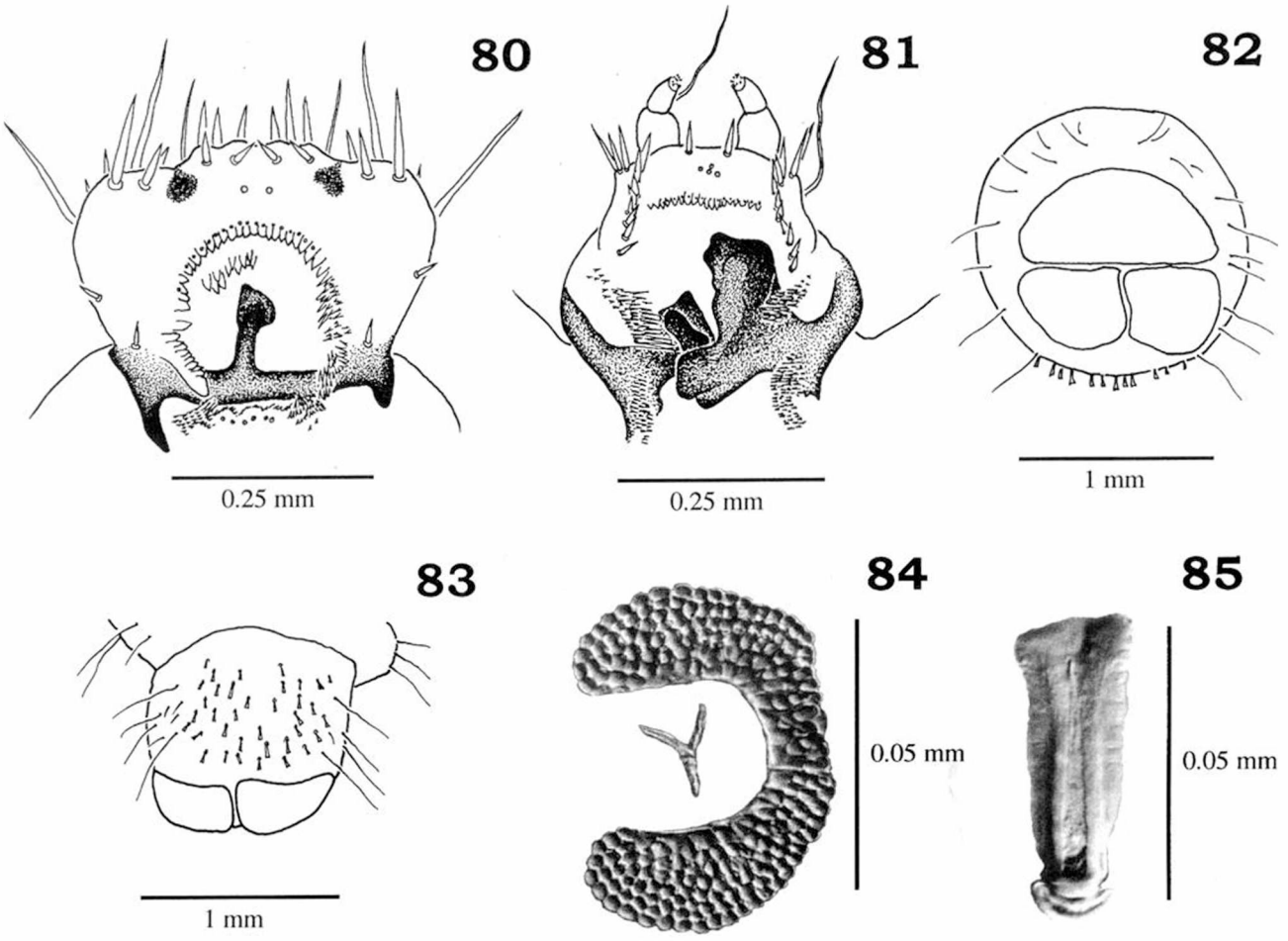
— Distance between the two lobes of the respiratory plate equal to or slightly less than the dorsoventral diameter of the bulla. Respiratory plate with maximum row of 4–6 holes . 8
8 Raster with teges of 32–33 setae; stipes with 20–26 blunt stridulatory teeth ..... *A. platensis* (Blanchard)
— Raster with teges of 38–60 setae; stipes with 10–23 blunt stridulatory teeth ..... *A. simulator* Harold
9 Stipes with 9–11 blunt stridulatory teeth .... *A. brevis* Fall
— Stipes with 19–28 stridulatory teeth .. *A. strigicauda* Bates

DISCUSSION

Morphological relationships

Keys are generally considered artificial and not intended to show phylogenetic relationships, but this is frequently apparent. Our results did not show phylogenetic relationships among the *Ataenius* species. Nevertheless, our data allowed us to reconsider the inclusion of *A. simulator* within the genus *Ataenius*. Some authors considered this species as belonging to the genus *Parataenius* Balthasar (Dellacasa, 1987), while others included it among *Ataenius* species (Cartwright, 1974; Deloya, 1994). Our results showed few differences between the larvae of *Ataenius* studied and *A. simulator*. Only *A. opatrinus* showed some peculiar traits, such as the presence of palidia and the shape of respiratory plate, but these characteristics often distinguish the larvae of closely related species (Ritcher, 1966; Verdú et al., 1997). According to our results, *A. simulator* and *A. opatrinus* should be classified in *Ataenius*.

The morphology of the studied *Ataenius* larvae is more homogeneous than is seen in the *Aphodius* larvae (Madle, 1935, 1936; Jerath, 1960; Ritcher, 1966; Walter, 1982; Kim & Lumaret, 1986; Verdú & Galante, 1995, 1997). This is probably a consequence of their feeding patterns. Many Aphodiini species, particularly the species of *Aphodius*, show coprophagous habits, which is a derived feed-



Figs 80–85: *Ataenius strigicauda* Bates. 80 – epipharynx; 81 – hypopharynx; 82 – caudal view of last abdominal segment; 83 – raster; 84 – thoracic spiracle; 85 – tegillum.

ing behaviour from the primitive saprophagous habits of the Aphodiinae (Halffter & Edmonds, 1982). However, the Eupariini, especially the species of *Ataenius*, are basically saprophagous (Cambefort, 1991), feeding efficiently on humus. Their larvae also occasionally eat roots (Wegner & Niemczyk, 1981; Cambefort, 1991; Ratcliffe, 1991). The evolution from saprophagy to coprophagy was the most important shift involving the species diversification of laparostict Scarabaeoidea (Cambefort, 1991; Scholtz & Chown, 1995). This evolutionary trend required ethological, physiological and morphological diversification with special modification of the mouthparts (Halffter & Matthews, 1966; Hata & Edmonds, 1983; Stebnicka, 1985), while the saprophagous species retained more primitive and undifferentiated mouthparts.

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