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DESCRIPTION OF THE IMMATURE STAGES OF SIX SPECIES OF *SPHAENOGNATHUS,* WITH COMPARATIVE NOTES ON PHYLOGENY AND NATURAL HISTORY (INSECTA: COLEOPTERA: LUCANIDAE)

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ABSTRACT

Third instar larvae of six Andean species of *Sphaenognathus* and pupae of *Sphaenognathus lindenii* are described and illustrated, with comparative notes on larvae of the related genus *Chiasognathus.* Keys are provided to larvae of genera of Chiasognathini and to species of *Sphaenognathus* for which larvae are known. A character considered diagnostic for Chiasognathini is to have all setae on the raster uniformly inclined laterally. The absence of a basal tooth on the mandible in *Sphaenognathus peruvianus* supports its placement in the subgenus *Chiasognathinus.* Derived larval characters are presented to support three monophyletic taxa: the tribe Chiasognathini, the genus *Sphaenognathus,* and a species-group containing *S. lindenii, S. oberon,* and *S. metallifer.*

INTRODUCTION

The family Lucanidae is of worldwide distribution and includes about a thousand described species (Benesh, 1960). According to Blackwelder (1944), there are 128 species in the Neotropical region. The larvae of several species of Lucanidae have been described. Significant publications on larvae of this group include Hayes (1929), Van Emden (1935, 1941, 1952), Medvedev (1952), Ritcher (1966) and Alderson (1975*a,* 1975*b*). In the Neotropical region, larvae of only four species have been described: *Sclerostomus ruficollis* Luederwaldt, *Pholidotus spixi* Nagel, *Pycnosiphorus femoralis* (Guérin), and *Chiasognathus granti* Stephens (Nagel, 1934; Cekalovic, 1982; Cekalovic and Castro, 1983; Costa et al., 1988). Most lucanid larvae live in decaying logs (Arnett, 1973; Borror et al., 1981), but the larvae of at least one species live in the soil (Milne, 1933).

The larvae described in the present work are in the tribe Chiasognathini, represented by *Chiasognathus* and *Sphaenognathus.* At present, according to Benesh (1990) and incorporating the synonymies made by Lacroix (1969), *Chiasognathus* includes four species, all from Chile. *Sphaenognathus* includes about 40 Neotropical species (Bartolozzi et al., 1992) and an additional species from Australia described by Moore (1978), thus implying a Gondwanian distribution for the tribe with ancient connections across Antarctica.

The only species of the tribe for which the larva has been described is *Chiasognathus granti* Stephens (Cekalovic and Castro, 1983). Notes on adults of *Chiasognathus* were published by Montalegre (1925), Ureta (1934), and Mathis (1981); information on the adults of *Sphaenognathus* was provided by Howden and Campbell (1974), Perrault (1991), Bartolozzi et al. (1992), and Bartolozzi and Onore (1993). The phylogeny of Lucanidae based on adults was discussed by

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Holloway (1960, 1968, 1969), Lacroix (1969), and Howden and Lawrence (1974). Phylogenetic hypotheses based on larvae were discussed by Van Emden (1952) and Lawrence (1981).

MATERIALS AND METHODS

To collect larvae, soil was sampled in areas where adults had been found. The soil was dug to a depth of 20 cm, and larvae, pupae, and associated adults were collected. Intact larvae were fixed by boiling gently in water for 3–5 min, and then preserved in 80% ethanol. The pupae were maintained alive in moist boxes until they became adults that were then killed and mounted for identification.

To study the larvae, the mandibles were removed using two strong needles, and then successively the labium and maxillae were removed using scissors. Larval structures submerged in 80% ethanol were examined at 50× with a stereomicroscope. The determination of sex in larvae was made by the presence (male) or absence (female) of Herold's organs as described by Menees (1957). The shape of the last two antennomeres and number and position of teeth of the stridulatory organs of the mesothoracic and metathoracic legs were used as characters to identify the larvae to genus. To distinguish species the following characters were used: number of teeth on the left mandible, shape of epipharyngeal pterotormae, shape of the prothoracic lateral sclerome, number of teeth on plectrum and pars stridens, shape of the thoracic spiracle and setation of lateral anal lobes and raster. The terminology used follows that of Edwards (1930), Böving (1936), Ritcher (1966) and Britton (1970).

I borrowed material from the following institutions or persons: CMNH, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; CV, Carlota Vergara Collection, Santiago, Chile; FSCA, Florida State Collection of Arthropods, Gainesville, Florida, USA; IZAV, Instituto de Zoologia Agricola, Universidad Central de Venezuela, Maracay, Venezuela; OSUO, Department of Entomology Collection, Oregon State University, Corvallis, Oregon, USA; QCAZ, Museo del Departamento de Biologia de la Pontificia Universidad Católica del Ecuador, Quito, Ecuador; WSUC, James Entomological Collection, Washington State University, Pullman, Washington, USA.

NATURAL HISTORY

In 1986, L. Coloma found a great number of adults of *Sphaenognathus oberon* in Casha Totoras, Bolivar Province, Ecuador. With the intention of finding larvae of this stag beetle in the vicinity, I searched carefully in rotten logs and old stumps. No larvae were found in rotting wood, so I extended the search to the soil where digging and sifting soon revealed several larvae of *S. oberon.* Investigating the same habitat at other localities, I found the larvae of *S. lindenii, S. metallifer, S. nobilis, S. peruvianus* (Fig. 1), and *S. subtilis.*

I never found eggs in the natural habitat, so in March, 1988, I dissected a dozen freshly killed females. These contained immature eggs in various stages of development. The number of eggs varied from 12–96. First instar larvae were found in groups up to a maximum of 54 individuals. They were in the first 3–10 cm of topsoil which was rich in humus and roots. Very often a dead female was found buried in the soil close to the group of larvae. Species of plants typically found growing in the topsoil near larvae were: *Salpichroa* sp. (Solanaceae), *Gynoxys buxifolia* (Asteraceae), *Orthrosanthus chimboracensis* (Iridaceae), *Equisetum bogotense* (Equisetaceae), *Barnadesia spinosa* (Asteraceae), *Hypericum laricifolium* (Hypericaceae), *Lachemilla orbiculata* (Rosaceae), *Ribes andicola* (Saxifragaceae), *Hesperomeles pernettifolia* (Rosaceae), *Chusquea* sp. (Poaceae), and *Elaphoglossum* sp. (Lomariopsidaceae).

Second instar larvae were less frequently encountered in the soil than third instar larvae. Third instar larvae were distributed uniformly, roughly equidistant from one another. They were buried 10–20 cm deep, and there was a maximum of 36 specimens per square meter. In some areas larvae were numerous, while in other, apparently identical, sites no larvae were found. In uniform habitat, the females may be arbitrary when choosing oviposition sites. Perhaps they settle

when they encounter some obstruction to flight, such as small bushes, and then lay their eggs.

Soil and fragments of roots were found in dissections of the gut, thus indicating that larvae may eat decomposing organic materials mixed with soil and small roots. When dug from the soil, larvae rolled into the characteristic C-shape of scarabaeiform larvae and remained inactive. Specimens unearthed at dusk and left on the surface were found in the same place the following morning. As the sun came up, they desiccated and died. Unearthed larvae of *S. lindenii* have the terga of abdominal segments 3–5 covered with moist soil, suggesting some special property of the cuticle or some secretion in those specific areas. I observed the same phenomenon in recently uncovered larvae of *Sphaenognathus oberon* and *S. metallifer.*

When disturbed, the larvae of *S. lindenii* produced vibrations using a stridulatory apparatus. Simultaneously and rhythmically, the metathoracic trochanter was rubbed against the mesothoracic coxa. No sound audible to human ears was produced, but vibrations could be felt when the stridulating larvae was held in hand. The stridulation may be used by larvae for protecting or marking the territory where they feed, as suggested by the evenly spaced distribution of larvae in the soil. Mature third instar larvae were 10–20 cm deep in suboval cavities with internal dimensions about 35 by 70 mm. Sometimes these cavities contained numerous white Collembola. I found dead larvae in the soil, covered by a white fungus. Others were full of brown liquid and very soft. One contained a dipteran puparium. Close to farms, domestic pigs actively dig the soil searching for the white grubs, which they eat voraciously. Dogs also follow farmers when they are preparing or plowing the soil, eating the larvae, pupae, and adults as they are turned up.

Pupae were in cavities as described above, each with its larval exuvium retracted to the caudal end. The pupae (Fig. 50–52) reposed on their dorsal surfaces and rotated their abdomens when disturbed. Pupae were found in the soil from November to February and adults from December to March. First, second, and third instar larvae, however, were found throughout the year, suggesting a life cycle of more than a single year.

In my opinion the subterranean habit of the larvae may be an adaptation that protects them from the rapid temperature changes in the upper layers of the soil that occur at the high elevations where they live.

KEYS AND DIAGNOSES

Chiasognathini Felsche, 1889

Diagnosis.—All setae on the raster inclined laterally, never medially or erect (Fig. 44–49).

Key to Larvae of Genera of Chiasognathini

1. Antenna with subapical segment swollen distally with an acute projecting lobe, medial to which is a suboval sensory spot facing medially (Fig. 7); apical segment pyriform. Mesocoxa with pars stridens consisting of a single row of teeth expanded proximally into a field of teeth as wide as several teeth, each tooth subequal in size to those in the main row (Fig. 35). Metatrochanter with plectrum consisting of row of fewer than 48 teeth (Fig. 40) ..... *Chiasognathus*

1′. Antenna with subapical segment distally rounded with sensory spot facing laterally (Fig. 6); apical segment subconical. Mesocoxa with pars stridens consisting of a single row of teeth, proximally with at most a patch of very small sparse granules (Fig. 36–39). Plectrum of metatrochanter consisting of row of more than 48 teeth (Fig. 41–43) ..... *Sphaenognathus*

Genus *Chiasognathus* Stephens, 1831

I have seen larvae and associated adults of the following species: *Chiasognathus granti,* 1 male, Chile, Cayutue, Lago Todos Los Santos, Llanguihue, 14 October 1969, J. Solervinces A.; *Chiasognathus* sp., 1 female, Chile, Mañiuales, L. Peña; *C. granti,* 14 larval skins, Chile, Lago Penihueico, Volcán Chosuenco, August 1988, O. Skew, ex boar stomach; *C. granti,* 2 males, XI Region, Coyhaique [no further data]. All specimens examined with mandibles worn; material deposited in QCAZ, CMNH, and CV.

Genus *Sphaenognathus* Buquet, 1838

Larva C-shaped, subcylindrical and thickened posteriorly (Fig. 1); mediolateral length, including head, 45–86 mm; color whitish blue when teneral and whitish yellow when fully developed.

Head capsule globose (Fig. 1–4), 8.0–11.6 mm wide, dark to light reddish brown with anterior pattern of clypeus yellowish brown; epicranial suture impressed, yellowish, approximately as long as frontal suture (epicranial suture appears shorter in Fig. 4 due to angle of view); surface of cranium bare to lightly punctate with 2–8 dorsoepicranial setae; stemma circular to ovate, not pigmented, without definite margin, not or slightly raised above head surface; frontal suture distinct, often asymmetrical; frons lightly punctate, becoming rugosopunctate anteriorly, with an ovate depression at top of epicranial suture corresponding to ocellar area; on each side, 1 or 2 setae at anterior angle, 1 or 2 exterior frontal setae, and 0 or 1 anterior frontal setae; clypeofrontal suture distinct, impressed. Clypeus trapezoidal, 3.0–3.7 times as long as wide, 1 or 2 anterior clypeal setae and 1 or 2 exterior clypeal setae on each side; preclypeus lightly sclerotized, rugosopunctate. Labrum suboval, rugosopunctate, wider than long, with 2 anterior labral setae, 10–20 posterior labral setae. Apex of epipharynx (Fig. 8, 9, 11–14), in frontal view, with 13–18 long, thick setae directed anteromedially; haptomerum with at least two truncate coarse heli; chaetopariae consisting of 18–93 long setae and numerous small setae directed medioapically; tormae united, laeotorma and dexiotorma almost symmetrical; pterotormae symmetrical, with apex rounded, acute or broadly truncate; epitorma with rounded apex and deeply impressed in surface of pedium; haptolachus with three suboval nesia, the medial nesium sometimes hardly distinct from sclerotized sensory cone, the right nesium larger than left nesium; a patch of small setae on each side of sensory area. Mandibles subtriangular (Fig. 2, 15–23), asymmetrical, brownish; dorsa of mandibles (Fig. 16, 17, 19–23) with small dorsomolar setae on base of molar area, one large caudolateral seta at scissorial notch and one large lateral seta on molar area; ventral surface of mandibles (Fig. 15, 18) with patch of ventromolar setae and a patch of ventrolateral setae; basolateral angle with ventral subtriangular process; basolateral angle with rounded postartis; scissorial area of left mandible (Fig. 15, 16) with 4–5 teeth (unknown in *S. subtilis*), inner margin of left mandible between scissorial and molar areas with or without basal tooth (Fig. 15, 16, 19–23); teeth of molar area (Fig. 15, 16) not well-defined, with masticatory concave area projecting

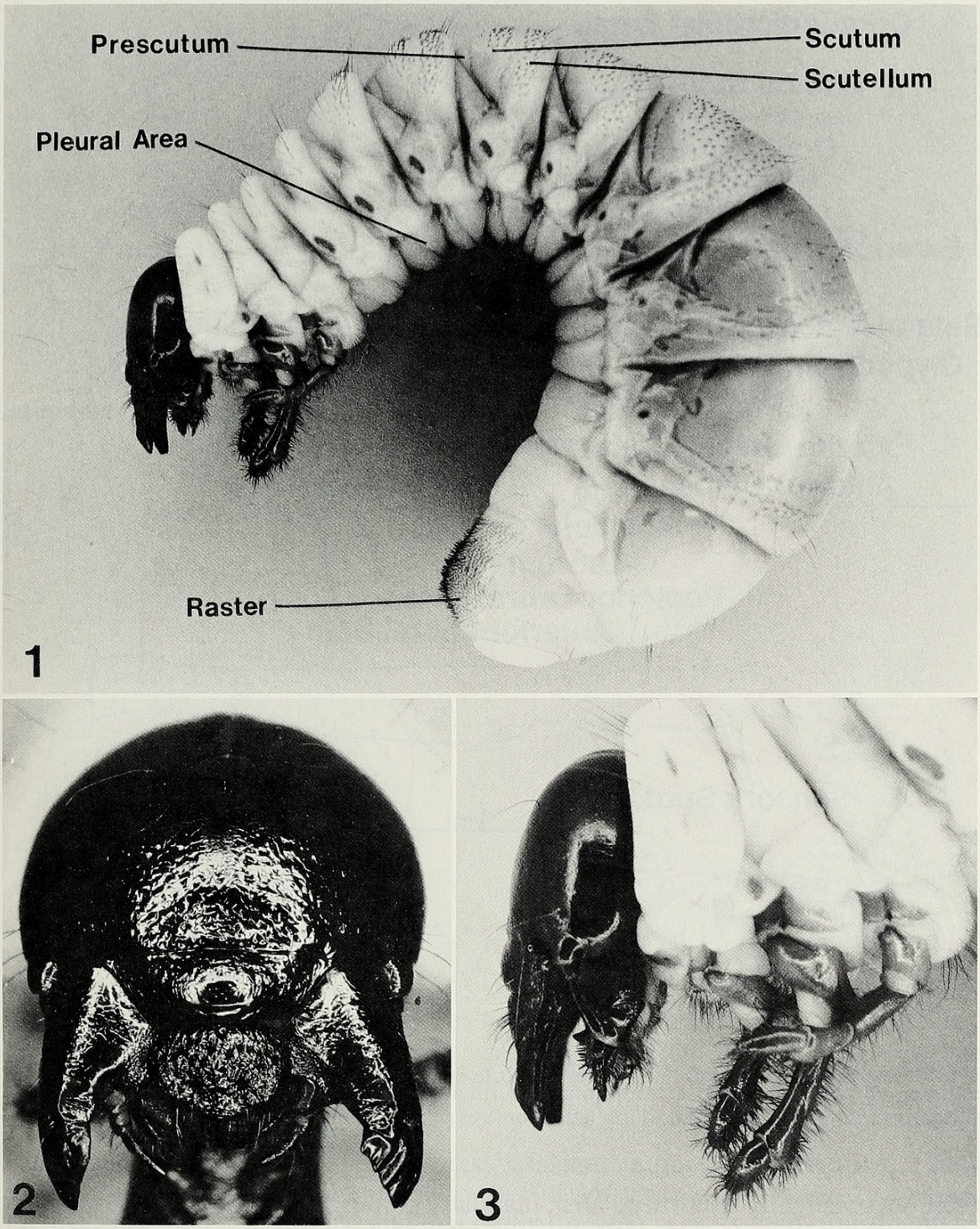

Fig. 1–3.—Third instar larva of *Sphaenognathus peruvianus*. 1, left lateral view; 2, head, frontal view; 3, head and thorax, left lateral view.

anteriorly and retracted posteriorly; acia present (Fig. 16); scissorial area of right mandible with teeth often not well-defined; molar area with masticatory area convex. Maxillae (Fig. 25, 26) each with galea and lacinia separate; galea with strong subconical uncus and 5–7 large setae lateral to uncus; lacinia with terminal subconical uncus, 10–17 large setae behind uncus; stipes with large strip of small

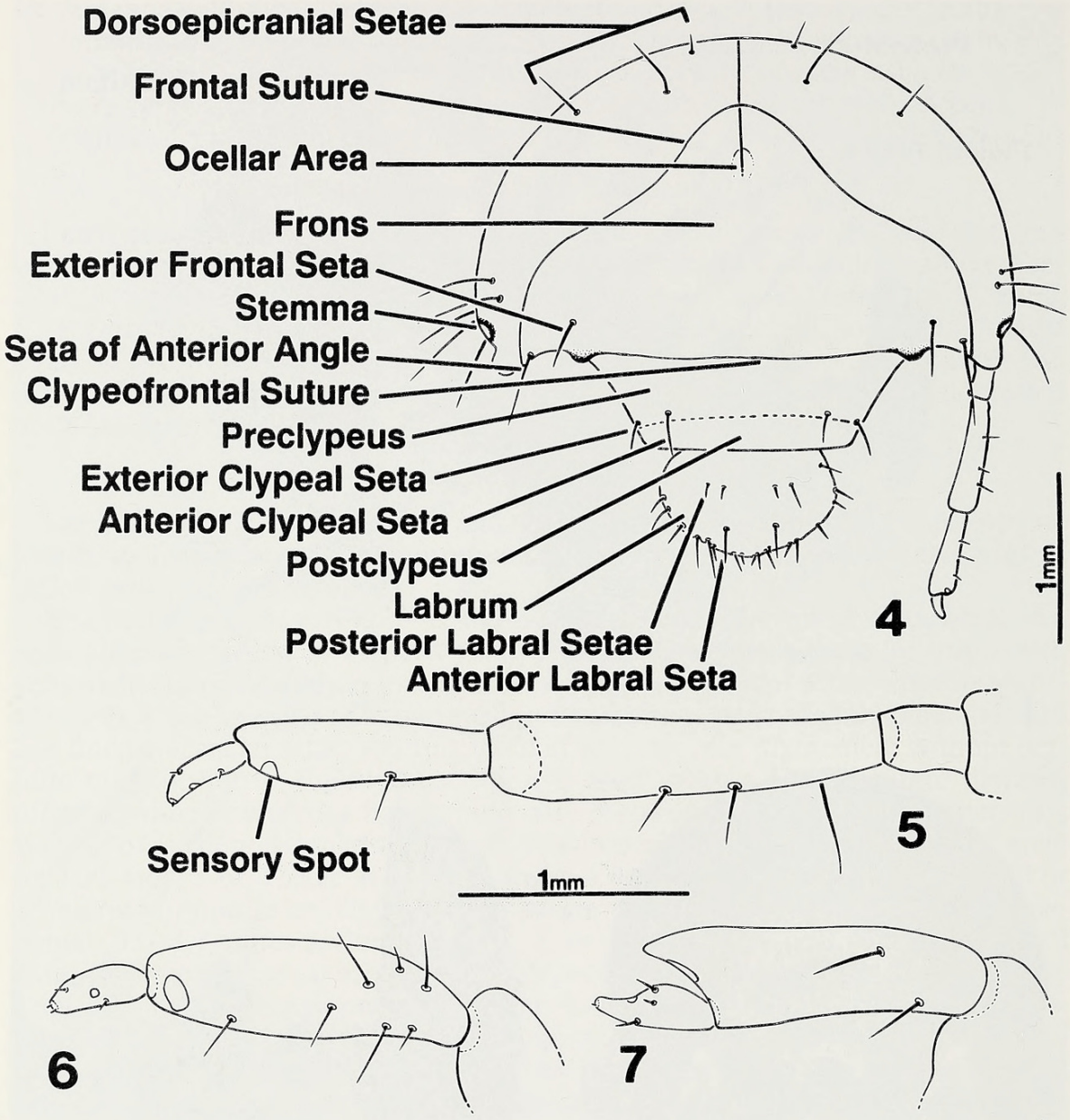

Fig. 4–7.—Third instar larvae of Chiasognathini. 4, *Sphaenognathus nobilis,* head; 5, *S. subtilis,* left antenna, dorsal view; 6, *S. oberon,* third and fourth antennomeres of right antenna, lateral view; 7, *Chiasognathus granti,* third and fourth antennomeres of right antenna, lateral view.

teeth set in a lightly sclerotized area; maxillary palpus with four palpomeres; basal palpomere as long as wide, with subcircular unpigmented area; second palpomere shorter than basal, subconical with subcircular unpigmented area; third palpomere subcylindrical, as long as second palpomere; apical palpomere subconical, longer than basal palpomere; palpomere 1–3 setose, apical palpomere glabrous. Labium (Fig. 24): labial palpi with two palpomeres, apical palpomere subconical, twice or more length of basal palpomere; hypopharyngeal sclerome heavily sclerotized, concave medially, asymmetrical; sublateral lobes of sclerome reduced to two unpigmented spots, the right spot smaller than left; sclerome with left side of anterior margin with strong conical teeth directed dorsally. Antennae (Fig. 4–6)

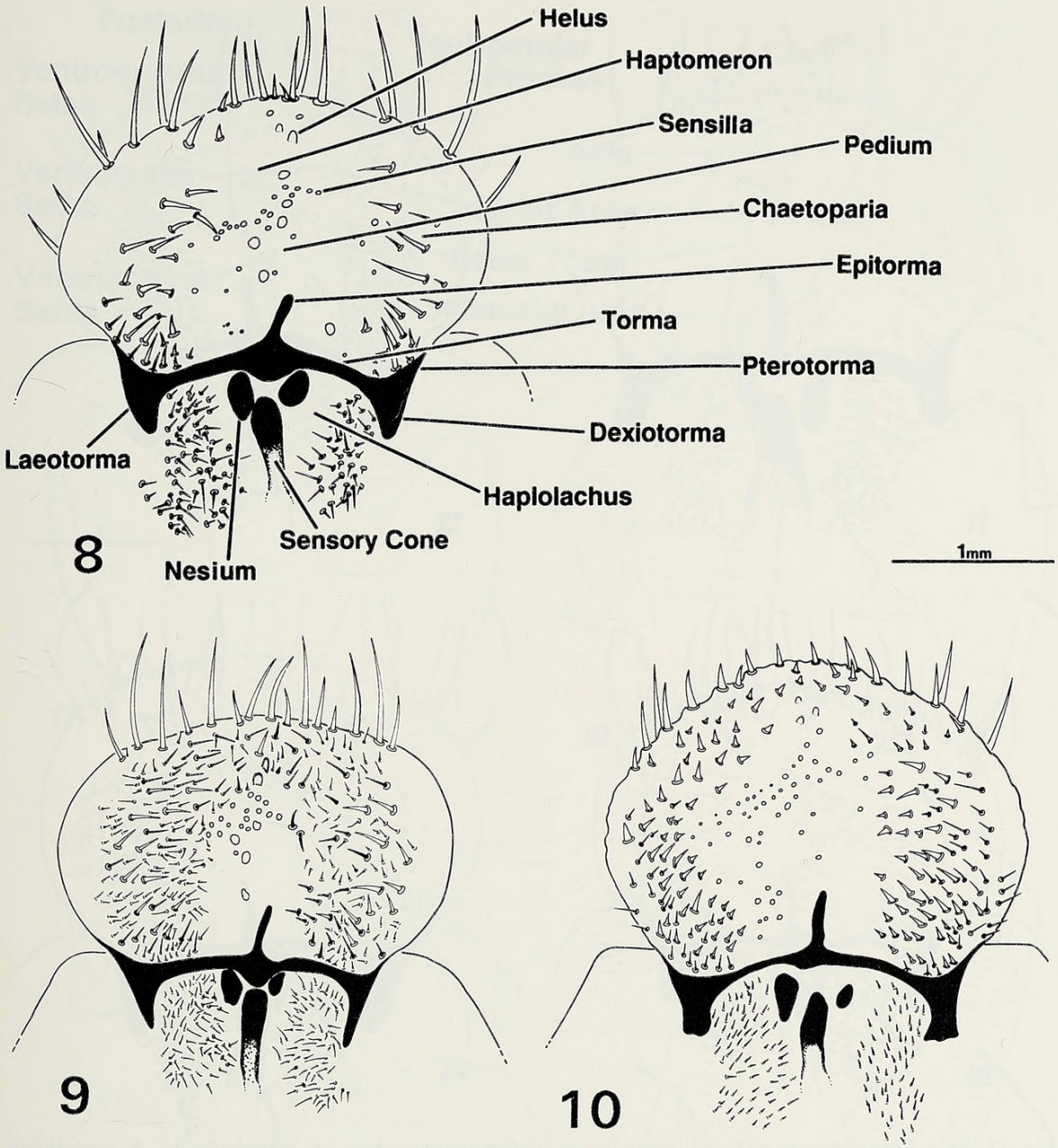

Fig. 8–10.—Epipharynges of third instar larvae of Chiasognathini. 8, *Sphaenognathus nobilis*; 9, *S. peruvianus*; 10, *Chiasognathus granti.*

geniculate, each with four antennomeres; basal antennomere subcylindrical, about as long as apical; second antennomere clavate, longer than third; third antennomere clavate with a subapical and externally directed sensory spot; fourth antennomere subconical, externally directed and with a sensory spot; second to fourth antennomeres setose.

Thorax (Fig. 3, 27) divided into prothorax, mesothorax, and metathorax; prothoracic dorsum with two narrow transverse rows of long setae, anterior row with many setae, posterior row with few setae; each side of prothorax with sclerotized furrow, continuous (Fig. 27) or interrupted below the middle (Fig. 3); mesothorax divided into two dorsal areas, posterior one with row of long setae; metathorax with dorsum similar to mesothorax; pleural area of mesothorax and metathorax

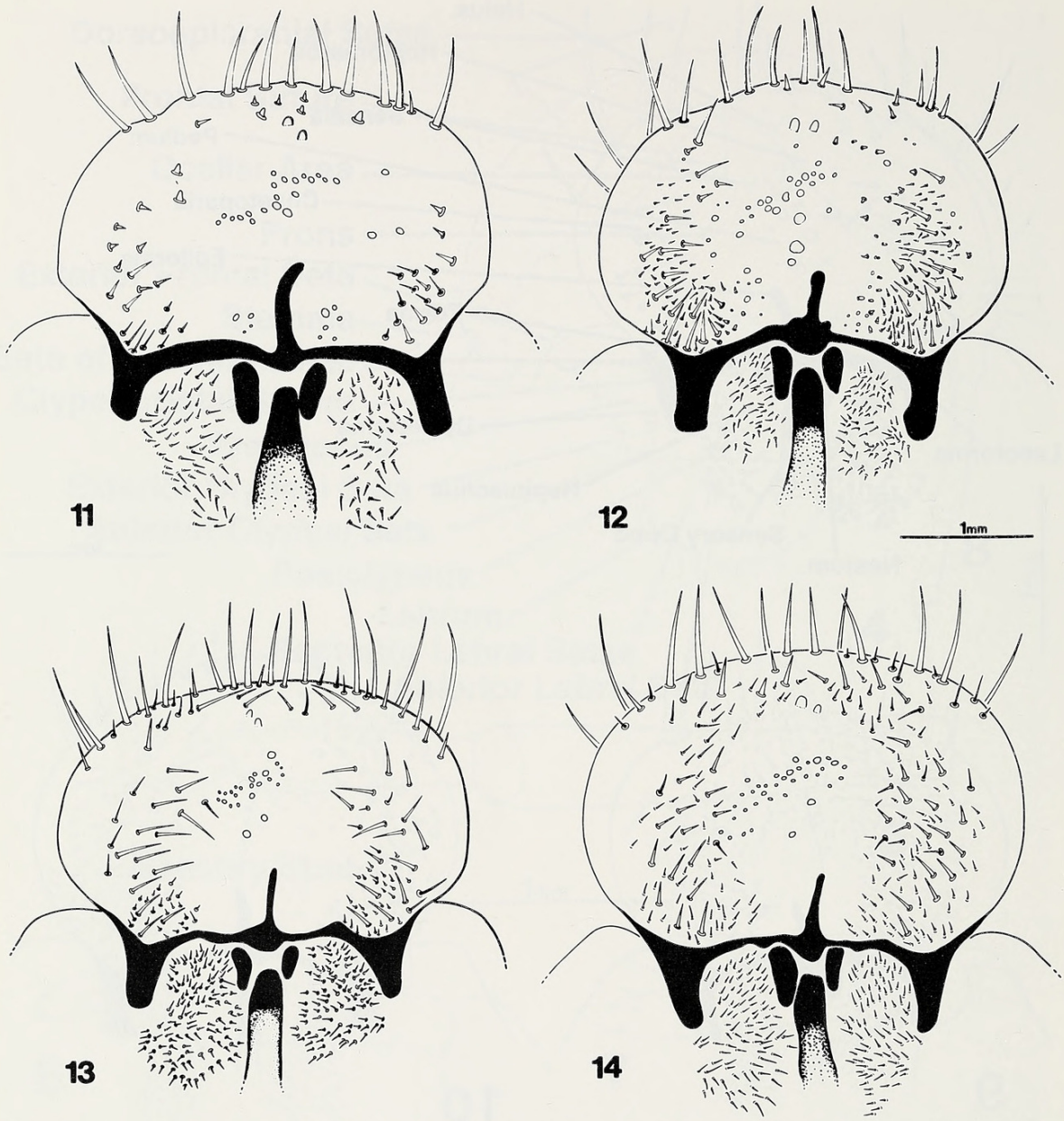

Fig. 11–14.—Epipharynges of third instar larvae of *Sphaenognathus*. 11, *S. subtilis*; 12, *S. metallifer*; 13, *S. lindenii*; 14, *S. oberon*.

each with a tubercle with a patch of long setae. Prothoracic legs (Fig. 31) slightly shorter than mesothoracic and metathoracic legs (Fig. 33, 34); metathoracic legs directed anterolaterally and perpendicular to those of mesothorax and prothorax. Each leg with setose coxa, trochanter, femur, tibia, and tarsungulus (Fig. 31, 33, 34); tarsungulus abruptly attenuated at apex forming very short median tooth, flanked by two setae rising from same position on each side (Fig. 32); coxae of mesothoracic legs (Fig. 36–39) with a stridulatory area or pars stridens, consisting of a slightly curved, longitudinal row of subconical teeth raised into slight carina, lateral end of carina diffusing into small patch of granules, medial end with very small patch or no patch of granules; trochanter of each metathoracic leg (Fig. 41–43) with a stridulatory area or plectrum consisting of a single longitudinal row of

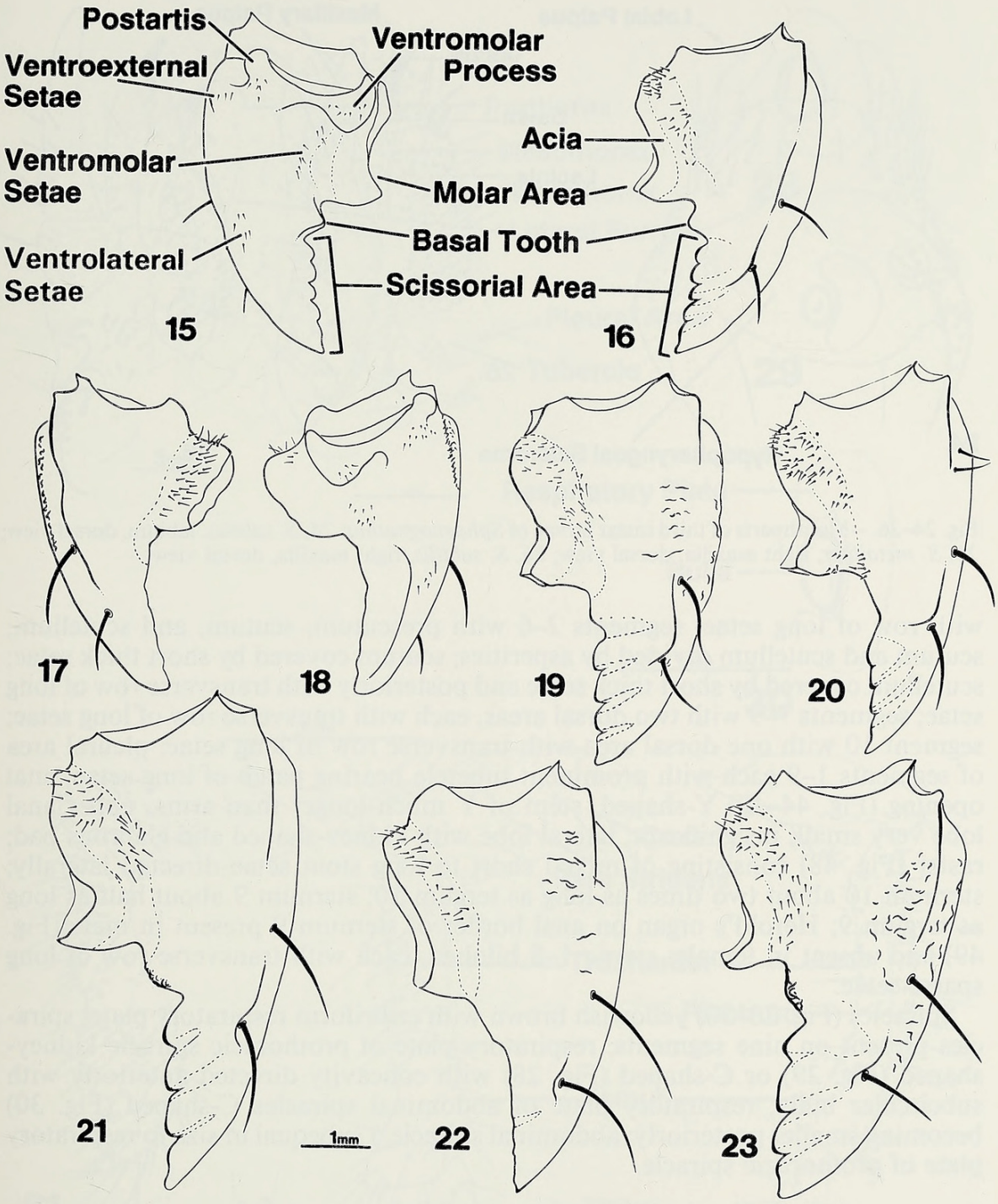

Fig. 15–23.—Mandibles of third instar larvae of *Sphaenognathus*. 15, *S. nobilis,* left mandible, ventral view; 16, *S. nobilis,* left mandible, dorsal view; 17, *S. nobilis,* right mandible, dorsal view; 18, *S. nobilis,* right mandible, dorsal view; 18, *S. nobilis,* right mandible, ventral view; 19, *S. metallifer,* left mandible, dorsal view, 20, *S. peruvianus,* left mandible, dorsal view; 21, *S. lindenii,* left mandible, dorsal view; 22, *S. subtilis,* left mandible, dorsal view; 23, *S. oberon,* left mandible, dorsal view.

short rounded, suboval or elongate teeth; teeth decreasing in size or becoming elongate distally; trochanter swollen apically with a moderate projecting lobe.

Abdominal terga 1–8 becoming longer posteriorly (Fig. 1); tergum 9 about same length as tergum 6; abdominal segment 1 with two dorsal areas, posterior area

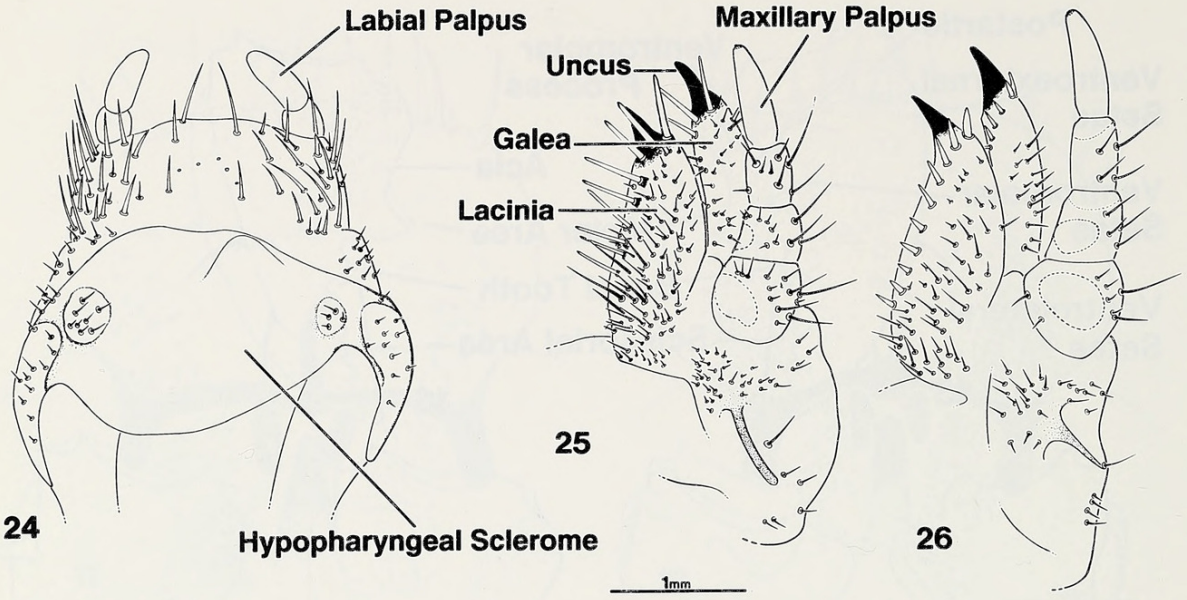

Fig. 24–26.—Mouthparts of third instar larvae of *Sphaenognathus*. 24, *S. subtilis*, labium, dorsal view; 25, *S. metallifer*, right maxilla, dorsal view; 26, *S. subtilis*, right maxilla, dorsal view.

with row of long setae; segments 2–6 with prescutum, scutum, and scutellum; scutum and scutellum divided by asperities; scutum covered by short thick setae; scutellum covered by short thick setae and posteriorly with transverse row of long setae; segments 7–9 with two dorsal areas, each with transverse row of long setae; segment 10 with one dorsal area with transverse row of long setae; pleural area of segments 1–9 each with prominent tubercle bearing patch of long setae; anal opening (Fig. 44–48) Y-shaped, stem of Y much longer than arms; upper anal lobe very small, insignificant; lateral lobe with kidney-shaped and glabrous pad; raster (Fig. 48) consisting of mixed short to long stout setae directed laterally; sternum 10 about two times as long as tergum 10; sternum 9 about half as long as tergum 9; Herold's organ on anal border of sternum 9 present in male (Fig. 49) and absent in female; sterna 1–8 bilobed, each with transverse row of long sparse setae.

Spiracles (Fig. 28–30) yellowish brown with cribriform respiratory plate; spiracles present on nine segments; respiratory plate of prothoracic spiracle kidney-shaped (Fig. 29) or C-shaped (Fig. 28) with concavity directed anteriorly with subcircular bulla; respiratory plate of abdominal spiracles C-shaped (Fig. 30) becoming smaller posteriorly; abdominal spiracle 5 subequal in size to respiratory plate of prothoracic spiracle.

Key to Known Larvae of *Sphaenognathus*

1′. Prothorax with lateral sclerotized furrow clearly interrupted by a nonsclerotized area (Fig. 3). Raster with more than 900 short to long setae (Fig. 1) ..... *Sphaenognathus peruvianus*

1′. Prothorax with lateral sclerotized furrow continuous, not interrupted by a nonsclerotized area (Fig. 27). Raster with fewer than 900 short to long setae (Fig. 48) 2

2(1′). Anal lobes glabrous (Fig. 46) ..... *Sphaenognathus subtilis*

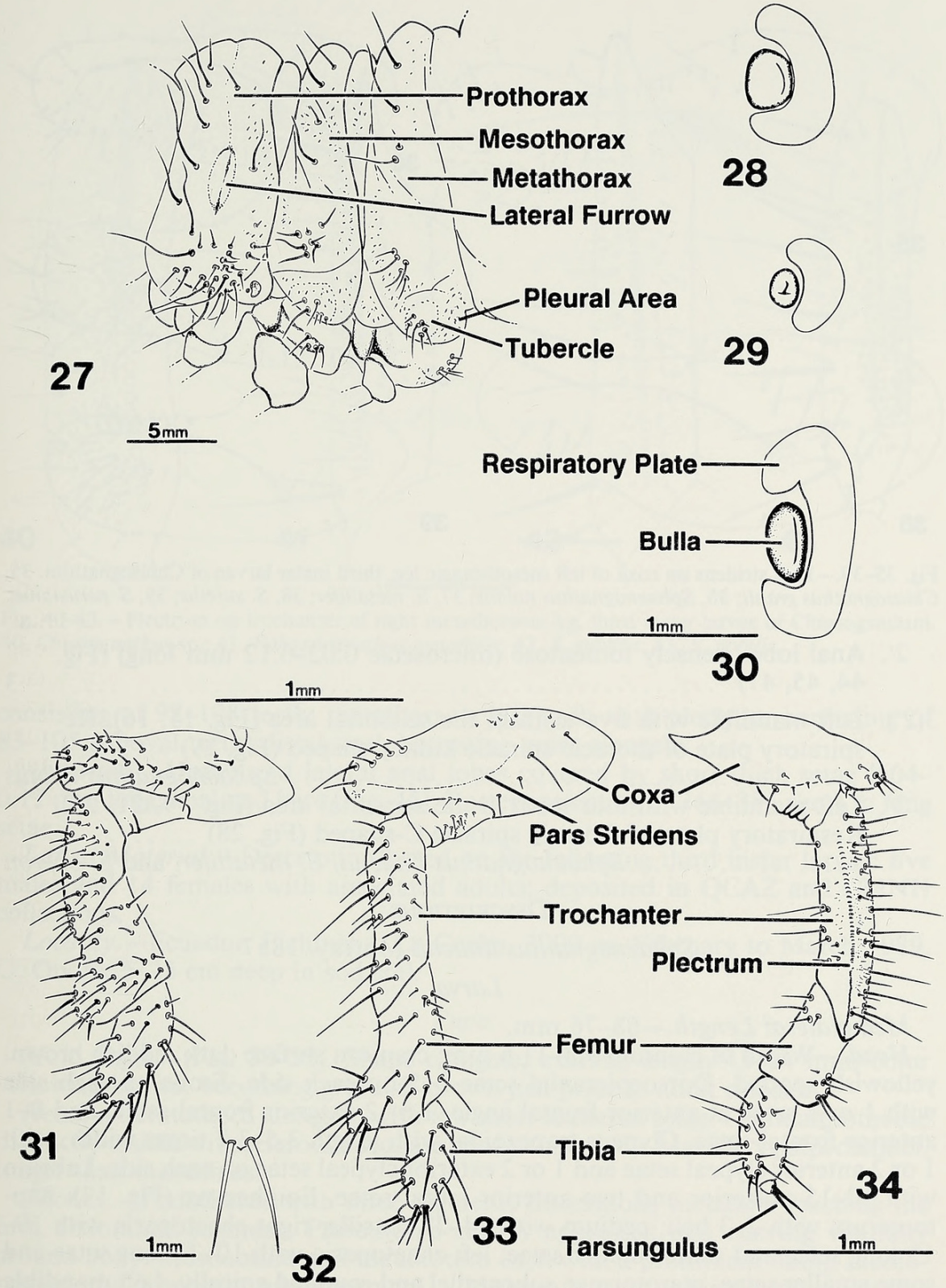

Fig. 27–34.—Third instar larvae of *Sphaenognathus*. 27, *S. nobilis*, thorax, left lateral view; 28, *S. subtilis*, left thoracic spiracle; 29, *S. nobilis*, left thoracic spiracle; 30, *S. nobilis*, left spiracle, abdominal segment 3; 31, *S. peruvianus*, right prothoracic leg; 32, *S. peruvianus*, tarsungulus of right prothoracic leg; 33, *S. metallifer*; left mesothoracic leg; 34, *S. peruvianus*, right metathoracic leg.

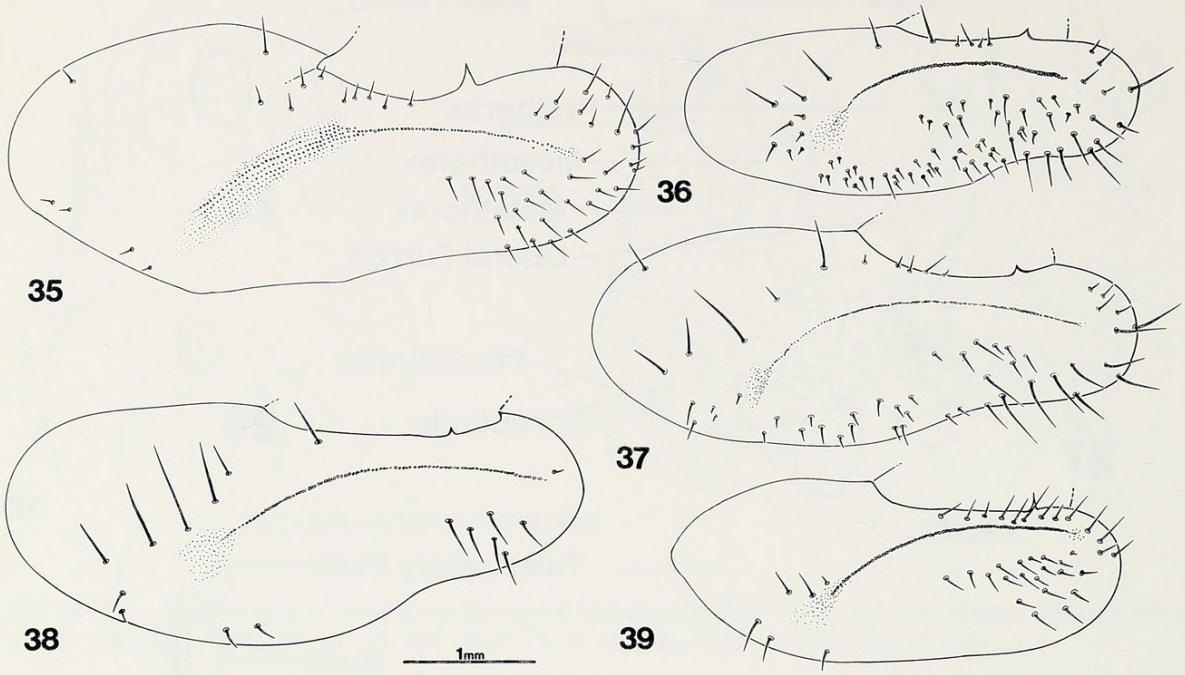

Fig. 35–39.—Pars stridens on coxa of left mesothoracic leg, third instar larvae of Chiasognathini. 35, *Chiasognathus granti*; 36, *Sphaenognathus nobilis*; 37, *S. metallifer*; 38, *S. subtilis*; 39, *S. peruvianus*.

2′. Anal lobes densely tomentose (microsetae 0.02–0.12 mm long) (Fig. 44, 45, 47) 3

3(2′). Left mandible with five teeth in the scissorial area (Fig. 15, 16). Respiratory plate of thoracic spiracle kidney-shaped (Fig. 29) .... *Sphaenognathus nobilis*

3′. Left mandible with four teeth in the scissorial area (Fig. 19, 21, 23). Respiratory plate of thoracic spiracle C-shaped (Fig. 28) ....*Sphaenognathus lindenii, S. metallifer,* and *S. oberon*

Descriptions

Sphaenognathus lindenii Murray, 1857

Larva

Mediolateral Length.—68–76 mm.

Head.—Width of cranium 9.3–11.6 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–5 on each side. Frons on each side with 1 or 2 setae at anterior frontal angle, 1 or 2 exterior frontal setae, and 0–1 anterior frontal setae. Clypeus trapezoidal with length 3.5–3.7 times width, with 1 or 2 anterior clypeal setae and 1 or 2 exterior clypeal setae on each side. Labrum with 10–15 posterior and two anterior labral setae. Epipharynx (Fig. 13): haptomerum with 2–3 heli; pedium with 24–27 sensilla; right chaetoparia with 10–15 long setae and some smaller setae; left chaetoparia with 10–24 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four blade-like scissorial teeth, basal tooth conical and dull (Fig. 21). Maxillae each with 5–6 large setae lateral to uncus of galea and 13–16 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens

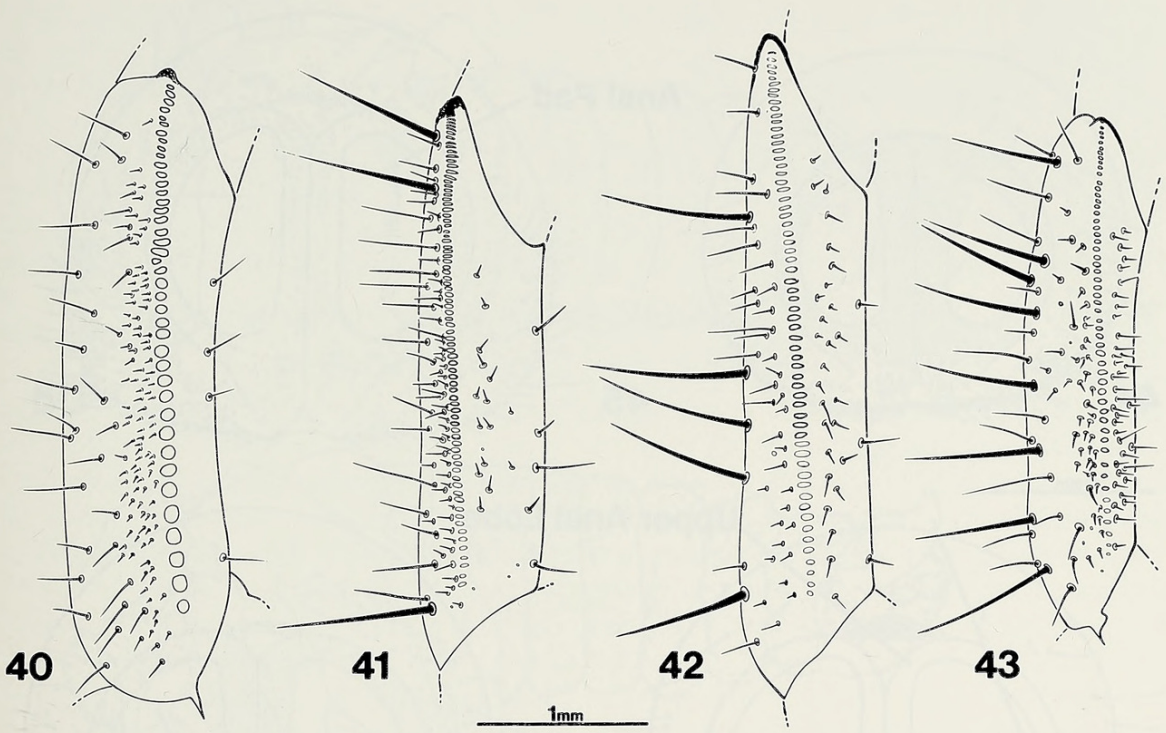

Fig. 40–43.—Plectrum on trochanter of right metathoracic leg, third instar larvae of Chiasognathini. 40, *Chiasognathus* sp.; 41, *Sphaenognathus metallifer*; 42, *S. subtilis*; 43, *S. nobilis*.

consisting of 92–108 teeth; metathoracic legs each with plectrum consisting of 83–105 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.04–0.12 mm long; anal pad bare (Fig. 45). Raster consisting of 366–386 short to long setae.

Larval Material.—Description based on the following third instar larvae: five males and 14 females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Pichincha, La Cocha, 3000 m, February to March 1989, G. Onore, 5–25 cm deep in sod soil.

Pupa

Male Pupa.—(Fig. 50–52). Shape elongate, exarate; length 43–54 mm; color yellowish brown, becoming greenish brown just prior to adult eclosion.

Head.—Ceratotheca elongate, with few short scattered setae. Ophthalmothecae distinctly visible with sclerotized lunate border anteriorly. Maxillary palpi distinct, longer than mandibles.

Thorax.—Podothecae with three segments discernible; metatarsi reaching the fifth abdominal segment. Pterothecae closely appressed and curving ventrally around body. Mesonotum and metanotum each with a prominent bump medioposteriorly; pronotum subtrapezoidal, 1.75 times as wide as long, with two prominent bumps medioposteriorly; pronotum, mesonotum, and metanotum with few scattered, short setae.

Abdomen.—Abdominal sterna with small scattered setae; apical segment with genitalia distinctly visible between urogomphi; nine abdominal terga visible; terga 1–8 with a transverse row of small setae and at posterior border a transverse row

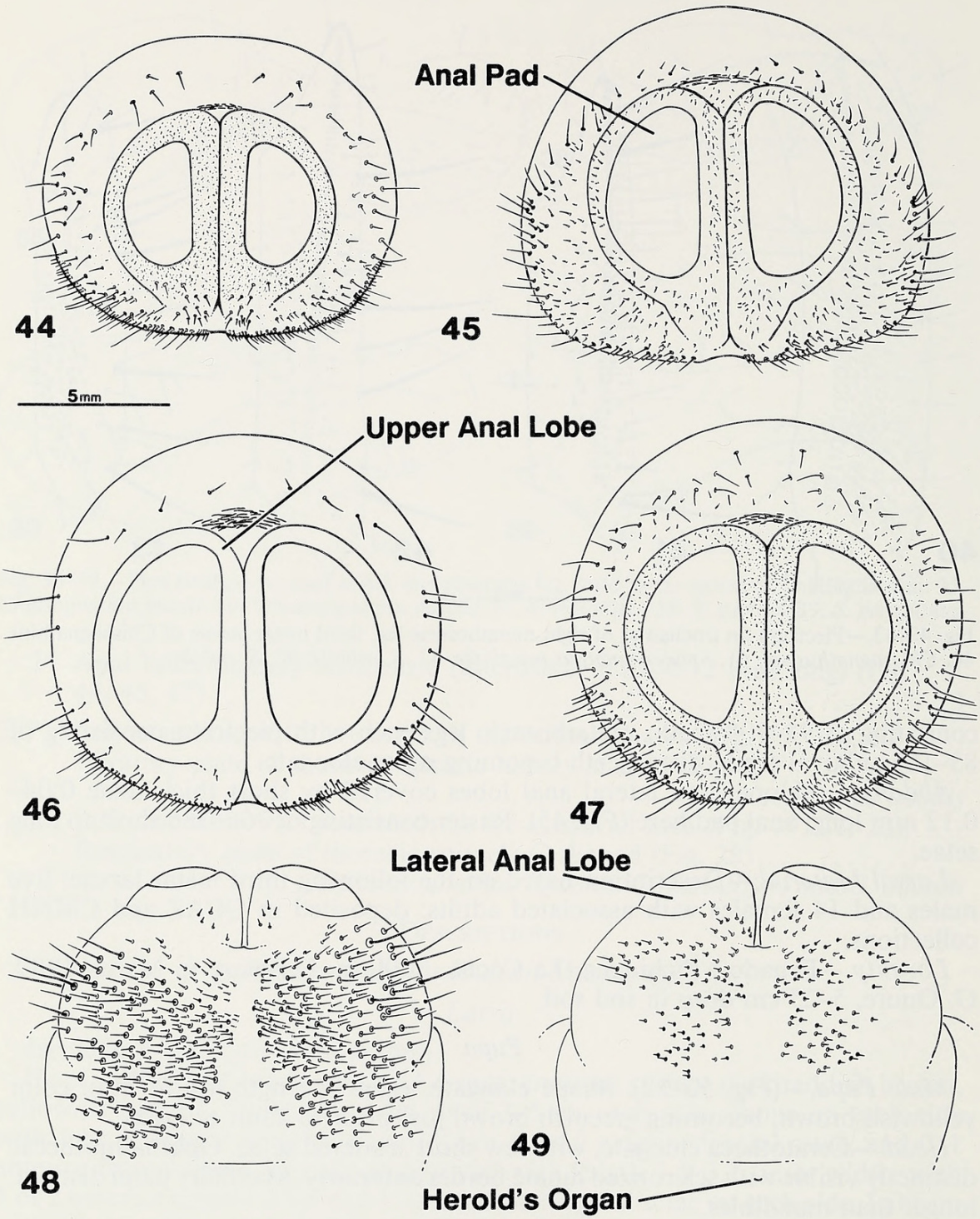

Fig. 44–49.—Posterior abdominal structures of Chiasognathini. 44, *Sphaenognathus nobilis,* caudal view of last abdominal segment; 45, *S. lindenii,* caudal view of last abdominal segment; 46, *S. subtilis,* caudal view of last abdominal segment; 47, *S. metallifer,* caudal view of last abdominal segment; 48, *S. subtilis,* sternum of last abdominal segment; 49, *Chiasognathus granti,* sterna 9–10 of male larva showing Herold's organ.

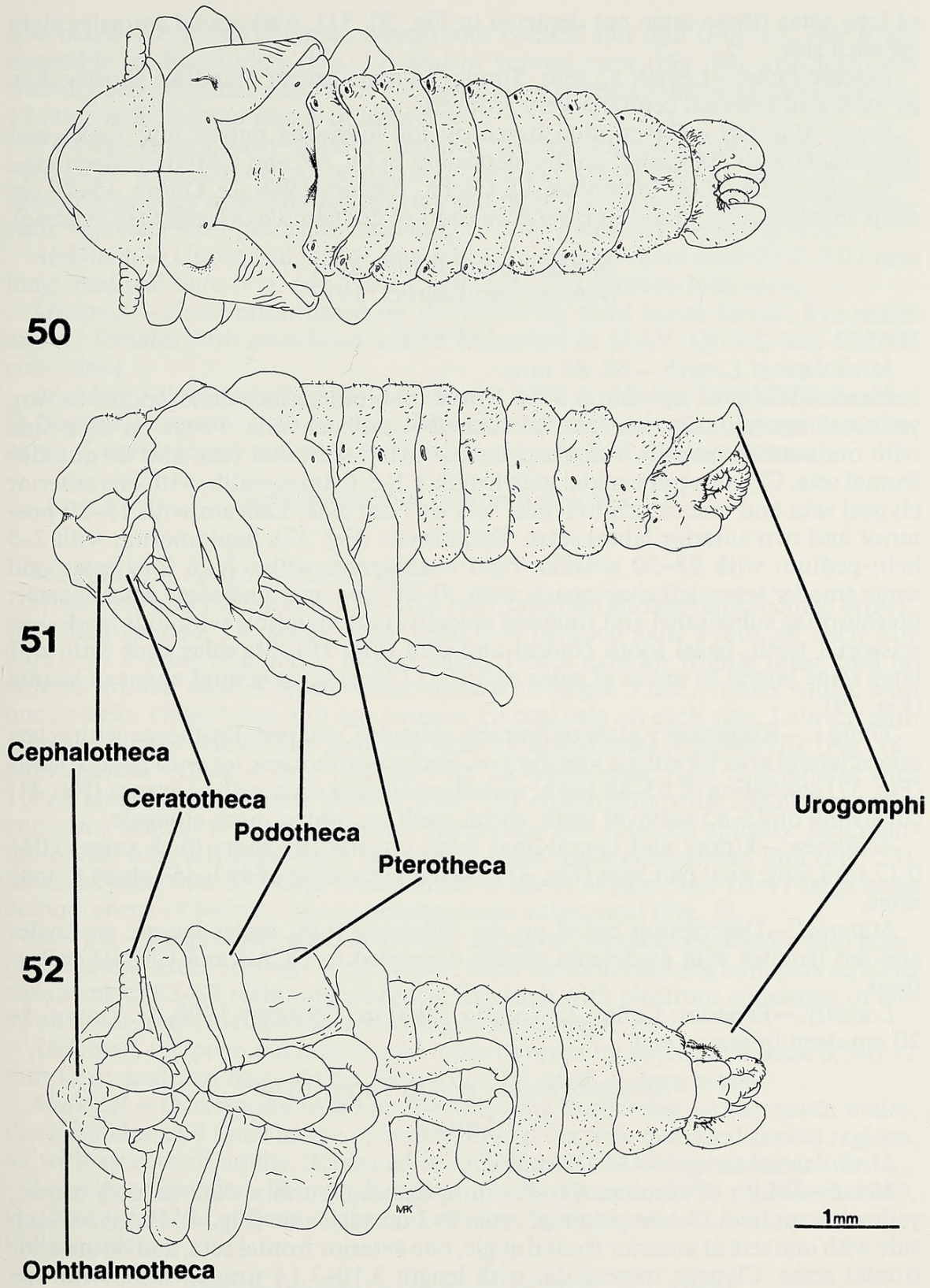

Fig. 50–52.—Pupa of *Sphaenognathus lindenii* (very fine setae on abdominal terga not shown). 50, dorsal view; 51, left lateral view; 52, ventral view.

of long setae (these setae not depicted in Fig. 50, 51). Abdominal spiracles eight on each side.

Female Pupa.—Length 52 mm. Similar to male except mandible shorter than in male and external genitalia very reduced.

Pupal Material.—Description based on the following pupae: four males and one female with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Pichincha, La Cocha, January 1988, G. Onore, 15–20 cm deep; in pupal cells, in sod soil; between roots of *Lachemilla orbiculata* (Rosaceae).

Sphaenognathus metallifer
Bomans and Lacroix, 1972

Larva

Mediolateral Length.—68–86 mm.

Head.—Width of cranium 8.8–10.1 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–4 on each side. Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal seta. Clypeus trapezoidal with length 3.1–3.6 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 15–20 posterior and two anterior labral setae. Epipharynx (Fig. 12): haptomerum with 2–5 heli; pedium with 28–50 sensilla; right chaetoparia with 17–26 long setae and some smaller setae; left chaetoparia with 20–27 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four blade-like scissorial teeth, basal tooth conical and dull (Fig. 19). Maxillae each with 5–7 large setae lateral to uncus of galea and 15–17 large setae behind uncus of lacinia (Fig. 25).

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens (Fig. 37) consisting of 83–88 teeth; metathoracic legs each with plectrum (Fig. 41) consisting of 73–85 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.04–0.12 mm long; anal pad bare (Fig. 47). Raster consisting of 462–464 short to long setae.

Material.—Description based on the following third instar larvae: six males and ten females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Cañar, El Tambo, 2900 m, February 1990, G. Onore, 5–20 cm deep in grassy soil.

Sphaenognathus nobilis Parry, 1874

Larva

Mediolateral Length.—45–72 mm.

Head.—Width of cranium 8.0–9.1 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–3 on each side (Fig. 4). Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal setae. Clypeus trapezoidal with length 3.10–3.14 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 8–12 posterior labral seta and two anterior labral setae. Epipharynx (Fig. 8): haptomerum with 2–4 heli; pedium with 23–31 sensilla; right chaetoparia with 15–16 long and some smaller setae; left chaetoparia with 13–18 long and some smaller setae; pterotormae rounded apically and internally directed. Left mandible with

five blade-like scissorial teeth, basal tooth conical and dull (Fig. 15, 16). Right mandible in dorsal view (Fig. 17) and in ventral view (Fig. 18) with teeth not well-defined. Maxillae each with 4–6 large setae lateral to uncus of galea and 15–17 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle kidney-shaped (Fig. 27, 29). Prothorax with sclerotized lateral area forming a long furrow (Fig. 27). Each mesothoracic leg with pars stridens consisting of 83–86 teeth (Fig. 36); metathoracic legs each with plectrum consisting of 50–57 suboval teeth (Fig. 43).

Abdomen.—Upper and lateral anal lobes covered by short setae 0.02–0.07 mm long; anal pad bare (Fig. 44). Raster with 586–730 short to long setae.

Material.—Description based on the following third instar larvae: five males and 13 females with associated adults; deposited in IZAV, QCAZ, and CMNH collections.

Locality.—Venezuela: Merida, La Mucuy, 2700 m, 18 Apr 1989, G. Onore and C. Bordon. In topsoil 3–15 cm deep, between roots of cultivated *Cupressus macrocarpa* (Cupressaceae) and native *Podocarpus rospigliosi* (Podocarpaceae).

Sphaenognathus oberon Kriesche, 1922

Larva

Mediolateral Length.—62–86 mm.

Head.—Width of cranium 10.0–10.6 mm; cranium surface dark reddish brown, yellowish spotted. Dorsoepicranial setae 2–4 on each side. Frons on each side with 1 or 2 setae at anterior frontal angle, 1 or 2 exterior frontal setae, and no anterior frontal setae. Clypeus trapezoidal with length 3.6–3.7 times width, with one anterior clypeal seta and one exterior clypeal seta on each side. Labrum with 10–15 posterior labral setae and two anterior labral setae. Epipharynx (Fig. 14): haptomerum with 2–4 heli; pedium with 28–64 sensilla; right chaetoparia with 16–25 long setae and some smaller setae; left chaetoparia with 23–30 long setae and some smaller setae; pterotormae subparallel and rounded apically. Left mandible with four scissorial teeth blade-like, basal tooth conical and dull (Fig. 23). Maxillae each with 5–7 large setae lateral to uncus of galea and 10–17 large setae behind uncus of lacinia. Apical antennomere subconical (Fig. 6).

Thorax.—Respiratory plate of thoracic spiracle C-shaped. Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens consisting of 85–87 teeth; metathoracic legs each with plectrum consisting of 60–83 suboval teeth, distal teeth becoming more elongate.

Abdomen.—Upper and lateral anal lobes covered by short thick setae 0.5–0.12 mm long; anal pad bare. Raster with 412–508 small to long setae.

Material.—Description based on the following third instar larvae: seven males, three females, and three larvae of undetermined sex with damaged genital regions, all with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Bolivar, Santiago, Casha Totoras, 2900 m, March 1989, G. Onore, 10–25 cm deep in the soil covered by cultivated *Solanum tuberosum* (Solanaceae).

Sphaenognathus peruvianus (Waterhouse, 1869)

Larva

Mediolateral Length.—58–76 mm (Fig. 1).

Head.—Width of cranium 8.0–10.0 mm; cranium surface reddish brown, yellowish spotted (Fig. 2, 3), 3–8 dorsoepicranial setae on each side. Frons on each

side with one or two setae at anterior frontal angle, one or two exterior frontal setae, and 0–1 anterior frontal setae. Clypeus trapezoidal with length 3.4 times width, with one anterior clypeal seta and one or two exterior clypeal setae on each side. Labrum with 19 posterior labral setae and two anterior labral setae. Epipharynx (Fig. 9): haptomerum with two heli; pedium with 21–29 sensilla; right chaetoparia with 30–41 long and some smaller setae; left chaetoparia with 30–52 long and some smaller setae; pterotormae subtriangular and slightly internally directed. Left mandible with four blade-like scissorial teeth and without basal tooth (Fig. 2, 20). Maxillae each with five large setae lateral to uncus of galea and 15–16 large setae behind uncus of lacinia.

Thorax.—Respiratory plate of thoracic spiracle C-shaped (Fig. 3). Prothorax with sclerotized lateral area consisting of furrow interrupted by a nonsclerotized area, the part of furrow ventral to interruption shorter than dorsal (Fig. 3). Prothoracic leg (Fig. 31). Each mesothoracic leg with pars stridens (Fig. 39) consisting of 79–88 teeth; metathoracic legs each with plectrum (Fig. 34) consisting of 66–82 conical teeth, distal teeth becoming more elongate. Tarsungulus of prothoracic, mesothoracic, and metathoracic legs (Fig. 32).

Abdomen.—Upper and lateral anal lobes covered by very sparse, scattered short setae 0.02–0.06 mm long; anal pad bare. Raster with 940–990 short to long setae.

Material.—Description based on the following third instar larvae: seven males and seven females with associated adults; deposited in QCAZ and CMNH collections.

Locality.—Ecuador: Loja, 4°16′S, 79°20′W, 2800 m, 24 March 1990, G. Onore, 5–15 cm in topsoil.

Sphaenognathus subtilis Lacroix, 1987

Larva

Mediolateral Length.—81 mm.

Head.—Width of cranium 10.8 mm; cranium surface dark reddish brown. One dorsoepicranial seta on each side. Frons on each side with one seta at anterior frontal angle, one exterior frontal seta, and no anterior frontal seta. Clypeus trapezoidal with length 3.2 times width, with one anterior clypeal seta on each side; one exterior clypeal seta on the left side and two setae on the right side. Epipharynx (Fig. 11): haptomerum with two heli; pedium with 50 sensilla; right chaetoparia with 12 long setae and some smaller setae; left chaetoparia with six long setae and some smaller setae, pterotormae rounded apically. Left mandible with scissorial teeth and the inner margin of the scissorial area worn (Fig. 22). Maxillae (Fig. 26) each with 6–7 large setae lateral to uncus of galea and 12–17 large setae behind uncus of lacinia. Labium (Fig. 24). Antenna (Fig. 5).

Thorax.—Respiratory plate of thoracic spiracle C-shaped (Fig. 28). Prothorax with sclerotized lateral area forming a long furrow. Each mesothoracic leg with pars stridens (Fig. 38) consisting of 84 teeth; metathoracic legs each with plectrum (Fig. 42) consisting of 62 suboval teeth, distal teeth becoming elongate.

Abdomen.—Anal lobes and anal pad bare (Fig. 46). Raster (Fig. 48) with about 324 small to long setae.

Material.—Description based on one female third instar larva, fully developed, associated with adults; deposited in CMNH collection.

Locality.—Ecuador: Napo, Cosanga, 1500 m, G. Onore. Under rotten log in grass-covered soil.

DISCUSSION

For this study I examined larvae of the following genera: *Ceratognathus, Cerucchus, Chiasognathus, Dorcus, Figulus, Lamprima, Lissapterus, Lissotes, Lucanus, Platycerus, Sinodendron, Sphaenognathus, Syndesus,* and *Rhyssonotus.* I assessed the characters of *Pholidotus* from the description and illustrations of Costa et al. (1988). The characters discussed below indicate that the genera most closely related to *Chiasognathus* and *Sphaenognathus* are *Rhyssonotus* and *Pholidotus,* and only these genera are discussed further. The same relationships were found by Lacroix (1969) and Holloway (1960) in their phylogenetic interpretations based on adults.

The following larval characters have been considered useful in distinguishing various groups of Lucanidae.

1. *Mandible.* The number of teeth in the left mandible has been used for distinguishing higher taxa of Lucanidae (Van Emden, 1935, 1941; Ritcher, 1966; Lawrence, 1981). However, this character is a problem to assess in larvae that have not recently molted, due to normal wear of the mandibles. The teeth are divided into two categories: the teeth of the scissorial area and the teeth basal to the scissorial area (between the scissorial area and the molar area) which I here designate "basal teeth" (Fig. 15, 16). The mandibles in *S. lindenii, S. metallifer* (Fig. 19), and *S. oberon* have four scissorial teeth; the same condition is found in *Rhyssonotus* sp. Costa et al. (1988) illustrated four scissorial teeth in *Pholidotus spixi. Sphaenognathus nobilis* has five scissorial teeth (Fig. 15, 16), and the condition is unknown in *S. subtilis* and *Chiasognathus granti.* Two basal teeth are present in *Rhyssonotus,* and one basal tooth in *S. lindenii, S. oberon, S. metallifer,* and *S. nobilis* (Fig. 15, 16, 19, 21, 23). Basal teeth are absent in *S. peruvianus* (Fig. 20). This absence is interpreted as derived, and strengthens the reestablishment by Bartolozzi et al. (1992) of *Chiasognathinus* (Didier and Séguy, 1953) as a distinctive and perhaps monophyletic subgenus of *Sphaenognathus* containing *S. peruvianus* and *S. gaujoni* (Oberthür).

2. *Prothorax.* A sclerotized, anteriorly projecting lobe on the prothorax was used as a character by Ritcher (1966) and Lawrence (1981). This structure is not present in *Chiasognathus* and *Sphaenognathus.* A second character, the lateral sclerotized furrow (Fig. 1, 27), is continuous in all known larvae of *Sphaenognathus* except *S. peruvianus* wherein the furrow is interrupted by a nonsclerotized area. The latter condition is considered derived, and occurs as well in *Rhyssonotus.* The character was not illustrated for *Pholidotus* by Costa et al. (1988).

3. *Mesothoracic legs.* The shape, number and position of teeth of the pars stridens of the mesocoxae have been used by Van Emden (1952), Ritcher (1966), Klausnitzer (1978), and Lawrence (1981). Larvae of species of *Sphaenognathus* have similar structures except for the number of teeth (Fig. 36–39). The same condition is present in *Pholidotus* and *Rhyssonotus. Chiasognathus* larvae differ in having a distinctive field of teeth at the proximal end of the main row of teeth on the pars stridens (Fig. 35).

4. *Metathoracic legs.* The plectrum of the metatrochanter is functionally related to the pars stridens. In the genera *Sphaenognathus* (Fig. 41–43), *Chiasognathus* (Fig. 40), *Pholidotus,* and *Rhyssonotus,* this structure is very similar with variation only in the number and shape of the teeth.

5. *Setation of anal sclerite.* The dense vestiture of setae in the area surrounding the anal pad separates *S. lindenii, S. metallifer, S. oberon,* and *S. nobilis* (Fig. 44, 45, 47) from *S. peruvianus* and *S. subtilis* (Fig. 46), which lack this vestiture.

Chiasognathus, Rhyssonotus, and *Pholidotus* have a reduced number of dense setae.

6. *Epipharynx.* The basic anatomy of the epipharynx is similar in *Sphaenognathus* (Fig. 9, 11–14), *Chiasognathus* (Fig. 10), *Pholidotus,* and *Rhyssonotus.* Perhaps the most important character common to the above-mentioned genera is the vestiture of setae lateral to the nesia of the haptolachus. In Chiasognathini, the sensilla in the pedium and the setae of the paria seem to have the same origins and they are sometimes represented as "emerging setae"; in the haptomerum there are two or more coarse nail-like spines which I interpret as heli following Böving (1936).

7. *Tarsungulus.* Van Emden (1941), Medvedev (1952), Paulian (1959), and Ritcher (1966) used the number of setae present on the tarsungulus as a character separating Lucaninae from Dorcinae and some other subfamilies. *Sphaenognathus* (Fig. 32), *Chiasognathus, Pholidotus* and *Rhyssonotus* have two setae on the tarsungulus. This character indicates that they should be included in Dorcinae. However, other characters support a relationship with Lucaninae.

8. *Raster.* The setae of the raster, localized in patches, are all inclined laterally in species of Chiasognathini (Fig. 1, 44–49).

A larval diagnosis for the family Lucanidae remains speculative with so few larvae available for study. Larval features suggest that Chiasognathini is related to Lucaninae and Dorcinae in agreement with Holloway's analysis of adults. That author concludes, "There appears to be no valid reason, at the present time, for recognizing as distinct groups the . . . Chiasognathinae, Dorcinae . . . ; probably all . . . belong in Lucaninae" (Holloway, 1960).

The most recent larval keys to lucanid subfamilies, based primarily on Palearctic and Nearctic genera, will not place all Chiasognathini in Lucaninae because *S. peruvianus* lacks the tooth between the inner margin of the scissorial area and the molar area (Fig. 20), a character considered diagnostic for Lucaninae. An important character linking Chiasognathini to Lucaninae is the length of the dorsal surface of abdominal segment 10, being half or less the length of the ventral surface of that segment (Fig. 1).

Known larvae of *Sphaenognathus* are very similar in anatomy with the exception of *S. peruvianus,* which presents features distinctive enough to justify revalidation of the subgenus *Chiasognathinus.*

PHYLOGENETIC NOTES

Although characters of larvae do not permit complete resolution of the phylogeny of the species described here, several apomorphic characters support the monophyly of three taxa as follows.

1. The monophyly of a lineage consisting of all examined species of Chiasognathini is supported by four characters tentatively considered to be apomorphic. Chiasognathini is also characterized by the presence of larval stemmata, but this is plesiomorphic and not phylogenetically informative.

a. All setae on the raster inclined or directed laterally. Other Scarabaeoidea have the setae uniformly directed medially or in many different directions.
b. Reduction in size of the third anal lobe. The third lobe is not reduced in *Syndesus* and other Scarabaeoidea.
c. Presence of a basal tooth on the scissorial margin of the mandible. This is also present in Lucaninae, although absent in other Scarabaeoidea. Its

absence in *Sphaenognathus peruvianus* is hypothesized to represent a secondary loss.

d. Presence of short thick setae on the anal lobes. Such short thick setae are absent in *Syndesus,* but their occurrence in other Lucanidae is not known. They appear to have been secondarily lost in *Sphaenognathus subtilis.*

2. *Chiasognathus* shares three characters with *Syndesus* that may be considered plesiomorphic for Chiasognathini. The derived condition of each of these characters may represent synapomorphies for *Sphaenognathus* as here delimited.

a. Teeth on the pars stridens in a single row. The pars stridens consists of a field of multiple, scattered teeth in *Chiasognathus* and *Syndesus.*

b. Apex of penultimate antennomere not extended past the base of apical antennomere. In *Chiasognathus* and *Syndesus* the distal end of the penultimate antennomere is modified, and the unmodified condition in *Sphaenognathus* is interpreted as a secondary apomorphic reduction.

c. Apical antennomere oblate to cylindrical. This antennomere is pyriform or conical in *Chiasognathus* and *Syndesus.*

3. The monophyly of a group consisting of *Sphaenognathus lindenii, S. oberon,* and *S. metallifer* is supported by one synapomorphy.

a. Presence of minute, slender setae on the anal lobe. These tiny setae are absent in other Chiasognathini, *Syndesus,* and many other genera of Lucanidae.

Alterations in the existing classification of Chiasognathini based on the above characters would be premature, and must wait until a more extensive analysis of characters from all development stages has been completed.

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