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DESCRIPTION OF IMMATURE STAGES OF *PHILOLITHUS DENSICOLLIS* AND *STENOMORPHA PUNCTICOLLIS* WITH NOTES ON THEIR BIOLOGY (COLEOPTERA, TENEBRIONIDAE, TENTYRIINAE).

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ABSTRACT

Mature larvae of the tribe Asidini are characterized by an unsclerotized body, dorsally concave mandibles with preapical gibbosity and submarginal setose area, granulate cranium, swollen preepipleurum, and huge granulate forelegs with contiguous coxae surrounded by an enlarged sternellum. The pygidial terminus is rounded in *Philolithus densicollis* (Horn) and bifurcate in *Stenomorpha puncticollis* (LeConte). First-instar larvae lack granules on cranium and forelegs, have 2 setae on the labrum, possess egg bursters, and are very similar in both species. Eggs are large, averaging 2.5 mm in length in *P. densicollis* and 3.1 mm in *S. puncticollis*. Pupae are not known. The two species are sympatric in eastern Washington state. Adults occur in autumn, living only one month. A female deposits about 1 egg per day. Eggs of *P. densicollis* hatch quickly and the first winter is passed in an early larval stage. Eggs of *S. puncticollis* apparently overwinter and hatch in early spring. The full life cycle probably takes two years. Cold temperature of the second winter breaks a developmental diapause and leads to adult eclosion the following autumn; *S. puncticollis* emerges somewhat later than *P. densicollis*. The prolonged immature phase as a subterranean scavenger is seen as a major adaptation to xeric environments.

Introduction

Up to the present time there have appeared no descriptions of the immature stages of any North American species in the tenebrionid tribe Asidini. The only significant information on the biology of any of these beetles has come from ecological studies at the Hanford Reservation, Washington (Rickard and Haverfield, 1965; Rickard, 1970; Hinds and Rickard, 1973), and at the Nevada Test Site (Tanner and Packham, 1965).

In the process of conducting systematic studies of the tribe Asidini (Brown, 1971), I have reared immature stages of many species, with the intention of describing them all together in a single monograph. However, completion of that project is several years away. As there are active ecological studies being conducted at the Hanford Reservation, it is important to make available the findings of life history studies pertinent to that region. Also there is current interest in the higher classification of the Tenebrionoidea with much attention focused on larvae, lending additional importance to the prompt dissemination of information on the morphology of immature Asidini.

Philolithus densicollis (Horn) and *Stenomorpha puncticollis* (LeConte) are the dominant ground-dwelling beetles found in southeastern Washington in autumn (Rickard, 1970). Both species were redescribed and illustrated (adults) by Boddy (1965). Brown (1971) transferred *P. densicollis* from *Pelecyphorus* Solier to *Philolithus* Lacordaire.

On 11 October 1968 I received living adults of both species from Dr. W. H. Rickard of the Battelle Pacific Northwest Laboratories, which he had removed from pit traps at the Hanford Reservation near Richland, Washington, on 5 October 1968. The following information is based on studies of those insects, supplemented by observations of other species of *Philolithus* and *Stenomorpha.*

Materials and Methods

Upon receipt, the living adults were sexed. The male has the apical segment of the maxillary palpus larger than that of the female (Brown, 1971), a feature that is reasonably easy to see in living specimens. Each female was given a number and placed in a separate container. About half the females each had a single male; the rest were alone.

The culture containers consisted of standard 16 oz. (.475 1) plastic food containers with about 20 mm of sand that had been washed and passed through a U.S. Standard No. 30 sieve (590-micron opening). The beetles were fed lettuce and ground-up chicken feed. The sand was watered periodically to stimulate oviposition.

On approximately 5-day intervals, the cultures were checked and adult mortality recorded. When any female died, the culture was checked for eggs. After the first 10 days all cultures were checked for eggs.

Eggs were recovered by passing the substrate sand successfully through U.S. Standard No. 20 (841 micron opening) and No. 30 sieves. Virtually all eggs were caught on the No. 20 sieve. Eggs were picked up singly with a small, dampened camel-hair brush.

The eggs were incubated in 60 mm by 15 mm covered plastic petri dishes. These were maintained in a moisture saturated environment by placing the dishes on a wire rack over water in plastic shoe boxes which were kept in a controlled temperature room at 70 F (21.1 C). The dishes were checked at intervals ranging from 4 to 7 days and the following series of data recorded; number of viable eggs (creamy color), number of dead eggs (brown color), number of first-instar larvae, and number of second-instar larvae. The number of larvae removed for preservation or culturing was also noted.

The larvae are actively cannibalistic, and attempts at mass rearing were not successful. Two rearing methods were used. The first requires little attention and is ideal for long-term rearing of asidine larvae when periodic checks for exuviae are not needed. The container consists of a common 8 oz (.238 l) clear plastic, disposable cold-drink cup. About 15 mm of plaster of paris containing 10 percent powdered charcoal by volume is poured in and a section of plastic Tygon tubing, one-half inch (12.7 mm) inside diameter inserted into the center of the fresh plaster. This serves as a watering tube. After the plaster hardens, a thin layer of plain sand is added, the larva placed on the sand, and the cup filled about half way with a sand-and-food mixture. This arrangement requires watering about once a week, and changing of food every three to four months. It offers the larva a moisture gradient similar to its natural habitat.

The second method used in this study was a modification of Wade and St. George's (1923) salve boxes as developed by R. E. Somerby (1972). It consists of a round plastic box 45 mm in diameter and 15 mm deep with a 5 mm layer of the plaster-of-paris and charcoal mixture. The tight-fitting lid has a 15 mm round hole covered with fine nylon netting. The plaster-of-paris is saturated with water, a thin layer of sand added, the larva placed on the sand, and covered with a sand-and-food mixture. The sand must be changed about once a week.

For the present study the sand used was river sand that had been washed, passed through a No. 30 sieve (590-micron opening), and sterilized. The food was common chicken feed that was ground up, passed through the No. 30 sieve, and sterilized. No effort was made to define a diet. Larvae have also been reared on ground-up rabbit pellets, oatmeal, alfalfa, or dry dog food. The food was mixed homogeneously with sand at a ratio of 10 parts sand to 1 part food by volume.

The first larvae were cultured on 14 November 1968. Rearing was terminated on 25 March 1969 because I was leaving Riverside, California where the work was being carried out. Larvae were killed and fixed in van Emden's solution (Emden, 1942), and later transferred to 80% ethyl alcohol with 4% glycerine.

Drawings of fresh eggs were made with an AO Spencer stereoscopic microscope with 2X objectives and a 10 mm grid with 1 mm squares in the 10X eyepiece. Overall views of larvae were drawn from specimens in alcohol. The labium, maxillae, and epipharynx were dissected from alcohol specimens and dry exuviae. A No. 2 insect pin with the point beaten flat and honed on a whetstone was used as a scalpel. This instrument was found superior to those commercially available for such minute dissections. Drawings were made by the author using a Wild M-5 stereoscopic microscope with drawing tube. The scale was drawn from a stage micrometer.

The terminology is based on that of Wade and St. George (1923). The descriptive sequence follows that of Spilman (1963).

The primary specimens and voucher adults are deposited in the Peabody Museum of Natural History, Yale University. Additional specimens will be deposited in the United States National Museum, Battelle Pacific Northwest Laboratories, and in the collection of the author.

DESCRIPTIONS

Tribe Asidini

MATURE LARVA. Body elongate, straight, weakly moniliform and semicylindrical dorsally (Figs. 2A, 5A), relatively flattened ventrally; generally unsclerotized except for mandibles, claws, and urogomphi; overall color creamy white to yellowish.

Head prognathus, golden brown in color, covered dorsally with darker, globular granules, at least on anterior half; setae short and sparse dorsally, becoming longer and denser laterally and ventrally. Apparently four poorly defined ocelli present. Clypeus transverse, united with frons, but set off by a deep sulcus (Fig. 1C, *c*); density of granules on clypeus equal to or exceeding density on frons. Labrum (Figs. 3C, 5C) emarginate and densely setose apically, with a median transverse band of flattened, spinose setae; sclerotized only on basal third and connected to clypeus by a broad, unsclerotized membrane. Epipharynx (Figs. 3D, 6D) with dense midlateral series of prostrate spinose setae facing medioposteriorly. Antenna (Figs. 3A, 6A) glabrous, arising from a fleshy swelling near ventral fossa of mandible; total length about two thirds that of mandible; first and second segments slender but each slightly swollen apically, the first longer than the second; third segment minute, set in center of flattened apex of second segment and bearing a single terminal seta. Mandible (Figs. 3A, 6A) bidentate, strongly developed and darkly sclerotized especially at apex and mola; distinctly concave dorsally, convex ventrally; lateral margin carinate, broadly expanded, with a preapical gibbosity (Fig. 3A, *pg*), usually more prominent on right mandible; dorsal margin between apex and mola sometimes with a small gibbosity or tooth on right mandible, occasionally on left (Fig. 6A, *t3*); submargin of mandible ventrally with an elongate, membranous area densely packed with long setae; mola relatively flat. Maxilla (Figs. 3B, 6B) with mala and stipes fused, bearing numerous long setae; mala reaching to about apex of mandibles, bearing on inner margin a double row of stout, pointed, recurved spines, becoming longer at apex of mala; palpus slender, three segmented; cardo flattened, transverse; articulating area swollen and prominent. Submentum and gula appear fused with cranium, sutures often not visible; setae numerous and long. Labium (Figs. 1C, 3B, 6B) slightly shorter than maxillae, bearing numerous long setae; mentum barrel shaped, slightly longer than wide; prementum smaller, trapezoidal, connected to mentum by a broad, glabrous membrane; ligula a single median apical projection; palpi two segmented, the second segment slightly smaller and narrower than the first. Hypopharynx with a large irregular fleshy lobe (Fig. 1C, *h*) bearing numerous setae directed toward pharynx (p); hypopharyngeal sclerome (*hs*) strongly sclerotized and tooth-like, partially embedded in fleshy tissue of hypopharynx but remaining firmly attached to cranium by the hypopharyngeal bracon when maxillae and labium are removed; hypopharyngeal bracon (Figs. 3A, 6A) in two parts, the lateral part integrated with cranium in region of ventral mandibular fossa, the median part bearing the sclerome separated from the lateral part by a distinct membranous area.

Prothorax with sparse, fine setae dorsally; tergum semicylindrical, wider than long, and longer than meso- or metathorax; usually with a pigmented anterior border and narrower posterior border; sternum (Fig. 1A) with eusternum, prehypopleurum and preepipleurum fused into a single collar-like unit; preepipleurum swollen, visible from above, completely separated from epipleurum, and set off from prehypopleurum by a deep sulcus; epipleurum fused with prothoracic tergum, lacking any visible suture; sternellum (articulating membrane of Schulze, 1962) greatly developed, swollen and shaped somewhat as a quarter sphere, almost surrounding coxae, and bearing scattered short, stiff setae on basal area. Mesothorax shorter than all other segments, widest in middle, with scattered, fine, short setae dorsally, and more numerous, long setae ventrally; sternum with eusternum and sternellum fused into a lumpy swollen central mass, bordered laterally by the folded epipleurum; preepipleurum bearing very large, elliptical first thoracic spiracle, which is deeply sunken and almost hidden by protruding sternal tissue. Metathorax similar to mesothorax, but longer, and from above more nearly resembling abdominal segments. Second thoracic spiracle much smaller than first spiracle, borne on preepipleurum and usually hidden.

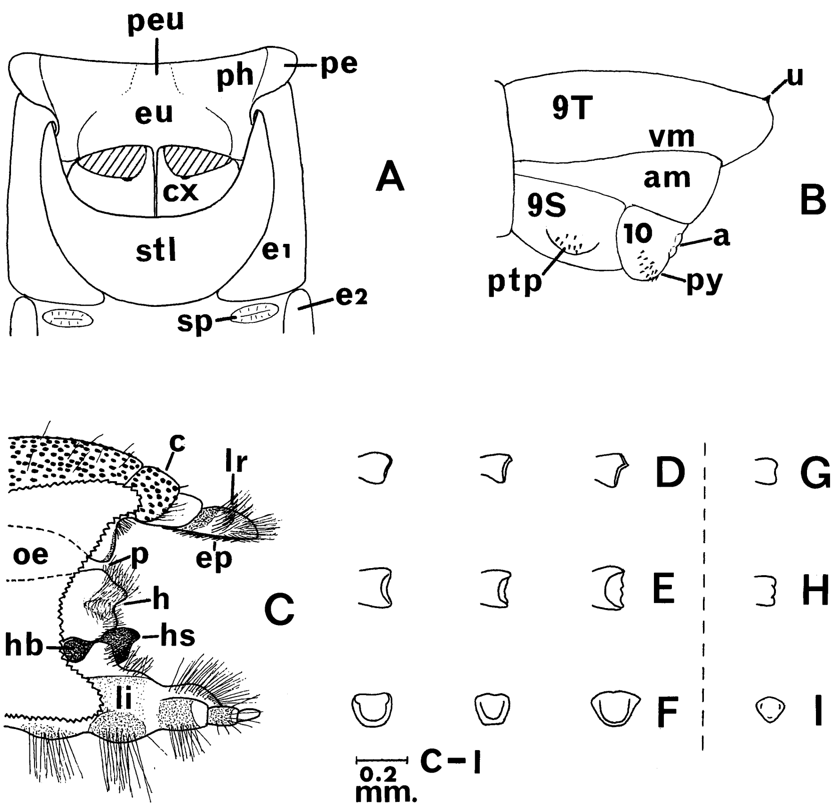

FIG. 1. Larval morphology of generalized Asidini: A) sternum of prothorax and part of mesothorax, legs removed; B) terminal abdominal segments, lateral view; C) lateral view of head with right mandible, maxilla, and part of cranium removed (jagged line); D–F) *Philolithus densicollis,* outline of hypopharyngeal sclerome of 3 specimens to show variation; D) right, lateral view (orientation of 1C); E) ventral view (aboral side facing viewer, see Fig. 3A); F) apical view (aboral side at bottom of drawing); G–I) *Stenomorpha puncticollis,* outline of hypopharyngeal sclerome; G) right, lateral view; H) ventral view (see Fig. 6A); I) apical view. Terminology: *a* = anus; *am* = articulating membrane; *c* = clypeus; *cx* = coxa; *e1* = prothoracic epipleurum; *e2* = mesothoracic epipleurum; *ep* = epipharynx; *eu* = eusternum; *h* = hypopharynx; *hb* = hypopharyngeal bracon; *hs* = hypopharyngeal sclerome; *li* = labium; *lr* = labrum; *oe* = oesophagus; *p* = pharynx; *pe* = preepipleurum; *peu* = preeusternal subdivision of eusternum; *ph* = prehypopleurum; *ptp* = preterminal pseudopod; *py* = pygopod; *sp* = 1st thoracic spiracle; *stl* = sternellum; *u* = urogomphus; *vm* = ventral margin of pygidium; *9S* = 9th abdominal sternum; *9T* = 9th abdominal tergum (pygidium); *10* = 10th abdominal segment.

Abdominal segments 1 to 7 very similar in size and shape; each widest in middle, convex laterally in dorsal view and slightly wider than long (Figs. 2A, 5A); dorsum generally glabrous, but setae present laterally and ventrally; spiracles elliptical, located laterodorsally, about one-sixth segment length behind anterior base (Figs. 2B, 5B), with a single nearby seta dorsad; a small oblique sclerotized stigma located in approximately the same plane but about one-fifth segment length ahead of posterior base, with a single seta directly anterior; sternum undifferentiated except for lateral fold of epipleurum, more flattened than the evenly convex dorsum, but may be swollen and protruding in turgid specimens. Abdominal segment 8 similar to preceding but more abruptly widened laterally, and with dorsal setae more evident, especially posteriorly. Abdominal segment 9 varying from a rounded (Fig. 2A) to deeply bifurcate terminus (Fig. 5A); urogomphi weak to well developed; dorsum variously armed with stout spines and setae; sternum about half the length of tergum and bearing a ventrolateral swelling (preterminal pseudopod, Fig. 1B, *ptp*) armed with several stout spines. Abdominal segment 10 with distinct lobed, but not elongate pygopodia (*py*), variously armed with stout spines; anus dorsal to pygopodia and located between their bases, surrounded by four broadly joined papillae generally forming a circle. United ninth sternum and tenth segment retractile into a cavity in ninth tergum (Fig. 2C) and joined to it by a wide articulating membrane (Fig. 1B, *am*); tenth segment always partially exposed and never enclosed by ninth sternum when retracted.

Prothoracic leg (Figs. 3E, 6E) greatly enlarged, almost twice the length, and two to three times the girth of the other legs; coxa massive, left and right coxae contiguous along a straight midline, partially to completely concealed by sternellum (Fig. 1A, *stl*); trochanter conical, arising from ventral surface of coxa, but appearing anterior because of normal position of legs in preserved specimens, bearing numerous globular granules similar to those on head, becoming especially dense at apex; femur massive, roughly triangular, arising on dorsoanterior portion of trochanter, with similar granules, ventrally with a set of comb-like, thick, long setae arranged in an irregular row, and dorsally with numerous thinner, often longer setae; tibia and tarsungulus immovably united, but divided into three segments, the tibia, unsclerotized basal part of tarsungulus, and strongly sclerotized claw; tibia often with large granules and with a single ventral row of long thickened setae forming a comb extending onto unsclerotized base of claw, dorsally with numerous, irregularly placed, long, thin setae; claw large, equal in length to trochanter, asymmetrical, curved and strongly concave ventrally, convex dorsally, and blunt to sharply pointed apically. Meso- and metathoracic legs much smaller, very similar to each other; coxae separated by at least half of one coxal diameter, and not concealed by sternellum, bearing scattered setae but no distinctive spines; orientation of legs lateral rather than anterior; configuration of trochanter, femur, tibia and tarsungulus similar to prothoracic legs except for smaller size and relatively more elongate members, the claw especially thin; granules lacking but two irregular rows of thick spines present, one posterior and one ventral, running from trochanter to tarsungulus, with thinner and longer setae on other surfaces.

SECOND-INSTAR LARVA. Closely resembles mature larva in form, but with fewer granules, setae and spines (Figs. 3F-K, 6F-H), and with antennae relatively stouter.

FIRST-INSTAR LARVA. Differs from all other instars in the following characters. Body compact, widest in middle (Figs. 4A, 7A), unsclerotized and pale white in color except for tips of mandibles, claws, egg bursters, and urogomphi.

Head surface faintly rugulose and lacking any granules (Figs. 4B, 7B). Ocelli apparently four in number. Labrum bearing only two distinct conical, spinose setae. Clypeus apparently lacking setae. Antenna relatively broader than in later instars; second segment swollen, longer and broader than first. Mandible lacking ventral membranous setose area, and bearing a distinct conical spine near dorsal base.

Prothorax longer than other segments, lacking any pigmentation or granulation; may or may not bear spine-like egg bursters. Mesothorax and metathorax subequal, about two-thirds as long as prothorax; spine-like egg bursters present dorsolaterally.

Abdominal segments 1 to 8 subequal, similar in length to meso- and metathorax; body widest at about third or fourth abdominal segments; spine-like egg bursters present dorsolaterally on all segments. Abdominal segment 9 with terminus rounded to weakly emarginate; urogomphi small, usually terminal; dorsal spines lacking; sternum with faint swelling in position of preterminal pseudopod, spines lacking. Abdominal segment 10 lacking spines on pygopodia.

Prothoracic leg lacking granules, but with one to three distinct pigmented spines each on ventroposterior surface of trochanter, femur, and tibia. Meso- and metathoracic legs with few faint, unpigmented spines.

EGG. Elongate elliptical, slightly narrower at one end than the other (Figs. 4C, 7C); width approximately one-third length, widest point slightly off center toward blunt end; in cross section, outline forms a circle flattened at one pole (Fig. 4D). Surface smooth and shiny, with no sculpturing visible under dissecting microscope. Color creamy white when fresh, becoming brownish yellow with age. Size relatively large, always greater than 2 mm in length.

REMARKS. The above detailed description at the tribal level is testimony to the extreme uniformity of the larvae of North American Asidini that have been seen to date. The mature larvae can be briefly characterized by the unsclerotized, fleshy appearing body, the dorsally concave mandibles with preapical gibbosity and submarginal setose area, the pronounced granulation of the cranium, the collar-like eusternum and swollen pre-epipleurum, the huge granulate prothoracic legs with contiguous coxae surrounded by the enlarged sternellum, the distinctly swollen and spinose preterminal pseudopodia of the ninth abdominal sternum, and the lobed, but not prolonged spinose pygopodia. This is based on examination of larvae of the genera *Astrotus* LeConte, *Philolithus* Lacordaire, *Gonasida* Casey, *Glyptasida* Casey, *Pelecyphorus* Solier, *Asidina* Casey, *Trichiasida* Casey, *Asidopsis* Casey, *Stethasida* Casey, and *Stenomorpha* Solier (Brown, unpublished); a representation sufficiently diverse that the addition of data from other genera will probably not alter characterization in any significant degree. Whether the Palearctic and African Asidini fit this picture is unknown as yet. However, the illustration of posterior abdominal segments of *Asida lutosa* Solier from Russia (Ogloblin and Kolobova, 1927, fig. 24) is very similar to the North American Asidini.

Descriptions of the other genera must await later monographic treatment, but a brief discussion of the variation at the generic level may be of value at this time. The first-instar larvae are so uniform that they are very difficult to separate at the generic level. The only obvious variation seen in later instars of the genera observed is the shape of the pygidium and development of the urogomphi. The larvae fall into three main groups; 1) *Astrotus, Philolithus, Gonasida,* and *Glyptasida* with the pygidium rounded posteriorly and the urogomphi very small; 2) *Pelecyphorus, Asidina,* and *Trichiasida* with the pygidium emarginate to weakly bifurcate posteriorly and with moderate-sized urogomphi; and 3) *Asidopsis, Stethasida,* and *Stenomorpha* with the pygidium deeply bifurcate and the urogomphi large.

Differentiation of genera and species within these three groups will be difficult in most cases. Much further study is needed of the specimens on hand before the problems can be resolved. For the purposes of this paper, no attempt is made to distinguish generic from specific characters of *Philolithus densicollis* and *Stenomorpha puncticollis.* These two species are largely sympatric; no other species of Asidini occur in their ranges.

Morphological changes during the growth of the larvae add to the difficulties in characterizing genera and species. The second through final prepupal instars are very similar in general appearance, but differ in quantitative characters such as number of setae, spines, granules, and of course in overall size. As the larva grows larger, the surface area increases, allowing an increase in number of spines, granules, etc. Also there are more subtle changes with age; the bifurcation of the pygidium becomes deeper, the antennae become thinner, and bald spots (areas devoid of setae or granules) develop on the cranium and pygidium.

The higher classification of the family Tenebrionidae is in an unsettled state. However there is a growing body of evidence from both adult and larval morphology that the family has two fundamental divisions, the "tentyroid" and "tenebrioid" lines (Blaisdell, 1939; Koch, 1955; Kelejnikova, 1971; Doyen, 1972). However, there is little agreement as to the subdivisions or ranks of the two lines. Doyen (1972) considers the two lines to be of family rank (Tentyriidae and Tenebrionidae) whereas Watt (1966, 1972) includes both lines within one family (Tenebrionidae). Further study is needed, particularly of immature stages, before the controversies can be settled. For the present, I am considering both lines as belonging in one family, the Tenebrionidae, with the tentyroids constituting the subfamily Tentyriinae, and the tenebrioids divided into several subfamilies as listed by Watt (1966) and including Alleculinae, Lagriinae and Nilioninae as proposed by Doyen (1972) and Watt (1972).

The larvae described here confirm the placement of the Asidini in the Tentyriinae. They also add significant information regarding characters of importance in larval classification. Scopin (1964) emphasized the structure of the pygidium. He stated that urogomphi are always absent in Tentyriinae (his "Tentyromorpha" and "Asidomorpha"). The larvae of *Stenomorpha* have large urogomphi, the first such recorded case in the Tentyriinae. This case indicates that the pygidium is a relatively poor indicator of higher phyletic relationships in the Tenebrionidae. It points out the difficulty of generalized descriptions of higher categories, such as subfamily, based on few samples from limited parts of the world. However, a general picture of larvae of Tentyriinae is emerging based on a scattering of American, European, and African material. The mandibles possess a lateral strongly setose area that may be ventral, as in the Asidini, or dorsal in other tribes as pointed out by Doyen (1972). The pygopodia are armed with distinct spines and the forelegs are greatly enlarged (Skopin, 1964). Another character that has not been stressed before is the enlarged sternellum partly surrounding the contiguous procoxae. Other characteristics of Tentyriinae are the large eggs (Doyen, 1972) and the presence of only two spines on the labrum of the first-instar larva (Kelejnikova, 1971).

Based on the larval features discussed above, it is possible to clarify the status of other tribes. Marcuzzi and Rampazzo (1966) described larvae of the American genera *Coniontis* and *Coelus* (tribe Coniontini). They concluded that the placement of the Coniontini in the Tenebrioninae after the Eleodini (Gebien, 1910) was correct, perhaps because the pygidium is superficially similar to that of the Eleodini. However, a comparison of larvae of Coniontini with the Asidini shows that the Coniontini clearly belong in the Tentyriinae. The structure of the mandibles, prothoracic sternum, pygopodia and preterminal pseudopodia are typically tentyrine. On the basis of adult characters Casey (1908), and Blaisdell (1939) also considered the Coniontini to be tentyrine, and Doyen (1972) using adult and larval characters reaffirmed the placement of the Coniontini in Tentyriinae. Why Gebien (1910) placed the Coniontini in the Tenebrioninae is unknown, but the error has been transmitted into major works on North American Coleoptera (Leng, 1920; Arnett, 1960).

No other larvae of American Tentyriinae have been described. Larvae of two genera of Cryptoglossini, *Cryptoglossa* Solier and *Schizillus* Horn, have been reared (Brown, unpublished) and clearly belong in the Tentyriinae. Probably the most serious gaps in our knowledge of larvae of the American Tentyriinae are the large tribes Epitragini and Eurymetopini.

Key to Mature Larvae of Asidini in Eastern Washington.

Terminus of pygidium rounded; urogomphi small and slightly preterminal; ventral margin of pygidium lacking spines; tibia of prothoracic leg with 6 to many granules posteriorly; prothorax with sparse small granules dorsally .... *Philolithus densicollis*

Terminus of pygidium bifurcate; urogomphi large and terminal; ventral margin of pygidium armed with small spines; tibia of prothoracic leg with 2 to 5 granules posteriorly; prothorax lacking granules ....
Stenomorpha puncticollis

Philolithus densicollis (Horn)
Figures 1–4

MATURE LARVA. Length 29 mm; head capsule width 2 mm. About 8th to 9th instar (out of estimated 11 instars), 4 specimens of about equal size.

Cranium densely granulate over most of dorsal surface (Fig. 2A); granules less numerous posteriorly and suppressed along epicranial suture and paired median and lateral bald spots; a few short setae present between granules. Labrum (Fig. 3C) with transverse median row of moderate length, flattened spines. Epipharynx (Fig. 3D) with dense midlateral series of prostrate spines directed medioposteriorly, some spines present on basal membrane. Antenna (Fig. 3A) with apex of second segment symmetrical. Mandible (Fig. 3A) with preapical gibbosity (*pg*) well developed, convex, slightly more prominent on right mandible; left mandible with a small but distinct tooth on inner dorsal margin; no similar tooth on right mandible. Hypopharyngeal sclerome (Fig. 1D-F) deeply excavate (Fig. 1E), trapezoidal in cross section (Fig. 1F), bicuspidate; the wider adoral margin more prolonged apically and bearing cusp at each corner; the narrower aboral margin excavated, appearing stepped in lateral view

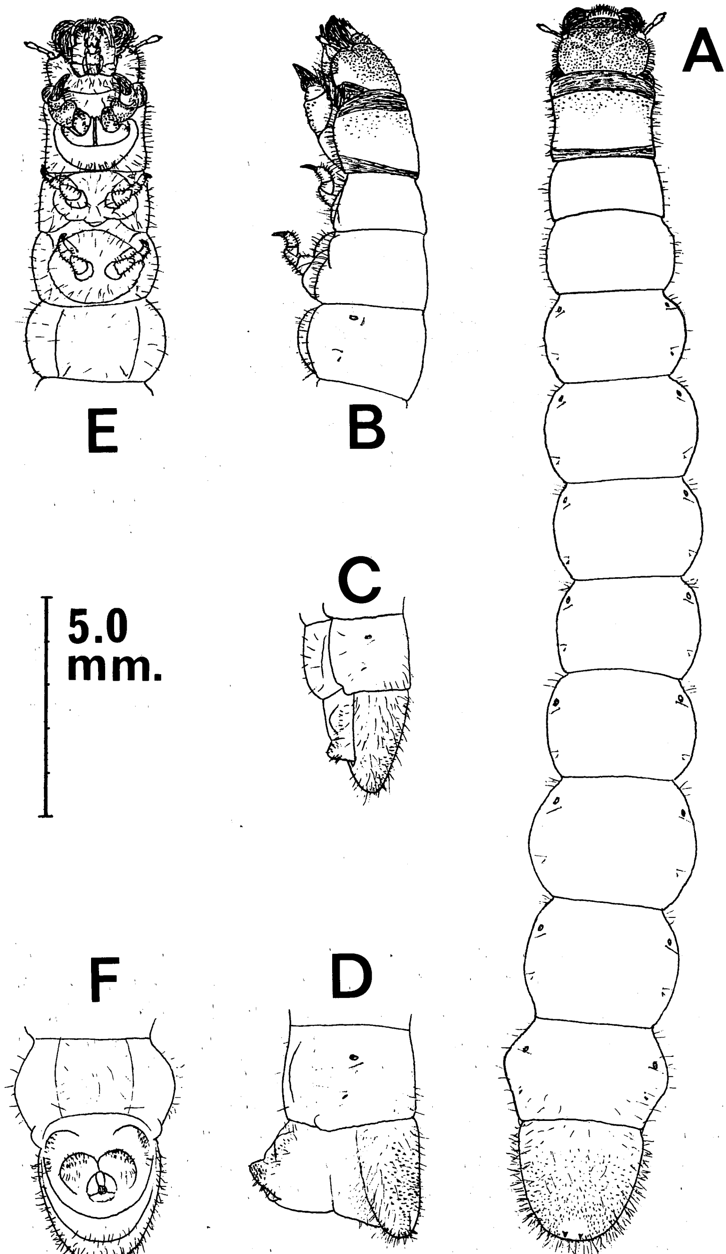

FIG. 2. *Philolithus densicollis,* mature larva: A) overall, dorsal view; B) anterior, lateral view; C) posterior, lateral view, ventral segments retracted; D) same, ventral segments extended; E) anterior, ventral view; F) posterior, ventral view.

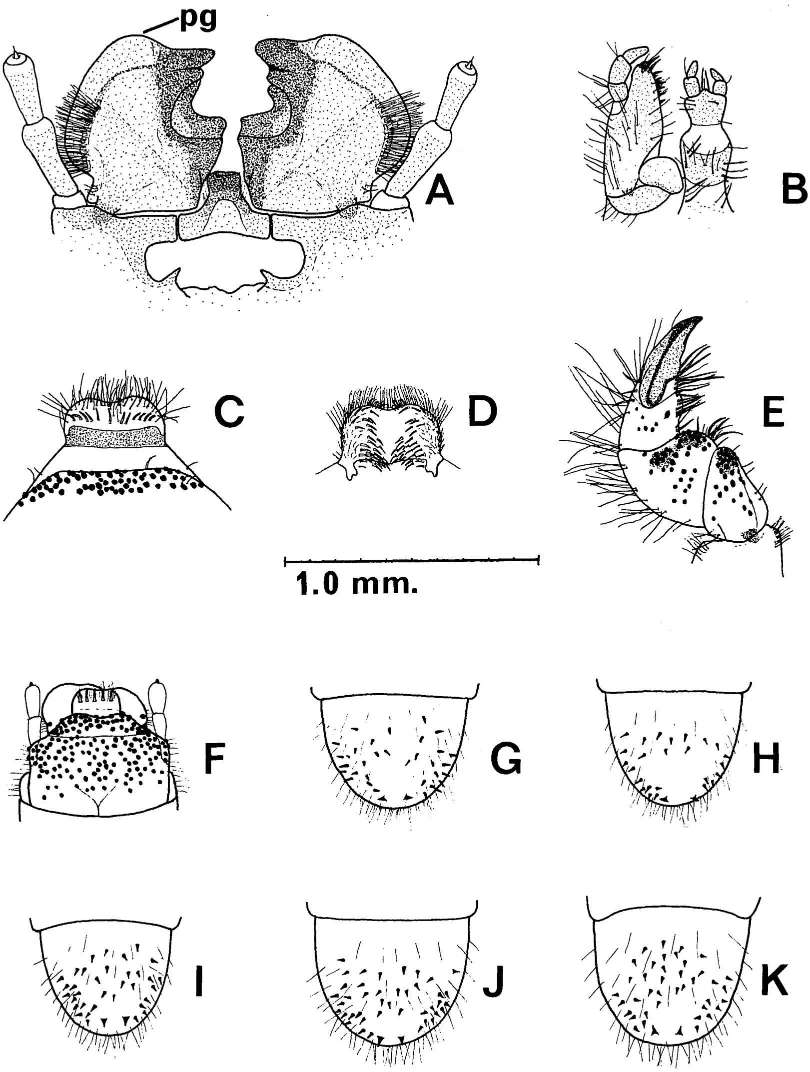

FIG. 3. *Philolithus densicollis:* A–E) details of intermediate stage larva: A) buccal area with maxillae and labium removed, ventral view (*pg* = preapical gibbosity of mandible); B) right maxilla and labium, ventral view; C) labrum, dorsal view; D) epipharynx; E) right prothoracic leg, posterior view; F) 2nd instar larva, head, dorsal view; G–K) 2nd instar larva, pygidium, dorsal view, 5 specimens showing variation.

(Fig. 1D), cusp lacking; inner excavation vaguely keyhole shaped when viewed from apex (Fig. 1F); margin usually smooth and rounded, but may be sharp and irregular.

Prothorax (Fig. 3A, B) with a rather broad, golden-brown anterior border, and a narrower posterior border on the tergum; scattered granules present over anterior half of tergum; sternellum short, about two thirds as long as wide. Meso- and metathorax lacking pigmented borders and granules.

Abdominal segments 1 to 8 (Fig. 2A) glabrous dorsally except for posterior region of segment 8; but laterally with a cluster of fine setae near anterior segmental base; sternum (Fig. 2E,F) with a few setae anteriorly and fewer posteriorly, two being longer than the others. Pygidium of abdominal segment 9 rounded posteriorly; urogomphi (Fig. 2A) very small, upturned, placed ahead of terminus of pygidium at a distance about equal to their own length; surface of pygidium covered with sharp, stout, conical spines, distributed randomly over posterior three quarters of pygidium, a few posterior to urogomphi, but none in a small, flattened bald area between and anterior to urogomphi; rounded lateral border of pygidium with numerous long, fine setae, but ventral margin lacking setae or spines (Fig. 3C); articulating membrane with scattered minute setae; sternum about half as long as tergum; preterminal pseudopod broadly swollen, with irregularly distributed conical spines. Abdominal segment 10 with prominent pygopodia; spines widely distributed over pygopod surface and tending to be directed anteriorly.

Prothoracic leg (Fig. 3E) with fine setae present on coxa, but spinose setae or granules absent; trochanter with granules densely packed apically forming a callus, spinose setae lacking; femur with a broad posterior apical callus of densely packed granules, and with a ventral comb of long, spinose setae; tibia with granules less numerous, but becoming densely packed posteriorly in mature larva (Fig. 3E is of a mid-instar larva with weaker development of granules); a regular comb of long spinose setae running along entire ventral length of tibia and onward with a slight offsetting onto unsclerotized basal part of tarsungulus, and with a parallel row of finer setae just anterior; no single erect seta near posterior base of claw.

SECOND-INSTAR LARVA. Length 4.77–5.68 mm (average of 3 normally extended specimens = 4.87); head capsule width 0.57–0.60 mm (average of 5 specimens = 0.59). Total specimens = 7.

Generally similar in form to later instars. Cranium with relatively large granules distributed sparsely over anterior two thirds to three quarters (Fig. 3F). Labrum usually with 5 flattened spines in transverse band. Second antennal segment slightly longer and more swollen than first, symmetrical at apex. Mandible with a distinct globular granule at lateral margin near base. Prothorax lacking granules or pigmented borders. Pygidium with 24–41 elongate spines (average of 5 specimens = 34) unequally distributed on left and right sides (Fig. 3G-K); urogomphi only slightly larger than spines; preterminal pseudopod usually with 5 spines in a double row. Pygopod with 14–22 spines (average of 5 specimens = 17) distributed somewhat irregularly, the posterior 3 or 4 spines more isolated and tending to be shorter and thicker. Prothoracic leg with spines and granules as follows; trochanter with 8–10 globular granules (average of 5 specimens = 9) and no spines; femur with 11–26 globular granules (average of 5 specimens = 15), and 2 ventral small pale colored spines; tibia with 2 posterioventral globular granules, 2 large anterioventral spines and 1 smaller together forming a comb; unsclerotized base of tarsungulus with 2 long thin spines.

FIRST-INSTAR LARVA. Length 4.08 mm; head capsule width 0.49 mm. Total specimens = 4, all with similar measurements.

Mandible with a large spindle-shaped spine at lateral margin near base (Fig. 4B). Prothorax with egg bursters present but extremely weak (Fig. 4A); egg bursters conical, spine-like, well developed on meso- and metathorax, and on abdominal segments 1 to 8; a distinct, long thin seta visible just behind egg burster on segment 8, and similar but extremely faint seta visible behind each egg burster on segments 2 to 7, but not visible on other segments. Pygidium of abdominal segment 9 with a few

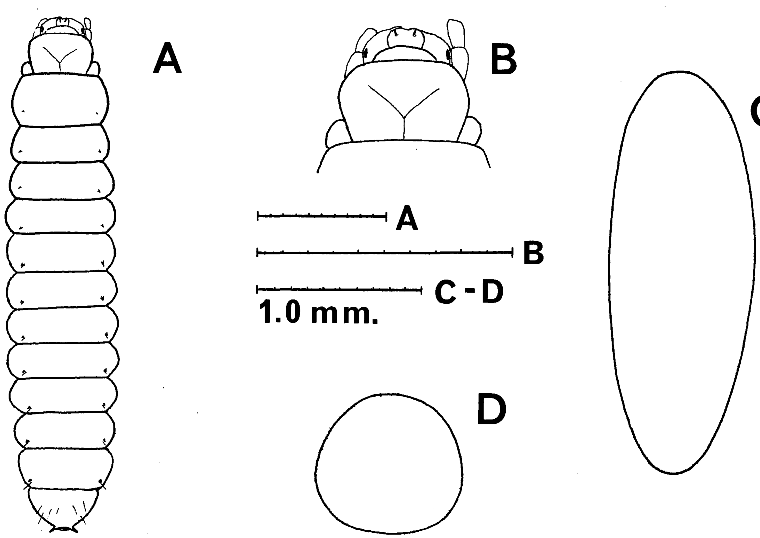

FIG. 4. *Philolithus densicollis:* A) first instar larva, overall dorsal view; B) same, head, dorsal view; C) egg, lateral view; D) egg, cross section.

scattered, faint setae; urogomphi slightly preterminal on pygidium, strongly divergent; terminus of pygidium rounded. Prothoracic leg with following arrangement of spines; trochanter with 2 short thick spines located ventrally near apex; femur with 1 similar spine ventrally and a much smaller spine posteriorly; tibia with 1 long thin spine midventrally, 1 shorter thin spine mid-ventro-posteriorly, and 1 thick short spine midposteriorly.

EGG. (Fig. 4C, D). Length 2.42–2.97 mm (average of 19 eggs = 2.55); width 0.82–0.95 mm (average of 19 eggs = 0.91); average width/length = 0.360.

REMARKS. Although the specimens upon which the description of the mature larval stage is based were probably not final instars, they were well enough advanced to be considered "mature" larvae. Chaetotaxy of the second instar larvae did not show much promise for constant characters at species level. For example, the position and number of spines on the pygidium were different and asymmetrical on each specimen examined (Fig. 3G-K). Spines and granules on the legs were highly variable. The hypopharyngeal sclerome (Fig. 1D-F) was more uniform and may prove to be a useful character.

Stenomorpha puncticollis (LeConte)
Figures 5–7

INTERMEDIATE STAGE LARVA. Length 20 mm; head capsule width 1.6 mm. About 6th to 7th instar (out of estimated 11 instars), 1 specimen with above measurements and 1 smaller specimen.

Cranium moderately densely granulate over most of dorsal surface (Fig. 5A), granules rather sparse posteriorly, and suppressed along epicranial suture and several median and lateral bald spots; only a few short setae present between granules. Labrum (Fig. 6C) with a transverse median row of short to moderate length flattened spines. Epipharynx (Fig. 6D) with moderately dense midlateral series of prostrate spines directed medially, spines absent on basal membrane. Antenna (Fig. 6A) with apex of second segment asymmetrical. Mandible with preapical gibbosity well developed, convex, slightly more prominent on right mandible; both mandibles with a distinct third tooth on inner dorsal margin (Fig. 6A, *t3*), slightly more developed and farther from apex on left mandible. Hypopharyngeal sclerome (Fig. 1G-I) vaguely triangular in cross section with adoral margin convex (Fig. 1I); tricuspidate (Fig. 1H), the cusps subequal, the single aboral cusp flatter and broader.

Prothorax (Fig. 5A) with anterior border narrow and weakly pigmented;

posterior border unpigmented (but may be pigmented in more mature larva); granules absent on tergum; sternellum short, about one-half as long as wide. Meso- and metathorax lacking pigmented borders and granules.

Abdominal segments 1 to 8 (Fig. 5A) glabrous dorsally and laterally except for a few setae near spiracles and stigmas; sternum (Fig. 5D, E) with few setae. Pygidium bifurcate posteriorly (Fig. 5A) and with a broad median depressed area extending to base of forks; urogomphi large, upturned, and terminal (Fig. 5C); surface of pygidium covered with sharp, stout, conical spines distributed unevenly over posterior 9/10, leaving numerous bald areas, fine short setae scattered dorsally and laterally; ventral margin of pygidium (Fig. 5C, E) with a band of small but distinct and numerous spines; articulating membrane glabrous; sternum about one-half as long as tergum (Fig. 5C); preterminal pseudopod broadly swollen, with irregularly distributed conical spines. Abdominal segment 10 with prominent pygopodia, spines of varying sizes directed anteriorly, distributed in a transverse band of about 3–4 irregular rows.

Prothoracic leg (Fig. 6E) with fine setae present on coxa, but spinose setae or granules absent; trochanter with granules tightly packed apically, rapidly becoming sparse subapically, a single seta present midposteriorly; femur with a broad posterior apical callus of densely packed granules, and with an irregular ventral cluster of short to medium length spinose setae, a single seta present midposteriorly; tibia with 2 globular posterioventral granules (up to 5 in larger larvae), with a ventral comb of 2 to many moderately long spinose setae, and a parallel row of finer and longer setae just anterior; unsclerotized basal part of tarsungulus with a similar but slightly offset comb, a single erect seta present near posterior base of claw.

SECOND-INSTAR LARVA. Length 5.23–5.54 mm (average of 3 specimens = 5.38); head capsule width 0.59–0.64 mm (average of 3 specimens = 0.60). Total specimens = 3.

Generally similar in form to later instars. Cranium with relatively large granules distributed moderately densely over anterior three-quarters (Fig. 6F). Labrum witn 4–5 flattened spines in transverse row. Second antennal segment slightly longer and more swollen than first, only slightly asymmetrical at apex. Mandible with an indistinct globular granule at lateral margin near base. Prothorax lacking granules or pigmented borders. Pygidium with 12–16 spines (average of 3 specimens = 13) mostly located laterally (Fig. 6G, H); urogomphi much larger than spines, terminal and upturned; bifurcation of pygidium less pronounced than in later instars; preterminal pseudopod with 5–6 spines in an irregular double row. Pygopod with 12–16 subequal spines (average of 3 specimens = 14) in a double transverse row. Prothoracic leg with spines and granules as follows; trochanter with 8–9 globular granules and no spines; femur with 16–19 globular granules (average of 3 specimens = 18) and 2 ventral, small, curved pale spines; tibia with 2 posterioventral globular granules, 2 large

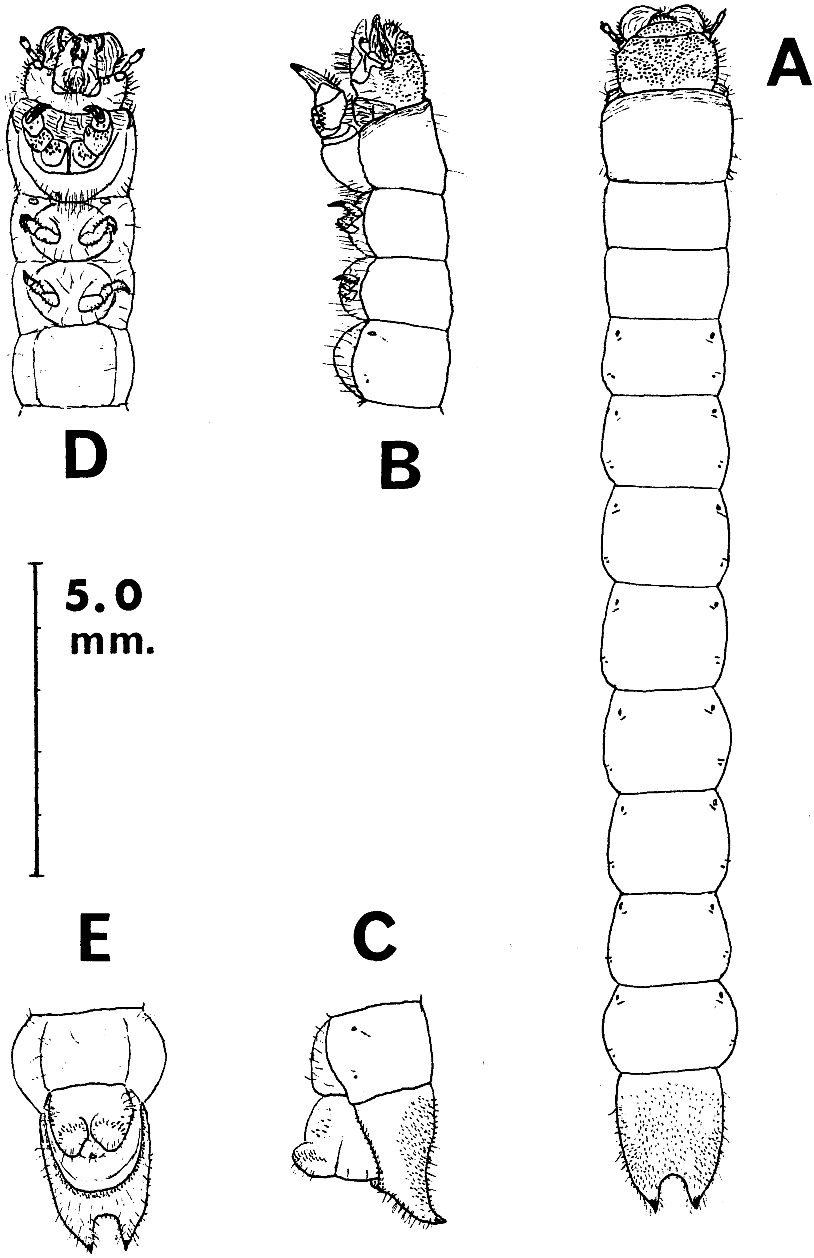

FIG. 5. *Stenomorpha puncticollis,* intermediate stage larva: A) overall dorsal view; B) anterior, lateral view; C) posterior, lateral view; D) anterior, ventral view; E) posterior, ventral view.

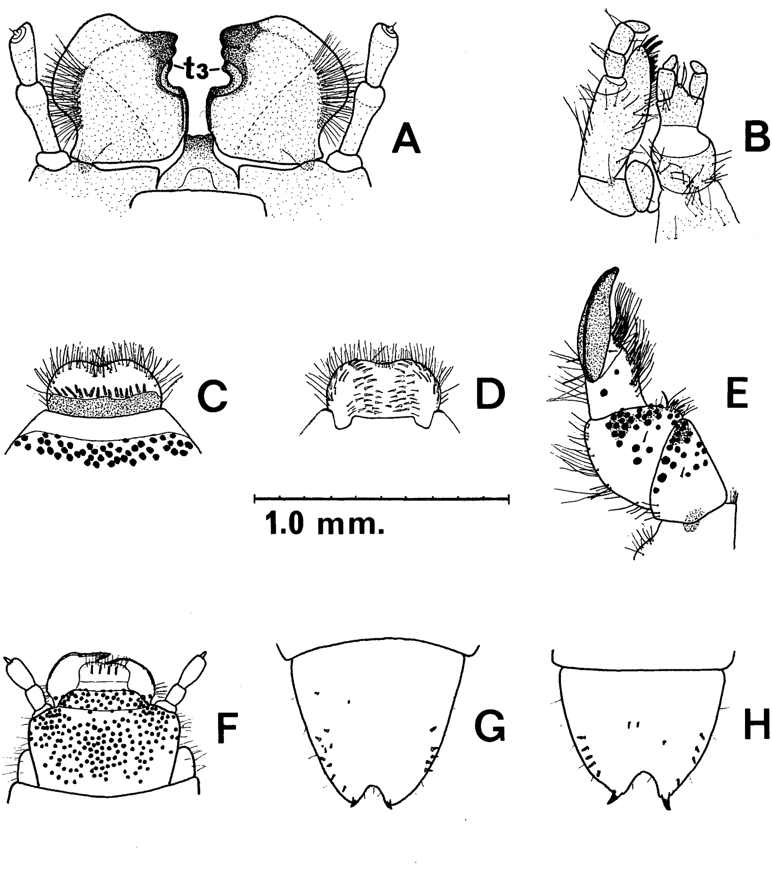

FIG. 6. *Stenomorpha puncticollis:* A–E) details of intermediate stage larva; A) buccal area with maxillae and labium removed, ventral view (*t3* = inner dorsal tooth of mandible); B) right maxilla and labium, ventral view; C) labrum, dorsal view; D) epipharynx; E) right prothoracic leg, posterior view; F) 2nd instar larva, head, dorsal view; G, H) 2nd instar larva, pygidium, dorsal view, 2 specimens showing variation.

anterioventral spines, and 1 much thinner and slightly more ventral; unsclerotized base of tarsungulus with 1–2 long thin spines.

FIRST-INSTAR LARVA. Length 4.15–4.38 mm; head capsule width 0.55 mm. Total specimens = 2.

Mandible with a large, spindle-shaped spine at lateral margin near base (Fig. 7B). Egg bursters not visible on prothorax, but present on all other thoracic and abdominal segments except pygidium, increasing in size posteriorly; no setae visible behind egg bursters. Pygidium with a few scattered faint setae; urogomphi terminal, directed dorsally and only slightly divergent; terminus of pygidium weakly emarginate. Prothoracic leg with the following arrangement of spines; trochanter with 2 short thick spines located ventrally near apex; femur with 1 similar spine located ventrally and a much smaller spine posteriorly; tibia with 1 long, moderately thin spine midventrally, 1 very short spine mid-ventro-posteriorly, and 1 slightly longer and thicker spine midposteriorly.

EGG. (Fig. 7C). Length 2.92–3.41 mm (average of 18 eggs = 3.08); width 1.04–1.21 mm (average of 18 eggs = 1.12); average width/length = 0.364.

REMARKS. After completion of the description and illustrations of the intermediate stage larva, I obtained from the United States National Museum a series of larvae from Roosevelt, Washington, collected 7 April 1942 and determined as *Euschides puncticollis* LeC. by M. C. Lane in 1942. *Euschides* is a synonym of *Stenomorpha*. Comparison with the reared larvae confirms that they are indeed *S. puncticollis*. There were 4 larvae about the size of the largest described here, and 3 larvae of much larger size. The large larvae measure about 35–40 mm in length, 3.5 mm in head capsule width, and fit the description of the intermediate-stage larva quite well. The only modifications of that description would involve characters that change with larval growth. The number of granules on the cranium increases; the comb of setae and spines on the prothoracic leg becomes denser; and the granules on the trochanter and femur become very numerous and tightly packed. One large specimen had 5 granules on one tibia, but all others had 2–4 granules, indicating that 5 is probably the maximum number for tibial granules. A narrow, faintly pigmented posterior border is visible on the tergum of the prothorax. The dorsum of the pygidium is depressed and concave in the posterior two-thirds, a feature not so strongly developed in younger larvae. This characteristic appears to be unique among larvae of the genus *Stenomorpha* and will probably serve to separate *S. puncticollis* from other larvae in the genus.

The presence of two distinct sizes of larvae in the USNM series strongly suggests that two generations were collected at one time. This lends added weight to the hypothesis of a two-year life cycle that will be discussed in the next section of this paper.

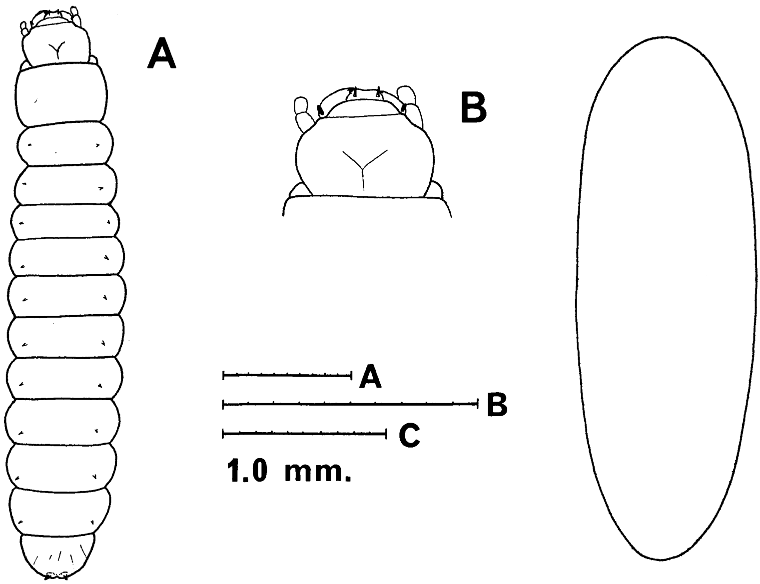

FIG. 7. *Stenomorpha puncticollis:* A) first instar larva, overall dorsal view; B) same, head, dorsal view; C) egg, lateral view.

BIOLOGICAL NOTES

ADULT LONGEVITY. The beetles were placed on sand substrate on 12 October 1968, one day after receipt. All beetles were alive on arrival, but parts of the legs of most specimens of *S. puncticollis* had been chewed off, while only a few of *P. densicollis* showed such damage.

Since the beetles could have been in traps several days before being removed on 5 October, it is reasonable to estimate 1 October as the average date of trapping. The major difficulty in estimating longevity from field-collected specimens is that the date of eclosion is unknown. In the case of the species considered here, many years of trapping indicate that the first adults appear in mid-September (Rickard and Haverfield, 1965; Rickard, 1970). Therefore it is unlikely that any of the individuals were more than 15 days old by 1 October.

Trauma during travel could also influence laboratory-observed longevity. Compared with other Asidini I have collected, the longevity figures in Table 1 appear somewhat low. For example, a series of 69 living specimens of *Philolithus actuosus* (Horn) collected at Twentynine Palms, California,

TABLE 1. Mortality of *P. densicollis* and *S. puncticollis* adults.

Date of death	Days after receipt	Probable days after trapping	*P. densicollis* Females	*P. densicollis* Males	*P. densicollis* Total	*S. puncticollis* Females	*S. puncticollis* Males	*S. puncticollis* Total
12-X	1	12	2	3	5	1	2	3
16-X	5	16	2	3	5	5	6	11
21-X	10	21	17	5	22	12	10	22
25-X	14	25				2		2
30-X	19	30	1		1	4	1	5
4-XI	24	35				1		1
8-XI	28	39	1		1	1		1
		Totals	23	11	34	26	19	45
Average longevity after receipt, days			10.0	6.2	8.7	11.6	7.9	10.1
Average longevity after trapping, days			21.0	17.2	19.7	22.6	18.9	21.1

on 9 September 1966 showed an average longevity of 24.5 days, with a maximum of 43 days. These specimens suffered a minimum of travel trauma as they were collected at dusk and transported by automobile at night to Riverside in little more than an hour. Other species of *Philolithus* and *Stenomorpha* are similar in longevity (Brown, unpublished).

By assuming that the adults of *P. densicollis* and *S. puncticollis* had eclosed an average of 10 days before trapping, a rough estimate of about 30 days for adult life is derived. It is clear that even after adjusting the data on mortality by estimating times of trapping and eclosion, both species are short lived as adults. This is completely consistent with data reported by Rickard (1970). However death appears to be a genetic factor, rather than environmental; in other words, the insects do not seem to be killed by winter cold, but die of old age. A major evolutionary adaptation of species in the tribe Asidini to xeric environments appears to be a reduction of the adult phase and a prolongation of the larval phase in the more hospitable subsoil environment.

Adults will feed readily on food provided them. However, when some adults of *Philolithus actuosus* were denied food and moisture, they continued to live an almost normal period and females laid eggs.

The data in Table 1 seem to indicate that *S. puncticollis* lived longer than *P. densicollis*, and that females of both species lived longer than males. Student's *t*-test was applied with the following results. The difference between means of total longevity of *P. densicollis* and *S. puncticollis* was not significant ($.2 < p < .3$). The difference between means of female and male longevity in *S. puncticollis* was significant ($.02 < p < .05$); the difference between means of female and male longevity in *P. densicollis* was almost, but not quite significant ($.05 < p < .1$). The data of Rickard and Haverfield (1965) show that *S. puncticollis* appears somewhat later in the season than *P. densicollis.* Therefore, it is possible that the specimens of *S. puncticollis* sent to me were younger, but the sample was not adequate to show this. The differential longevity of females and males may be a function of earlier eclosion of males. Attention in future pit trap surveys to the proportions of females and males recovered throughout the season may cast further light on this matter.

OVIPOSITION. Females in the tribe Asidini, including *P. densicollis* and *S. puncticollis*, have a well-developed ovipositor that is about half as long as the entire insect. The apical coxites are strongly sclerotized and function as drill bits. Eggs are laid to a depth of about 1 cm in the soil. The female is able to penetrate a very hard soil crust to deposit her eggs. They notably prefer damp spots in the soil for oviposition, a behavior that aids in reducing the risk of dessication. In contrast, tenebrionids in the genus *Eleodes* simply drop their eggs on the surface or partially bury them in loose soil or litter.

TABLE 2. Oviposition by females of *P. densicollis* and *S. puncticollis.*

	P. densicollis	*S. puncticollis*
Total females	23	26
Females laying eggs	11	5
Percentage of females laying eggs	47.8	19.2
Total eggs laid	60	29
Average eggs/laying female	5.5	5.8
Maximum eggs from 1 female	16	13

Even more than with longevity, these data seem depressed when compared with that of other Asidini, due possibly to trauma in shipment. For example, of the 34 female *Philolithus actuosus* in the California sample mentioned before, 22 (64.7%) laid eggs, with an average of 26.1 eggs per laying female, and a maximum of 60. Compared with figures reported for *Eleodes* (an average of 287 eggs per female, Wakeland, 1926; and 300 from a single female in a 24-hour period, Matteson, 1966), even the figures for *P. actuosus* seem low. However, the total biomass of eggs in the two groups may not be so different, considering that asidine eggs are much larger than eleodine eggs. Also because of their more careful placement, there is probably higher survival among eggs of the Asidini, than those of *Eleodes*.

Estimates of the rate of oviposition are difficult to make. The physiological strain of egg production on tiny species such as *P. densicollis* and *S. puncticollis* must be great, as the length of an egg is fully 20% of the length of the beetle. The fact that the eggs of these species are not much smaller than those of other species of Asidini having adults three times as large indicates that there must be a strong adaptive advantage for the production of large eggs by these beetles. Comparing data in Tables 1 and 2 shows that an average of one egg was laid every other day. Data from other species of Asidini that suffered less trauma in transport, suggest that one egg each day is probably a better estimate. For those females of *P. densicollis* and *S. puncticollis* that lived longer, eggs were recovered several times in numbers that indicated that egg production was fairly regular, rather than in spurts.

EGG INCUBATION. While *P. densicollis* and *S. puncticollis* are similar in longevity and oviposition, they differ in egg incubation periods. The eggs of *P. densicollis* hatched about 2 weeks after oviposition; the eggs of

TABLE 3. *P. densicollis* and *S. puncticollis* egg hatch at 70 F (21.1 C)

Days after recovery of eggs	*S. puncticollis* Viable eggs	Dead eggs	New 1st instar	*P. densicollis* Viable eggs	Dead eggs	New 1st instar
0	29			55		
7	26	3		45	10	
14	23	3		19	5	21
18	23			11		8
24	23			0		11
30	23					
38	23					
43	23					
53	20	1	2			
63	11	1	8			
71	9	1	1			
81	8		1			
93	3	5				
103	2	1				
114	2					
122	0	2				
Total hatch			12			40
Average days to hatch			62.6			17.5
Average viability			41.4%			72.7%

S. puncticollis took 2 months. Also the viability of *S. puncticollis* eggs appeared lower. (Of the original 60 eggs recovered from *P. densicollis,* only 55 are listed in Table 3 as "viable" because 5 were accidentally destroyed in handling.)

The first eggs of *S. puncticollis* were observed to have hatched on 23 December 1968. The rest hatched in early January. In southeastern Washington the near-surface soil temperature at this same time would have been close to freezing and the eggs probably would not have hatched until the spring. The evidence indicates therefore that *S. puncticollis* passes its first winter in the egg stage, while *P. densicollis* winters as an early instar larva. This could explain the later appearance of *S. puncticollis* adults.

FIRST LARVAL MOLT. The first-instar larva is inactive and does not feed. Although individual first instars were not isolated to determine time to the first molt, virtually all first instars of *P. densicollis* and *S. puncticollis* molted to second instars in less than two weeks. The second instar is active, burrows into the soil, and feeds. It appears to be much more resistant to dessication than the first instar.

While it may appear that *P. densicollis* obtains a strong developmental head start by its rapid egg hatch, its lead over *S. puncticollis* is probably only slight. Controlled temperature experiments with other species of *Philolithus* and *Stenomorpha* (Brown, unpublished) showed that temperatures of 40 F (4.4 C) or below completely stopped larval development. Thus, the majority of overwintering *P. densicollis* larvae remain in the second instar. By the time *S. puncticollis* hatches in the spring and rapidly molts to second instar, *P. densicollis* may not have reached any further than third or fourth instar.

LATER LIFE STAGES. Since study of *P. densicollis* and *S. puncticollis* was terminated before pupation, speculations on their later development must be extrapolated from studies of other species (Brown, unpublished).

It is clear from all the life history studies that have been conducted to date, that the larvae of the Asidini are subterranean scavengers of organic detritus. No living plant material was used in successfully rearing several species from egg to adult. The larvae are well adapted for their underground existence, the scooped mandibles and enlarged forelegs serving as excellent digging tools. Digging is accomplished by downward thrusts of the forelegs and opposing upward thrusts of the head. Forward leverage is achieved by expansion of the spinose abdominal terminus. The larvae easily bore through hardened plaster of paris, but do not ingest it. They do not appear to feed by passing the soil in which they burrow through their alimentary tract, but rather by selection of the edible material encountered in the soil. Larvae in the large cup cultures almost never came to the surface. Their unsclerotized bodies are poorly suited for exposure to surface conditions. *Eleodes* larvae in contrast, often surface and graze on plants and seeds. Therefore, it seems probable that developing asidine larvae are relatively independent of transient surface events such as rainfall, plant growth, and fires. Deep-boring larvae would be adversely affected only by a very prolonged drought. Specimens have been collected at depths exceeding 1 m. Growth rates would be effected by soil temperature. Rainfall and temperature probably have a particularly profound effect on survival of eggs, early instar larvae, and pupae.

Estimation of the total life cycle time from laboratory data is difficult because of differences in temperature regime and food. Temperatures used in the laboratory were probably above the average encountered in the field. While growth of early instar larvae probably almost stops for 3–4 months of winter in the field, the laboratory specimens were kept at 70–80 F. A two-month period of under 50 F (10 C) was needed to break diapause in late instar larvae before pupation occurred. Only here did the laboratory regime resemble the field. Overall the warmer lab temperature probably resulted in faster growth. The food medium used was more concentrated and probably more nutritious than food encountered in the field. This also could have accelerated larval growth.

Pupation is probably in cells near the surface or under protective objects, as the emerged adults are too fragile to dig through much soil. The majority of pupations in the lab were 1–2 years after oviposition, with an average of about 1.5 years. Taking into account the accelerated growth in the lab, it is probable that 2 years is the normal duration of the life cycle for most Asidini in the field. The role of cold in breaking an apparent developmental diapause in late instars is critical. From 4-5 months after restoration of normal temperature the larvae will pupate. Thus there seems to be a temperature-entrained biological clock that governs pupation in late summer and early fall. Preliminary experiments with varying photoperiods indicate that the light-dark cycle has no effect.

Larvae of other species of *Philolithus* and *Stenomorpha* had a variable number of instars before pupation, generally around 11–12. The pupal stage lasted only about a month. Larvae not subjected to a cold period continued to add instars and eventually died.

Although *P. densicollis* and *S. puncticollis* are smaller than the other species studied, it is probable that they also have a 2-year life cycle with about 11 instars. It is assumed that both species require prolonged low temperature in late instars before pupation occurs. Although future study may alter details of this hypothesis, it should serve as a useful model in ecological studies of these insects.

The occurrence of adult Asidini in the field is often characterized by massive but very local population outbreaks. *P. densicollis* is particularly well known for this phenomenon (Boddy, 1965). This may indicate an evolutionary trend toward periodic population explosions that dampen the effects of predation by simply swamping predators. As with all Tentyriinae, the Asidini lack defensive secretions. Population outbreaks were considered by Alexander and Moore (1962) to be significant in the evolution of periodical cicadas.

Acknowledgments

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