New Genus and Species of Triorophini, Including Immatures, Reproductive Structures, and Notes on Biology and Phylogeny (Coleoptera: Tenebrionidae)

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ABSTRACT A new genus and species of Triorophini, *Troglogeneion zapoteca*, is described from Oaxaca, Mexico. The immature stages and adult female external and internal reproductive structures of *Troglogeneion* are described. Larval evidence supports the close relationship of the tribes Tentyriini, Epitragini and Triorophini. Evidence from female internal reproductive tracts supports the retention of Triorophini as a separate tribe. This new genus represents a significant geographic range extension for the tribe Triorophini.

IN JULY of 1982, a large aggregation of triorophines was found beneath a large boulder and adjacent rocks in a large cavernlike grotto near the Yagul Ruins, Oaxaca, Mexico. These specimens represent a considerable geographic range extension for the tribe Triorophini, as well as a new genus and species.

Materials and Methods

In the laboratory (in September 1982), adults were transferred to a plastic, open-top, rearing container filled ¾ with a fine sterilized sand (able to pass through a 0.8-mm sieve). A plastic tube was pre-inserted into the sand in the center to the bottom to allow the addition of water to the lower layers of sand without wetting the top. Occasionally, a small amount of water was sprinkled on top of the sand. Cultures were kept at room temperature (uncontrolled at approximately 21°C) and fed mixtures of dry dog food, cereals, assorted grains, and various bits of vegetable matter. The rearing container was examined regularly to detect eggs or larvae by sifting the sand through the sieve. Every 3 months, the sand was sterilized to prevent fungal or acarine infestation by washing with water and by oven-drying.

Rearing procedures were similar to those of Brown (1973). To prevent cannibalism, larvae were transferred to smaller containers with pre-mixed sterilized sand (10 parts sand to 1 part food) over a 2-cm layer of plaster of paris with a watering tube inserted into the plaster. Enough water was added to moisten the lower 1 cm of sand.

Immature specimens were killed in boiling water and transferred to 70% EtOH for preservation. Larval structures were cleared in hot 10% KOH and examined in temporary glycerin mounts. Female internal cuticular structures were prepared and examined using a method similar to that suggested by Tschinkel and Doyen (1980).

Troglogeneion, gen. nov.

Body elongate, ovate, apterous.

Head slightly deflexed, abruptly narrowed behind eyes; clypeus produced, feebly trilobed, central lobe terminating in obtuse point with serrate margins, lateral lobes broadly rounded; supraorbital carinae feeble, extending from about middle of eyes to about ½ distance from eyes to epistomal margins; eyes slightly flattened, truncate posteriorly, indented to ½ width by epistomal canthus; mentum hexagonal; maxillary palpus approximately equal in length to first 3 antennal segments; posterior margin of submentum with fossa equal to width of mentum, lateral areas of fossa with deep, laterally elliptical pits, median area shallower (Fig. 3); gena laterally from fossa to eyes forming a deep pit at about midlength; antennae slender, gradually broadened, last 3 antennomeres slightly enlarged, flattened.

Pronotum (Fig. 4 and 5) subquadrate, surface slightly convex anteriorly, less so posteriorly, anterior margin truncate, apical angles slightly produced, sides broadly arcuate, beaded.

Scutellum visible, subquadrate.

Elytra convex, inflated, punctate-striate, each elytron with 10 rows of punctures, intervals slightly elevated, epipleura widest at apex, gradually narrowing.

Ventral Surface. Prosternal process convex between procoxae, posteriorly reflexed, mesosternum not excavate; meso-, metacoxae about equally separated; intercoxal process of abdomen acute; first 3 visible sterna about equal in length, slightly convex, 4th, shorter, flat.

Legs moderate in length, slender; meso-, metafemora gradually becoming slightly inflated to

middle, slightly less near apex; profemora shorter, apex more inflated; tibia slender.

Reproductive Structures. Male aedeagus (Fig. 6) with tegmen inverted (ventral), median lobe free, sinuately curved, lateral penis rods approaching along dorsal midline, fused on ventral apical surface.

Female Reproductive Organs (Fig. 7). Ovipositor moderately sclerotized, with numerous, minute, scattered setae; paraproct elongate (2-fold length of coxites); paraproct baculi (ventral) and protiger baculi (dorsal) heavily sclerotized, protiger baculi widely separated; coxites shorter, lobes 2–4 fused, baculi of coxite lobe 1 heavily sclerotized, transverse; gonostyles short, minute, ventrolateral. Internal reproductive tube with vagina elongate, membranous; bursa copulatrix dorsal; common oviduct entering vagina ventrally; spermathecae bursa-derived, composed of 10 separate comblike ducts, ventroapical on bursa copulatrix on nonglandular common tube leading to spermathecal accesory gland; spermathecal accessory gland enlarged, elongate, unbranched (three individuals examined).

Diagnosis. This genus may be distinguished from all other Triorophini by the deep subgenal and submental pits and by the abruptly narrowed head behind the eyes (Fig. 3). *Triorophus* has deep submental pits but lacks the abruptly narrowed head behind the eyes; in *Triorophus*, the base of the mandibles is inflated, visible from above and deeply interrupts the epistomal margin (figure 14.73 in Arnett [1960]). *Troglogeneion* males lack the secondary sexual patch of setae near the medial area of the first abdominal sternum, characteristic of males of *Triorophus* and several other genera of Triorophini (Doyen 1982).

The following changes in Arnett's 1960 key (p. 648), incorporating the previous additions proposed by Doyen (1982, p. 90), will separate *Troglogeneion* from other Triorophini.

1. Posterior margin of submentum behind lateral margins of mentum without two deep, laterally elliptical pits (sometimes with single median pit or depressed area) 2
   Posterior margin of submentum behind lateral margins of mentum with two deep, laterally elliptical pits (Fig. 3) ... 8
8(1). Head abruptly narrowed behind eyes (Fig. 3), base of mandibles not visible from above; epistomal lobe (dorsal view) broad, projecting, not interrupted; frontal clypeal area not inflated .... Troglogeneion
   Head not abruptly narrowed behind eyes, base of mandibles inflated, visible from above, deeply interrupting epistomal margin; frontal clypeal area strongly inflated (Arnett's Fig. 14.73) .. Triorophus

***Troglogeneion zapoteca*, sp. nov.**
(Fig. 1–7)

Type. Length 10.1 mm, width 4.5 mm; color nigropiceous (Fig. 1).

Head (Fig. 2 and 3) to posterior transverse groove (preocciput) 1.3-fold wider than long, widest across eyes; surface convex posteriorly to slightly convex anteriorly on frons, moderately but deeply punctate, more dense near margins; punctures variable in size, from 1 to about ¼ size of eye facet; eyes 4–5 facets in width at narrowest, upper lobe 7 facets wide, 4 facets wide ventrally; mentum with anterior, lateral margins equal in length, posterior margin slightly less than twice length of other margins; anterior, anterolateral surfaces bearing uneven row of long, fine setae; maxillary palpus ratio of segment lengths 4:15:10:20; antennae with apical segments reaching elytra when head retracted, 10th segment wider than long, ratio of segment lengths 23:12:19:17:13:13:13:12:11:11:14.

Pronotum (Fig. 4 and 5). Widest anterior to midlength, surface slightly convex anteriorly, less so posteriorly, moderately, deeply, unevenly punctate, punctures of mainly 2 unequal sizes (larger 5-fold size of smaller); each bearing short seta with approximately 6 sensory pits surrounding the seta; anterior margin slightly beaded on lateral ⅓, basal margin sinuatolobate, medial lobe slightly produced posteriorly to elytral margin.

Elytra. Rows of punctures on elytra moderately deep, regular, punctures not in sulci, each bearing a short seta, seta shorter than diameter of puncture; intervals with 2–3 irregular rows of minute punctures of about ⅛ size of large punctures; epipleura gradually narrowing in width to ½ distance posteriorly, then subparallel to apex.

Ventral Surface. Thoracic pleura, sterna with deep large punctures, each bearing a short, fine seta; sterna with surfaces sparsely, finely punctate, central punctures bearing setae of about 4-fold as long as puncture diameter, sternal ratios (anterior to posterior) 15:15:12:7:10.

Legs. Protibia with tuft of short setae on apical ⅓; tarsi with ventral surface bearing stiff tufts of yellowish setae, interrupting plantar surfaces, slightly less so on apical tarsomere. Tarsal length ratios as follows: protarsus 11:6:6:6:20; mesotarsus 18:10:8:8:22; metatarsus 33:14:10:31.

Variation in Size. Sixty one specimens were measured in elytral length and width. Elytral length: mean = 8.26; SD = 0.411. Elytral width: mean = 5.60; SD = 0.664. Females average slightly larger than males.

Holotype. Male. Mexico, Oaxaca, 1 mi E Yagul ruin, 5,800 ft, Acacia scrub, VII-2-82, collected under rocks in limestone cliff-overhang caves, Rolf L. Aalbu col. (California Academy of Sciences, San Francisco [CASC]).

Allotype. Same data (CASC).

Paratypes. Same data, 80.

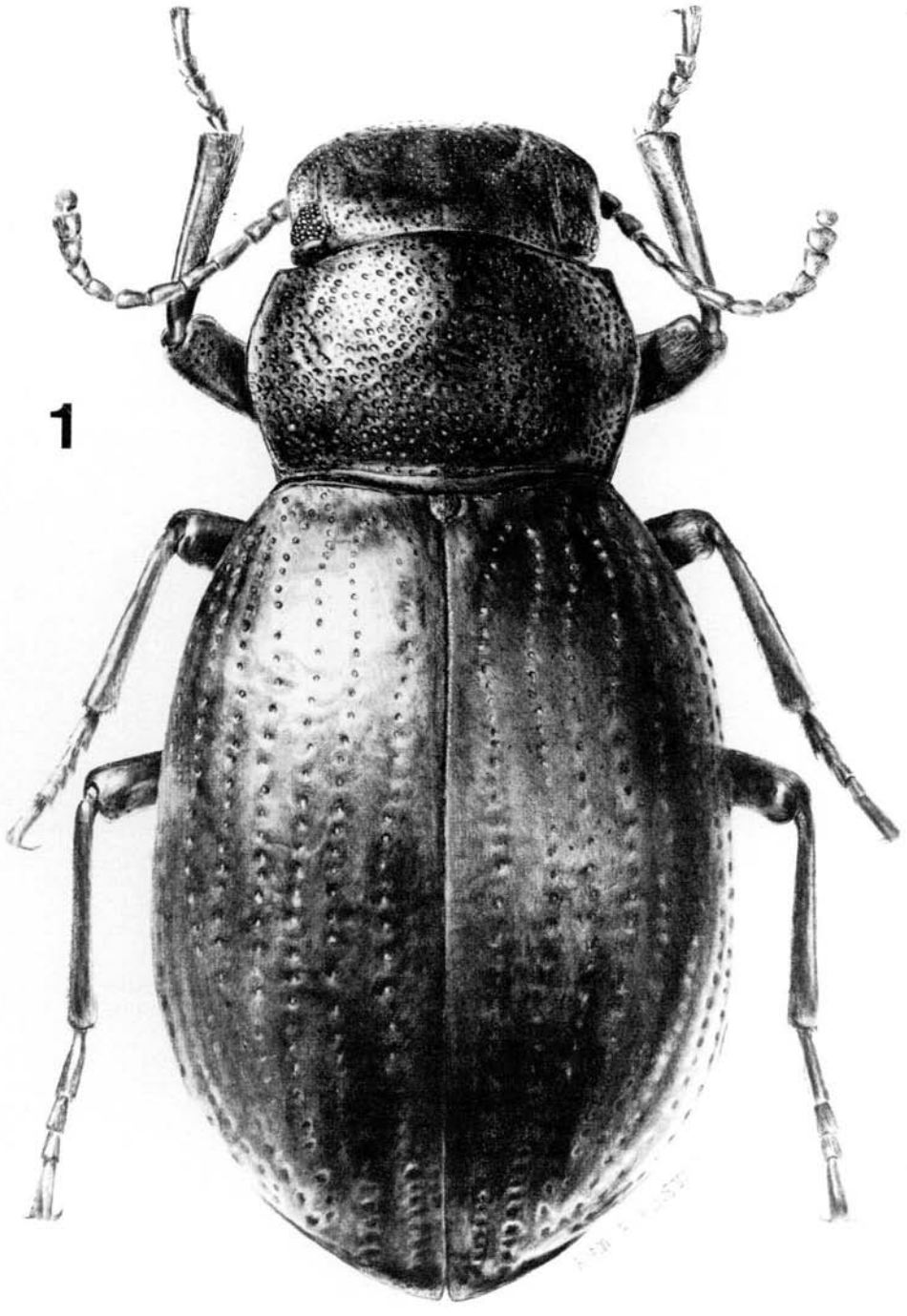


Fig. 1. *T. zapoteca,* adult, dorsal aspect.

Paratype Distribution. U.S. National Museum, Washington, D.C. (USNM), 4; British Museum of Natural History, London (BMNH), 4; University of California, Berkeley (CISC), 5; Calif. Dept. of Food and Agriculture, Sacramento (CDAE), 5; Kirby W. Brown collection (KWBC), 5; Richard L. Berry collection (RLBC), 5; Musee National d'Histoire Naturelle, Paris (MNHP), 4; Rolf L.

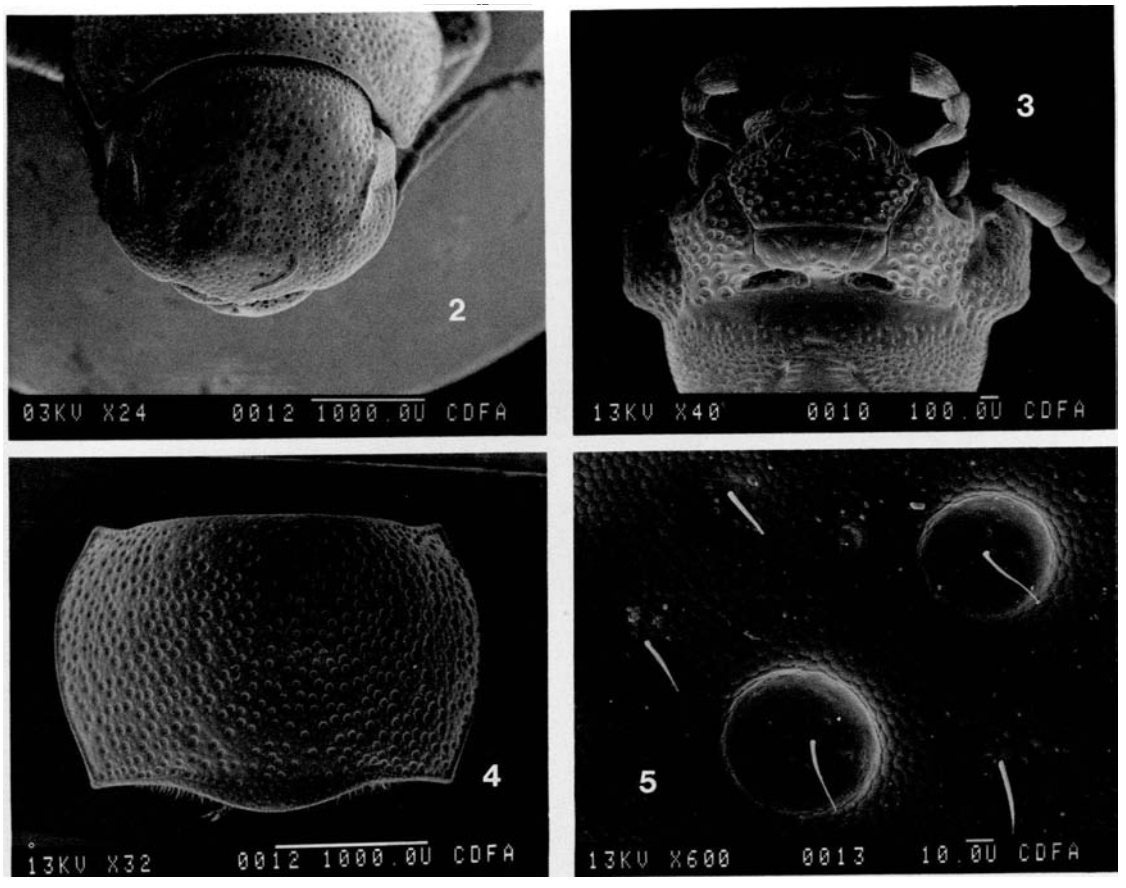


Fig. 2–5. *T. zapoteca*, various adult structures. (2) Head, dorsal aspect. (3) Head, ventral aspect. (4) Pronotum, dorsal aspect. (5) Pronotum: close up of punctures, showing surrounding sensory pits.

Aalbu collection (RLAC), 48; same data except C. A. Triplehorn col. (Ohio State University, Columbus [OSUC]), 4; same data except Yagul ruins, VII-4-75, C. A., W. E., and B. W. Triplehorn cols., 3 (OSUC).

Etymology. Troglogeneion: trogle, Gr. f. hole; geneion Gr. n. chin. Zapoteca is taken from the Aztec word zapotec, which denotes a tribe of people, descendants of the Olmec tribe from the Gulf Coast, who first settled in the Oaxacan valley and are thought to have built the city of Yagul.

Description of the Immature Stages of *T. zapoteca*

Mature Larva (Fig. 8–19). Length 25 mm, body elongate, cylindrical, cream colored; mandibles, tarsal claws, spinelike setae on apex of abdomen, legs, and head moderately to heavily sclerotized, dark brown to black; cranium lightly sclerotized, color light brown, pronotum, legs, less so, yellow; meso-, metathorax only very slightly sclerotized near posterior margins, light yellow in color. Ratio of segment lengths (Fig. 8): H-10:P-9:MST-8:MTT-8:A1-12:A2-14:A3-16:A4-14:A5-15:A6-15:A7-12:A8-11:A9-15.

Head (Fig. 9). Prognathous, slightly depressed dorsoventrally; cranium quadrate, anterior angles truncate, cuticle smooth, lightly sclerotized, with few sparse setae dorsally; lateral margins with many, moderately long, spinelike setae arranged in 3–4 uneven longitudinal rows and sparse, longer (3- to 4-fold), thinner setae; small pigment spot near posterior base of each antenna, subgena medially with cluster of long, slender setae. Antennae articulated on prominences just ventrad of anterior laterad truncate margins of cranium; basal segment very slightly expanded near apex, about 4-fold as long as wide; second segment clavate, slightly shorter than first; 3rd segment slender, cylindrical, about as long as width of 1st segment, apex with very short, slender seta, sensorium circular. Clypeus with 6 setae in transverse row near posterior margin. Labrum evenly arcuate, with 4 transverse rows of setae: 1 anterior row of 5 long spinelike setae on latero-anterior margins and 6 long slender setae on medial anterior margin, 2

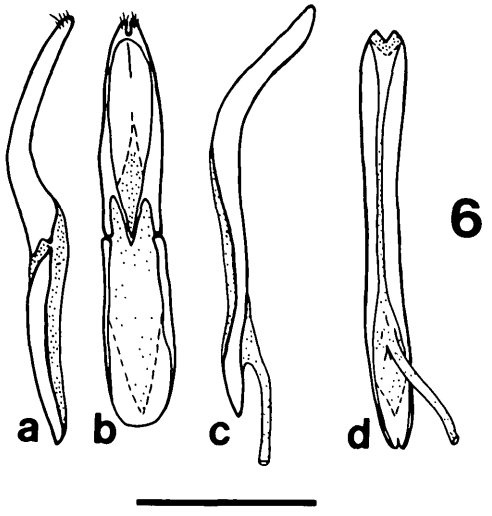


Fig. 6. *T. zapoteca,* male reproductive structures. Genitalia; lateral aspect of aedeagus (a), dorsal aspect (b), lateral aspect of median lobe (c), dorsal aspect (d) (Bar = 0.5 mm).

medial rows of 12 short, thick, spinelike setae, 1 posterior row with 2 similar setae laterally and 2 shorter setae medially. Epipharynx (Fig. 10) with anterior margin invaginated ventrally, with two rows of marginal epipharyngeal setae: 1st row directed anterodorsally, 2nd row directed posteroventrally, fitting over anterior margin of mandibles, medial microspinules of epipharynx (not illustrated) arranged into 3 subparallel pairs, posterior pair largest. Mandibles (Fig. 11 and 12) with basal semimembranous patch on posterior dorsolateral surface with numerous (about 30), erect, short, stout, spinelike setae; both incisor lobes bidentate with subapical tooth on ventral surface, molar surface slightly concave. Maxillae (Fig. 13) with mala bearing row of spinelike setae directed anteromedially, finer setae scattered on ventral surface, maxillary palpus with 2nd segment slightly longer than first, 3rd segment approximately equal in length to first. Labium (Fig. 14) with prementum, mentum clearly defined, prementum with scattered, long setae on lateral, anterior margins, mentum with few scattered setae on posterior, lateroventral margins. Ligula (Fig. 15) bearing approximately 30 fine setae; hypopharyngeal sclerome strongly sclerotized, directed anteriorly, anterior margin concave, feebly bilobed.

Thorax. Prothorax with tergal surface yellowish in color; laterodorsal surface with scattered, fine setae of unequal sizes, extending medially with an unequal row near anterior and posterior margins and with few scattered setae extending medially from midlateral area of tergum terminating on each side with a seta on midlateral surface. Sternum broad, marked medially with anteroposterior convex band of very fine tubercles, broadening toward mid anterior margin of coxae, marked medially with clump of long, fine setae; sternal-coxal-trochantin articulation areas sclerotized; intercoxal process very slender, trochantin triangular; sternellum surface convex, enclosing coxae posteriorly to midlateral region, replaced in anterior lateral region by triangular proepimeron. Prothoracic legs (Fig. 16) enlarged, coxae subquadrate; trochanter subconical, about ½ length of femur, medial margin with short, spinelike seta followed proximally by a long seta and 4 shorter, very fine setae; femur robust, medial margin with pectin of five stout, blunt, spinelike setae arranged in slightly decreasing lengths, lateral margins with row of long, delicate setae; tibia robust, medial margin with pectin of 7 stout setae approximately twice length of those on femur, followed proximally by an 8th shorter, spinelike seta; lateral margins with row of long, delicate setae, approximately 3-fold as long as pectal setae; tarsangulus with short, transverse, weakly sclerotized basal segment bearing single, stout, spinelike seta; distal segment formed into moderately sclerotized claw. Meso-, metathorax very lightly sclerotized, surface creamy yellow; laterodorsal surfaces with scattered, fine setae of unequal sizes, extending medially near anterior margins and with an unequal row near posterior edge of tergum. Mesothoracic (Fig. 17), metathoracic legs similar, about ⅔ size of prothoracic legs, more slender; trochanter with medial margin bearing short spinelike seta, followed proximally by 4 longer, more delicate setae; femur with 2 rows of stout, spinelike setae interspaced with more delicate setae: 1st row on medial margin with 2 stout, spinelike setae interspaced with more delicate, slender seta; 2nd row on posterolateral surface composed of 4 spinelike setae; more slender setae present on dorsal surface; tibia with 2 rows of 3 spinelike setae, corresponding in location to femoral rows, slightly decreasing in length and stoutness from apex; tarsangulus as in prothoracic leg but smaller, not as robust.

Abdomen. First abdominal segment subquadrate, about 1.6-fold wider than long; 2nd through 6th submoniliform, subequal in length, 7th, 8th shorter; 9th abdominal tergum (Fig. 18) subconical in dorsal aspect; with scattered, dorsally directed, spinelike setae and numerous finer, longer setae on lateral and apical areas; membranous area between tergite and sternite of 9th abdominal segment with tuft of few, fine setae; 10th abdominal segment (Fig. 19) modified as enlarged pygopodial lobes set laterally with 11 spinelike setae arranged in an uneven ellipse and with scattered longer, fine setae posteriorly and laterally; spiracles annular with peripheral air tubes.

Eggs. Elongate elliptical, color creamy white, 1.8 mm long, 0.7 mm wide, surface smooth, shiny, with no sculpturing visible at 1,000× magnification.

First-instar Larva (Fig. 20). Length 3.2 mm, shape more compact than mature larva; meso-

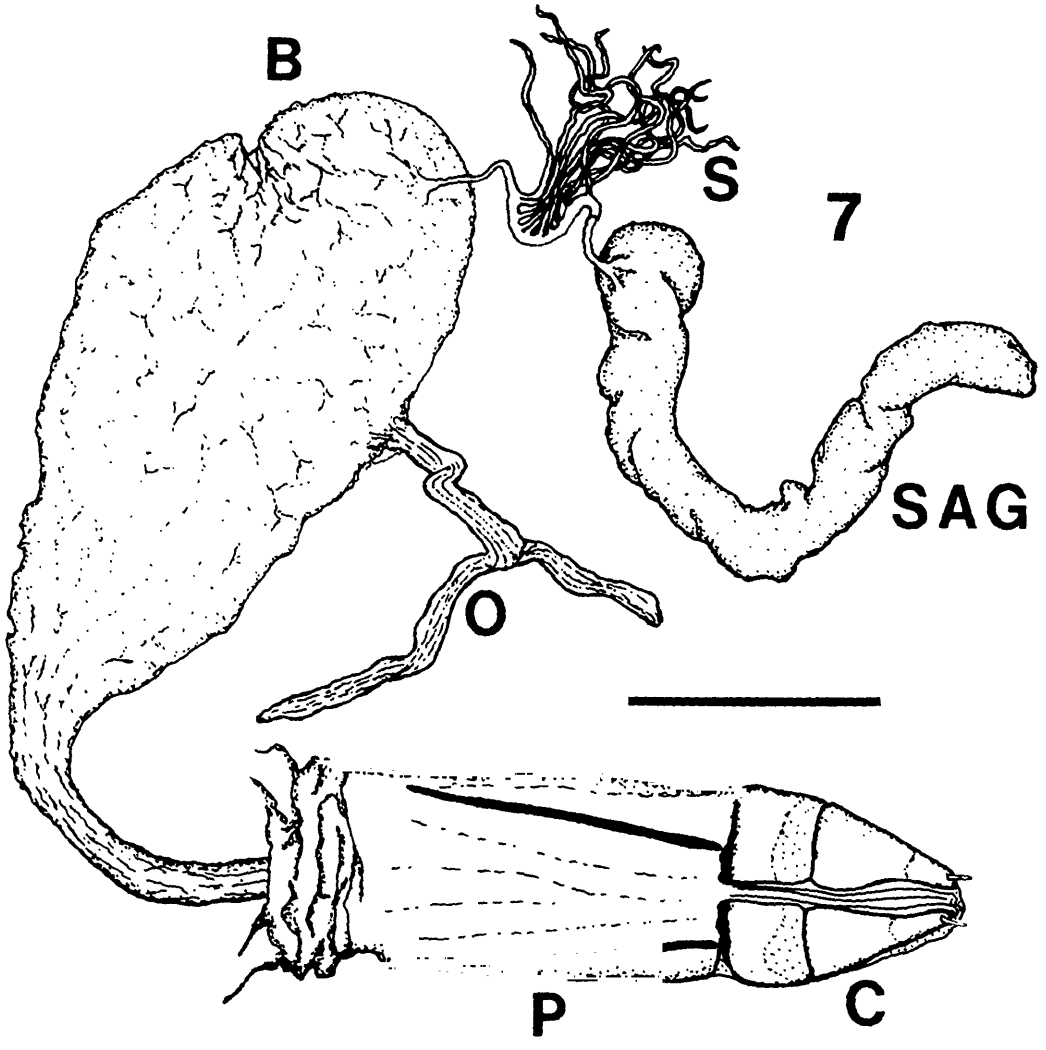


Fig. 7. *T. zapoteca*, female reproductive structures: ventral aspect of ovipositor (a), with coxites (C) and paraproct (P); dorsal aspect of female internal genital tube (b), with oviduct (O), bursa copulatrix (B), multiple spermathecae (S) and spermathecal accessory gland (SG) (Bar = 1.0 mm).

thorax reduced, widest near the middle, white except for tips of mandibles, protarsal claws, spicules on head and prothoracic legs, and junction of episternum, trochantin and procoxa on prothorax. Ratio of segment lengths: H-18:P-11:MST-10:MTT-9:A1-9:A2-13:A3-13:A4-14:A5-15:A6-12:A7-13:A8-8:A9-15.

Head. Proportionally larger than in mature larva, with visible eye spots, on mediolateral margins; labrum deeply incised in anterior medial area, somewhat inflated, with 2 spicules on upper anterior lateral surfaces; antenna with 2nd segment much larger in proportion than in mature larva; mandibles with upper membranous surface with one spicule.

Thorax. Prothorax proportionally larger than in adult. Protibia with 1 spicule on medial margin; femur with 1 spicule near apical medial margin.

Second-instar Larva. Length 5.1 mm, shape similar to mature larva.

Head. With visible eye spots on mediolateral margins, labrum with 6 spicules on upper anterior surface (two center spicules smaller in size) and 2 lateral spicules on lower anterior surface; antenna with 2nd segment much larger in proportion than in mature larva; mandibles with upper membranous surface with seven spicules.

Thorax. Prothoracic legs: tibia with 3 spicules on medial margin, 2 apical spicules larger; femur with two medial spicules near apical margin.

Pupa (Fig. 21 and 22). Length 10 mm, moderately elongate, slightly depressed, weakly pigmented except tips of mandibles and lateral lamellae of abdominal segments.

Thorax. Prothorax convex, shape as in adult, posterior angles acute, lateral margins with nu-

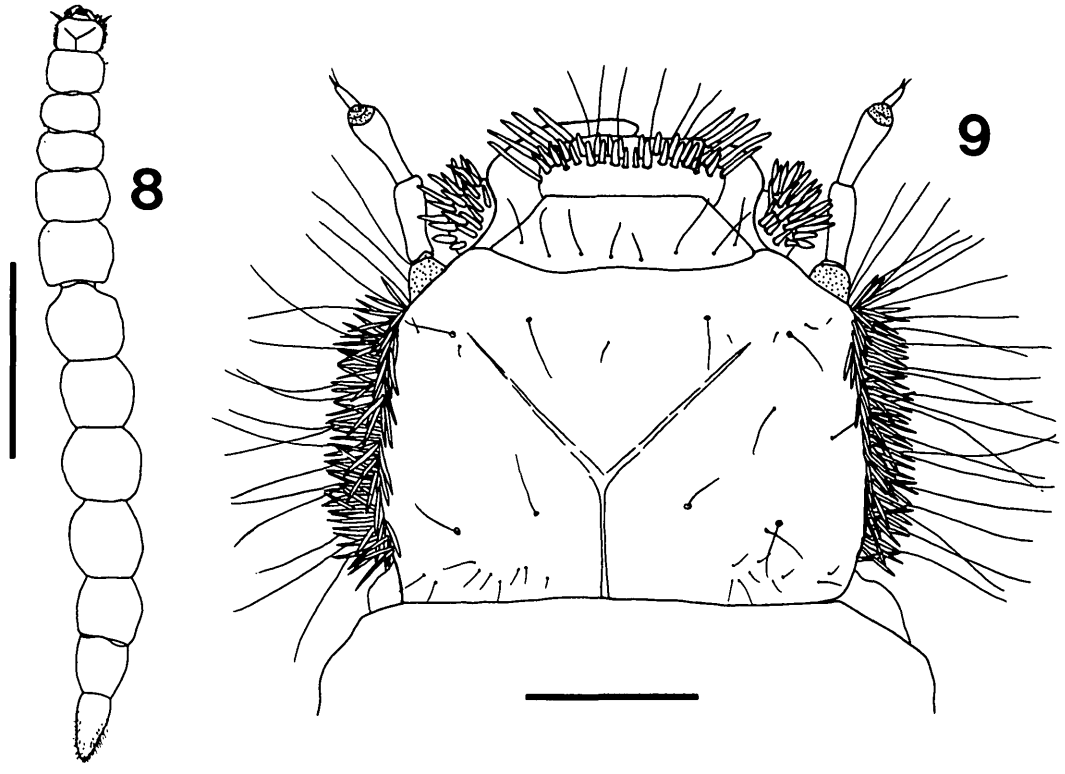


Fig. 8 and 9. *T. zapoteca*, various larval structures. Length of scale lines in parentheses. (8) Dorsal aspect of mature larva (5.0 mm). (9) Dorsal aspect of head (Bar = 0.5 mm).

merous very fine, short setae. Meso-, metathorax transverse. Elytra visible as lateral cream-color lobes. Wing visible as translucent lobes, smaller than elytra (although adult is apterous), no venation visible.

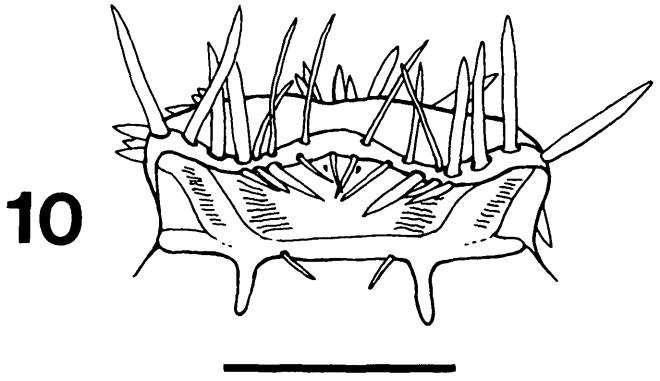
Abdomen. Subparallel, terga 2–6 with prominent subequal sclerotized "gin-traps" composed of strongly sclerotized serrate anterior margins with numerous sharp, small teeth and corresponding very weakly sclerotized indentations on posterior margins of preceding segments; terga 7–8 bare; tergum 9 with a pair of short, slender urogomphi, slightly curved laterad, tips weakly sclerotized.

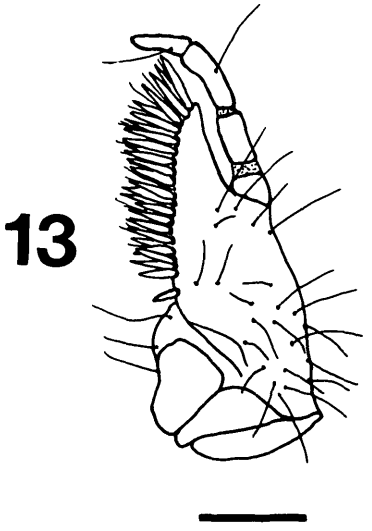
Biological and Rearing Notes

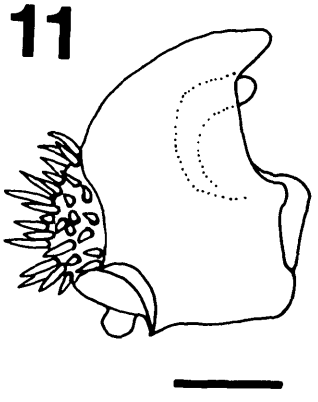
T. zapoteca represents a considerable southern extension of the range of Triorophini, from the Chihuahuan desert of northern Mexico. Specimens of Triorophini are usually found singly or occasionally in pairs, wandering at night in rocky areas with fine, sandy soil, in open flat sandy deserts on sand, or occasionally on brushy vegetation. Many were trapped in short duration, dry pitfall traps or long duration, ethylene glycol pitfall traps (Aalbu 1977). Adults seem to be strictly nocturnal, remaining under rocks or plant debris during the day.

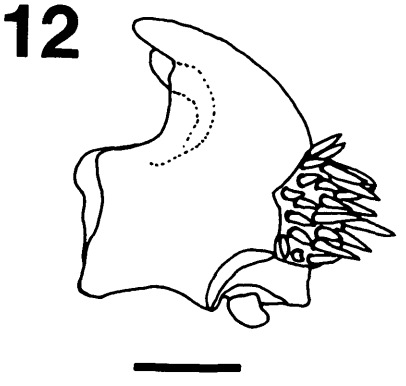
The area around the Yagul Ruins is a limestone formation of hills bordering the Oaxacan river valley to the west, often eroded, into high cliffs with many deep grottos and caves with floors composed of scattered loose rocks in a very fine, powderlike sandy soil very high in organic matter due to the many animals such as rodents, bats, and cattle that use them for shelter. Most of the specimens of *T. zapoteca* were found in aggregations of approximately 10–40 in crevices under a flattened boulder approximately 1 m in diameter. Others were singly or in pairs also on the underside of the boulder, in the soil under the boulder, or beneath adjacent smaller rocks.

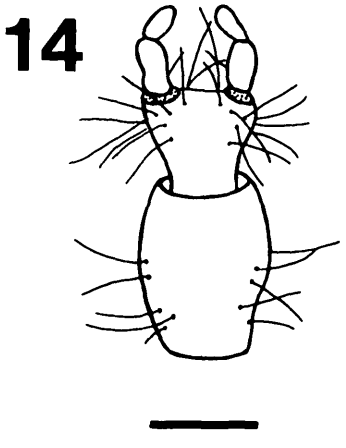
Where known, Tentryiinae oviposit in damp soil or sand, usually after rains, when ephemeral moisture is used to the greatest advantage (Brown 1973, Watt 1974) although Watt (1974) also reports that *Tentyria schaumi* will oviposit in dry sand. *T. zapoteca* oviposits in dry sand, even when given a choice of moist sand. Eggs are laid singly, approximately 0.5 cm beneath the surface. Immature stages take approximately 7 months to reach maturity with the pupal stage lasting approximately











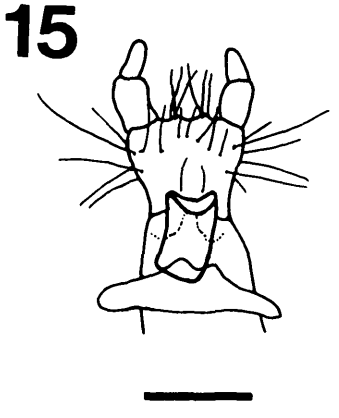


Fig. 10–15. *T. zapoteca*, various larval mouthpart structures. (10) Epipharynx. (11) Dorsal aspect of left mandible. (12) Dorsal aspect of right mandible. (13) Ventral aspect of right maxilla. (14) Ventral aspect of labium. (15) Dorsal aspect of hypopharynx showing hypopharyngeal sclerome and bracon (Bars = 0.25 mm).

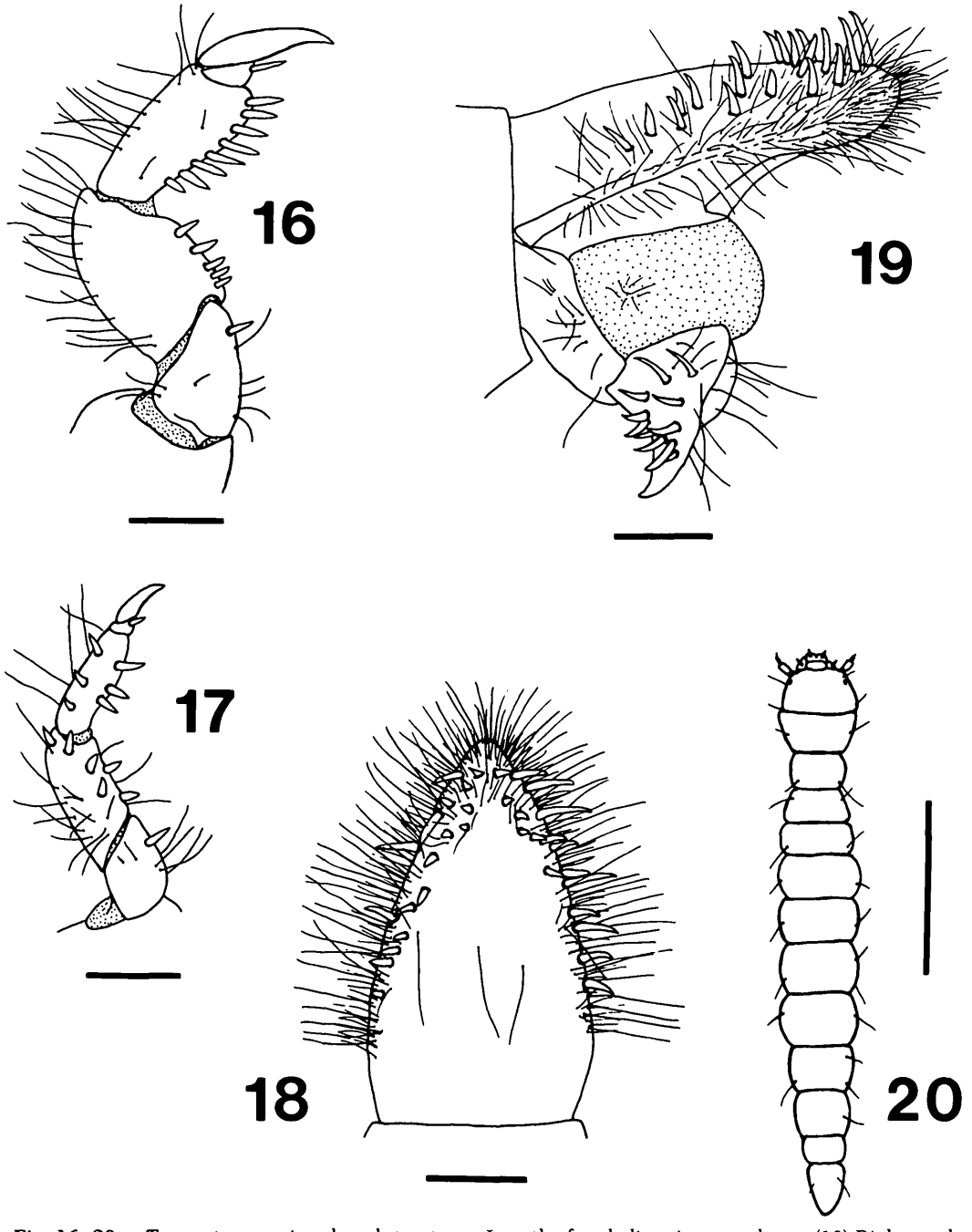


Fig. 16–20. *T. zapoteca,* various larval structures. Length of scale lines in parentheses. (16) Right prothoracic leg, posterior aspect (Bar = 0.25 mm). (17) Right metathoracic leg, ventral aspect (Bar = 0.25 mm). (18) Abdominal segment 9, dorsal aspect (Bar = 0.5 mm). (19) Abdominal segments 9 and 10, lateral aspect (Bar = 0.5 mm). (20) First-instar larva, dorsal aspect (Bar =1.0 mm).

20 days. In the laboratory, adults live 1–2 years. There is probably one generation per year in nature.

Phylogenetic Relationships

The tenebrionid subfamily Tentyriinae includes many groups which are ecologically and morphologically specialized. Many are regionally restricted to varied biogeographical areas. As a consequence of these similar "morphotypes," which may have independently evolved in similar ecological areas, there have been differing opinions over tribal limits and their phylogenetic positions within the subfamily Tentyriinae, especially in reference to the following currently accepted tribes of

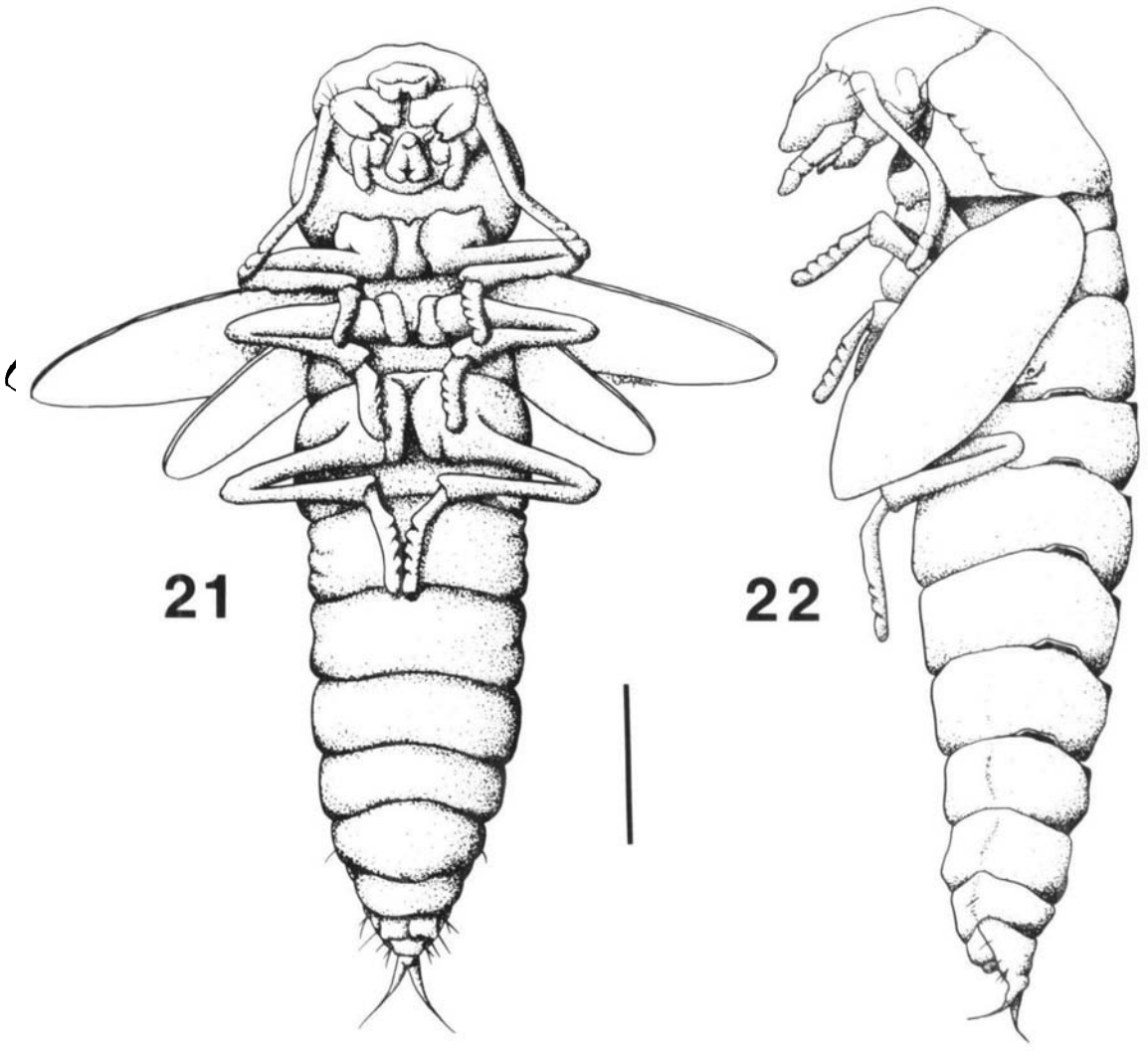


Fig. 21 and 22. *T. zapoteca,* pupa. (21) Ventral aspect. (22) Lateral aspect (Bar = 2.0 mm).

Tentyriinae: Epitragini, Tentyriini, Eurymetopini, Trimytini, Auchmobiini, Trientomini, Craniontini, and Triorophini. Many of the earlier divisions proposed have been on the basis of unreliable, superficial characters of the front of the head, antennae, or the setal patterns on the tarsi. Most recently, Watt (1974), without giving specific reasons, suggested that the Triorophini and Thinobatini (a South American tribe) be included in the Tentyriini sensu Koch (1955) or be merged with other North American tribes (for classifications, *see* Lacordaire 1859, Horn 1870, Casey 1907, Koch 1955, 1962, Watt 1974).

The tribe Triorophini presently encompasses the following genera: *Triorophus, Micromes, Trichiotes, Oxygonodera, Triphalus, Stibia, Triphalopsis, Orthostibia,* and *Troglogeneion. Troglogeneion* offers the first opportunity to critically examine the immature stages of Triorophini in reference to other closely related tribes within the Tentyriinae. To present additional information on relationships, I have also added notes on the female reproductive system.

Immature Stages

Mature Larvae. Tentyriine larvae are poorly known in comparison to the rest of the Tenebrionidae. Of the few that have been described, only a fraction have been described in sufficient detail necessary for critical character comparison. Consequently, most attempts to establish keys to higher categories such as tribes within the Tentyriinae have not proved reliable when tested with new material. Recently, works by Brown (1973), Watt (1974), Doyen (1972, 1974, 1976), Doyen and Lawrence (1979), Schulze (1974), and others have added much to the knowledge of the immature

stages of tentyriines with more detailed descriptions of immature stages including, in some of these, also descriptions of eggs, 1st instar larvae and pupae of the species.

The larvae of "tentyriines" have been distinguished from other tenebrionid larvae by Skopin (1960, 1962) and Kelejnikova (1963, 1970). These, however, in most cases separated from the tentyriines groups such as the asidines, molurines, akidines, eurychorines, erodiines now considered to be tentyriines. Probably the most recent combination of characters used to distinguish tentyriine larvae was proposed by Watt (1974), although two of Watt's characters were found to be unreliable by Brown (1973): 1) dorsolateral surface of mandibles with membranous elevation bearing numerous setae (in certain cases, as in the Asidini, ventrolateral); and 2) urogomphi absent (mature larvae of *Stenomorpha* [and other Asidini] have large urogomphi and many nontentyriines lack urogomphi).

Kelejnikova (1970) distinguished the larva of Tentyriini from other tentyriine tribes although very few other tribes (Epitragini and Adesmiini) were used for comparison. Among distinguishing features listed, the following are of particular interest: 1) head with borders of hairs and setae (setae and spicules) along sides; 2) labrum with (at least) a transverse row of spicules in middle, lateral rows of setae (or spicules) extending forward from (lateral) ends of transverse row along anterior margin of labrum, medially discontinued but replaced by 4 spicules (or setae) centrally; 3) middle of epipharynx with 2 spicules (2 very short, stout spicules) and 4–6 microscopic ones; 4) hypopharynx (hypopharyngeal sclerome) cup-shaped; 5) tormae merged into a single sclerite; 6) clypeus with "numerous" long setae along posterior margin (apparently as few as seven in *Scythis* (*see* Knor 1977); 7) "tibiotarsus" with pecten of long stout spicules on inner surface; and 8) femur and trochanter with "platforms" bounded by spicules and setae on inner surface. The mature larvae of *Troglogeneion zapoteca* seem to fit clearly within this group agreeing with all of these characters with perhaps the exception of the four setae in the middle of the anterior surface of the labrum (six in *Troglogeneion*).

Kelejnikova also proposed keys for the identification of Palearctic tribes and described genera of Tentyriinae. In the tribal key, Tentyriini were lumped together with Zophosini later distinguished by Schulze (1974) by apparent lack of a sclerotized hypopharyngeal sclerome. These were distinguished from the Epitragini by the presence in the Epitragini of a "tuft of setae" (or spicules) on the membranous area between the tergum and sternum of the 9th abdominal segment. This character has been found to be unreliable: it is present in *Troglogeneion* and absent in some epitragines (*see* Doyen 1974, p. 162). In the key to the genera of Tentyriini, *T. zapoteca* can be fit along with *Gnathosia* Fischer into her couplet 5(6). *Troglogeneion* may then be distinguished from *Gnathosia* by the presence in *Troglogeneion* of 5 spicules on the inner surface of each profemora (8 in *Gnathosia*) and a tuft of setae on the membranous surface between the tergum and sternum of the 9th abdominal segment (apparently absent in *Gnathosia*).

First-instar Larvae (Larvulae). First-instar larvae of many Coleoptera have been found to be different from later instars (Crowson 1981). In tentyriines, larvulae do not feed and are immobile. Kelejnikova (1971) suggested that these better represented the "initial" or plesiomorphic condition, more useful in character analysis because later instar larvae tend to be more specialized for a particular ecological niche. She examined labral and clypeal spicules and found the larvulae of the Tentyriinae examined, including some Akidini and Tentyriini, to have a clypeus with four setae and a labrum with two spicules in the middle of the disc. The Tentyriini examined (*Anatolica* Eschscholtz, *Onymacris* Allard, and *Tentyria* Latreille) were further modified in having the labrum "deeply incised" anteriomedially. Tenebrionoids have four setae on the clypeus, a labrum which is not incised with a basic setal formula of 3-2-3 (six lateral setae and 2 mid setae or spicules).

The larvula of *T. zapoteca* showed clear relationships to the Tentyriini larvulae characterized by Kelejnikova in having a cleft labrum with two spicules. *Troglogeneion* differed from the Tentyriini larvulae by the absence of any setation on the clypeus. Kelejnikova (1971) did not mention the setal patterns found on the dorsolateral membranous portion of the mandibles. In this respect, the larvulae of *Troglogeneion* agree with the larvulae of Asidini examined by Brown (1973) and the larvulae of Zophosini examined by Schulze (1974) in having only one spicule on each mandible. They also agree with asidines in lacking setation on the clypeus, having the antennae broader than later instars (with the second segment swollen) and having the prothorax longer than all other segments (characters not mentioned by Kelejnikova or Schulze). *Troglogeneion* differs from the asidine and zophosine larvulae by the absence of egg bursters (short, thick, sclerotized spicules present dorsolaterally on most segments except head) although in one species examined by Schulze (*Cardosis fairmairei*), the egg bursters were extremely fine, not strongly sclerotized and only detectable on three abdominal nota. *Troglogeneion* also differs from the asidines described but agrees with the zophosines in the presence of the anteriorly cleft labrum.

Pupae. Very few tentyriine pupae have been described. Watt (1974) characterized the pupa of *Nyctoporis* (Nyctoporini) and Doyen (1976) described the pupa of *Coelus* (Coniontini) and compared these to *Coniontis*. The pupa of *Coelus* was similar to that of *Troglogeneion* in having a de-

flexed, hypognathous head (opisthognathous in *Nyctoporis*). *Troglogeneion* differs from *Coelus* in having gin traps on segments 2–6 composed of only anterolaterally directed spines and opposing indentations on the preceding segments (in *Coelus* the gin traps were found on abdominal segments 2–7 and were composed of both anterolaterally directed spines and weak, posteriorly directed spines; on segment 8, only weak anterior spines). *Nyctoporis* differs from both of these in having prominent lateral lamellae on terga 1–6 on which the gin traps (sclerotized on both sides) are located.

The larvae and larvulae of the Triorophini are very similar to those of the Tentyriini and Epitragini described. From characteristics and diagnostic keys presented by Kelejnikova (1970), the larvae of Tentyriini and Epitragini seem to be more generalized than other tentyriine tribes. It is possible that the above diagnosis of Tentyriini by Kelejnikova will encompass a number of the tentyriine tribes. The following combination of characters modified from Watt (1974), Brown (1973), and Kelejnikova (1970, 1971) may be used to characterize the known immature stages of Tentyriinae: Larvulae with labrum bearing two spicules in middle of disc (except Pimeliini and Platyopini[1]). Mature larva 1) with antennae 3-segmented; 2) mola prominent, strongly sclerotized, without fine, transverse ridges; 3) gula distinct; 4) prothoracic sternellum greatly enlarged; 5) legs modified for digging; tarsungulus divided into a heavily sclerotized apical lobe and a weakly sclerotized base; 6) front legs sometimes much stouter and always with different setal pattern than others; 7) hypopharyngeal sclerome usually concave anteriorly, rarely convex, never tridentate, dorsal surface smooth; and 8) dorsolateral or ventrolateral surface of mandibles with a membranous elevation bearing numerous setae.

Female Reproductive Structures

The internal female reproductive structures have been examined in very few members of the tenebrionid subfamily Tentyriinae. Watt (1974) was apparently the first, illustrating the internal cuticular tract of *Tentyria schaumi* Kraatz. Although Watt uses a different terminology (also used by Sokoloff [1972]), especially in the relationship between the spermathecae and spermathecal accessory gland, his drawing seems to indicate the absence of multiple spermathecae. I have followed the terminology used by Happ and Happ (1970) and adopted by Tschinkel and Doyen (1980). Tschinkel and Doyen examined 10 species of tentyrioids in detail although most of these were not specified. They found both the ovipositors and internal tubes of tentyriines extremely variable in relation to other tenebrionids, many exhibiting characters they considered apomorphic.

A comparative study of the female internal and external reproductive structures of the Tentyriinae is in progress. At the present time, 70 genera representing 30 tribes have been examined. The genera of Triorophini so far examined (including species of *Triorophus, Micromes, Oxygonodera, Triphalopsis, Triphalus, Stibia,* as well as *Troglogenion*) differ consistently from the genera of Tentyriini examined (including species of *Tentyria, Pachychila,* and *Mesostena*) in the following characteristics: 1) presence of a secondarily derived, dorsal bursa copulatrix (bursa copulatrix absent in Tentyriini); 2) spermathecae multiple, thin, elongate, arranged comblike on a common thin tube between bursa and spermathecal accessory gland (spermatheca single, or with few thick short tubules inserted at apex of vagina in Tentyriini); 3) spermathecal accessory gland inserted apically on spermatheca (basally on spermatheca or directly on vagina in Tentyriini). These combinations of character differences oppose close relationship of these tribes.

Other presumably closely related tribes, such as the Trimytini, Thinobatini, Eurymetopini, Auchmobiini, Epitragini, Trientomini, and Craniontini have also been examined in relation to the Triorophini. In all these, the internal tract is significantly different enough from triorophines to at least temporarily support the retention of the current status of the tribe. Examination of additional genera and tribes of Tentyriinae will elucidate these relationships.

[1] Although the Pimeliini and Platyopini share a number of characters with the Tentyriinae (including tegmen ventral and defensive glands absent), and are generally considered tentyrioids, membranes are exposed on the apical two abdominal sternites and larvulae bear a setal formula of 3-2-3 on the labrum, as in tenebrionines.

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