Zootaxa 1111: 1–19 (2006)
www.mapress.com/zootaxa/

ISSN 1175-5326 (print edition)
ZOOTAXA
ISSN 1175-5334 (online edition)
1111

Description and behaviour of *Goniotropis kuntzeni* larvae (Coleoptera: Carabidae: Paussinae: Ozaenini) and a key to genera of Paussinae larvae

WENDY MOORE[1] & ANDREA DI GIULIO[2]

[1]*Department of Entomology, University of Arizona, Tucson, Arizona, 85721, USA.*
wmoore@ag.arizona.edu
[2]*Dipartimento di Biologia, Università "Roma Tre" Viale G. Marconi 446, I-00146 Rome, Italy*
digiulio@uniroma3.it

Abstract

Goniotropis species are large, parallel-sided paussine beetles common in the New World tropics and ranging from southern Arizona to northern Argentina. Specimens of *Goniotropis kuntzeni* Bänninger were collected in southern Arizona and larvae were reared under laboratory conditions. The egg, first instar larva and second instar larva are described and illustrated, providing the first larval description for this genus. *Goniotropis* larvae live in burrows that they construct and seal with their terminal disk (which is composed of modified urogomphi and dorsal plates). They feed by trapping live insect prey with the moveable components of their terminal disk, and then they bring the captured prey into their gallery to consume. Burrowing and feeding behaviours of *Goniotropis kuntzeni* larva closely resemble those previously described for *Pachyteles* species. A key to the genera of paussine larvae is provided.

Key words: Carabidae, Paussinae, Ozaenini, *Goniotropis kuntzeni*, larva, Arizona, bombardier beetle

Introduction

The carabid tribe Ozaenini contains approximately 181 described species classified in 24 genera (Lorenz 1998; Deuve 2001a, 2001b, 2002, 2004). Over 90 percent of Ozaenini species live only in tropical regions; however, there are a few exceptions. For example, the distribution ranges of five ozaenine species include areas north of the US/Mexico border. The distribution ranges of *Goniotropis kuntzeni* Bänninger, *G. parca* LeConte, *Ozaena lemoulti* Bänninger, and *Pachyteles gyllenhali* (Dejean) include southernmost Arizona and the distribution range of *Physea hirta* LeConte includes southernmost Texas (Ball and McCleve 1990).

Accepted by V. Grebennikov: 18 Nov. 2005; published: 20 Jan. 2006

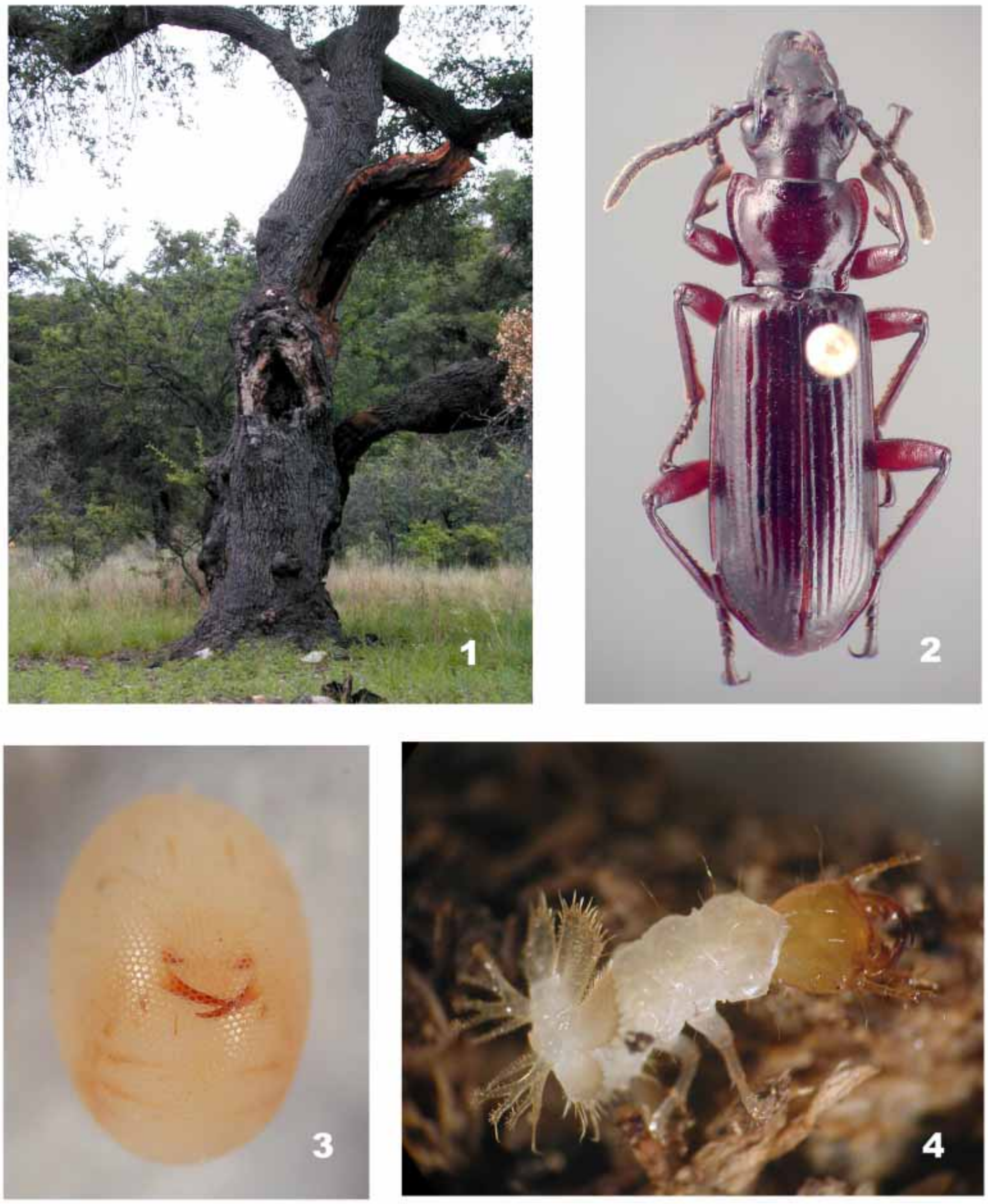
In this paper, we describe the external morphology of the egg, and first and second instar larva of *Goniotropis kuntzeni* Bänninger from southern Arizona, providing the first such descriptions for this New World genus containing 15 described species (Lorenz 1998). We also provide an updated key to the genera of Paussinae larvae based on larval morphology. The last key to paussine larvae was published in 1992 (Luna de Carvalho). Since that time our knowledge has grown significantly with the descriptions of larvae in the genera *Itamus* Schmidt-Goebel, *Pachyteles* Perty, *Arthropterus* W.S. MacLeay and *Goniotropis* Gray and the re-descriptions of larvae in the genera *Physea* Brullé and *Platyrhopalopsis* Desneux.

Very little is known about the behaviour of ozaenines. These beetles are night active predators on arthropods. Although most species in the carabid subfamily Paussinae are myrmecophilous (obligate associates of ants), within the tribe Ozaenini only members of the genus *Physea* Brullé are known to be myrmecophilous. Whereas adults of most other ozaenine lineages are found under stones, bark, and rotting wood, those of *Goniotropis* species are found on trees at night as they probe holes in the bark in search of prey (W. Moore and T.L. Erwin personal communication).

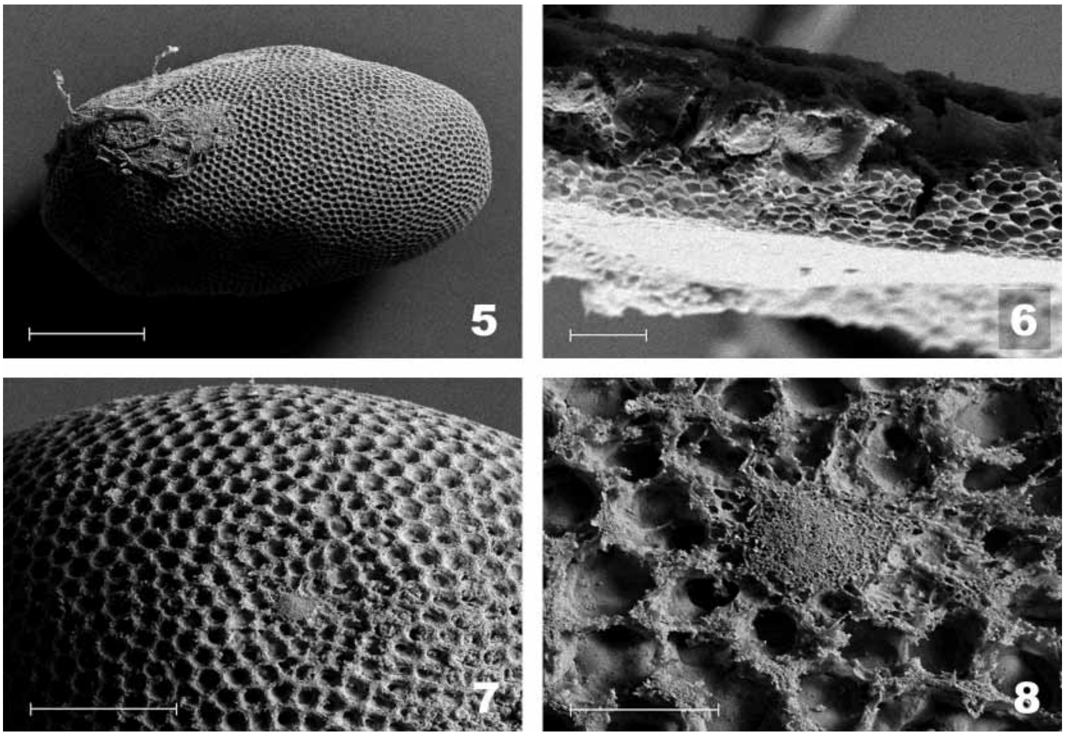
Ozaenine larvae are known for nine species in four genera (*Itamus*, *Sphaerostylus*, *Pachyteles* and *Physea*) (see Di Giulio and Moore 2004). Paussinae larvae share an unusual and unique trait: the ninth abdominal segment is enlarged and fused with the eighth abdominal tergite. This fusion displaces the urogomphi and the tenth segment into a vertical plane, forming, together with the flattened epipleurites of the eighth segment, a terminal disk (Fig. 4), which is an apomorphy of the subfamily (Bousquet 1986). Whereas it is likely that myrmecophilous larvae use the terminal disk as a symphilous organ (Oberprieler 1985; Bousquet 1986; Luna de Carvalho 1989; Di Giulio and Moore 2004), free-living larvae use it as a door to the galleries they construct in wood or sand. In addition, these larvae use the moveable components of the terminal disk to trap their prey (Costa *et al*. 1988; Di Giulio and Vigna Taglianti 2001).

Materials and Methods

Adults (Fig. 2) were collected at night (9–11 p.m.) from the bark of mature Emory oaks (*Quercus emoryi* Torrey) (Fig. 1) in southern Arizona (Santa Cruz County, Walker Canyon, 31°22.819'N 111°03.994'W, 1214m) by W. Moore and R.C. Brusca on 21 July 2001 and 12 August 2003 after the onset of summer rains. Walker Canyon is located just north of the US/Mexico border in the Madrean Evergreen Woodland biotic community of the Sonoran Desert (Brown 1994). This habitat contains two species of oak; Emory oak and the Mexican blue oak *(Quercus oblongifolia* Torrey*)*, as well as species of mesquite and sycamore trees. *Goniotropis kuntzeni* adults were collected only from the oldest living specimens of *Quercus emoryi.* These mature trees show damage from old age and the trunks are often partly hollow (Fig. 1). *Goniotropis parca* and *Ozaena lemoulti* are found on Emory oaks in Walker Canyon as well, but *G. kuntzeni* is the most abundant species. The large formicine ant, *Camponotus ocreatus* Emery, also frequents Emory oaks, and specimens were observed on trees both with and without *G. kuntzeni*, although there is no evidence of a direct association between these beetles and ants.

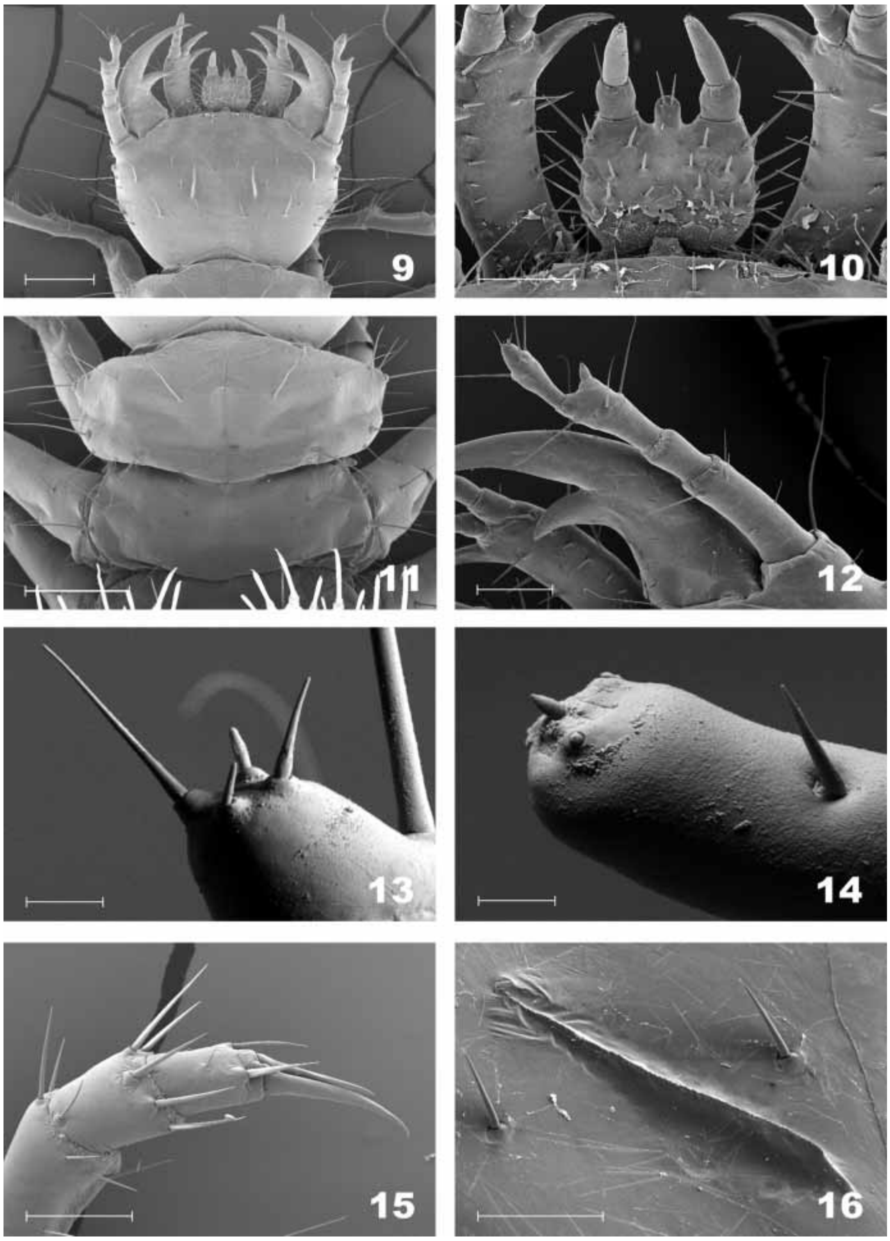


FIGURES 1–4. *Goniotropis kuntzeni*. 1—habitat, Emory Oak in Walker Canyon, Arizona; 2—adult male; 3—egg close to hatching, sclerotized mandibles are visible through the egg shell; 4—first-instar larva.

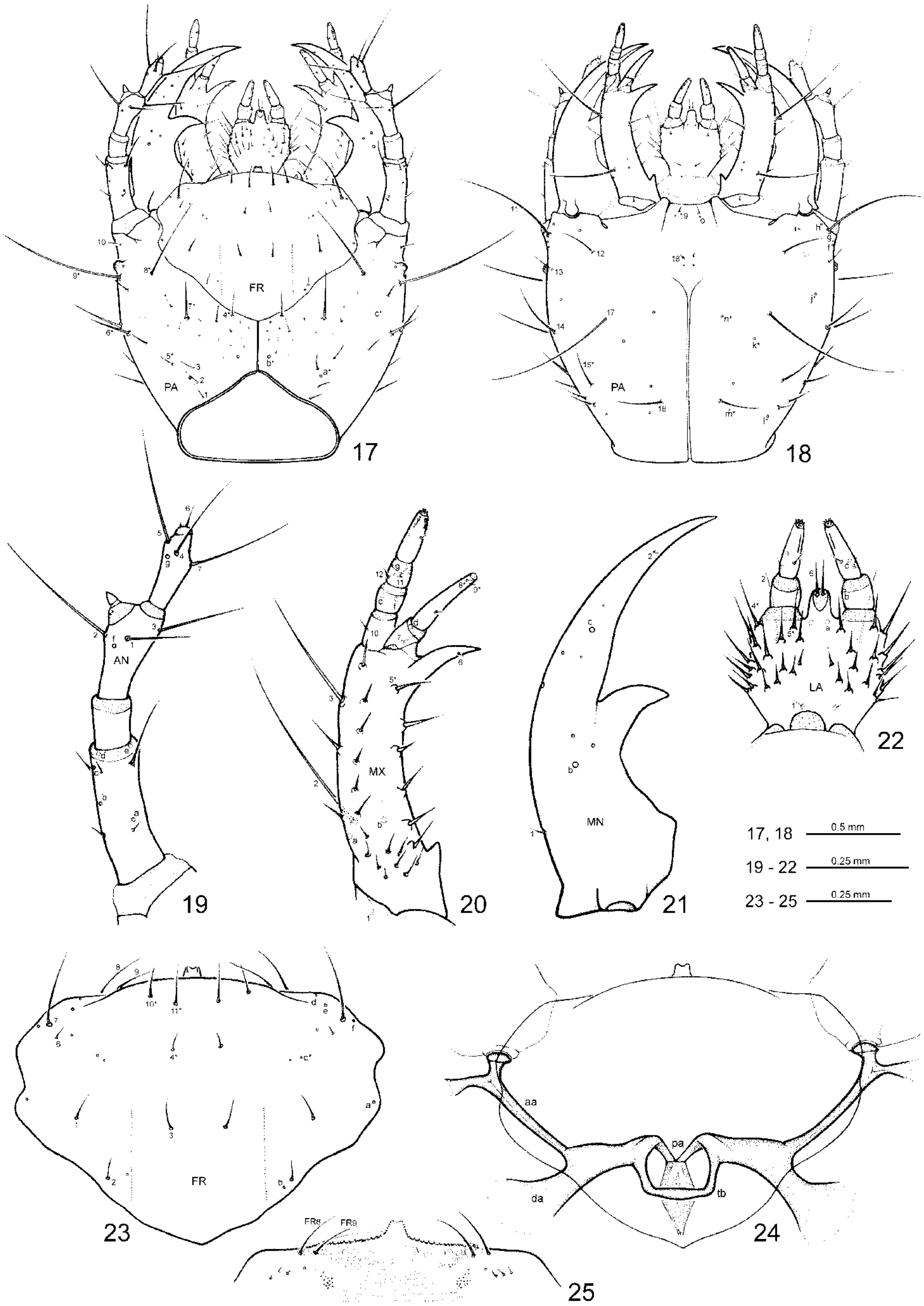


FIGURES 5–8. *Goniotropis kuntzeni* egg. 5—lateral view (scale: 500 µm); 6—cross section of egg shell (scale: 20 µm); 7—anterior pole with micropilar area (scale: 200 µm); 8—close-up of micropilar area (scale: 50 µm).

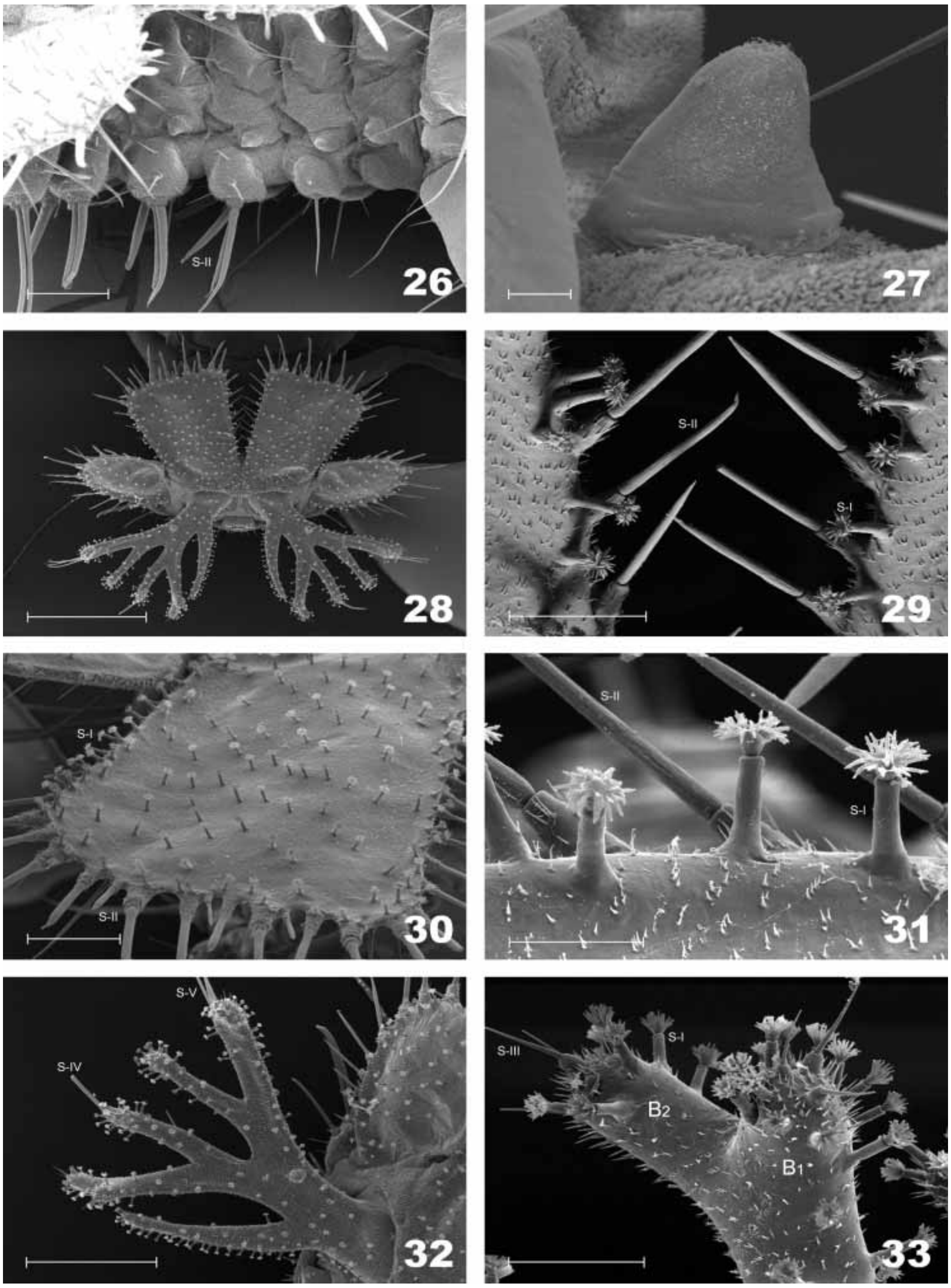
Goniotropis kuntzeni larvae were reared under laboratory conditions at the University of Arizona. Adult males and females were identified by the sexually dimorphic foretarsi. Females were placed in individual plastic chambers (5 cm X 5 cm) with peat moss (*Sphagnum* Linnaeus) dampened with distilled water. Chambers were kept at approximately 23°C near a window and thus the beetles experienced natural lighting conditions. Every three days they were fed a segment of fresh mealworm larvae (*Tenebrio* Linnaeus) and the food was removed after 12 hours to avoid fungal growth. After approximately one month, the females began to oviposit on the peat moss surface. Eggs were washed in a 1% chlorine solution to prevent fungal growth, rinsed with distilled water, and placed inside a small Petri dish lined with clean cotton tissue paper, which was moistened with distilled water daily to prevent desiccation. Eggs hatched after 18 to 21 days (n=12). Larvae were reared in individual rearing chambers (5 cm X 5 cm) with peat moss dampened with distilled water. They were fed living adult flies, *Drosophila mojavensis* Patterson and Crow. Most larvae were preserved as first instars. Two larvae molted to second instars 49 and 54 days after hatching. One larva was observed and photographed as it molted. The cuticle of the first instar cracked longitudinally along the dorsal surface of the thorax and second instar larva emerged from that fracture. First the head broke free from the exuvium and then, after approximately 10 minutes, the larva was able to shed the old cuticle from the terminal disk.



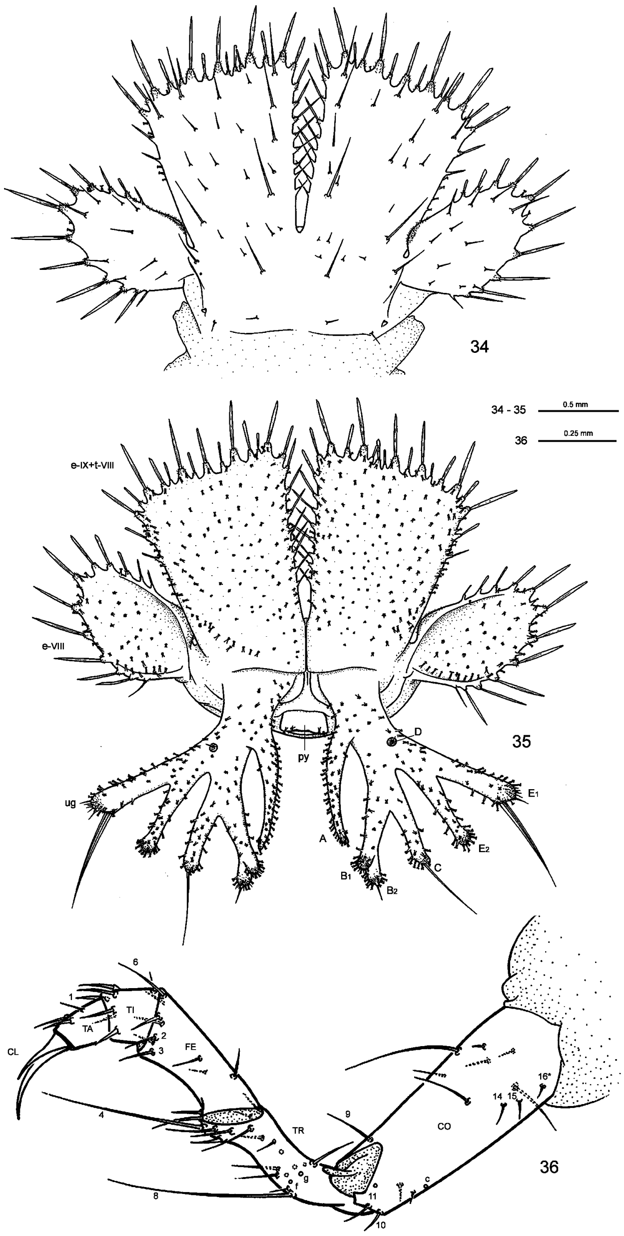
FIGURES 9–16. *Goniotropis kuntzeni* first instar larva. 9—head, dorsal view (scale: 500 µm); 10—labium, dorsal view (scale: 200 µm); 11—pronotum and mesonotum, dorsal view (scale: 500 µm); 12—right antenna, dorsal view (scale: 200 µm); 13—apex of right antennomere IV, dorsal view (scale: 20 µm); 14—apex of right galea, dorsal view (scale: 10 µm); 15—apex of prothoracic leg, anterolateral view (scale: 200 µm); 16—right egg burster (scale: 100 µm).



FIGURES 17–25. *Goniotropis kuntzeni* first instar larva. 17—head, dorsal view; 18—head, ventral view; 19—left antenna, dorsal view; 20—left maxilla, dorsal view; 21—left mandible, dorsal view; 22—labium, dorsal view; 23—frontoclypeolabrum, dorsal view; 24—tentorium; 25—epipharynx. aa, anterior arms of tentorium; AN, antenna; da = dorsal arms of tentorium; FR, frontoclypeolabrum; LA, labium; MN, mandible; MX, maxilla; pa = posterior arms of tentorium; PA, parietalia; tb = tentorial bridge.



FIGURES 26–33. *Goniotropis kuntzeni* first instar larva. 26—abdomen, right lateral view (scale: 200 µm); 27—abdominal spiracle I (scale: 20 µm); 28—terminal disk, apical view (scale: 1 mm); 29—sensilla S-II and S-I between dorsal plates (scale: 100 µm); 30—surface of dorsal plate (scale: 100 µm); 31—sensilla S-I and S-II on margin of dorsal plates (scale: 50 µm), 32—right urogomphus (scale: 500 µm); 33—bilobed apex of lobe B of urogomphus (scale: 100 µm). S-I, S-II, S-III, S-IV, S-V, abdominal sensilla.



FIGURES 34–36. *Goniotropis kuntzeni* first instar larva. 34—terminal disk, dorsal view; 35—terminal disk, apical view; 36—left prothoracic leg, posterior view. A, B_1, B_2, C, D, E_1, E_2, urogomphal lobes; CL, claws; CO, coxa; e, epipleurite; FE, femur; py, pygidium; t, tergum; TA, tarsus; TI, tibia; TR, trochanter; ug, urogomphus.

Additional images and videos of the larvae are available online on the *Goniotropis kuntzeni* page of the Tree of Life Web Project (http://tolweb.org/notes/?note_id=3140).

Seven eggs, 9 first-instars and 2 second-instars were preserved in 75% ethyl alcohol. Prior to preservation larvae were submerged in hot, distilled water for approximately one minute. One first instar specimen was mounted on a slide with Canada Balsam and was studied and drawn by using both Olympus SZX12 and Leitz Laborlux S microscopes equipped with drawing tubes. One egg and one first-instar specimen were critical point dried, sputtered with gold, mounted on stubs, and photographed with a Philips XL30 scanning electron microscope (L.I.M.E. laboratory, University "Roma Tre," Rome).

Larvae were deposited in the University of Arizona Collection of Arthropods, the W. Moore Collection (Tucson, Arizona) and the A. Di Giulio - A. Vigna Taglianti Collection (Rome, Italy).

For general terminology of larval structures we refer to Lawrence (1991). The nomenclature of the tentorial apodemes follows Spence and Sutcliffe (1982). Notation of primary setae and pores follows the system of Bousquet and Goulet (1984), modified for *Metrius contractus* Eschscholtz (Bousquet 1986); according to this system we consider as "additional" the setae not recognised as homologous to the ancestral primary carabid pattern both in first and second larval instars. When all the primary setae were recognised on the sclerites and parts of the body, only the additional setae are mentioned. As some of the sensilla of *Goniotropis* larvae present on the abdomen and terminal disk are homologous to those recognised by Bousquet (1986) in *Metrius contractus* (sensilla S-I to S-V), by Di Giulio *et al.* (2000) in *Pachyteles* spp. (sensilla S-I to S-VII), and by Di Giulio and Moore (2004) in *Arthropterus* sp. (sensilla S-I to S-VIII), we adopted the same nomenclature used by these authors. Notations for microsculpture and urogomphal lobes follow that proposed by Bousquet (1986) for *Metrius contractus*, and later modified by Vigna Taglianti *et al.* (1998) for the Ozaenini. An asterisk (*) following a coded seta indicates that the homology between the structure on the *Goniotropis* larva and the corresponding code is questionable.

Taxonomic Treatment

Egg morphology. Egg (Figs. 3, 5) ovoid, length about 2 mm, maximum width about 1 mm. Anterior pole with micropilar area (Figs. 7–8) small and finely perforated, diameter about 40 µm. Egg-shell (chorion) (Fig. 6) consists of 1 external and 1 internal layer; external layer composed of a honeycombed, regularly perforate grid, net-like with sub-hexagonal meshes; diameter of each mesh about 30 µm; internal layer (aerenchyma) about 15–20 µm thick, spongy, containing air filled cavities, similar to egg-shell type A described by Kaupp *et al.* (2000).

Diagnosis of first and second instars. Coronal suture long; frontal sutures weakly sinuate; labral spine small, subrectangular, apex two-lobed; last palpomere of maxilla elongate; prementum subquadrate or slightly transverse, with elongate ligula; stipes slender, long, inwardly curved, with strong triangular basal tooth; lacinia short; mandibles elongate and slender with short, sharp and slender retinaculum; last antennomere long, club-shaped; abdominal epipleurites progressively larger from segment I to VIII; terminal disk wide, about twice as wide as head; lateral plates (epipleurites VIII) of terminal disk transverse, slender and elongate, projecting laterally, well separated from dorsal plates; dorsal plates (epipleurite IX + tergum VIII) subrectangular, wider at apex than at base, widely separated in middle; urogomphal lobe A shorter than B; urogomphal lobe B_2 slightly longer than B_1.

Description: First instar.

Measurements. Body length about 7.4 mm (from tip of mandibles to apex of terminal disk); cephalic capsule maximum width (at base of antennae) 1.58 mm, medial length (from occipital foramen to anterior margin of frontoclypeolabrum) 1.08 mm; prothorax maximum width 1.36 mm, medial length 0.76 mm; terminal disk maximum width (at level of lateral plates) 2.89 mm; dorsal plates length (from base, near articulation, to medial apex) 1.44 mm.

Habitus and coloration. Body soft, weakly sclerotized, not physogastric. Abdomen short, bellows-like (Fig. 26), contracted dorsally elevating large terminal disk (Fig. 4). Body whitish, terminal disk well sclerotized and yellowish, cephalic capsule and mouthparts strongly sclerotized and light brown (Fig. 4). Terebra, retinaculum and apex of mandibles, laciniae, anterior margin of frontal sclerite, egg-bursters and claws thickly sclerotized and reddish brown to piceous.

Microsculpture. Cephalic capsule, mouthparts, thoracic tergites and legs smooth, without or with only sparse, pointed microsculpture (Figs. 9–12, 15, 16). Labral spine and anterior margin of epipharynx with strongly spinulate microsculpture, resulting in a serrate anterior margin (Figs. 10, 25); lateral and anteromedial part of epipharynx with thin, elongate sculpticells medially directed; posteromedial part of epipharynx with many short rows of anteriorly directed spines; hypopharynx with many long concentric comb-like rows, each composed of hundreds of small anteriorly directed teeth; epi- and hypopharyngeal microsculpture, together with associated setae, forming a mouth filter apparatus; basal third of prementum (Fig. 10) with pointed microsculpture on dorsal surface. Membranous areas of body and sclerites of the abdomen rugulose to rugose (Figs. 26–27), with pointed or multi-pointed sculpticells, sparse near setae. Surface of plates and urogomphi of terminal disk (Figs. 29, 31, 33), as well as pygidium, with pointed to multi-pointed microsculpture.

Chaetotaxy. Frontoclypeolabrum (Figs. 9, 23) without additional setae; setae FR_1, FR_2 and FR_3 subequal in length; setae FR_1 and FR_3 at anterior third of egg bursters, seta FR_2 at basal third of egg bursters, posterolateral to egg bursters; FR_4* small, slightly shorter than FR_3, anteromedial to frontal area; seta FR_5 absent, possibly replaced by a pore; FR_6 small, slightly medial and posterior to FR_7; seta FR_7 longer than other frontal setae, almost twice as long as FR_1; setae FR_8 and FR_9 moderately long, medially directed, inserted ventrally at anterior corners of median prominence; setae FR_{10}* and FR_{11}* just behind transverse frontal keel; seta FR_{11}* slightly posterior to and longer than FR_{10}*; labral spine with 2 minute anteriorly directed setae on dorsal surface. Parietale (Figs. 17–18) with several small additional setae between PA_8* and basal stem of epicranial suture; 3 ventrolateral spine-like additional setae posterior to PA_{14}; PA_8* elongate, at same level as PA_9*. Antennomere I (Figs. 12, 19) with 5 additional setae: 2 short dorsolateral setae on basal half, and a crown of 3 longer setae subapically; II without additional setae; III with seta AN_1 displaced anteriorly; IV with AN_6 short (Fig. 13, 19). Mandible (Fig. 21) without additional setae; seta MN_1 short; 6 additional pores on dorsal surface between MN_1 and MN_2: 2 anterior to MN_b*, 3 at the level of anterior insertion of retinaculum and 1 anterior to MN_c. Setal group gMX (Fig. 20) on stipes composed of approximately 20 spine-like setae distributed as follows: 5 setae along occlusal margin (Fig. 10), 7–8 setae along dorsolateral margin and 6–8 near base; 2 additional setae on lateral side of stipes; seta MX_5* dorsal; seta MX_6 small, subapical, in a medial groove of lacinia; MX_d* ventral at apex of galeomere I; seta MX_8* subapical, close to MX_9*; small sensorial area (composed of 3 short lateral and 1 longer medial basiconic sensilla) present at apex of galeomere II (Fig. 14); maxillary palpomere IV with small dorsolateral additional seta on medial side, 1 ventral pore and 3 longitudinal subapical digitiform sensilla and apical sensorial area composed of several papillae. Prementum (Figs. 10, 22) with about 30 additional spine-like setae on lateral and dorsal surfaces, inserted in protuberances; seta LA_1 close to midline; labial palpomere II with 2 additional setae, 1 mesodorsal and 1 small ventrolateral, 3 longitudinal subapical digitiform sensilla and apical sensorial area composed of several papillae. Each side of epipharynx (Fig. 25) with 3 small additional setae and 1 pore posterior to couple FR_8-FR_9. Pro-, meso- and metanotum (Fig. 11) with 2 or 3 additional setae and several pores (mostly anterior) on each side of ecdysial line; seta PR_{14} elongate on discal area. Trochanter (Fig. 36) with spiniform setae present mostly on ventral side, including a long TR_4; TR_8 about as long as TR_4 but thinner. Meso- and metasternum with MS_4* extremely long. Abdominal tergites I–VII (Fig. 26) with reduced setation. Tergal side of dorsal and lateral plates of terminal disk (Fig. 34) with stiff pointed setae (sensilla S-VII) of various sizes, with cylindrical bases protruding from plates: about 25 on each dorsal plate (epipleurite IX + tergite VIII) and about 10 on each lateral plate (epipleurite VIII); margins of dorsal and lateral plates (Figs. 34–35) with sensilla S-II (and a few sensilla S-I); each dorsal plate with about 15 S-II of two sizes, large and small S-II evenly dispersed in alternate positions along distal margin; inner margin of each dorsal plate (Fig. 29) with 8–9 S-II obliquely directed, increasing in size from base to apex; margin of each lateral plate with 12 sensilla S-II, short S-II at base of lateral plate and long S-II at apex of lateral plate; ventral side of terminal disk with numerous sensilla S-I (Fig. 29, 31, 33) sparsely distributed: about 150 S-I on each dorsal plate, mostly basally and medially, and about 50 on each lateral plate. Epipleurites (Fig. 26) of abdominal segments I–II with inconspicuous or moderately long and thin setae; those of segments III–VII with several setae and strong, elongate sensilla S-II. Hypopleurites of segments I and VIII without setae, II and VII with setae, III–VI with setae and sensilla S-II. Sternal area of segments I–II and VI–VIII with setae, those of III–V with setae and elongate sensilla S-II. Urogomphi (Figs. 32–33, 35) with many S-I, mainly on dorsal and apical areas of branches; branch B with 2–3 S-III apically (Fig. 33), branch C with 1 apical and 1 subbasal S-IV, branch E_1 with 4–5 S-III apically and 1 S-V subapically on ventral side, branch D with 1 S-III apically. Pygidium with few sensilla S-I.

Head. Cephalic capsule (Figs. 9, 17–18) transverse (width/length ratio = 1.46), hyperprognathous, slightly rounded laterally, regularly tapered at basal half into a distinct neck; maximum width at antennal insertions about twice as wide as at occipital foramen, occipital foramen dorsally displaced; tentorium (Fig. 24) with posteromedial processes joined forming a subrectangular bridge (tentorial bridge). Frontoclypeolabrum (Figs. 9, 23) shield-like, transverse (width/length ratio = 1.36), with surface medially convex and laterally concave; basal stem of epicranial suture elongate, anterior frontal arms only slightly sinuate; egg-bursters (Fig. 16) keel-like, composed of two longitudinal, multispinulate carinae, each consisting of about 80 apically directed teeth, anteriorly preceded by a larger triangular spine; carinae parallel, about one third frontoclypeolabrum length, widely separated, placed between FR_1 and FR_3. Frontoclypeolabrum (Figs. 10, 23, 25) with two anterior margins: dorsal margin smooth, moderately curved and anteriorly prominent, forming a transverse keel (see Di Giulio *et al.* 2003 and Di Giulio and Moore 2004 for a discussion on homology) extended to adnasalia, ventral margin serrate, slightly sloping anteriorly, medially produced into a subrectangular labral tooth (labral spine *sensu* Beutel 1992) partially 2-lobed apically; adnasalia slightly rounded and slightly protruding. Parietale (Figs. 17–18) with one stemma; ocular and cervical grooves absent; ventral walls of parietale medially fused forming a complete single gular suture (Fig. 18). Antennae (Figs. 12, 19) 4-jointed, slightly shorter than mandibles, forwardly directed; antennomere I about 3 times longer than II; III about 2 times longer than II; IV slightly shorter than III; III with small, conical sensorial appendage. Mandibles (Figs. 12, 21) long and slender, falcate, sharp at apex, about 3 times as long as their basal width, evenly curved along lateral margin; penicillus absent; terebra double-edged: dorsal cutting edge slightly convex beyond retinaculum, then concave near apex; ventral cutting edge regularly concave; retinaculum subtriangular, with pointed apex slightly curved inward. Maxilla (Figs. 10, 20) with undivided cardo, long and slender stipes, 4-jointed palp, 2-jointed galea and 1-jointed lacinia; stipes distinctly curved inward, about 4 times as long as their basal width; conspicuous mesal stipital protuberance present subbasally on inner side, triangular, forwardly directed and acute at apex. Setal notches present along inner side; maxillary palpomeres gradually decreasing in length from I to III; IV digitiform, distinctly longer than others, about as long as II and III combined. Galeomere I short; II cylindrical, stick-like, 3 times as long as I, slightly curved inward at distal half. Lacinia (Fig. 10) elongate and curved, strongly sclerotized, basally fused with stipes and apically pointed. Labium

(Figs. 10, 22) with sclerotized prementum and 2-jointed palp; prementum subquadrate or slightly transverse with setal notches present on dorsal surface and sides; ligula long, about as long as labial palpomere I; labial palpomere I short and wider than II; II digitiform, about 2 times as long as I.

Thorax. Tergites (Fig. 11) moderately sclerotized (mostly pronotum) decreasing in length from pro- to metanotum, sternites slightly or not sclerotized. Pronotum wider than meso- and metanotum, transverse, two times wider than long, with setiferous protuberances on sides. Meso- and metanotum rounded laterally, widely transverse, about two and a half times wider than long, with anterior margin slightly concave; longitudinal ecdysial line well marked on pro- and mesonotum, less evident, but present, on metanotum.

Spiracles. Thoracic and abdominal spiracles (Fig. 27) annular with conical, protruding peritremes. Mesothoracic spiracles anterolaterally positioned on mesopleura, diameter almost 2 times wider than diameter of abdominal spiracle I. Abdominal spiracle I diameter slightly wider than diameter of abdominal spiracles II–VII, II–VII subequal (Fig. 26), VIII extremely small, placed basally between insertion of dorsal and lateral plates of terminal disk (Fig. 34).

Legs. Legs long, 5-jointed (Figs. 15, 36), progressively longer from foreleg to hindleg. Coxa cylindrical, elongate, about as long as trochanter and femur combined; trochanter obliquely truncate and ventrally expanded at apex, about as long as femur and tibia combined; femur about twice as long as tibia, slightly increasing in size from base to apex; tibia cylindrical, about as long as tarsus; tarsus more slender than tibia, conical, tapered from base to apex, with 2 sharp claws; anterior claw long, regularly curved from base to apex; posterior claw shorter, thinner and almost straight.

Abdomen. Abdominal segments I–VII (Fig. 26) slightly or not sclerotized, bellows-like, generally upcurved, with abdominal apex (terminal disk) elevated. Abdominal sclerite boundaries barely discernable, recognised by reduction of pointed microsculpture, reduction of protrusion, and presence of setae or sensilla S-II; segments progressively wider from I to VII. Each segment dorsally flattened, with swollen, setiferous pleural and sternal areas. Hypopleurites I, VII and VIII relatively small, II–VI larger and protruding. E pipleurites conical, distinctly protruding, gradually larger in size from I to VIII; epipleurites VIII (Figs. 34–35) flattened and enlarged into 2 sclerotized lateral plates, smaller than dorsal plates; lateral plates slender, suboval, transverse, almost 2 times wider than long; epipleurites IX greatly enlarged and fused with tergum of segment VIII into a terminal disk (= anal plate *sensu* Bousquet 1986); terminal disk (Figs. 28, 34–35) completely divided into 2 rectangular, sclerotized plates (dorsal plates), slightly enlarged from base to apex and widely separated in middle (Fig. 30); lateral plates widely separated from dorsal plates; lateral plates, dorsal plates and urogomphi articulated at base by membranes, dorsal and lateral plates move against urogomphi. Median, inner and outer sternites gradually narrowed from segments I to VI; median sternite absent in segments VI to VIII; sternum VI to VIII without sclerites. Urogomphi and pygidium generally oriented in a vertical plane (Figs. 4, 28, 35); urogomphi (Figs. 28, 32, 35) wide, branched, each composed of 7 slender, slightly flattened lobes: A, B_1, B_2, C, D, E_2, E_1 (respectively from inner to outer) mostly developed on a single plane; lobe A inserted more basally than others, slender, slightly curved and tapered to tip, not reaching apex of lobe B; lobe B stout and vertically two-lobed at apex (Fig. 33), B_2 (ventral) slightly longer than B_1 (dorsal); lobe C as long as E_2; lobes E_2 and E_1 slightly club-shaped; lobe E_1 subparallel sided, slightly stronger than others; lobe D small, dorsal, emerging perpendicularly to plane of other branches, from base of branch E; pygidium (Fig. 35) flat, subrectangular, medioventral between urogomphal insertions.

Second instar. No significant morphological differences were observed between first and second instar larvae, other than those associated with larger body size of the second instar, including relative dimensions of structures, a slightly richer chaetotaxy and a stronger sclerotization of head, mouthparts, sclerites, terminal disk and urogomphi. Characters that differ from the first instar are reported below.

Measurements. Body length about 1 cm (from tip of mandibles to apex of terminal disk); cephalic capsule maximum width (at base of antennae) 2.2 mm, medial length (from occipital foramen to anterior margin of frontoclypeolabrum) 1.6 mm; prothorax maximum width 2 mm, medial length 1.2 mm; terminal disk maximum width (at level of lateral plates) 4 mm; dorsal plates length (from basal folding to medial apex) 2 mm.

Differences from first instar larva. Cephalic capsule more curved laterally and strongly tapered to the occipital foramen. Frontoclypeolabrum with labral spine more elongate and slender, with associated stronger denticulation and pubescence of anterior margin of epipharynx; anterior frontal arms of epicranial suture almost straight; egg-bursters absent; a pair of minute setae, possibly representing setae FR_5*, present at level of pore FR_C. Antennae slightly longer and thinner; antennomere I with 5–6 small setae on the basal half and a crown of 3 longer setae subapically; antennomere II with a long, lateral seta on outer side; antennomere IV longer and more clavate. Mesothoracic spiracles with cylindrical, larger peritremes. Urogomphi with lobes more slender and elongate; lobe B_1 and B_2 subequal in length.

Behaviour. The behaviour of *G. kuntzeni* larvae, observed under laboratory conditions, resembles that described by Di Giulio and Vigna Taglianti (2001) for *Pachyteles*. *Goniotropis kuntzeni* larvae dug burrows in the peat moss and they closed off their burrow with their terminal disk. They fed by trapping live insect prey *(Drosophila mojavensis*) with the moveable components of their terminal disk, and then they brought the captured prey into their burrow to consume. The larvae were also observed to forcefully squirt clear fluid, of unknown chemical composition, from their anus when disturbed.

Key to the Genera of Paussinae Larvae

Names of species with described larvae are provided in brackets following each genus. An illustrated version of this key is available online on the Paussinae pages of the Tree of Life Web Project (http://tolweb.org/notes/?note_id=3430).

1. Abdomen linear, with segments VIII–IX not modified; segment IX with pair of tubular urogomphi (rarely reduced or absent) .... most Carabidae
- Abdomen upcurved, with segments VIII–IX (mostly epipleurites and tergites) highly modified, transformed into a transverse sclerotized terminal disk composed of flat plates; segment IX with pair of branched or plate-like urogomphi.........(Paussinae)…2
2. Head hyperprognathous (bent upwards); neck constricted; coronal suture present; sensorial appendage on antennomere III small and conical; mandibles long and slender, sickle-shaped; urogomphi multi-lobed; tarsi with 2 claws; pygidium between urogomphi near the middle of the terminal disk ....(Metriini, Ozaenini)…3
- Head prognathous; neck not constricted; coronal suture absent; sensorial appendage on antennomere III large, bulbous or conical; mandibles short and broad, subtriangular; urogomphi flattened, plate-like, not lobate; tarsi with 1 claw; pygidium ventral to urogomphi and terminal disk…(Paussini) 8
3. Anterior margin of frontoclypeolabrale with four small subequal teeth just behind the anterior margin of frontal sclerite; stipes of maxillae without a basal tooth; urogomphi with 5 lobes, lobe A short, lobe D at the common base of lobes B-C, lobe E undivided ....*Metrius* Eschscholtz [*M. contractus* Eschscholtz]
- Anterior margin of frontoclypeolabrale not toothed, instead smooth transverse keel present anteriorly on frontal sclerite; stipes of maxillae with an acute basal tooth at inner side; urogomphi with 6 or more lobes, lobe A elongate; lobe D at the base of lobe E; lobe E subapically divided into E_1 and E_2 lobes ....(Ozaenini)…4
4. Transverse keel well behind anterior margin of frontoclypeolabrale; labral tooth wide, slightly rounded anteriorly, clearly visible in dorsal view; prementum tapered from the base to the apex; urogomphi with short, flattened and partially fused lobes, lobes B, D and E_1 pointed at tip; dorsal plates of terminal disk concave with large, protruding sensorial areas near the middle.................................... *Physea* Brullé [*P. setosa* Chaudoir]
- Transverse keel just behind anterior margin of frontoclypeolabrale; labral tooth small, anteriorly truncate, partially covered by the transverse keel in dorsal view; prementum subrectangular or subquadrate, with parallel sides; urogomphi antler-like with long and slender lobes, lobes B, D and E_1 rounded at tip; dorsal plates of terminal disk flat or only slightly convex without protruding sensorial areas 5
5. Prementum subrectangular, longer than wide; ligula dome-like, moderately protruding; antennomere IV short and cylindrical; second galeomere conical .... *Pachyteles* Perty [*P. mexicanus* Chaudoir, *P. vignai* Deuve, *P. digiulioi* Deuve, *Pachyteles* sp. (van Emden 1942), *Pachyteles* sp. (Costa *et al.* 1988)]
- Prementum subquadrate or slightly transverse; ligula elongate; antennomere IV long

and clavate; second galeomere stick-like, elongate and cylindrical.............................. 6

6. Urogomphi with lobes A and E_2 flattened, truncate and partially two-lobed at apex (according to the drawings of Paulian 1947); lobe B undivided.................................... ....*Sphaerostylus* (Subgenus *Afrozaena*) Chaudoir [*S. luteus* Hope]

- Urogomphi with lobes A and E_2 cylindrical, tapering to the tip and undivided; lobe B divided into B_1 and B_2 lobes…... 7

7. Lacinia slightly longer than galea; dorsal plates of terminal disk subtrapezoidal, distinctly wider at apex than at base, medially adjacent; lateral plates wide and short; lobe A slender, about as long as lobe B; lobe D slender and long .... *Itamus* Schmidt-Goebel [*I. cavicola* (Moore)]

- Lacinia shorter than galea; dorsal plates of terminal disk subrectangular, only slightly wider at apex than at base, deeply divided medially; lateral plates elongate and slender; lobe A robust, distinctly shorter than lobe B; lobe D short ....…*Goniotropis* Gray [*G. kuntzeni* Bänninger]

8. Several setae on dorsal surface of the head, thoracic tergites and of perimeter of terminal disk clavate and riddled (sensilla S-VIII); lacinia present, apically with strong hook-like spines along occlusal margin; antennomere IV with stick-like, apical sensory appendix; mandible without prostheca; leg with articulated trochanter, femur, tibia and tarsus; urogomphi with irregularly raised margin ....…*Arthropterus* W.S. MacLeay [*Arthropterus* sp. (Di Giulio and Moore 2004)]

- Setae on dorsal surface of the head, thoracic tergites and perimeter of terminal disk not clavate; lacinia absent; antennomere IV simple, without stick-like, apical sensory appendix; mandible with digitiform prostheca; leg with fused trochanter, femur, tibia and tarsus; urogomphi with regularly rounded margin…. 9

9. Prementum narrowing apically; first maxillary palpomere basally articulated with stipes, resulting in a 4-jointed palp; sutures between trochanter, femur, tibia and tarsus visible; sensillum S-I with inflated apex; sensilla S-II on margin of terminal disk replaced by long fine setae.............*Platyrhopalopsis* Desneux [*P. melleii* (Westwood)]

- Prementum widening apically; first maxillary palpomere basally fused with stipes, resulting in a 3-jointed palp; trochanter, femur, tibia and tarsus completely fused, without suture remnants; sensillum S-I with simple truncate apex; sensilla S-II on margin of terminal disk strong and short, with frayed apex .... *Paussus* Linnaeus [*P. cultratus* (Subgenus *Bathypaussus*) Westwood, *P. cucullatus* (Subgenus *Cochliopaussus*) Westwood, *P. curtisi* (Subgenus *Curtisipaussus*) Westwood, *P. horni* (Subgenus *Edaphopaussus*) Wasmann, *P.* aff. *distinguendus* (Subgenus *Klugipaussus*) Reichensperger, *P. afzelii* (Subgenus *Lineatopaussus*) Westwood, *P. kannegieteri* (Subgenus *Semipaussus*) Westwood, *P. cridae* (Subgenus *Spinicoxipaussus*) Gestro], *P. granulatus* (Subgenus *Granulopaussus*) Westwood

Discussion

Larvae are now known for five of the 24 Ozaenini genera. Although the number of described larvae is relatively small, larval characters have proven useful for revealing relationships within this subfamily (Di Giulio *et al*. 2003, Di Giulio and Moore 2004). Larval character states present in *G. kuntzeni* but absent in other described ozaenine larvae may be revealed to be apomorphies of the species, genus or more inclusive clades as additional ozaenine larvae are described. Most of the larval characters that are unique to *G. kuntzeni* are those of the terminal disk. For example, the terminal disk of *G. kuntzeni* is very wide, about twice as wide as the head; the lateral plates are slender, elongate, laterally projecting, and well separated from dorsal plates; lobe A is shorter than lobe B; and lobe B2 slightly longer than lobe B1 in first instar. In addition, the mandible has a short, sharp and slender retinaculum and the abdominal epipleurites are progressively expanded and protruding from segments I to VIII.

Goniotropis kuntzeni larvae share some character states with other ozaenine larvae. For instance, the following *G. kuntzeni* characteristics are also present in the Old World genus *Itamus*: the head capsule is distinctly curved laterally and strongly tapered to the occipital foramen; the coronal suture is elongate; the mandible is elongate and slender; the stipes is curved and slender with a strong triangular basal tooth, and the last antennomere is elongate and club-shaped. *Goniotropis kuntzeni* and *Pachyteles mexicanus* (Chaudoir) have similarly shaped subrectangular dorsal plates that are widely separated in the middle. At this time the phylogenetic relationship between *Goniotropis* and other ozaenine genera is uncertain based on larval morphology.

Adults and larvae of Paussinae exhibit varying degrees of association with ants and although the natural history of most species is not well known, the external morphology of the larvae provides clues about their behaviour. For example, myrmecophilous larvae, such as those of *Arthropterus*, *Platyrhopalopsis* and *Paussus* and possibly the ozaenine genus *Physea*, have an immobile terminal disk with fused plates. On the other hand, non-myrmecophilous larvae are burrow-trappers (Costa *et al.* 1988, Bousquet 1986, Di Giulio and Vigna Taglianti 2001). These larvae use the moveable components of their terminal disk to capture insects and bring their prey into their gallery to consume. The discovery that *Goniotropis kuntzeni* have mobile plates of the terminal disk that they use to trap live insect prey, suggests that these larvae are not myrmecophilous, despite the observation that the ant *Camponotus ocreatus* were consistently found on the same Emory oak trees as the *Goniotropis kuntzeni* adults.

This is the first report of a paussine larva forcefully ejecting a clear liquid from their anus when disturbed. We recommend that future behavioral studies of Paussinae larvae include investigations of this phenomenon. It would be interesting to determine the chemical composition of this fluid and its potential role in defence or in the capture of prey as well as its presence in other paussine larvae.

Acknowledgements

We are grateful to Scott McCleve for his advice on collecting methods and collection localities for ozaenine species in southern Arizona and to David Maddison for his advice on techniques for rearing carabid larvae and for providing lab space for this study. We also thank Teri Markow for supplying *Drosophila mojavensis* as food for the larvae. This study was supported by an NSF Dissertation Improvement Grant (DEB 0309221) to W. Moore and D.R Maddison.

References

Ball, G.E. & McCleve, S. (1990) The Middle American genera of the tribe Ozaenini with notes about the species in southwestern USA and selected species from Mexico. *Quaestiones Entomologicae*, 26(1), 31–116.

Beutel, R.G. (1992) Study on the systematic position of Metriini based on characters of the larval head (Coleoptera: Carabidae). *Systematic Entomology,* 17(3), 207–218.

Bousquet, Y. (1986) Description of first-instar larva of *Metrius contractus* (Coleoptera: Carabidae) with remarks about phylogenetic relationships and ranking of the genus *Metrius*. *The Canadian Entomologist,* 118(4), 373–388.

Bousquet, Y. & Goulet, A. (1984) Notation of primary setae and pores on larvae of Carabidae (Coleoptera: Adephaga). *Canadian Journal of Zoology,* 62, 573–588.

Brown, D.E. (1994) *Biotic Communities: Southwestern United States and Northwestern Mexico*. University of Utah Press, Salt Lake City, 342 pp.

Costa, C., Vanin, S.A., & Casari-Chen, S.A. (1988) *Larvas de Coleoptera do Brasil.* Museu de Zoologia, Universidade de Sao Paulo, Sao Paulo, Brazil, 282 pp.

Deuve, T. (2001a) Contribution á la connaissance des Coléopteres Paussidae Ozaeninae Néotropicaux. *Revue Française dEntomologie (N.S.),* 23(4), 237–252.

Deuve, T. (2001b) Le genre *Eustra* Schmidt-Goebel, 1846, insectes (Coleoptera, Paussidae, Ozaeninae) a genitalia femelles orthotopiques. *Zoosystema,* 23(3), 547–578.

Deuve, T. (2002) Une nouvelle *Eustra* troglobie du karst de Maros, Sulawesi (Coleoptera, Paussidae). *Nouvelle Revue d'Entomologie,* 19(2), 193–195.

Deuve, T. (2004) Nouveaux Ozaenini neotropicaux (Coleoptera, Paussidae). *Revue Française d'E ntomologie (N.S.),* 26(3), 117–130.

Di Giulio, A., Fausto, A.M., Taddei, A.R. & Vigna Taglianti, A. (2000) The terminal disk of *Pachyteles* larvae (Coleoptera, Carabidae, Paussinae): a morphological study. In: Natural History and Applied Ecology of Carabid Beetles, Proceedings of the IX European Carabidologists Meeting (26–31 July, 1998, Camigliatello, Cosenza, Italy). (Eds. P. Brandmayr, G. Lövei, T. Zetto Brandmayr, A. Casale & A. Vigna Taglianti) pp. 89–93. (Pensoft, Sofia, Moscow).

Di Giulio, A., and Vigna Taglianti, A. (2001) Biological observations on *Pachyteles* larvae (Coleoptera: Carabidae: Paussinae). *Tropical Zoology,* 14, 157–173.

Di Giulio, A., Fattorini, S., Kaupp, A., Vigna Taglianti, A. & Nagel, P. (2003). Review of competing hypotheses of phylogenetic relationships of Paussinae (Coleoptera: Carabidae) based on larval characters. *Systematic Entomology,* 28, 509–537.

Di Giulio, A. & Moore, W. (2004) The first-instar larva of the genus *Arthropterus* (Coleoptera: Carabidae: Paussinae): implications for evolution of myrmecophily and phylogenetic relationships within the subfamily. *Invertebrate Systematics,* 18(2), 101–115.

Kaupp, A., Guggenheim, R. & Nagel, P. (2000) Egg-shell structure of Paussinae and other Carabidae, with notes on its phylogenetic relevance (Coleoptera). *In*: Brandmayr, P., Lövei, G., Brandmayr, T.Z., Casale, A. & Vigna Taglianti, A. (Eds.) *Natural History and Applied Ecology of Carabid Beetles, Proceedings of the 9th International Carabidologist Meeting, Cosenza, Italy.* Pensoft Publishers, Sofia, Moscow, pp. 111–115.

Lawrence, J.F. (1991) Order Coleoptera. *In*: Stehr, F.W. (Ed.), *Immature Insects. Vol. 2.* Kendall/Hunt Publishing Company, Dubuque, Iowa, pp. 144–298.

Lorenz, W. (1998) *Systematic List of Extant Ground Beetles of the World. (Insecta Coleoptera "Geadephaga": Trachypachidae and Carabidae incl. Paussinae, Cicindelinae, Rhysodinae). First Edition.* Published by the author, Tutzing, Germany, 502 pp.

Luna de Carvalho, E. (1989) Essai monographie des Coléoptères Protopaussines et Paussines. *Memorias do Institudo de Investigaçao Científica Tropical, Segunda Série,* 70(1987), 1–1028.

Luna de Carvalho, E. (1992) Revisao do estudo das larvas de Carabideos Paussinae e de subfamilias afins (Coleoptera: Adephaga). *Elytron (Bulletin of the Association of Coleopterology),* 5(1991), 285–310.

Oberprieler, R.G. (1985). Paussidae. *In*: Scholtz, C.H. & E. Holm (Eds.) *Insects of Southern Africa.* Butterworth, Durban, South Africa, pp. 196–198.

Paulian, R. (1947) La larve de *Pseudozaena (Afrozaena) luteus* [sic] Hope (Col. Carab. Ozaenidae). *Bulletin du Muséum National d'Histoire Naturelle,* 2, 335–339.

Spence, J.R. & Sutcliffe, J.F. (1982) Structure and function of feeding in larvae *Nebria* (Coleoptera:Carabidae). *Canadian Journal of Zoology*, 60, 2382–2394.

Vigna Taglianti, A., Santarelli, F.M., Di Giulio, A. & Oliverio, M. (1998) Phylogenetic implications of larval morphology in the tribe Ozaenini (Coleoptera: Carabidae). *In*: Ball, G.E., Casale, A. & Vigna Taglianti, A. (Eds.) *Phylogeny and Classification of Caraboidea (Coleoptera: Adephaga). Proceedings of a Symposium. XX International Congress of Entomology.* Museo Regionale Di Scienze Naturali, Torino, Italy, pp. 273–296.