

REVISION OF THE NEW WORLD SHORT-WINGED FLOWER BEETLES  
(COLEOPTERA: KATERETIDAE). PART I. GENERIC REVIEW  
AND REVISION OF *ANTHONAEUS* HORN, 1879

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ABSTRACT

A revision of the genus *Anthonaenus* Horn is provided as the initial step of a multiphase project to completely revise the entire New World Kateretidae fauna. *Anthonaenus*, a previously monospecific genus of short-winged flower beetles, was formerly known from the type species *Anthonaenus agavensis* (Crotch). This species is a specialist on flowers of *Hesperoyucca* (Engelm.) Baker (Agavaceae) in southern California, USA. *Anthonaenus bajaensis*, **new species**, is described from Baja California, Mexico, and a redescription of *A. agavensis* is provided for comparative morphology. The larva of *A. agavensis* is described for the first time and the relationship of *Anthonaenus* to other New and Old World Kateretidae genera is discussed in the context of both larval and adult morphology.

Key Words: Cucujoidea, *Yucca*, *Hesperoyucca*, Agavaceae, taxonomy, larva, morphology

RESUMEN

Como primer paso de un proyecto que contempla la revisión completa de la fauna de Kateretidae del Nuevo Mundo, en el presente trabajo se proporciona una revisión del género *Anthonaenus* Horn. *Anthonaenus*, un género inicialmente monoespecífico de coleópteros braquípteros florícolas, fue definido por la especie tipo, *Anthonaenus agavensis* (Crotch). Esta especie se especializa en las flores de *Hesperoyucca* (Engelm.) Baker (Agavaceae) en el sur de California, EEUU. Se describe *Anthonaenus bajaensis*, **nueva especie**, de Baja California, México, y se redescrive *A. agavensis*, comparándola con la nueva especie. Se describe por primera vez la larva de *A. agavensis* y se discute la relación de *Anthonaenus* con otros géneros de Kateretidae del Nuevo y Viejo Mundo, en el contexto de la morfología larvaria y la del adulto.

Kateretidae are a comparatively small family of Cucujoidea with approximately 100 species contained within 14 genera worldwide (Audisio 1993; Jelínek and Cline 2010). Kateretidae share a long and intertwined taxonomic history with the closely related family Nitidulidae, within which the family was once considered a subfamily. The family has also had some nomenclatural instability (see Audisio *et al.* 1994, Audisio 1995, and Cline 2006). Kateretid taxa, however, possess many diagnostic characters that both unite and separate them from Nitidulidae, and the related Smicripidae (see Audisio 1993 and Cline 2005 for reviews). The most notable adult diagnostic feature is the presence of a long, slender maxillary galea, which is absent in Nitidulidae, as well as a typically asymmetrical (in dorsal view) male aedeagus

with tegminal parameres always articulated with the phallobase but never fused to it. Notable larval diagnostic characters include the absence of a mandibular prosthema and urogomphi, and the presence of distinct posteriorly diverging hypostomal rods (see Jelínek and Cline 2010, Jelínek *et al.* 2010, and Cline 2010 for recent morphological reviews of Kateretidae, Nitidulidae, and Smicripidae, respectively).

The Old World Kateretidae fauna contains ten genera (see Jelínek and Audisio 2007 for a review of Palearctic taxa), including *Anamartus* Jelínek, 1976, *Brachyleptus* Motschulsky, 1845, *Brachypterolus* Grouvelle, 1913, *Brachypterus* Kugelann, 1794, *Heterhelus* Jacquelin du Val, 1858, *Jelinekiella* Kirejtshuk, 2000 (= *Jelinekia* Kirejtshuk, 1986, *nec* Cobos, 1981, Buprestidae; see Kirejtshuk

2000), *Kateretes* Herbst, 1793, *Notobrachypterus* Blackburn, 1892, *Platamartus* Reitter, 1892, and *Sibirhelus* Kirejtshuk, 1989. Some of these genera have been completely revised relatively recently, including *Anamartus* (Jelínek 1976; Audisio 1980, 1993) and *Brachyleptus* (Jelínek 1980; Audisio 1989, 1993); however, most remain incompletely revised. Four Holarctic genera are known, including *Brachypterus*, *Brachypterolus*, *Heterhelus*, and *Kateretes*. Within the New World, six genera occur in the Nearctic (Habeck 2002 did not recognize the synonymy of *Boreades* Parsons with *Heterhelus*, which is tentatively followed herein), consisting of the following: *Amartus* J. LeConte, 1861, *Anthonaenus* Horn, 1879, *Brachypterolus*, *Brachypterus*, *Heterhelus*, and *Kateretes*. The Neotropical region contains two additional genera, i.e. *Cercometes* Reitter, 1875 and *Neobrachypterus* Jelínek, 1979. Therefore, the New World Kateretidae fauna is represented by a total of eight genera (Fig. 1), half of which are endemic to the western hemisphere, two in the Nearctic (*Amartus* and *Anthonaenus*) and two in the Neotropics (*Cercometes* and *Neobrachypterus*) (Blackwelder 1945). *Neobrachypterus* was relatively recently revised (Jelínek 1979), but *Cercometes* has not received thorough treatment since its inception (Reitter 1875). Each of the New World genera is currently under revision by the authors, and work herein represents the first stage of a multiphase project to completely revise the entire New World Kateretidae fauna.

*Anthonaenus* species were thought to be geographically restricted from Santa Barbara County south to San Diego County in California, U.S.A. (Parsons 1943). However, a new record from Plumas County, California further extends the range of *Anthonaenus agavensis* (Crotch) northward within the Sierra Nevada mountains, and records from Marin and Sonoma counties extend the range northward into the Coastal Ranges of California. Likewise, the new species described herein increases the range of the genus southward into Baja California, Mexico. We suspect that populations of *Anthonaenus* will likely be discovered in neighboring states in the southwestern United States and Mexico, as the host plant genus is known to occur throughout the region. Both Horn (1879) and Parsons (1943) reported *A. agavensis* from host plants in the genus *Agave* L. (Agavaceae), hence the specific epithet of the type species for the genus. However, Udovic (1986), during his research on the pollination biology of *Yucca whipplei* (Torr.) Trel. (now = *Hesperoyucca whipplei*; Agavaceae) south of the Los Angeles basin in the Ryan Oak Glen Reserve northeast of Escondido, found specimens of *A. agavensis* only on *H. whipplei* and none on *Agave*. Herein, adults of *A. agavensis* are reported for the first time on flowers of *Yucca schidigera* Roez ex Ortgies (Mojave yucca) and *Yucca brevifolia*

Engelm. (Joshua tree) (both Agavaceae), flowers of *Malacothrix glabrata* A. Gray (Asteraceae), and flowers of *Ceanothus* L. (Rhamnaceae), as well as on non-flowering bushes of *Cercocarpus* Kunth (Rosaceae). However, *H. whipplei* is the only host from which larvae have been collected or reared and thus is likely the only true host for *A. agavensis*; nevertheless, further field observations should be undertaken on both *Y. schidigera* and *Y. brevifolia* to confirm host preferences. The new species is known only from flowers of *Hesperoyucca peninsularis* (McKelvey) Clary (Agavaceae), which is endemic only to Baja California. *Hesperoyucca* (Engelm.) Baker currently contains three species: *H. whipplei*, *H. peninsularis*, and *Hesperoyucca newberryi* (McKelvey) Clary. No specimens of *Anthonaenus* have yet been collected from the latter species, which is only known to occur in northwestern Arizona (Mohave Co.).

*Anthonaenus*, unlike all other Kateretidae genera, possess a strongly dorso-ventrally compressed body. This flattened body plan is undoubtedly linked to the floral morphology of the host plants in the monocotyledonous family Agavaceae. Although the body is markedly flattened, there are similarities of this genus to *Amartus*, another Kateretidae taxon endemic to western North America (see diagnosis and discussion below). Current work is being pursued by us not only to monograph all New World genera, but also to provide a phylogenetic treatment using cladistic methods for the entire world fauna (all 14 genera), using both morphological and molecular datasets. Following that quantitative analysis, the relatedness of these two genera, and all genera, will be further pursued; however, that is beyond the scope of this manuscript and awaits quantitative scrutiny utilizing all known genera.

## MATERIAL AND METHODS

The following museums and institutions loaned specimens: American Museum of Natural History (AMNH); California Academy of Sciences (CAS); California State Collection of Arthropods (CSCA); Field Museum of Natural History (FMNH); Florida State Collection of Arthropods (FSCA); Los Angeles County Natural History Museum (LACM); Museum of Comparative Zoology at Harvard University (MCZ); Michigan State University (MSUC); Northern Arizona University (NAUC); The Ohio State University (OSUC); Texas A&M University (TAMU); San Diego Natural History Museum (SDMC); University of California-Riverside (UCR); University of California-Berkeley (UCB); the United States National Museum - Smithsonian Institution (USNM); the first author's collection (ARCC), which is currently housed in the Plant Pest Diagnostics Center in Sacramento, California, and the second

author's collection (CAR), which is currently housed in the Zoological Museum of the Department of Biology "C. Darwin", Sapienza Rome University, Rome, Italy.

Specimen label data are reported verbatim with the following indicators: a backslash "/" denotes label breaks when more than one label was present; each line on a label is separated by a semicolon ";". Numbers of specimens are represented within parentheses "(O)" prior to the collection data.

Genitalia, the metendosternite, and mouthparts were extracted, manually cleaned with minuten pins or KOH, and placed on glycerin slide mounts for observation and imaging. Genitalia drawings were made using an Olympus® BX50 compound microscope attached to a camera lucida. All external images and mouthpart drawings were made through a camera lucida attached to a WILD® Heerbrugg or Nikon® SMZ1500 dissecting microscope. Multiple images were acquired and montages compiled using CombineZ® freeware, and subsequently touched up using Adobe® Photoshop®. Scale bars were calibrated with an ocular micrometer using SPOT® Advanced software on images taken with a digital camera attached to the Nikon® SMZ1500. Scanning electron micrographs were prepared at the California Department of Food & Agriculture Plant Pest

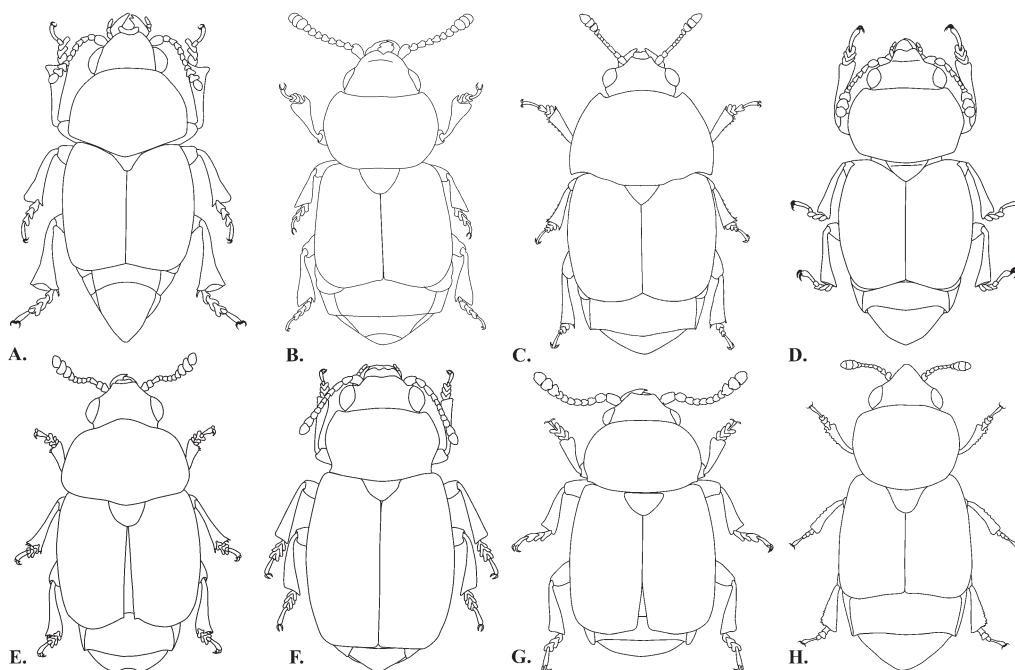
Diagnostics Center using a JEOL model JSM 6300 SEM; specimens used for SEM images were partially desiccated, thereby producing a more "lobed" appearance to the body segments.

Total length and width values are averages for representative specimens analyzed. Total length is defined as distance between apex of labrum and apex of pygidium; total width is distance between elytral humeri; total depth is greatest height of specimen when viewed laterally, typically from metaventricle to elytra. Head length is the distance from the labral apex to the occiput along the midline, and head width is the greatest distance across the head at the temples. Pronotal length is the distance at the midline from the anterior to posterior margin, and pronotal width is the greatest distance across the pronotum. Metasternal length is the distance at the midline from the anterior to posterior margin, and metasternal width is the greatest distance across the metaventricle.

#### GENERA OF NEW WORLD KATERETIDAE

##### 1) *Amartus* J. LeConte, 1861 (Fig. 1A)

This genus currently contains two species. Both species are known to occur on species of *Eschscholzia* Chamisso (Papaveraceae), and are



**Fig. 1.** Dorsal habitus drawings of New World Kateretidae genera. A) *Amartus tinctus* (Mannerheim) (modified from Hatch 1961), B) *Anthonaenus agavensis*, C) *Brachypterolus pulicarius* (modified from Jelinek and Cline 2010), D) *Brachypteris urticae* (F.) (modified from Hatch 1961), E) *Cercometes deyrollei* Reitter, F) *Heterhelus sericans* (LeConte) (modified from Hatch 1961), G) *Kateretes scissus* Parsons, H) *Neobrachypteris nigropiceus* Jelinek (modified from Jelinek 1979).

sympatric in the northwestern United States. The host plants listed by Jelínek and Cline (2010) were a misprint. *Eschscholzia* is the only known larval host plant.

2) *Anthonaenus* Horn, 1879 (Figs. 1B, 2–9)

Following the revision below, there are now two species in this genus. Both species occur in southwestern North America. *Hesperoyucca* (Agavaceae) is the only known larval host, although adults have also been collected from other plants.

3) *Brachypterus* Kugelann, 1794 (Fig. 1C)

This genus currently contains four species in the Nearctic (Parsons 1943), three of which are endemic to the region and one of which is Holarctic. The genus is widespread in North America. All species are known to occur on *Urtica* L. (Urticaceae) (Parsons 1943; Jelínek and Cline 2010).

4) *Brachypterosus* Grouvelle, 1913 (Fig. 1D)

This Holarctic genus currently contains one Nearctic species, *Brachypterosus pulicarius* (L.), which is Holarctic in distribution. In North America this species is known to occur on *Linaria* Mill. (Scrophulariaceae) (Parsons 1943).

5) *Cercometes* Reitter, 1875 (Fig. 1E)

This genus currently contains five species in South America (Grouvelle 1913). This is clearly a polyphyletic genus. We are currently delimiting the new genera needed to accommodate monophyletic groupings of the species. These taxonomic emendations and new taxa will be treated in the subsequent installation of this series of revisions. No host data is available for any taxa currently regarded as “*Cercometes*”.

6) *Heterhelus* Jacquelin du Val, 1858 (Fig. 1F)

This Holarctic genus currently contains four Nearctic species. One species, *Heterhelus (Boreades) abdominalis* (Erichson), was previously considered in its own monotypic genus, but subsequently was relegated to subgeneric status (Audisio 1993). Two species were previously listed as *Kateretes* (= “*Cateretes*”) by Parsons (1943), and one species, *Heterhelus crinitus* Murray, was omitted from the fauna by all subsequent authors. Nearctic species are known to reproduce on *Sambucus* L. (Adoxaceae or Caprifoliaceae, according to different classifications).

7) *Kateretes* Herbst, 1793 (Fig. 1G)

This genus currently contains one Nearctic species, *Kateretes scissus* Parsons. Previously, three species were recorded from North America (Parsons 1943), however, the other two species are in fact members of *Heterhelus*. This single Nearctic species is distributed in eastern North America. Although no host data are available for

this species, other members of this Holarctic genus reproduce on *Juncus* L. (Juncaceae) (Audisio 1993; Jelínek and Cline 2010).

8) *Neobrachypterus* Jelínek, 1979 (Fig. 1H)

This genus currently contains 10 species and is widely distributed in the Neotropics from Mexico to Argentina. No host data is currently available for any of the inclusive species (Jelínek 1979).

## REVISION OF *ANTHONAEUS* HORN, 1879

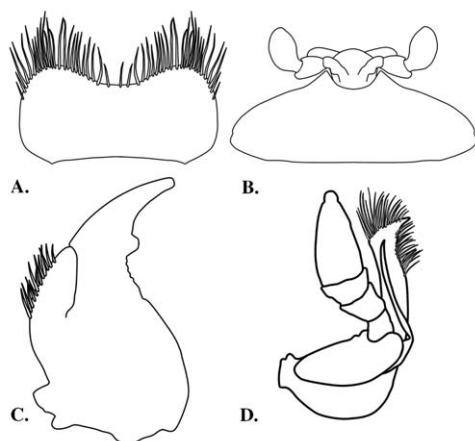
*Anthonaenus* Horn 1879: 273; gender - masculine

Type Species: *Colastus agavensis* Crotch 1874: 76 (by monotypy)

**Adult Diagnosis.** Differs from all other Kateretidae by the following combination of characters: body dorso-ventrally compressed; mandible with prominent subapical tooth; prosternum elongate,  $>1.5\times$  the length of the prosternal process.

**Adult Description.** Body overall dorso-ventrally compressed; elongate, widest near visible abdominal tergite 1; body densely punctate and finely setose; setae light brown to golden in color; pronotum and elytra fimbriate.

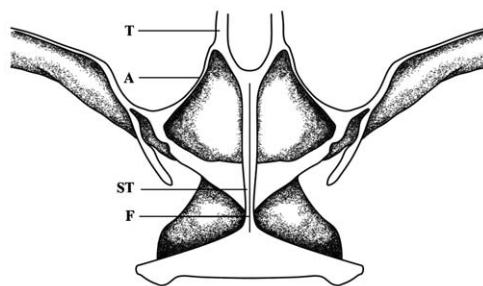
Head broadly triangular, wider than long, narrower than pronotum; vertex transverse; frontoclypeal region with transverse, shallow sulcus; occipital line well developed medially. Temples short and posteriorly arcuate. Eyes well developed, moderately protruding laterally, finely faceted, interfacetal setae absent. Clypeus with anterior margin moderately to deeply concave; lateral anterior angles acute. Labrum transverse, anterior margin concave with visible portion appearing moderately bilobed, antero-lateral lobes broadly rounded, strongly setose on anterior margin (Fig. 2A). Mandibles well developed; broadly widened basally; apex acuminate; distinct subapical tooth present; lateral setigerous furrow present with elongate setae; ventro-medial articulation dicondylic; mola not well developed with faint, short, oblique lines; prostheca indistinct (Fig. 2C). Maxilla with galea and lacinia elongate and narrow; cardo and stipes well developed, subequal in length; stipes with lateral margin lunate; galea with apical third densely setose with short and elongate setae, apex moderately hook-shaped, lacinia thinner than galea and subequal in length, palp 4-segmented with terminal segment conical and equal in length to segments 1–3 combined (Fig. 2D). Mentum transverse, well developed, clearly demarcated from submentum and gula; anterior margin with deep concavity in medial third (Fig. 2B). Labium with 3-segmented palp, palpi well separated at base by width of basal segment, terminal segment obovate and slightly longer than segment 2 (Fig. 2B). Antennal grooves absent on ventral side of head. Antennae 11-segmented;



**Fig. 2.** Mouthparts of *Anthonaenus agavensis*. A) Labrum, dorsal view, B) Mentum and labium, ventral view, C) Left mandible, dorsal view, D) Left maxilla, dorsal view.

scape moderately enlarged,  $1.8\text{--}2.0\times$  length of pedicel; segments 2–8 similar in shape, becoming dilated apically; segments 9–11 forming a loose club, 9–10 similar in size and shape, segment 11 subequal to 9–10 combined, apex acuminate and appearing appendiculate.

Pronotum moderately transverse, narrower than bases of elytra, finely fimbriate, anterior angles broadly rounded but distinct, posterior angles indistinct. Prosternum relatively elongate,  $\sim 1.5\times$  longer than prosternal process, demarcated from proepisternal by well defined suture. Prosternal process narrow, parallel-sided, extending slightly beyond posterior margin of procoxal cavities, not expanded laterally behind procoxal cavities, apex truncate to broadly evenly convex, in lateral view with posterior margin rounded with no vertical face. Procoxal cavities externally narrowly open. Mesonotum with scutellum visible, large, hemispherical with apex rounded. Mesosternum large and conspicuous, flattened, at same level as metaventrite, posterior mesosternal process twice as wide as prosternal process and extending to midway between the mesocoxal cavities with truncate posterior margin. Metaventrite transverse, subequal to  $2\times$  length of mesosternum; discrimen present along posterior two-thirds of midline only, not apparent in anterior third. Metendosternite of cucujoid-hylecoetoid type, anterior tendons arising medially from furca, sclerotized lateral arms of furca well-developed with blunt apices, lateral parts of ventral process of furca obliquely oriented to base of furca, stalk of furca short and lyriform with heavily sclerotized ventral median flange, base of furca wide and broadly attached to metaventrite (Fig. 3).



**Fig. 3.** Metendosternite of *Anthonaenus agavensis*. A – lateral arms of furca, F – ventral flange of furca, ST – stalk of furca, T – anterior tendons of furca.

Elytra abbreviated, not covering last two visible abdominal tergites; epipleuron broad in basal half, then dramatically narrowing in apical half; lateral margins not explanate; apical margins broadly evenly rounded; humeral angles vaguely indicated, not prominent; sutural striae visible; pubescence fine and short, fimbriate. Visible abdominal ventrite 1 projecting between metacoxae, with broadly rounded apex. All ventrites with fimbriate margins. Male pygidium with deeply concave posterior margin exposing “anal sclerite”.

Legs normal, *i.e.* no sexual dimorphism apparent, with all femora shallowly caniculate for reception of tibiae; widest near middle. Tibiae with paired unequal apical spurs. Tarsi 5-5-5; tarsomere 4 small and situated between weakly bilobed tarsomere 3, tarsomeres 1–3 weakly bilobed with dense setose pad; tarsomere 5 moderately elongate, equal to length of tarsomeres 1–2 combined; claws simple.

Male genitalia with tegminal parameres not fused to each other or phallobase, symmetrical. Median lobe (penis) asymmetrical. Female genitalia with coxites slightly diverging apically and possessing short apical lateral styli.

**Variation.** Some specimens may possess lighter colored elytra than the body, or the entire body may appear uniformly colored.

**Larval Diagnosis.** Due to the scarce knowledge of New World Kateretidae larval forms, in particular Neotropical taxa, there is great difficulty in ascertaining the true affinities of *Anthonaenus* solely based on immature forms. However, original observations based on Nearctic taxa, including an upcoming description of *Amartus* larvae, suggest that a relationship to *Amartus* can be supported by the following shared characters: frontal sutures distant at base; epicranial stem absent; sensory appendage on antennal segment three-fourths length of terminal segment; spiracles annular-biforous; inner margin of mandible with three or more well developed sub-apical teeth; mandibular mola with one or more



tooth-like projections; and tarsi without adhesive lobe. Inclusion of Neotropical genera such as *Neobrachypterus* and *Cercometes* would greatly advance our understanding of this genus and New World taxa in general; however, immatures from these genera remain unknown.

#### Mature Larval Description (3<sup>rd</sup> Instar)

Length 3.5–5.5 mm, width 0.8–1.1 mm across abdominal segment 3. Body elongate, subparallel, moderately convex, widest near A3, urogomphi and pregomphi absent. Overall, body almost circular in cross-section. Only head well sclerotized, T1 with faint rugosities anteriorly and laterally, legs moderately well sclerotized, remainder of body integument pale whitish/cream colored and overall lightly to unpigmented with some faint scale-like sculpturing present. Dorsal body setae short, simple, scattered, and erect, not borne on short tubercles (Figs. 4A and 4B).

Head (Fig. 5A). Prognathous, narrower than T1, not concealed by prothorax, surface mostly smooth with faint rugose areas antero-medially. Dorsal posterior margin of capsule deeply indentate medially. Clypeus bearing 2 pairs of macrosetae, each pair near antero-lateral angles, other microsetae may be present; clypeofrontal protuberances absent. Frontoclypeal suture distinct. Epicranial stem absent, frontal sutures “V-shaped” but separate from each other. Median endocarina absent. Four stemmata present on each side of head, but weakly developed. Antenna 3-segmented with relative antennomeral lengths from base to apex 1.0:1.2:0.8. Antennal base broad, pseudorectangular to somewhat globular. Segment 1 simple, somewhat rounded laterally, asetose. Segment 2 transverse, 2–3 macrosetae present apically, and with a sensory appendage 0.75× length of segment 3. Segment 3 cylindrical, smaller than either of preceding 2 segments, bearing 1 long apical

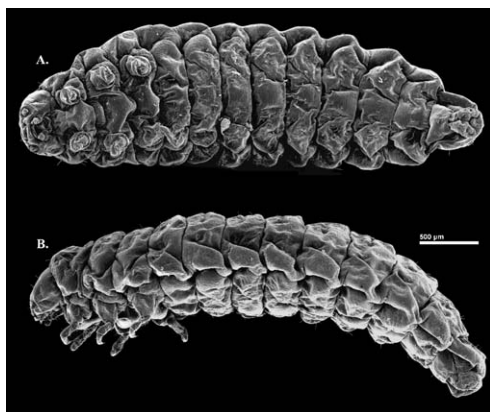


Fig. 4. SEM images of *Anthonaenus agavensis* 3<sup>rd</sup> instar. A) Ventral view, B) Lateral view.

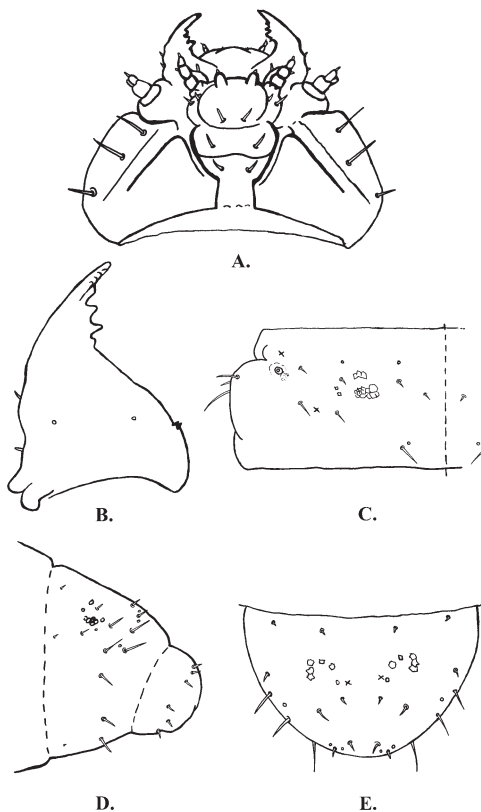


Fig. 5. Larval features of *Anthonaenus agavensis* 3<sup>rd</sup> instar. A) Ventral view of head, B) Ventral view of right mandible, C) Dorsal view of left-hand portion of abdominal tergite 5, D) Lateral view of abdominal segments 9-10, E) Dorsal view of abdominal tergite 9.

macroseta. Labrum free, moderately large, transverse. Hypostomal rods long, diverging posteriorly. Mandibles symmetrical, apical tooth with grooved dorsal cutting margin; typically 3 subapical teeth present along medial margin; prostheca absent; mola with tooth-like projection and granular grinding surface; base of mandible broadly widened with strongly dicondylic articulation (Fig. 5B). Ventral mouthparts retracted. Maxilla with bluntly rounded undeveloped asetose mala. Maxillary palp 3-segmented, segments 1 and 2 subequal, segment 3 slightly smaller than 1 or 2 and possessing terminal sensory setae. Mentum/submentum moderately transverse; ligula not well developed. Labial palpi simple, short, widely separated, 1-segmented with terminal seta.

Prothorax narrower and longer than meso- and metathorax, and with more distinct granular surface sculpturing. Length ratio of prothorax/mesothorax/metathorax 1.5:1.0:1.0. Meso- and metathorax equal in length, with metathorax somewhat wider.

All thoracic terga with widely scattered short, elongate macrosetae. Legs well developed, widely separated, 2 tarsungular setae present. Ten abdominal segments total (Figs. 5C-E), moderately lobed laterally. Abdominal segments 1-8 similar in shape; A9-10 smaller and more globular in shape; A10 broadly with apical margin broadly evenly convex. Spiracles annular-biforous, not borne on tubercles. Pregomphi and urogomphi absent. Anal opening "Y-shaped", with superior slits appearing lyriform, not angulate.

**Notes.** Horn's original description (1879: 273), albeit short and somewhat generalized, provided an adequate differentiation of *Anthonaenus* from the rest of the New World Kateretidae fauna. However, the first robust assessment and thorough description of the genus was completed by Parsons (1943) in his treatment of the entire Nearctic Nitidulidae and Kateretidae (= Parsons' Cateretinae).

### *Anthonaenus agavensis* (Crotch)

*Colastus agavensis* Crotch 1874: 76; original description

*Carpophilus agavensis* (Crotch); generic combination by LeConte (1875)

*Anthonaenus agavensis* (Crotch); generic combination by Horn (1879)

**Type Specimens Examined.** Holotype (MCZ). Cal./*Anthonaenus*; *agavensis*; Crotch./Type; 8313.

**Other Specimens Examined.** >700, including the following: (4) S. Cal./Ac. 5409, Coll Chase Palm; (5) CA: 14 mi. NW, Redlands: *Yucca*, May 31, 1961, G.H. Nelson, Coll./*Anthonaenus agavensis*, 10015 (Crotch), G.H. Nelson, '75; (4) CA: Orange Co., 9 mi E San Juan, Capistrano, April 26, 1969, E.E. Ball, Coll./*Anthonaenus agavensis* (Crotch), A.R. Cline 2003; (12) Baldwin Lk., VI-5-48, CA/D.J. & J.N., Knull Collrs.; (28) Santa Rosa M., V-27-46, CA/D.J. & J.N., Knull Collrs.; (4) Boulevard, CA, VI-12-51/D.J. & J.N., Knull Collrs.; (9) Jacumba, CA, VI-12-51/D.J. & J.N., Knull Collrs.; (10) Pinon Flat, Santa Rosa M., VII-1-41, CA; (2) 5 miles NW of Julian, Calif., IV-30-1985, W.F. Chamberlain; (4) M. Albright, Los Angeles Co., Cal.; (3) Big Tujunga, Can. L.A. Co. Cal./coll. Dwight Pierce, *Yucca whipplei*; (1) G.P. Mackenzie, Little Rock, Calif., 6-18-44; (1) Ventura Co., Calif./coll. Dwight Pierce, *Yucca whipplei*; (1) Sonoma Co., CA; (1) III-11-1965, Orange Co., Calif., L. San Juan P.C. / R.J. Hamton, collr., III-11-1965; (1) Julian, San Diego Co. CA, 4-28-53; (10) L.A. Co. Calif., Tajunga Can., 4-24-1938/*Yucca whipplei*, C.A. Fessenner; (1) San Jacinto Mts., Calif., 2873; (1) Calif. L.A. CA, San Dimas Cyn, June 23 1968, E. Giesbert Coll.; (4) 2 mi W of Jacumba, San Diego Co., Calif., 2 April 1966, Richard S. Funk; (1) Onion Junction, S. Bernardino Co., CA, T 2N, R 6W, S26,

V-15-79, coll. by H.L. Murray; (1) San Diego, VI-1-29, Calif./Col. by H. Dorn/Pres. by E. Liljebblad/Det. by (1939) H.R. Dodge/*Anthonaenus agavensis* (Crotch); (1) San Diego, V-14-30, Calif./Col. by H. Dorn/Pres. by E. Liljebblad/*Anthonaenus agavensis* (Crotch)/Det. by (1939) H.R. Dodge; (1) 10 mi N Redlands, San Bernardino Mts., VI-5-1954, Calif., G.H. Nelson/ 3500 elev./ on yucca/10015/N.M. Downie Colln., 1992, Acc. Z-18, 343, Field Museum; (1) Cal., Santa Barbara Co., La Purisima Mission, 3-30-53, H. Hacker Coll./10022 Schuh '71/N.M. Downie Colln., 1992, Acc. Z-18, 343, Field Museum; (1) San Bernadino Co., CAL, May/3670; (2) G.P. Mackenzie, Little Rock, Calif., 6-18-44/10015/N.M. Downie Colln., 1992, Acc. Z-18, 343, Field Museum/*Anthonaenus agavensis* (Crotch); (2) CNHM, 1955, Carl Brancsik Colln., ex Eduard Knirsch/*Anthonaenus agavensis* (Crotch), det. A. Kirejtshuk 1999; (8) S. Diego Co., CALIF., Cardiff-by-Sea, Apr. 21-26 1967, D. Davis, 50'/from flowers *Yucca whipplei*; (3) Los Ang. Co., CAL.; (2) Cal.; (4) Cal./Collection C.V. Riley; (1) Cal./Coll Hubbard & Schwarz; (1) Cal./3032/Collection Belfrage; (8) Los Angeles Co., CAL./Coquillet Collection; (1) Calif., San Diego Co., 2 mi S Rincon Springs, 27 March 1971, R. Turnbow/*Anthonaenus agavensis* (Crotch), det. Connell '79; (1) Tecate, Califa, March 1966, R. Duke Coll./yucca 66-6868/*Anthonaenus agavensis* (Crotch), det. Connell '66/Compared with Paratype *Colastus agavensis* Crotch MCZ 8313 type is a ♀ conspecific 1-39-69 WAC; (4) San Diego Calif., 4-12-49, E.P. VanDuzee/*Anthonaenus agavensis* (Crotch), 10015, det. L.R. Gillogly; (16) 2 mi. E Lyons Vy., San Diego Co., Calif., III-26-61/*Yucca whipplei*/J. Powell Collector; (6) Calif., Kern Co., Frazier Park, 2 mi W., VII-20-63/*Yucca whipplei*/J. Powell Collector; (3) Alpine, 5 mi E. San Diego Co., Calif., III-31-61/*Yucca whipplei*/J. Langston Collector; (2) Descanso Rgr. Sta., San Diego Co., Calif., III-31-61/*Cercocarpus sp.* / R.L. Langston Collector; (14) Calif., S. Berdo. Co., Highland, 8 mi NE, IV-14-65/. Doyen Collector; (2) Mt. Palomar, San Diego Co., Calif., VI-28-63/*Yucca whipplei*; (23) Calif., S.L.O. Co., La Panza Cpg., IV-25-64/*Yucca whipplei*/J. Powell Collector; (2) Calif: S. Berdo. Co., City Cr. NE. of Highland, IV-16-65/*Yucca whipplei*/R.L. Langston Collector; (9) L.A. Co., Calif., VII-20-63/ San Fernando 7 mi NW Cal/*Yucca whipplei*/J. Powell Collector; (40) CA: San Diego Co., III-IV-1974, *Yucca whipplei*, J. Powell; (1) Buckman Spgs., 5-18-27/10015; (1) Little Sycamore Cyn., Ventura Co., 500', Calif., IV-24-66/*Yucca whipplei*/J. Powell Collector; (2) Crystal Lake, Los Angeles Co., Calif., VI-29-50/CJ. Weinman Collector/B. Adelson Collection; (2) Los Prietos, Sta. Barb. Co. Calif., VI-23-65/R. W. Gear Collector; (2) Los Prietos, Sta. Barb. Co. Calif., VI-23-65/E. M. Omi Collector; (2) Cardiff, San Diego Co., Calif., 3-22-67/*Yucca whipplei*/J. Powell

- Collector; (2) 3 mi. N Refugio Beach, Calif., Sta. Barb. Co., June 21, 1965/*Yucca whipplei*/J. Powell Collector; (1) Quatal Canyon, NW corner Ventura Co., Calif., V-9-59/*Yucca whipplei*/J. Powell Collector; (1) Tanbark Flat, Los Angeles Co., Calif., VI-25-50/T.R. Haig Collector; (26) 2 mi. NE. Lakeside, San Diego Co., Calif., III-29-61/*Yucca whipplei*/J. Powell Collector; (3) Calif: S. D. Co., 5 mi. SE. Julian, VI-11-65, J.T. Doyen; (5) Calif., 3 mi. W. Amboy, San Bernardino Co., IV-6-1966, J. Doyen; (3) Calif: Riv. Co., Whitewater CYN., IV-11-65/*Yucca whipplei*/G. Buckingham Collector; (1) R. R. Cyn., 5 mi. E. Elsinore, Riv. Co. Calif., IV-13-65/J. Powell Collector; (1) East Highlands, San Bernardino Co. Calif., IV-26-62/*Yucca*/F.R. Cole Collector; (1) Calif: Riv. Co., 5 mi., SE. Valle Vista, IV-12-63/*Yucca whipplei*/J. Powell Collector; (4) Tujunga, VII-1-40, Calif., J. Schwartz/J.W. Green Collection; (11) Cajon Pass, S Bern Co., Cal, V-24-41/Van Dyke Collection; (13) Borego Desert, Calif., II-9-1941/*Yucca*/L.R. Gillogly Collector/L.R. Gillogly Collection; (1) San Diego Co., CAL., IV-8-1925/F.E. Blaisdell Collector/Blaisdell Collection; (21) San Diego Co., CAL., IV-8-1925/Van Dyke Collection; (4) Lebec Cal, Alt. 4000 ft., V-13-1928/JO Martin Collector; (4) Calif: S. Berdo. Co., Highland, 8 mi. NE., IV-14-65/J. Doyen Collector; (2) Calif: S. Berdo. Co., Highland, 8 mi. NE., IV-14-65/*Yucca whipplei*/J. Doyen Collector; (1) R. R. Cyn., 4 mi E. Elsinore, Riv. Co., Calif., IV-14-65/*Yucca whipplei*/J. Powell Collector; (2) 2 mi E Lyons Vy., San Diego Co., Calif., III-26-61/*Yucca whipplei*/J. Powell Collector; (2) San Diego Co., Cal., 4-27-1965/*Yucca whipplei*/R.D. Hancock J.L. Johnson Collector; (3) S. Bndino Cal./05-13/A. Fenyes Collection; (2) Cajon Pass, S Bern Co., Cal., V-19-37/Coll. & Pres. by E. Guedet; (10) Descanso Cal., San Diego Co., Apr. 25 1920/EPVanDuzee Collector; (6) Capistrano Calif., III-16-41/*Yucca*/L.R. Gillogly Collector/L.R. Gillogly Collection; (1) San Diego Co., Cal./F. E. Blaisdell Collector/Blaisdell Collection; (1) San Diego, CAL./F. E. Blaisdell Collector; (1) L.A. Co. Cal./Van Dyke Collection/3670; (4) POWAY, CAL/F. E. Collector/Blaisdell Collection; (2) Fairfax Cal, V-9-20/EPVanDuzee; (6) S' Bernardino Mts., Cal., 3000', V-5-52, Bryant Lot 40-41; (2) S' Bernardino Mts., Cal., 3000', V-5-52, Bryant Lot 40-41/on large stemmed yucca; (3) Hurkey Cr. P. C., S. Jacinto Mts., Calif., VI-21-60/E.L. Sleeper Collr.; (1) Hurkey Cr. P. C., S. Jacinto Mts., Calif., V-21-60/E.L. Sleeper Collr.; (2) Calif: S. L. O. Co., LaPanza Cng., IV-25-64/Collr: J. Doyen; (1) Tujunga, Calif., IV-30-44/*Yucca*/L.R. Gillogly Collector/L.R. Gillogly Collection; (2) Vista, Calif., VII-31-40 / *Yucca*/L.R. Gillogly Collection; (1) Vista Cal., V-28-40/*Yucca*/L.R. Gillogly Collector/L.R. Gillogly Collection; (1) Alpine, San Diego Co., CAL., IV-9-1925/Van Dyke Collection; (1) Los Angeles Cal./Van Dyke Collection; (1) Los Ang. Co. Cal./Wickham/A. FENYES Collection; (1) Los Angeles Cal./L.R. Gillogly Collection; (1) Pinon Flat, Calif., San Jacinto Mts., 23-IV-1950/C. D. MacNeill Collector; (1) CAL: Riverside Co., Pinon Flat, IV-20-1962/C. MacNeill, D. Rentz & R. Brown Collectors; (1) Calif: Riv. Co., Whitewater Cyn., IV-11-65/*Yucca whipplei*/G. Buckingham Collector; (1) Fallbrook, Calif., III-6-1941/*yucca blossom*, L.R. Gillogly/L.R. Gillogly Collection; (1) Calif: S. Berdo. Co., City Cr., NE. of Highland, IV-16-65/*Yucca whipplei*/R.L. Langston Collector; (1) Calif: Riv. Co., Radec, 1 mi N., IV-12-65/*Yucca schidigera*/J. Powell; (1) Calif., Orange Co., San Juan Hot Springs, IV-30-67/D.R. Caruthers Coll. (37) USA: California: San Diego Co.; Cleveland National Forest; Hauser Canyon; 32°40'23"N, 116°34'04"W; 26-III-2002, yucca flowers; W.D. Shepard & C.B. Barr. (1) 2 mi. NE Lakeside; San Diego Co., Calif.; III-29-61/*Yucca whipplei*/J. Powell; Collector. (1) California; Hwy. 138; San Bernardino Co./Pinon Hills; (Desert Sprs)/G.H. Nelson; 27-IV-1986/Flr.; *Malacathrix glabrata* (14 larvae, pupae and adults) nr. Jacumba, San Diego Co., Calif.; IV-14-1985, ex: *Yucca whipplei* blossoms; coll. T.N. Seeno, Det. I.E. Savage. (1) 5 mi. S Gorman, Los Angeles Co.; Calif., IV-1-1971; ex: *Yucca brevifolia*; det. L.R. Gillogly, 1#780b. (15 adults and larvae) S. Bdo. Co., CA, VI-20-1975; ex: yucca; coll: E.L. Paddock. (2) G.F. Mackenzie; Little Rock; Calif. 6-18-44. (1) Pac Sl; En Ag. (63) USA: CA: San Bernardino Co.; 4 km SE Wrightwood, Lone Pine; Cnyon, 34°19.03'N/117°34.93'W, elev. 5388'; 21-28-MAY-2005, A.R. Cline; Ex. *Yucca whipplei*. (8) USA: CA: San Bernardino Co.; 10.5 km SE Wrightwood, Swarthout; Canyon Rd., 34°17.911'N; 117°30.51'W, elev. 3643'; 24-MAY-2005; A.R. Cline, Ex. *Yucca whipplei*. (2) California; San Bernardino Co.; 20-VI-1975, E.L. Paddock; *Yucca* sp. flowers. (3) USA: CA: Los Angeles Co.; 9 km SE Wrightwood, Lone; Pine Canyon; 34°18.17'N; 117°31.81'W, elev. 4127'; 21-28-MAY-2005, A.R. Cline; Ex. *Yucca whipplei*. (1) USA: CA: Los Angeles Co.; 3 km NW Wrightwood, 1 mi. N on Ball Flat Rd., 34°23'06"N; 117°41'19"W, elev. 7300'; 27-MAY-2005, A.R. Cline & S.D. Gaimari; Ex. Sweeping/beating. (1) USA: CA: San Bernardino Co.; 9 km SE Wrightwood, Lone Pine; Canyon, 34°18.17'N; 117°31.81'W, elev. 4127'; 21-28-MAY-2005, A.R. Cline; Ex. *Yucca whipplei*. (1) Tujunga, Cal.; VII-15-1990; E.K. Wearing. (4) CAL, 4 mi. E. Poway, San Diego Co.; 29-MAR-1972/*Yucca whipplei*/J.S. Heppner collr. (2) Capistrano, Calif., III-16-1941. (1) Onion Junction, San Bernardino Co., CA; T2N, R6W, S26; V-15-1979. (4) 2 mi. W Jucumba, San Diego Co., Calif; 2-Apr-1966; Richard S. Funk. (6) Alpine, Calif.; San Diego Co.; III-27-1968/S.M. Hogue collr./R.L. Penrose collr. (1) Los Angeles Co.; Pinyon Hills Calif.; VI-17-1975, R. Aalbu. (1) California, San Bernardino Co.;



Hwy. 138/Pinyon Hills (Desert Sprs.)/G.H. Nelson; 27-IV-1986 / Flr. *Malacothrix glabrata*. (15) USA: CA: San Bernardino Co.; 4 km SE Wrightwood, Lon Pine; Canyon, 34°19.03'N; 117°34.93'W, elev. 5388'; 21–28-MAY-2005, A.R. Cline; Ex. flower of *Ceanothus* sp. (30) Calif. San Diego Co.; 1.3 mi. W Jacumba; 14-April-1983; ex. *Yucca whipplei*; coll: T.N.Seeno. (3) Coyote Wells, Calif.; Imperial Co.; III-22-1970/A.J. Gilbert collr. (2) 10 mi. E. San Juan Capistrano; Orange Co., Calif.; IV-11-1970/ex: yucca/A.J. Gilbert collr. (1) Claremont; Los Angeles Co., Calif.; 4-29-1961, 220; Fred G. Andrews. (1) Portola; Plumas Co., Calif.; 12 June 1962, 327; Fred G. Andrews. (2) San Bernardino; San Bernardino Co.; Cal. IV-24-1970/yucca blooms/collr. E. A. Kane. (3) CA: San Bernardino Co.; 5 mi. E Mentone; Power house 3000'; V-11-1978, K. Cooper. (5) Calif.; San Diego Co.; Jacumba; III-6-1983/ex. Agave buds/coll: Ray Gil. (22) San Bernardino; San Bernardino Co.; Cal. VI-19-1975 / ex. yucca/Drake and; Paddock; collectors. (3) "San Diego Co/Calif. 5-18-27, "Buckman Spgs", W.S. Wright/Collection. (1) unlabeled. (1) "591".

**Diagnosis.** See diagnosis for new species below.

**Adult Redescription.** Length 3.8–4.2 mm, width 1.8–2.0 mm. Body color reddish or orange-brown, elytra sometimes lighter than rest of body. Head broadly triangular (W:L = 1.8:1); punctures circular, interspaces granular to rugose and ~1–2 puncture diameters apart. Antennae moderately elongate, as long as length of head and half of pronotum combined; club oblong; club ~0.4 length of segments 1–8 combined; terminal antennomere with apical half conical and acuminate. Mentum moderately punctate, punctures similar to those on head, interspaces shining, smooth to alutaceous and separated by 0.25–0.50 puncture diameter, each puncture giving rise to a short stiff golden seta. Submentum and gula less densely punctate than mentum, interspaces smooth and shining, punctures separated by ~1 puncture diameter.

Pronotum moderately transverse (W:L = 1.7:1.0), widest near middle, flattened or somewhat concave in lateral view. Anterior angles distinct, rounded, obtuse. Posterior angles indistinct, broadly rounded. Lateral and posterior margins narrowly explanate, lateral margins broadly arcuate to posterior margin. Anterior margin medially concave. Posterior margin straight to slightly concave medially. Pronotal punctures similar in size and shape to those on head, interspaces granular to alutaceous, moderately shining, punctures separated by ~1 puncture diameter. Prosternum relatively elongate, ~1.6× longer than prosternal process. Apex of prosternal process truncate in ventral view. Prosternal punctures similar to those on mentum, interspaces mostly smooth, transverse reticulations present anteriorly, punctures widely separated by >2 puncture diameters. Mesonotum with

punctures similarly shaped and spaced as those on pronotum. Mesosternum flattened, at same level as metaventricle, evenly concave posteriorly for reception of metaventricle; punctures faintly impressed, similar to those on prosternum, separated by 1–2 puncture diameters. Metaventricle transverse (W:L = 2.3:1.0); metasternal discrimen incomplete in anterior 0.33; posterior margin notched for reception of first visible abdominal ventrite; punctures faintly impressed, similar to those on mesosternum, widely separated by >2 puncture diameter, surface sculpturing alutaceous to granular. Elytral punctures similar to those on pronotum, deeply impressed, interspaces smooth to finely alutaceous, shining, punctures separated by ~1 puncture diameter. Visible abdominal ventrite 1 projecting between metacoxae with broadly rounded apex. Visible abdominal ventrites 2–3 equal in length, both slightly shorter than ventrite 1. Ventrite 4 elongate, length subequal to ventrites 1–3 combined. Hypopygidium with posterior margin evenly convex, apex densely punctate. Pygidium with posterior margin evenly convex, apex densely punctate.

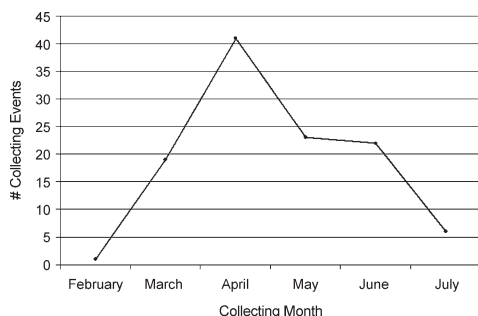
Protibiae greatly expanded in apical half; apical half of lateral margin and entire apical margin with blunt short pegs present. Meso- and metatibiae similarly shaped and armored, but pegs longer and more numerous.

Male genitalia well sclerotized. Sexual dimorphism apparent in males, which possess a deeply concave posterior margin of pygidium and exposed "anal sclerite". Tegmen with parameres broadly rounded apically (Fig. 8E). Abdominal sternite 8, *i.e.* spiculum gastrale, with anterior angles (Fig. 8C). Median lobe of aedeagus in lateral view with shallow apical notch (Fig. 8A). Female genitalia moderately sclerotized. Gonocoxites moderately long, not fused or adjacent along entire inner margin; tapered basally and apically; two primary setae present along apicolateral margin; apical styli small with three primary setae present. Spermatheca circular, ducts approximating each other (Fig. 9C).

**Etymology.** Specific epithet was derived from the generic name of the purported host plant.

**Distribution.** Label data and previously published records indicate the presence of *A. agavensis* in the following California counties: Los Angeles, Riverside, San Bernardino, Orange, San Diego, Imperial, Plumas, Santa Barbara, Ventura, Sonoma, Kern, San Luis Obispo, and Marin.

**Notes.** Adult phenology, according to the specimens examined (>700 specimens representing >110 separate collecting events over the past 90 years), indicates activity from February to July, with most activity in April (Fig. 6). This phenology is consistent throughout the range of the species, and is likely dependent on the local flowering incidence of the *Hesperoyucca* host plants.



**Fig. 6.** Phenological occurrence of *Anthonaenus agavensis* throughout its range in California, as derived from >110 unique collecting events representing >700 specimens over the past 90 years.

**Larval Description.** Gross morphology is given in the generic description above. Overall, pubescence fine and short, integument with scale-like microsculpture. Head with moderately elongate macrosetae present; 2 setae present on frontoclypeal region, 2 present on frons posterior to frontoclypeal pair; 3 setae present medially on epicranial (*i.e.* parietal) plate and 1 laterally on epicranial (parietal) plate. Head with rugose areas along medial anterior surface, becoming smooth along lateral and posterior surfaces. Prothoracic terga with rugose areas along anterior and lateral margins; macrosetae more elongate laterally than medially. Meso- and metathoracic terga with macrosetae more diffusely dispersed. Setal pattern on abdominal tergite 5 consisting of 3 macrosetae along lateral margin latero-posteriorly directed, all other macrosetae directed medio-laterad (Fig. 5C). Abdominal segments 9 and 10 with setae appearing band-like around both terga and sterna (Fig. 5D); segment 10 with elongate setae present along lateral margins, and most shorter macrosetae oriented in a medial or posterior direction (Fig. 5E). Abdominal segment 10 with apex broadly, evenly rounded.

### *Anthonaenus bajaensis* Cline and Audisio, new species

**Type Specimens.** HOLOTYPE ♂ (UCB) MEX: Baja Calif. Norte; 7 mi. SE Maneadero; 100' el. III-25-1973/collected by; J.A. Powell/[red label] HOLOTYPE; *Anthonaenus*; *bajaensis*; Cline & Audisio des. 2009. PARATYPES 1♂ (ARCC), 7♀ (2 ARCC, 5 UCB) with same data as holotype, except yellow paratype labels. PARATYPE 1♀ (CSCA) MEX: Baja Calif. N. 21; mi. N Chapala III-28-1973 Ex flower; *Yucca peninsularis*; J. Doyen/[yellow label] PARATYPE; *Anthonaenus*; *bajaensis*; Cline & Audisio des. 2009. PARATYPE 2♀ (UCB, ARCC) MEX: Baja Calif. Norte; Jaraguay Summit, 22; mi. NW Rancho Chapala; 2600' el. J.A.

Powell; *Yucca peninsularis*; III-27-73/[yellow label] PARATYPE; *Anthonaenus*; *bajaensis*; Cline & Audisio des. 2009. PARATYPE 1♀ (UCB) MEX: Baja Calif. Norte; 21 mi. NW Rancho; Chapala 2500' el.; III-27/28-1975; Szerlip & J.A. Powell/[yellow label] PARATYPE; *Anthonaenus*; *bajaensis*; Cline & Audisio des. 2009.

**Diagnosis.** Differs from *A. agavensis* in the following combination of characters: body overall more robust with darker body coloration; head more broadly triangular, W:L never >1.7:1.0; anterior margin of pronotum straight not concave medially; metasternum more strongly transverse with W:L always >2.8:1.0; terminal abdominal tergite and ventrite more densely punctate; ventral surface of pro-, meso-, and metasterna alutaceous to granular and less shining; protibial armature less developed along lateral margin; apex of pygidium in females more broadly rounded; relatively narrower aedeagal parameres, elongate rather than tapering shape of tegminal medial grooves, origination of setae from inner tegminal margin, median lobe in lateral view more robust and with deeper apical notch; ovipositor gonocoxites more developed laterally; terminal gonostyloid appendages larger and possessing two rather than three primary setae. This species is also only known to occur on *Y. peninsularis* in Baja California.

**Description.** Length 4.0–4.2 mm, width 1.9–2.0 mm (Fig. 7). Body color dark reddish or orange-brown, elytra sometimes lighter than rest of body. Some lowland specimens with elytra somewhat lighter than rest of body; all specimens from higher elevations unicolorous. Head broadly triangular (W:L = 1.6:1.0); punctures circular, interspaces smooth to granular with microreticulations laterally and ~1–2 puncture diameters apart. Antennae elongate, subequal to length of head and three-fourths of pronotum combined; club oblong; club ~0.3 length of segments 1–8 combined; terminal antennomere with apical half conical and bluntly acuminate. Mentum moderately punctate, punctures similar to those on head, interspaces completely granular and separated by 0.5–1.0 puncture diameter. Submentum and gula less densely punctate than mentum, interspaces alutaceous to granular with microreticulations laterally, punctures separated by ~1–2 puncture diameters.

Pronotum moderately transverse (W:L = 1.7:1.0), widest near middle, flattened or somewhat concave in lateral view. Anterior angles distinct, rounded, obtuse. Posterior angles indistinct, broadly rounded. Lateral and posterior margins narrowly explanate, lateral margins broadly arcuate to posterior margin. Anterior margin truncate to slightly shallowly concave. Posterior margin straight. Pronotal punctures dense, similar in size and shape to those on head, interspaces granular to alutaceous, moderately



Fig. 7. Dorsal habitus of *Anthonaeus bajaensis*, female paratype.

shining, punctures separated by  $\sim 0.5$ – $1.0$  puncture diameter. Prosternum relatively elongate,  $\sim 1.5\times$  longer than prosternal process. Apex of prosternal broadly evenly convex in ventral view. Prosternal punctures similar to those on mentum, interspaces mostly alutaceous to granular with some microreticulation present throughout, punctures separated by 1–2 puncture diameters. Mesonotum with punctures similarly shaped as those on pronotum,  $\sim 0.5$ – $1.0$  puncture diameter apart. Mesosternum flattened, at same level as metaventrite, truncate posteriorly for reception of metaventrite; punctures faintly impressed, similar to those on prosternum, separated by 1–2 puncture diameters. Metaventrite transverse ( $W:L = 2.9:1.0$ ); metasternal discrimen incomplete in anterior 0.33; posterior margin shallowly notched for reception of first visible abdominal ventrite; punctures more deeply impressed than those on mesosternum, separated by 1–2 puncture diameters, surface sculpturing smooth to granular. Elytral punctures similar to those on pronotum, deeply impressed, interspaces finely alutaceous to granular, moderately shining, punctures separated by  $\sim 1$  puncture diameter.

Protibiae greatly expanded in apical half; apical half of lateral margin with 2–3 short pegs present, entire apical margin with blunt short pegs present.

Meso- and metatibiae similarly shaped, pegs somewhat longer and also more numerous along apical half of lateral margin.

Visible abdominal ventrite 1 subequal to ventrites 2–3 combined. Visible abdominal ventrites 2–3 equal in length, both slightly shorter than ventrite 1. Ventrite 4 elongate, length subequal to ventrites 1–3 combined. Hypopygidium with posterior margin broadly convex, apex deeply densely punctate. Pygidium with posterior margin broadly convex almost truncate, apex deeply densely punctate.

Male genitalia well sclerotized. Tegmen with parameres narrowly rounded apically (Fig. 8F). Abdominal sternite 8, *i.e.* spiculum gastrale, with anterior angles projecting more laterad (Fig. 8D). Median lobe of aedeagus in lateral view with deep apical notch (Fig. 8B). Female genitalia moderately sclerotized. Gonocoxites moderately long, adjacent along most of inner margin; tapered basally and apically; 3 primary setae present along apico-lateral margin; apical styli well-developed and robust with 2 primary setae present (Fig. 9B). Spermatheca not observed.

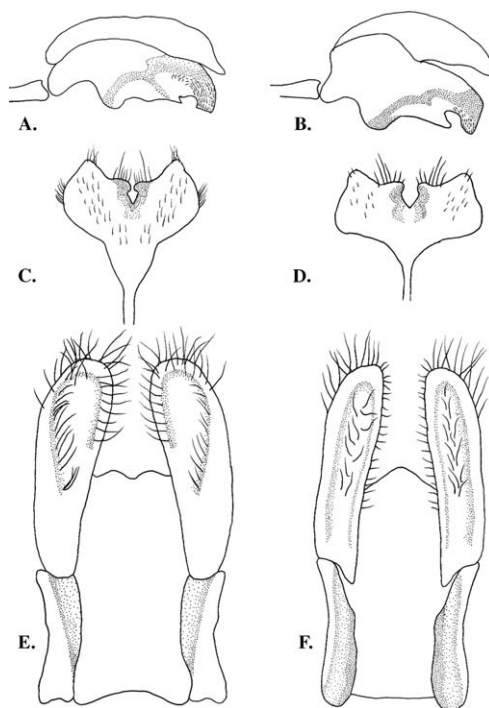
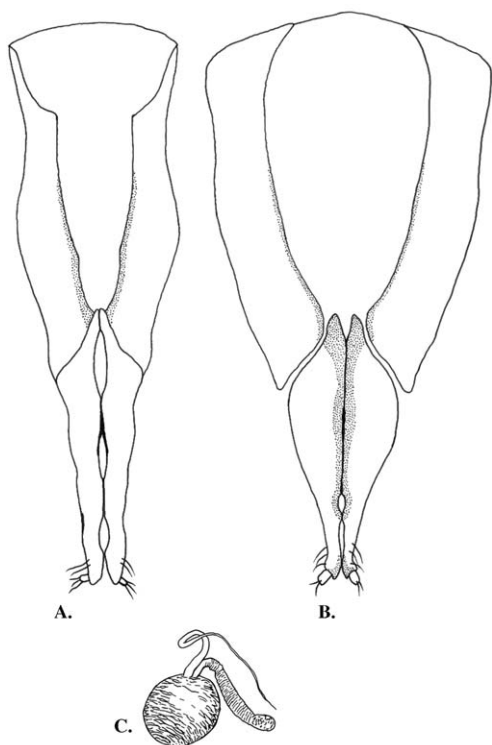


Fig. 8. Male genitalia. Lateral view of median lobe of aedeagus of A) *Anthonaeus agavensis* and B) *Anthonaeus bajaensis*. Ventral view of spiculum gastrale, *i.e.* abdominal ventrite 8 of C) *A. agavensis* and D) *A. bajaensis*. Ventral view of tegmen of E) *A. agavensis* and F) *A. bajaensis*.



**Fig. 9.** Female genitalia. Ventral view of ovipositor of A) *Anthonaenus agavensis* and B) *Anthonaenus bajaensis*, C) Ventral view of spermatheca of *A. agavensis*.

**Etymology.** The specific epithet is a derivation of the type locality.

**Biology.** All specimens were collected in late March, which coincides with the early emergence and flowering of *Hesperoyucca* in Baja California. Larvae have yet been collected for this species, but adults with biological data indicate they have been collected only from *H. peninsularis* inflorescences.

**Notes.** The holotype male has the genitalia and terminal two visible abdominal segments disarticulated and placed underneath the specimen in a glycerin vial.

## DISCUSSION

*Anthonaenus*, like *Amartus*, is only distributed in western North America. However, the range of *Anthonaenus* is restricted to more arid environments than that of *Amartus*, and the genus has not been shown to occur in neighboring Arizona, Oregon, or Nevada. Although this may be in part due to deficient collecting in southern Nevada, the same cannot be said for Arizona or Oregon where many specialist beetle collectors reside and frequent. Thus, the true range of *Anthonaenus* may be restricted to arid re-

gions of California in the north to Baja California Sur in the south. This range pattern is not uncommon in Coleoptera and is known for other genera, including *Phobetus* LeConte (Scarabaeidae), *Hesperorhapis* Fall and *Prasinalia* Casey (Buprestidae), *Schizopus* LeConte, *Dystaxia* LeConte, and *Glyptoscelimorpha* Horn (Schizopodidae), and others.

*Anthonaenus* demonstrates a morphological relatedness to *Amartus*, although this is somewhat obscured by the much more dorso-ventrally compressed body form of *Anthonaenus* and the corresponding flattening of other features. This adaptive compressed body morphology in *Anthonaenus* is likely associated with its host relationship to *Hesperoyucca*, a monocotyledonous plant, where adult females oviposit eggs within the constrained spaces of the developing flower bud and subsequent larval development proceeds within the developing flower and seed capsules. *Amartus* exhibits a host preference for *Eschscholzia*, a dicotyledonous plant, wherein oviposition and larval development occur on flowers and seeds morphologically dissimilar to *Hesperoyucca*. This host preference of *Amartus* for Papaveraceae is also shared with the Old World genera *Brachyleptus*, which is known from *Glaucium* Miller, *Papaver* L., and *Roemeria* Medikus, and *Anamartus*, which is known from *Glaucium* and *Hypocoum* L. (*Hypocoum* was recently considered a member of a related family, Hypecoaceae). The clade *Brachyleptus* + *Anamartus* could likely be sister to *Amartus* and *Anthonaenus* (this will be discussed in greater detail upon completion of the phylogenetic analysis, but is worth noting here; another member of this clade will almost certainly be the closely related Australian genus *Jelinekiella*), and also shares a similar habitat preference for relatively dry regions with a Mediterranean climate. However, *Anthonaenus* and *Amartus* share a similarly shaped ovipositor with deep medially cleft unfused gonocoxites possessing short terminal setose styli. *Brachyleptus* and *Anamartus* possess fused gonocoxites, but the apices are shallowly cleft with no terminal setose styli. Thus, the three genera (*Amartus*, *Brachyleptus*, and *Anamartus*) that specialize on Papaveraceae do not exhibit similar oviposition apparati; however, the two geographically close genera (*Amartus* and *Anthonaenus*) do possess similar ovipositor morphology. This retention of a similar egg-laying apparatus in *Anthonaenus* as in *Amartus* may reflect a recent radiation of *Anthonaenus* onto *Hesperoyucca*, with subsequent phylogenetic inertia in development of the ovipositor terminus. This hypothesis will be further tested upon completion of the phylogenetic reconstruction (utilizing both morphological and molecular data) for the entire Kateretidae.

Interestingly, *Eschscholzia* (host plant for *Amartus*) has its greatest species diversity in the southern deserts of California (D. Kelch, personal communication),



where *H. whipplei* (host plant for *A. agavensis*) is most abundant. Likewise, the early appearance of inflorescences of these plants is similar, and typically occurs from April to May. This overlap in flowering period may also have contributed to the host switching of early ancestors of *Anthonaenus*. However, the generalized ovipositor shape shared by *Anthonaenus* and *Amartus* may be considered plesiotypic in Kateretidae, and therefore not necessarily indicative of a strict phylogenetic relationship. In fact, the shared deep, transverse tentorial impression on the head, the shared shape of pronotum and head, the relatively similar plesiotypic structure of the ovipositor and of male genitalia, the distally dilated tibiae, and the shared larval host-plant Division (*i.e.* Monocotyledones) may suggest a relatively close phylogenetic relationship of *Anthonaenus* to the Holarctic genus *Kateretes*, whose members are associated as larvae with Cyperaceae and Juncaceae (Audisio 1993). This alternative phylogenetic hypothesis will also be explored and tested using the combined morphological/molecular phylogenetic reconstructions, but is beyond the scope of the present paper.

#### ACKNOWLEDGMENTS

We thank the museum and institution curators, collection managers, and directors that graciously loaned specimens or provided specimen data. Special thanks to Cheryl Barr at the University of California-Berkeley for her patience and generosity. Iris Savage and Megan O'Donnell helped prepare the drawings and figures. Dr. Dean Kelch, CDFA senior plant taxonomist, provided information and discussion on plants in the southwestern U.S. and Baja California, Mexico. Professor Jose Carlos Otero (Universidad de Santiago de Compostela, Spain) kindly provided the Spanish translation for the resumen. We also thank our friend and colleague Josef Jelínek for fruitful discussions of Nitidulidae and Kateretidae, and for reviewing an earlier draft of this manuscript. He continues to provide interesting and stimulating ideas on the evolution of these beetles.

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(Received 18 February 2010; accepted 7 July 2010. Publication date 20 September 2010.)