The Neotropical species *Askalaphium depressum* (Bates): Larval description, first diagnosis and illustrations of immature Ctenodactylini, with natural history notes on the genus and tribe (Coleoptera: Carabidae)

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**Abstract**

Adults and larvae of *Askalaphium depressum* (Bates) live in association with hispine chrysomelid beetles of the genus *Cephaloleia* Chevrolat, in the appressed leaf axils of the riverside reed, *Gynerium sagittatum* (Aubl.) P. Beauv. This reed is locally known in Amazonian Perú as Caña Brava. Both adult and larval *A. depressum* eat larvae of *Cephaloleia* species and larvae of an unidentified dipteran, and perhaps other insects living in the confines of the leaf sheaths of that plant species. The geographic range of Caña Brava reed extends from subtropical South America northward to México (and Florida), but *A. depressum* has been found thus far at only three Amazonian localities, probably indicating its cryptic microhabitat and lack of collecting, therein. Likely, the range of this commensal carabid species is more extensive and may approach the range of its host plant and hispine food. Structural features of second and third instar larvae of *A. depressum* are described for the first time. Larval character states that are shared with a related ctenodactyline, *Leptotrachelus dor-salis* (Fabricius), provide a basis for characterization of the tribe Ctenodactylini.

**Key words:** Carabidae, Ctenodactylini, *Askalaphium depressum* (Bates), larva, Perú, *Gynerium sagittatum*, Commensalism, Caña Brava Beetle, *Cephaloleia*

**Resumen**

Los adultos y las larvas de *Askalaphium depressum* (Bates) (Carabidae: Ctenodactylini) viven en asociación con coleópteros del género *Cephaloleia* Chevrolat (Chrysomelidae: Hispinae) en las axilas de las hojas de *Gynerium sagittatum* (Aubl.) P. Beauv., conocida en Perú como “caña brava”. Probablemente los adultos y las larvas de *A. depressum*, se alimentan de sus vecinos crisomelidos y de otros insectos que viven en las hojas de esta especie de caña. La caña brava se extiende desde América sub-tropical hasta México (y Florida), mientras *A. depressum* se ha reportado únicamente...
en tres localidades amazónicas; debido posiblemente a su micro-hábitat críptico y a la falta de colecciones entomológicas en caña brava. Probablemente el rango de distribución de este carabido comensalista, es mucho más extenso y podría aproximarse al rango de distribución de su planta hospedera y comida. En este artículo se describen por primera vez las características estructurales del segundo y tercer estadio larval de Askalaphium depressum. Los caracteres que son compartidos con otra especie de ctenodactilino, Leptotrachelus dorsalis (Fabricius), proveen una base para la caracterización de la tribu Ctenodactilini.

Palabras Clave: Carabidae, Ctenodactylini, Askalaphium depressum (Bates), larva, Perú, Gynerium sagittatum, Comensalismo, Coleoptero de caña brava, Cephaloleia

Introduction

In 1871, some years after his eleven incredibly productive years as an entomologist in the Amazon Basin, in part with his friend Alfred Russel Wallace, Henry Walter Bates described the adult of Ctenodactyla depressum. Bates collected his specimens at Tefé (formerly Ega) in Brazil in the 1850’s from “the close fitting folds of large aquatic grasses in which species of Cephaloleia, and other flattened forms of Hispidae, lie concealed in great numbers.” Then, 67 years later, Max Liebke (1938), the prolific German Entomologist, transferred Bates’ species to a new genus, Askalaphium Liebke. Another 43 years after that taxonomic action, Askalaphium depressum was “rediscovered” with canopy fogging techniques in Lower Floodplain Forest at Reserva Tambopata in southeastern Perú (Erwin 1985a). Erwin (1991) first reported the occurrence of Askalaphium depressum (Bates) as common in the leaf axils of Caña Brava (Gynerium sagittatum (Aubl.) P. Beauv.), a large reed (Fig. 1) that lives along all the broader waterways of the main Amazon drainage, as well as in many second order streams. Erwin (1997) subsequently provided an illustration of the adult of this striking carabid beetle (reproduced here in Fig. 2). Gynerium sagittatum is likely the same reed in which Bates first discovered this markedly depressed carabid beetle, as the plant is widely distributed along most of the Amazon tributaries and the main river itself. No specimens of A. depressum are known to have been collected between Bates’ Amazon expeditions in the 1850’s and 1984, some 130 years later.

Van Emden (1948) described the larva of Leptotrachelus dorsalis Fabricius, Ctenodactylini, the only known larva of the tribe until now. However, at that time “Colliurina” and “Ctenodactylina” were regarded as subtribes of Colliurini (Colliurini is now classified as an unrelated clade, Odacanthini), thus van Emden inadvertently gave a single combined description for both tribes, and then provided in a key the means to separate what he regarded as subtribes, but with very few important features listed. Van Emden provided illustrations for many other genera in his important contribution to knowledge of carabid larvae, but did not provide any for these particular ctenodactyline and odacanthine groups. Thompson (1979) summarized van Emden’s description, but did not add anything new to it, did not provide illustrations, nor did he sort the mixed characters of the two tribes.
These tribes, Ctenodactylini and Odacanthini, are now recognized as not being especially closely related (Erwin 1991).

**FIGURE 1.** A stand of Caña Brava reed, *Gynerium sagittatum*, along a 50-meter stretch of Zone 7, BIO-LAT Biodiversity Station, Pakitza, Perú.

**FIGURE 2.** Adult, dorsal aspect, of *Askalaphium depressum* (Bates). Specimen represented is from Rio Tambopata, Explorers Inn, Perú.

**FIGURE 3.** Larva, 3rd instar, dorsal aspect, of *Askalaphium depressum* (Bates). Specimen represented is from the BIO-LAT Biodiversity Station, Pakitza, Perú.
To correct these deficiencies, structural features of *A. depressum* are described, analyzed, and compared with those of the other known ctenodactyline larva, *L. dorsalis* (Fabricius), as well as a known odacanthine, *Odacantha melanura* Linnaeus, to sort out the mixed descriptions of van Emden. Further understanding of the Ctenodactylini is sought in features of the way of life of *A. depressum*, compared to other ctenodactyline genera.

**Specimens and methods**

As part of a student project in the BIOLAT Program in 1988 (Wilson & Sandoval 1996) of the Smithsonian Institution, one of us (RFM) collected and stripped crowns of 150 canes of *G. sagittatum* along a 50 meter transect (Fig. 1) of the plant in Zone 7, BIOLAT Biodiversity Station, Pakitza, Perú (11° 56’ 47” S, 071° 17’ 00” W) (see Erwin 1991, for a description of the various biotopes at Pakitza, including Zone 7, the varzea).

Thirty-some larvae were collected over a several day period. After feeding experiments and loss through humidity and fungus problems in the rearing containers, we secured 12 perfect specimens (seven 2nd instars, four 3rd instars) in 80% ethanol and it is upon these specimens that the following descriptions are based. The specimens are housed in the National Museum of Natural History, Smithsonian Institution, Washington, DC. One-half of the series is held in trust for MUSM in Lima, Perú, for when they obtain appropriate facilities for storage of important vouchering specimens.

Descriptive and larval preparation methods follow those suggested by the classic carabid larval method paper of Bousquet and Goulet (1984), particularly their coding system for setae and pores, and their description format. Additional setal and pore positions were discovered in this tribe and we have designated these in a sequence that follows the methods suggested by Bousquet and Goulet (1984). However, we recognize that their coding was limited to primary setae from the first instar, that is, those thought to be ancestral in carabids. Our addition of numbers for setae and pores are for comparative purposes within the clade Ctenodactylini and are not intended to be used for other clades. We have noted in the captions the final number for the primary codes for both setae and pores in Bousquet and Goulet (1984), the rest are for this tribe only. Our subsequent designations may be merely accessory setae common in later instars.

**Tribe Ctenodactylini**

Based on larvae of *Askalaphium depressum* (Bates).

**Recognition**

Head and body markedly depressed (Fig 3). Head wider than prothorax, gena markedly rounded (2nd Instar) or slightly subangulate (3rd Instar) behind stemmata. Neck
slightly constricted, short and broad, cervical groove and keel distinct. Maxilla with inner lobe present, unisetose, seta 2x length of lobe. Tarsus robust, subequal in length to that of tibia, dorso-apical surface multispinose, claws longitudinally ribbed (Fig. 23), short, about equal in length to diameter of tarsus. Urogomphi non-segmented, multi-nodose, infuscated. Pygidium with marked triangular patch of setae postero-ventrally.

Description of Third Instar

Coloration (Fig. 3). Mostly rich cream color with infuscated urogomphi and rufescent mandibles, frontale, and anterior margins of head capsule. Microsculpture. Head capsule with exceedingly fine transverse lines. Chaetotaxy. Head. Frontale (Fig. 4) with 9 setae (FR₁ - FR₁₁; FR₆,₉ replaced by pores) and 5 pores (FR₁ - FR₉) on each side. Parietale (Figs. 4, 5, 6) with 36 setae (PA₁ - PA₉₀) and 20 pores (PA₁ - PA₉; pores i, f absent) on each side. Antenna (Figs. 7, 7a, 7b): antennomere 1 with 2 pores (AN₁ - AN₉); antennomere 2 with 6 pores (AN₅ - AN₆); antennomere 3 with 3 setae (AN₁ - AN₃) and 2 pores (AN₁ - AN₅) and 3 small sensillae near base of sensorial appendage (Fig. 7a); antennomere 4 with 3 setae (AN₁ - AN₃) and 2 pores (AN₅ - AN₆) and 2 small apical sensilla (Fig. 7b). Mandible (Fig. 8) with 1 setae (MN₁) and 7 pores (MN₁ - MN₇). Labium (Fig. 9): prementum with 9 setae (LA₁ - LA₉) and 1 pore (LA₉) on each side; palpomere 1 with 1 pore (LA₉); palpomere 2 with 1 pore (LA₉) and with 3-5 minute pores or sensilla. Maxilla (Fig. 10, 10a, 11): cardo without setae; stipes with 10 constant setae (MX₁ - MX₁₄), MX₁, 8, 11, 12 absent; 10 pores (MX₁ - MX₄), MX₃, e, t, f, g absent, and a variable number of setae (gMX) on dorsal side; lacinia (Fig. 10a) with 1 setae (MX₁); galeomere 1 with 1 setae (MX₁) and no pores; galeomere 2 with apical setae, no pores; maxillary palpomeres without visible sensatory features. Thorax. Prothorax: Notum (Fig. 12, 13) with 14 major setae (PR₁ - PR₁₄), PR₁ absent, numerous small auxiliary setae, and 19 pores (PR₅ - PR₁₉) on each side; pleurite with 3 setae (PL₁ - PL₉), and 19 pores (PL₁ - PL₉) on each side; episternum (Fig. 13) with 11 setae (ES₁ - ES₁₉); epimeron (Fig. 13) with 1 seta (EM₁); prosternite (Fig. 14) with 7 setae (PS₁ - PS₇), gPS absent, and with 9 setae (PS₁ - PS₇) on each side. Mesothorax and Metathorax: Notum (Figs 15 - 16) with 14 setae (ME₁ - ME₁₄), numerous small auxiliary setae, and 12 pores (ME₁ - ME₁₂) on each side; episternum (Fig. 16) with 3 setae (ES₁, ES₅, ES₉) and 1 pore (ES₆); trochantin (Fig. 16) with 1 seta (TS₁); epimeron (Fig. 16) with 1 seta (EM₁); pleurite (Fig. 16) with 1 posterior seta (PL₁); sternum (Fig 14) with 10 setae (MS₁ - MS₁₀) and 2 pores (MS₁ - MS₁₀) on each side. Legs. Coxa (Figs. 17, 18, 19) with 13 setae (CO₁ - CO₁₉); CO₇, 10, 13, 17 absent, and 1 pores (CO₁). Trochanter (Fig. 18, 19) with 8 setae (TR₁ - TR₈) and 2 pores (TR₁ - TR₈). Femur (Fig. 20) with 10 setae (FE₁ - FE₁₀), FE₁ absent, and no pores. Tibia (Fig. 20) with 7 setae (TI₁ - TI₇) and 1 pore (TI₈). Tarsus (Fig. 20, 21, 22) with 1 constant seta (TA₁) and a marked setal brush; no pores. Anterior claw
(Fig. 20, 21, 22) with no setae; posterior claw with no setae. **ABDOMEN.** Tergite I (Fig. 24, 25) with 16 setae (TE₁ - TE₁₆) and 11 pores (TE₁₆ - TE₁) on each side. Tergites II - VIII as in Tergite I. Tergite IX and urogomphi (Fig. 26) with 16 setae (UR₁ - UR₁₆) and 7 pores (UR₆ - UR₇). Epipleurite (Fig. 25) with 5 setae (EP₁ - EP₅) and no pores. Hypopleurite (Fig. 25) with 3 setae (HY₁ - HY₃) and 1 pore (HY₄). Segment 7 with anterior sternites (Fig. 27) each with 2 setae (ST₁ - ST₂) and 3 pores (ST₆ - ST₇). Median sternites (Fig. 27) with 2 setae (ST₁ - ST₂) and 3+ pores (ST₆ - ST₇). Inner sternites (Fig. 27) with 2 setae (ST₁ - ST₂) and no pores. Outer sternites (Fig. 27) each with 3 setae (ST₁ - ST₃) and no pores. Sternal sclerite on segment IX with xx setae (ST₁ - ST₇) on each side. Segment 8 with anterior sternites (Fig. 27) each with 2 setae (ST₁ - ST₂) and 3 pores (ST₆ - ST₇). Median sternites (Fig. 27) with 2 setae (ST₁ - ST₂) and a reverse crescent-shaped pore array. Inner sternites (Fig. 27) with 2 setae (ST₁ - ST₂) and no pores. Outer sternites (Fig. 27) each with 1 seta (ST₁) and no pores. Sternal sclerite on segment IX with 3 setae (ST₁ - ST₃) on each side. Ninth abdominal tergite and urogomphi (Fig. 26) with 16 setae (UR₁ - UR₁₆) and 6 pores (UR₆ - UR₇). Pygidium (Fig. 28) with 19 setae (PY₁ - PY₁₉), and no pores.

**FIGURE 5.** Larval head capsule, parietale (PA), ventral aspect. 5, third instar; 5a, second instar. Primary setae: PA, 10-15. Primary pores: PA, e - l (pore i not present in second instar). Scale line equals 1.0 mm.

**FIGURE 6.** Larval head capsule, parietale (PA), lateral aspect. 6, third instar; 6a, second instar. Primary setae: PA, 11-19. Primary pores: PA, h - o (pore i not present in second instar). Scale line equals 1.0 mm.
FIGURE 7. Larval antenna (AN), third instar, right side dorsal aspect, 7, antenna; 7a, sensorial appendix; 7b, apex of antenomere 4. Primary setae: AN, 1-7. Primary pores: AN, a - g.

FIGURE 8. Larval mandible (MN), right side dorsal aspect, 8, third instar; 8a, second instar. Primary setae: MN, 1-2. Primary pores: MN, a - c.


FIGURE 10. Larval maxilla (MX), right side dorsal aspect, third instar, 10, maxilla; 10a, area near galea. Primary setae: MX, 1-12. Primary pores: MX, a – g.
**FIGURE 11.** Larval maxilla, right side ventral aspect, third instar. Primary setae: MX, 1-12. Primary pores: MX, a - g.

**FIGURE 12.** Larval prontoum (PR), dorsal aspect, third instar. Primary setae: PR, 1-14. Primary pores: PR, a - l.

**FIGURE 13.** Larval prothorax, left side lateral aspect, third instar: epimeron (EM); episternum (ES). Primary setae: EM, 1;

**FIGURE 14.** Larval prothorax and mesothorax, ventral aspect: prosternum (PS); mesosternum (MS); cc, coxal cavity; hy, hypopleurite; pt, prosternite. Primary setae: PS, 1-2; MS, 1-4. Primary pores: PS, nil; MS, nil.

**FIGURE 15.** Larval mesonotum (ME), dorsal aspect. Primary setae: ME, 1-14. Primary pores: ME, a - g.
**FIGURE 16.** Larval mesothorax, left side lateral aspect, third instar: epimeron (EM); episternum (ES); mesonotum (ME); trochantin (TS); pleurite (PL). Primary setae: EM, 1; ES, 1-4; TS, 1; PL, 1. Primary pores: EM, nil; ES, nil; TS, nil; PL, a - e.

**FIGURE 17.** Larval mesocoxa (CO), left side dorsal aspect; 17a, basal extremity of coxa. Primary setae: CO, 1-17. Primary pores: CO, a – e.

**FIGURE 18.** Coxa, trochanter, and basal part of femur, anterolateral aspect: mesocoxa (CO); trochanter (TR); femur (FE). Primary setae: TR, 1-8; FE, 1-6. Primary pores: TR, a – e; FE, a – b.

**FIGURE 19.** Coxa, trochanter, and basal part of femur, posterolateral aspect.

**FIGURE 20.** Middle leg, lateroventral aspect, except basal half of coxa: mesocoxa (CO); trochanter (TR); femur (FE); tibia (TI); tarsus (TA).
FIGURE 21. Claws and apical part of tarsus, posterolateral aspect: tarsus (TA); claws (UN).

FIGURE 22. Claws and apical part of tarsus, dorsal aspect.

FIGURE 23. Tarsus and claws, posterolateral aspect. [SEM]

FIGURE 24. First abdominal tergite (TE), dorsal aspect. Primary setae: TE, 1-11. Primary pores: TE, a - d.


FIGURE 27. Seventh, eight, and ninth abdominal segments (ST), ventral aspect: epipleurite (EP); as, anterior sternite; is, inner sternite; mes, median sternite; os, outer sternite; ss, sternal sclerite. Primary setae: ST, 1-6; EP, 1-2. Primary pores: ST, nil; EP, nil.
HEAD. Nasale short, slightly rounded with uneven margin; mandibles robust and with obvious serrations apico-medially; genae prominent, slightly wider than distance across stemmata, rounded to broad neck. Eyes of 6 markedly prominent stemmata. Antennomere 2 slightly longer than 1 and 3, 4 slightly shorter than 3. Mandible with prominent retinaculum, dentiform; terebral blade obviously serrate, pensillus absent. Ligula of labium produced, bisetose. Ratios of palptomere lengths can be deduced from the illustrations.

THORAX. Prothorax broadly quadrate; mesothorax transverse ovaloid, more narrowly ante- riad, broader mesially, narrow apically. ABDOMEN. Segments hexagonal, broad. Urogo- mphi about twice as long as prothorax is long. Legs. Tarsus markedly spinose.

Description of Second Instar

Coloration. Available specimens are somewhat paler in color than those of the 3rd instar, nearly white, with slightly infuscated urogomphi and flavous mandibles, frontale, and anterior margins of head capsule. Microsculpture. As in third instar. Chaetotaxy. HEAD. Frontale (Fig. 4a) with 10 setae (FR₁ - FR₁₁; seta 9 absent) and 6 pores (FR₇, FR₈) on each side. Parietale (Fig. 4a, 5a, 6a) with 22 setae (PA₁ - PA₂₂) and 21 pores (PA₁ - PA₁; pore ₇ absent) on each side. A few uncoded pores and very small setae occur asymmetrically. Mandible with small subapical seta (MN₂ not found in 3rd instar; pores MN₂₃, present. Otherwise, stages similar. Head. As in third instar, except nasale margin slightly less undulating; mandible (Fig. 8b) not robust and without obvious terebral serrations, retinaculum blunt, 3 pores and one apical seta, as well as scrobal seta A₁; genae less rounded than in 3rd instar, about as wide as head across stemmata. Thorax. As in third instar. Legs. As in third instar. ABDOMEN. As in third instar.

Natural History

As might be predicted from their exceedingly depressed form (Figs. 2, 3), these beetles are super-specialists (Erwin 1985b) for tight places. The notes taken by the astute 19th Cen-
tury Amazon entomologist, H.W. Bates, upon discovering adults in the 1850’s suggested this already. Both larvae and adults live in the appressed leaf bases of the reed, *G. sagittatum* (Fig. 1). On the basis of these observations, we postulate a commensal relationship between the species of *Askalaphium* and *Gynerium*, and because the adult and larval beetles eat the larvae of the hispine, *Cephaloleia* Chevrolat, with species of that genus, as well.

We found larvae and adults of *A. depressum*, on average in every fifth cane (n = 150 canes) of *G. sagittatum*. Thus, the population density of the beetle species may have been very high, and this might be true elsewhere, wherever this reed grows in large stands. Like most carabids, the larvae and adults ate dead or dying insects when offered in our field laboratory, however, we did not actually observe them feeding in the stands along the river, nor did we observe them walking about on the surfaces of the reed leaves in the day or at night, although fogging collections at Tambopata suggest that they are night active. The present study took place in October, the beginning of the rainy season at Pakitza (Erwin 1991). We did not find first instars, nor did we encounter pupae, thus seasonality may be an important factor in their life cycle. This aspect is open to future study.

Upon studying the structure of the larvae, we discovered the marked setal patch on the tarsus (Fig. 20), as well as the ribbed claws. These characters combined with the markedly depressed form suggest that the larvae move easily through the young, soft, fleshy, and appressed Caña Brava leaf substrate using the leverage gained by these setal attributes while seeking their prey. This aspect is also open to future study. For the purposes of conservation, we designate the species, the Caña Brava Beetle.

**Biogeography**

The reed, as a microhabitat for this commensal species of carabid is classified in the family Poaceae (= Arundinoideae), Arundinae. This reed is a very large, soil binding, rhizomatous perennial species, with individuals having culms that are 200–1000 cm high. The culm internodes are solid and the leaves are not basally aggregated, rather they are clustered towards the culm tips. The plant species is helophytic occurring on stream and riversides and other wet varzea places in the neotropics (Caribbean, Amazon, and Andean regions). Known localities for *A. depressum* are indicated in Fig. 29 (Tefé, Pakitza, and Tambopata). However, the recorded distribution of *G. sagittatum* is México to subtropical South America (and Florida, USA). We therefore predict that where the plant is found, at least in the Amazon Basin, so will the beetles be found, hence the distribution would be typical of most widespread varzea species with Amazonian river dynamics dictating dispersal potential (Erwin 1991). Whether or not the beetles have achieved northward movement across the Andes, or into Middle America is not known. This is still another aspect that is open to future study.

**Characteristics of Ctenodactylini**

Although van Emden (1948) mixed attributes of two unrelated tribes, Odacanthini and Ctenodactylini, some features of the latter may be extracted from his descriptions. His observations of members of the genus *Leptotrachelus* contain the following which we also found in larvae of *A. depressum*: epicranial suture short; cervical groove and keel present; maxilla with inner lobe present; neck not severely constricted; urogomphi nodal, yet not segmented. We located the collection of *L. dorsalis* larvae that van Emden studied (collected at Oxford, Indiana) in the NMNH, however, they are not in very good condition. We confirm his observations and add that second and third instars lack a pencillus and the terebral blade is serrate, but refrain from making a more detailed comparison until better specimens are discovered in future field work. These observations are at least a beginning in our understanding of the structural features of the larval stages for the carabid tribe Ctenodactylini. There are some poorly preserved specimens of *Odacanta melanura* Linnaeus in the NMNH collection, as well, and we studied these as well as possible considering their condition. These specimens differ from ctenodactyline larvae in that the mandible has a single seta pensillus and the maxilla lacks an inner lobe, other features are not discernible.

The postulated commensal association with monocotyledonous plants and larvae of a genus of chrysomelids provides an additional characteristic feature of ctenodactylines. Species representing other genera of the this tribe are known to occur commonly as adults on the culms of marsh grasses such as *Panicum dichotomiflorum* (*Leptotrachelus dorsalis*: Steiner 1984) in Maryland, USA, and *Paspalum* sp. (*Leptotrachelus* spp.: Erwin 1991) in the western Amazon Basin. Undescribed larvae of some genera of ctenodactylines were also found in the rotten stems and leaf axils of species of the plant genera *Heliconia* and *Calathea* in low wet places. Further discovery is necessary and subsequent documentation is required to define more accurately the Ctenodactylini, and to explore the patterns that must link these beetles evolutionarily and ecologically to the plants on which they live and the food which they eat.
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Literature cited


