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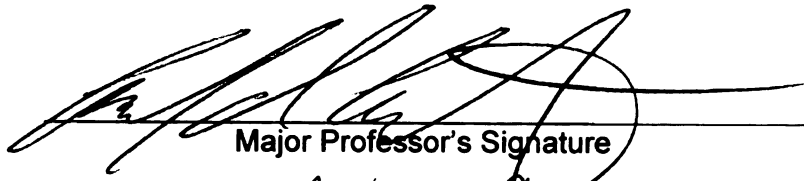
A Revision of *Camptocerus* Dejean  
(Coleoptera: Curculionidae: Scolytinae)  
With Notes on its Biology

presented by

Sarah Marie Smith

has been accepted towards fulfillment  
of the requirements for the

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A REVISION OF *CAMPTOCERUS* DEJEAN (COLEOPTERA: CURCULIONIDAE:  
SCOLYTINAE) WITH NOTES ON ITS BIOLOGY

By

Sarah Marie Smith

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## ABSTRACT

### A REVISION OF *CAMPTOCERUS* DEJEAN (COLEOPTERA: CURCULIONIDAE: SCOLYTINAE)

By

Sarah Marie Smith

The Neotropical ambrosia beetle genus *Camptocerus* Dejean was revised. The monophyly of the genus was tested using 66 morphological characters in a cladistic analysis. *Camptocerus* was monophyletic and 30 species are recognized. Six **new synonyms** are presented: *C. auricomus* Blandford (= *C. striatulus* Hagedorn), *C. inoblitus* (Schedl) (= *C. morio* (Schedl)), *C. niger* (Fabricius) (= *C. tectus* Eggers), *C. opacicollis* (Eggers) (= *C. infidelis* Wood; = *C. uniseriatus* Schedl), *C. suturalis* (Fabricius) (= *C. cinctus* Chapuis). Two species received **new status**: *C. charpentierae* Schedl and *C. hirtipennis* Schedl. Eleven **new species** of *Camptocerus* are described: *C. coccoformus*, *C. distinctus*, *C. dolei*, *C. igniculus*, *C. mallopterus*, *C. noel*, *C. petrovi*, *C. pilifrons*, *C. pseudoangustior*, *C. unicornus* and *C. zucca*. An illustrated key, diagnosis, distribution, hosts and images were provided for each species.

I report observations of *Camptocerus* attracted to felled *Protium amazonicum* Swart in southeastern Peru and the behavior of four species. An unusual behavior for scolytines was observed as three species aggregated to leaves surrounding potential hosts, bored into leaves and fed, a rare behavior for Scolytines. . Males competed for mates with physical contact. Ant predation killed ~50% of colonizing individuals for one species.

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## **CHAPTER ONE**

### **A Revision of *Camptocerus* Dejean (Coleoptera: Curculionidae: Scolytinae)**

## ABSTRACT

The Neotropical ambrosia beetle genus *Camptocerus* Dejean was revised. The monophyly of the genus was tested using 66 morphological characters in a cladistic analysis. *Camptocerus* was monophyletic and 30 species are recognized. Six **new synonyms** are presented: *C. auricomus* Blandford (= *C. striatulus* Hagedorn), *C. inoblitus* (Schedl) (= *C. morio* (Schedl)), *C. niger* (Fabricius) (= *C. tectus* Eggers), *C. opacicollis* (Eggers) (= *C. infidelis* Wood; = *C. uniseriatus* Schedl), *C. suturalis* (Fabricius) (= *C. cinctus* Chapuis). Two species received **new status**: *C. charpentierae* Schedl and *C. hirtipennis* Schedl. Eleven **new species** of *Camptocerus* are described: *C. coccoformus*, *C. distinctus*, *C. dolei*, *C. igniculus*, *C. mallopterus*, *C. noel*, *C. petrovi*, *C. pilifrons*, *C. pseudoangustior*, *C. unicornus* and *C. zucca*. An illustrated key, diagnosis, distribution, hosts and images were provided for each species.



## INTRODUCTION

Beetles of the subfamily Scolytinae (Coleoptera: Curculionidae) are ubiquitous in forests world-wide and contribute to the decomposition of dead vegetation. More than 6,000 species (Wood & Bright, 1992) specialize on plant parts, from root to fruit, as food resources for larvae and adults (Wood, 1982). Scolytines, along with the closely related subfamily Platypodinae, are collectively referred to as the bark and ambrosia beetles. The Scolytinae are primarily composed of two distinct ecological feeding groups; bark and ambrosia beetles. True bark beetles feed on phloem and cambium of live, declining or dead trees. Ambrosia beetles tunnel into the xylem of a host tree and cultivate a symbiotic fungal garden on which the adults and larvae feed. This ambrosial feeding habit has evolved multiple times within the Scolytinae (Farrell et al., 2001). The primary behavior of boring under bark and into sapwood hastens decomposition via the introduction of other xylophagous organisms.

Even though South America possesses one of the most diverse groups of scolytines in the world (Wood, 2007), the fauna is one of the least known (Bright, 1993; S. L. Wood, pers. comm.). Along with under-studied species diversity, little is known about South American scolytine biology and ecology, including tree host associations (Beaver, 1972). One such poorly known group is the tribe Scolytini and specifically the ambrosia beetle genus *Camptocerus* Dejean (Wood, 2007). This study was undertaken to taxonomically revise and redescribe *Camptocerus* (Scolytinae: Scolytini). Phylogenetic analysis based on adult morphological and ecological characters was incorporated to

determine monophyly of the genus, species validity, species relationships and the relationship of *Camptocerus* within the tribe Scolytini.

### **Natural History**

*Camptocerus* is unique among the genera in the tribe Scolytini because the larvae are xylomycetophagous (xylem and ambrosial fungus feeding) instead of phloeophagous (phloem feeding) (Beaver, 1972; Wood, 1972, 1982, 1986, 2007; Petrov, 2007). The female creates an entrance tunnel into the cambium where the male joins her. Infestation of moribund host material can start within one day, but typically occurs within 2-4 days and ceases after 3 to 10 days (Beaver, 1972). Personal observations in Peru indicate that *Camptocerus* can continue colonization for more than 26 days (Chapter 2). In a typical gallery, the entrance tunnel runs in a transverse plane toward the center of the stem. From this tunnel, the female adds one or two circumferential branches creating a maternal gallery (Wood, 2007). Females lay single eggs along the maternal gallery in wide niches cut at right angles to the gallery and on parallel sides. Niches are plugged with boring dust (Beaver, 1972). Females occupy the inner galleries and males protect the gallery entrance by plugging the holes with their abdomens (Beaver, 1972; chapter 2).

Larvae hatch and feed on xylem and the black mycelial growth of the ambrosia fungi lining the niche. Each larva enlarges its niche to a cradle as it grows and is capable of turning around within the cradle. The 7-10 week life cycle is longer than other xylomycetophagous scolytines and platypodines and may perhaps be due to the slow growth of the ambrosial fungus (Beaver, 1972). Females probably inoculate the tree with fungal spores stored in their mycangia upon attack (Beaver, 1972), but, the location of the mycangia have been previously unknown.

Several *Camptocerus* species have been known to colonize a single host tree and the species segregate themselves by trunk/branch size, with large species attacking the trunk and large branches (5- <30 cm) and small species attacking smaller branches (1- 5 cm) (Beaver, 1972; chapter 2). Depending on the site, a single host has been observed to contain between one and four (Beaver, 1972) and six species of *Camptocerus* (Smith, per. ob.).

*Camptocerus* species also perform leaf feeding, a rare and unusual behavior for Scolytines. *Camptocerus aeneipennis* adults have been found feeding on leaves of a *Thrysoodium* species (Anacardiaceae) in the Panama Canal Zone (von Wining, 1930). The beetles had chewed the leaf's central vein to form circular holes slightly smaller than the width of their bodies. Each beetle was lying in a hole with its mesosternum lying between the leaf surfaces, with heads directed toward the leaf's ventral surface. Once positioned, the beetles performed window feeding (feeding only on one surface of the leaf) a few mm from their present hole or up to 20 mm away. It is presumed that the beetles were using the leaves for maturation feeding (von Wining, 1930). This behavior has also been observed by *C. opacicollis* (Eggers), *C. noel* Smith & Cognato sp. n., *C. pseudoangustior* Smith & Cognato sp. n. (chapter 2), *C. aeneipennis* and *C. aterrimus* in southeastern Peru (S.M.Smith, pers. ob.) and by *C. suturalis* in Loreto province, Peru (A. Petrov, pers. com). Although these behaviors were not witnessed, feeding damage from *C. aeneipennis* and *C. auricomus* Blandford were also observed by me along Pipeline Rd in the Parque Nacional Soberania, Panama Province, Panama. This locality is along the Panama Canal and in the same area from which this behavior was first reported (von Wining, 1930).

*Camptocerus* exhibit a unique aggregation technique. It is apparent that *Camptocerus* also chew aggregation holes within 2 m of host tree. The behavior is similar to maturation feeding except that a hole is chewed in the leaf, but the material is not digested. In addition, there is never window-feeding damage near the hole. This behavior creates distinctive damage that is easily recognizable by perfectly formed circular holes located between two leaf veins (S.M.Smith, pers. ob).

Host records for *Camptocerus* are limited, but *Camptocerus* have been found colonizing eleven different tree families with host records reported for half of all species. *Camptocerus* are overwhelmingly collected from members of the Burseraceae (specifically *Protium* sp.), but they can also utilize species of Chrysobalanaceae, Clusiaceae, Euphorbiaceae, Fabaceae Lauraceae, Leguminosae, Meliaceae, Myrtaceae, Roseaceae, Sapindaceae to a lesser extent. *Camptocerus* have been observed to preferentially colonize *Protium* over other documented hosts (Beaver, 1972) and Beaver (1989) concluded that *Camptocerus* species are host specific on *Protium* . Host specificity is unusual for ambrosia beetles, which are typically polyphagous (Hulcr et al., 2007a).

The geographical range of *Camptocerus* extends from Veracruz, Mexico (Atkinson & Equihua- Martinez, 1986) to Chaco, Argentina (Bruch, 1914). To date, only four species have been found in Mexico and Central America. Of those, one is exclusive to Central America, two are distributed in Central and South America, one is distributed in Mexico, Central, and South America; 26 species are exclusively in South America (Table 1.1). Given this distribution pattern, Wood (1982) hypothesized that the genus originated in South America and has radiated north over time. In addition, the greatest

diversity of *Camptocerus* species (83%), as well as the other Scolytini, lies in the Amazon Basin (Wood & Bright, 1992; Wood, 2007) (Fig.1.2).

### Systematics

The tribe Scolytini is currently composed of approximately 209 species in four genera: *Camptocerus* Dejean 1821, *Cnemonyx* Eichhoff 1868, *Scolytus* Geoffroy 1762, and *Scolytopsis* Blandford 1896. The tribe likely originated in the Neotropics with all genera distributed in the New World, except for numerous Palearctic *Scolytus* (Wood, 1986). All genera are phloeophagous (phloem feeding) with the exception of the xylomycetophagous *Camptocerus*. All genera are monogamous except for a few species of Neotropical *Scolytus* (Wood, 1982). Members of the tribe are identified by a single apical, unarmed spine-like process that curves toward and extends beyond the process of the inner apical angle of the protibia and a seven-segmented funicle. All display a strongly sexually dimorphic head ornamented with hair-like setae, with the male frons variously excavated and female frons flat to convex (excavated in one *Scolytus* species). The eye is entire and the posterior area of head is subtruncate. The pronotum is unarmed with a costate lateral margin. In addition, the metapleural suture descends subventrally to the groove, receiving the groove on the costal margin of the elytra, then turns abruptly and parallels the groove near the metacoxal process (Wood, 1978, 1982, 1986).

*Camptocerus* has historically been diagnosed from the other genera of the tribe by a large, broad, and flat scutellum that is at least 1.5 times wider than long, the absence of a notch at the elytral base for scutellar reception, generally larger body size, gradually



ascending abdomen, extensively excavated male frons, suture 1 of antennal club marked internally by a septum, a usually finely sculptured elytra, by meso- and metathoracic tibiae acutely margined on apical anterior edge without supplemental denticles, and by xylomeycetophagy (Wood, 1982, 1986, 2007). *Camptocerus* species show marked sexual dimorphism of the frons and epistoma; the male frons is often strongly excavated and the female frons is flat to convex. The male frons is covered by more and longer setae than the female frons. The epistoma is elongated and rostrate-like in the male. Sexual dimorphism also occurs in the antennal scape and funicle and to various degrees in the elytral declivity. The female scape and funicle are similar to the male antenna but lack the long brush-like setae on funicle segments 2-7. It is difficult to distinguish between some members of *Camptocerus* and *Cnemonyx* due to similar morphology. They are most effectively identified by phloeophagous (*Cnemonyx*) or xylomeycetophagous (*Camptocerus*) feeding habits (S.L. Wood, pers. comm.). Unfortunately, many *Camptocerus* species have only been collected by passive methods (e.g. canopy fogging). As a result, species identity of approximately half of the *Camptocerus* species has been confirmed by field observations of xylomeycetophagy; feeding habits of the remaining species are unknown.

### **Taxonomic History**

*Camptocerus* was established as a monotypic genus by Dejean who designated *Hylesinus aeneipennis* Fabricius as the type species. However authorship of *Camptocerus* has been attributed to Latreille in the majority of taxonomic literature (Erichson, 1836;

LaPort de Castelneau, 1840; Lacordaire, 1866; Chapuis, 1869; Girard, 1873; Blandford, 1896; Hagedorn, 1910; Blackman, 1943; Blackwelder, 1947; Schedl, 1952; Schedl, 1962; Beaver, 1972; Wood, 1978, 1982, 1986; Beaver, 1989; Wood & Bright, 1992; Petrov, 2007; Wood, 2007) with three exceptions that also cite Dejean (Lacordaire, 1866; Beaver, 1972; Wood, 1972) and three that recognize Dejean (Chevrolat, 1838; Hopkins, 1914, 1915). Dejean is the rightful author; he named the genus and assigned a type species of *Hylesinus aeneipennis* Fabricius, but he did not provide a written description of the genus (Dejean, 1821). However, his action validated the name in accordance with the ICZN code article 12.2.5 (ICZN, 1999). In 1829, Latreille cited Dejean when he described the genus *Camptocerus* as “whose males have strongly bent antennae, furnished outside with long hairs; which are inserted at a notable distance from the eyes, which are elliptical and oblique.” It seems likely that other authors were unaware of the Dejean (1821) publication and credit was instead given to Latreille (Lacordaire, 1866).

The unique morphology exhibited by *Camptocerus* species has led to the creation and subsequent placement in the group (tribe) Camptocérides with the Palearctic genus *Diamerus* Erichson (Lacordaire, 1866). Ferrari (1867) recognized the Camptocérides as a subtribe. Chapuis (1869) elevated the Camptocérides back to a tribe and Blandford (1893) maintained this taxonomic position., until he later sunk the Camptocérides back to the level of subgroup (subtribe) (Blandford 1896). Blandford (1896) removed *Diamerus* from this group and placed the genera *Cnemonyx*, *Loganius* Chapuis, *Ceratolepsis* Chapuis into the subtribe. Hopkins (1915) elevated the subtribe to the subfamily Camptocerinae. Blatchey & Leng (1916) sunk the Camptocerinae back to a subtribe, which they named Camptocerini. Costa Lima (1956) departed from this

classification and followed Hopkins (1915) recognizing these genera at the subfamily level. Wood (1961) appeared to have placed the Camptocerini as a synonym of the tribe Scolytini.

Prior to Wood's 1972 anatomical revision, the tribe Scolytini consisted of two clearly defined genera (*Scolytus* and *Scolytopsis*) and five strikingly similar genera (*Camptocerus*, *Cnemonyx*, *Loganius*, *Ceratolepsis*, and *Coptosomus* Schedl). *Camptocerus*, *Ceratolepsis*, and *Coptosomus* possess meso- and metathoracic tibiae that are identical to the prothoracic tibiae, with a straight, sharp, and smooth anterior edge of the apical margin to the base of the outer apical spine. In *Cnemonyx* and *Loganius*, the surface of the tibial anterior edge of the apical margin to the base of the outer apical spine bears one or more denticles. Species with these denticles also have two to three sutures on the antennal club marked with setae, while species without denticles lack externally marked sutures but at least part of suture 1 is marked internally by a septum. Schedl (1962) noted that the characters used to diagnose these genera were inconsistent and formed a spectrum of variation. This caused him to synonymize *Ceratolepsis* with *Camptocerus*. However, Wood (1972) determined the genus *Camptocerus* was a distinct group without any synonymies; he found the characters used to identify *Ceratolepsis* (scales on antennal club), *Cnemonyx* (crenulations of elytral base), and *Coptosomus* (oddly placed antennal suture) were insufficient to clearly define species groups and transferred them to the oldest described genus, *Cnemonyx*. *Loganius* species were divided between *Cnemonyx* and *Camptocerus*.

Five *Camptocerus* species were among the first New World scolytines to be described (Illiger, 1807; Blandford, 1896). Since 1801, nine authors have contributed

species. In 1801, Fabricius described *Hylesinus aeneipennis*, *H. fasciatus*, *H. gibbus*, *H. niger*, and *H. suturalis*. In 1821, Dejean created the genus *Camptocerus* using *Hylesinus aeneipennis* as the type species and the remaining species were subsequently placed in *Camptocerus* by Wilhelm Erichson (1836). Several taxonomists have described *Camptocerus* species including Felicien Chapuis (1869), Walter Fielding Holloway Blandford (1896), Max Hagedorn (1910), Hans Eggers (1928, 1929, 1932, 1943), Mulsby W. Blackman (1943), Karl Schedl (1939, 1952, 1970, 1972, 1973), Stephen L. Wood (1969, 1972, 2007), and Alex Petrov (2007). To date, only *C. bolivae* has been moved to another genus (*Cnemonyx*). However, several *Loganius* species have been transferred to *Camptocerus*, including *C. inoblitus* (Wood, 1972), *C. major* (Schedl, 1952), *C. morio* (Wood and Bright, 1992), and *C. opacicollis* (Schedl, 1952; Wood, 1972). *Camptocerus terebrator* Lacordaire (1833) is a nomen nudum. This species does not meet the criteria outlined by the ICZN article 12.1 as there is no description, definition or indication of the species. Schedl (1976) also indicated that the species did not meet these requirements, but failed to recognize the name as a nomen nudum.

It is quite puzzling that *Camptocerus* has one of the longest taxonomic histories of American scolytines yet remains one of the least understood genera. In *Biologia-Centrali Americana*, Blandford (1896) noted that with the exception of *C. aeneipennis*, *Camptocerus* species were rare in collections and few were described. This situation persists to the present with several species represented by fewer than five individuals; *C. aeneipennis* remains common in collections. Indeed biological information exists for fewer than half of the known species with most data pertaining to *C. aeneipennis*.

Although the genus *Camptocerus* was recently reviewed by Wood (2007), an additional 11 new species have since been discovered. Examination of Dr. Terry Erwin's Ecuadorian Amazon rain forest canopy fogging samples collected between 1994 and 2006 yielded seven novel *Camptocerus* species. Museum loans and recent collecting by the authors in Guyana and Peru have also led to the discovery of an additional four new species and previously unknown females for three species, *C. charpentierae* Schedl, *C. costatus* Chapuis and *C. quadridens* Blackman. Currently, the genus is composed of 30 species, of which 19 are valid and an additional 11 species are described herein.

## Materials and Methods

Approximately 1182 *Camptocerus* specimens representing all taxa from a range of locations in Mexico, Central and South America were examined for this study. Five species of *Cnemonyx* and one species of *Scolytopsis* were also included in the ingroup. Five *Scolytus* species (two Neotropical, one Nearctic, and two Palearctic) were selected as the outgroup and as the root taxa.

The following entomological collection codens (following Evenhuis, 2007) and abbreviations are referenced in the text:

|      |   |
|------|---|
| AMNH | American Museum of Natural History, New York, New York, USA.  |
| BMNH | British Natural History Museum, London, United Kingdom.   |
| CASC | California Academy of Sciences, San Francisco, California, USA.   |
| CSCA | California State Collection of Arthropods, Sacramento, California, USA.                                     |
| DEI  | Deutsches Entomologisches Institute, Leibniz-Zentrum für<br>Agrarlandschaftsforschung, Müncheberg, Germany. |

|              |   |
|--------------|---|
| <b>FMNH</b>  | <b>Field Museum of Natural History, Chicago, Illinois, USA.</b>   |
| <b>IRSNB</b> | <b>Institute Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium.</b>   |
| <b>MECN</b>  | <b>Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.</b>   |
| <b>MNHN</b>  | <b>Muséum National d'Histoire Naturelle, Paris, France.</b>   |
| <b>MSUC</b>  | <b>Albert J. Cook Arthropod Research Collection, Michigan State University,<br/>East Lansing, Michigan, USA.</b>                    |
| <b>MUSM</b>  | <b>Universidad Nacional Mayor de San Marcos, Lima, Peru.</b>  |
| <b>MZUSP</b> | <b>Museum de Zoologia, Universidad de Sao Paulo, Sao Paulo, Brazil.</b>   |
| <b>NHMW</b>  | <b>Naturhistorisches Muesum Wien, Vienna, Austria.</b>  |
| <b>NMNH</b>  | <b>National Museum of Natural History, Smithsonian Institution,<br/>Washington, DC, USA (Including Stephen L. Wood Collection).</b> |
| <b>RJRC</b>  | <b>Robert J. Rabaglia collection, Maryland, USA.</b>  |
| <b>SEMC</b>  | <b>Snow Entomological Museum, Lawrence, Kansas USA.</b>   |
| <b>SMTD</b>  | <b>Staatliches Museum für Tierkunde in Dresden, Germany.</b>  |
| <b>STRI</b>  | <b>Smithsonian Tropical Research Institute Collection, Balboa, Panama.</b>  |
| <b>UCDC</b>  | <b>Bohart Museum of Entomology, University of California, Davis,<br/>California, USA.</b>   |
| <b>UMMZ</b>  | <b>Museum of Zoology, University of Michigan, Ann Arbor, Michigan,<br/>USA.</b>   |
| <b>UZMC</b>  | <b>Natural History Museum of Denmark, University of Copenhagen,<br/>Zoological Museum, Copenhagen, Denmark.</b>                     |
| <b>ZMMU</b>  | <b>Zoological Museum, Moscow State University, Moscow, Russia.</b>  |

Host plants were compiled from the following publications: Kleine, 1934; Bondar, 1950; Viana, 1965; Beaver, 1972; Atkinson & Equihua-Martinez, 1986; Maes & Equihua-Martinez, 1988; Wood & Bright, 1992; Wood, 2007; L. Kirkendall (per. comm.); A. Petrov (per. comm.). Distribution records were gleaned from the following sources: Chevrolat, 1838; Hagedorn, 1903, 1910; Kleine 1913, 1914; Bruch, 1914; Viana, 1914; Nunberg, 1962, Schedl, 1972; Beaver, 1972; Atkinson & Equihua-Martinez, 1986; Maes & Equihua-Martinez, 1988; Wood & Bright, 1992; Bright & Skidmore, 1997, 2002; Wood, 2007; A. Petrov (per. com.); T. Atkinson (per. com.). Plant nomenclature was checked using Discover Life ([discoverlife.org](http://discoverlife.org)) and the International Plant Names Index ([www.ipni.org](http://www.ipni.org)).

Specimens were examined using a Leica MZ16 compound microscope, illuminated with a SCHOTT 150W halogen light source (model ACE ®1). Images were taken with a Leica DFC 320 and montage images were assembled using Helicon Focus 3.50,5 (HeliconSoft) Following the protocol used by Wood (1982; 2007), measurements were made using an ocular micrometer on the same microscope and with the same light source as above calibrated with ROK 150 mm digital calipers (model DC-122A). Measurements were made perpendicular to the specimen's dorsal surface. Length was measured from the anterior margin of the pronotum to the apex of the elytra, excluding the head. Width was measured at the widest part of the pronotum, the base. Proportions are the ratio of the length to the width. A maximum of 20 individuals were selected for each species and encompassed the known species distribution.

Holotypes were designated with red labels. Lectotypes, allotypes and paratypes were designated with yellow labels.

## Morphological Characters

Traditional bark beetle generic and species level morphological characters were employed in this study (Hopkins, 1915; Wood, 1978; Knížek & Beaver, 2004).

Characters were taken from generic descriptions (Hagedorn, 1910; Wood, 1982, 1986, 2007), species descriptions, and personal examination of specimens. *C. aeneipennis* was used to determine intraspecific variation within a character due to its abundance in museum collections and wide geographic range. All characters were based on adult morphology and feeding habit. External anatomical terminology followed Hopkins (1909), subsequently used by Schedl (1931) and by Wood (1982, 1986, 2007).

Sculpturing terminology followed Torre-Bueno (1989). The elongated epistoma of male *Camptocerus* differed significantly from other bark beetles and I created new terminology to accommodate this structure. The male epistoma was defined as the area extending from the mandibular margin (here termed the apical epistomal margin) to the level of antennal insertion (Wood, 1982, 2007) (here termed the basal epistomal margin). The frons was considered the region of the head originating at the basal epistomal margin and terminating at the vertex of the head (Fig 1. 3).

Genitalia dissections were performed on male specimens of 35 of 40 taxa. Dissections were not performed for species not represented by males, or for species only known from a short series or holotype. Dissections were performed after soaking a specimen in 70% ethanol for ten minutes. In small species, a hooked #2 stainless steel insect pin was placed in the coxal cavity and was used to pry back the abdominal sternites up to tergite 6. The genitalia were then removed and placed in 20% KOH until cleared,



usually after 5-7 days and neutralized in 20% glacial acetic acid. For larger species, preparation was the same and the genitalia were removed by inserting a hooked pin into the genital opening between the eighth sternite and tergite. The genitalia were removed with the hook and cleared using the same methods as above. Genitalia were stored in glass genitalia vials filled with glycerin or by placing them on mounting cards in the manner recommended by the loaning institution.

Characters were scored from both sexes unless otherwise noted. *Camptocerus* exhibited strong sexual dimorphism; males exhibit a wide spectrum of morphological features while females display conserved morphology. As a necessary consequence, characters were predominately male based. Characters were scored for all taxa except for *C. annectens* Wood, and *C. major* (Eggers), which are only known from females. As a result these species were excluded from the phylogenetic analysis (60% of characters scored). Characters and character state numbers corresponded to data coded in the data matrix for each taxon. The characters matrix (Table 1.2) was constructed and edited from the online database MX (Yoder et al., 2006). Character transformations were evaluated using MacClade 4.0 PPC (Maddison & Maddison, 2000) and homology of characters and definitions of character states were re-examined and modified if necessary.

A total of 66 characters (24 binary and 42 multistate) were used in this study. Twenty-two characters were coded from the head including the antennae, 11 characters from the prothorax, 26 characters from the abdomen including the elytra and scutellum, 1 character from the mesosternum, 5 characters from male genitalia and 1 character based on feeding habit. Consistency and retention index values generated from MacClade 4.0 are listed next to each character.

## **Head**

1. *Antennal club sutures* (ci = 1.00; ri = 1.00)

0: zero

1: one

2: two

3: three

2. *Female apical epistoma emarginate at medial line* (ci = 1.00; ri = 1.00)

0: normal

1: emarginate

3. *Male apical epistoma emarginate at medial line* (ci = 1.00; ri = 1.00)

0: normal

1: emarginate

4. *Relative epistoma size compared to frons* (ci = 0.14; ri = 0.65)

0: less than one fourth

1: greater than or equal to one-fourth

5. *Vestiture on lateral margin of epistoma* (ci = 0.60; ri = 0.33)

0: setae entire

1: setae on lower half

2: middle

3: glabrous

6. *Male apical epistomal margin* (ci = 0.57; ri = 0.73)

0: unarmed

1: short transverse carina

2: tubercle

3: large tubercle extending length of epistoma

4: median lobe

7. *Male basal epistomal margin* (ci = 0.60; ri = 0.82) (Fig. 1.4)

0: transverse, concave carina

1: tumid above scape insertion

2: strongly developed transverse carina

3: weakly developed transverse carina

4: no demarcation

5: transverse carina with strongly developed lateral areas

6: short transverse carina

8. *Excavation of male frons* (ci = 0.40; ri = 0.57)

0: weak/feeble

1: strong

2: flat

9. *Male gena* (ci = 0.17; ri = 0.00)

0: triangular structure absent

1: triangular structure present

10. *Lateral margin of male epistoma* (ci = 0.50; ri = 0.83)

0: arcuate costa pointing distally

1: arcuate costa pointing proximally

2: vertical costa

3: costa angled inward

4: costa absent

11. *Male frons excavation size* (ci = 0.40; ri = 0.67)

0: excavation does not border ocular margin

1: excavation touches ocular margin

2: excavation absent

12. *Male frons armature* (ci = 1.00; ri = 1.00)

0: unarmed

1: tubercle

13. *Male frontal setae in two bands* (ci = 0.25; ri = 0.57)

0: absent

1: present

14. *Male frons vestiture on excavated area* (ci = 0.30; ri = 0.42) (Fig 1.5)

0: glabrous

1: few setae (less than 20); frons clearly visible

2: moderate setae (frons largely covered by setae); surface obscured but visible

3: dense setae; frons surface not visible

15. *Male scape* (ci = 0.80; ri = 0.96)

0: elongate and narrowly rounded distally

1: elongate and narrow

2: elongate and expanded distally

3: short and round

4: elongate and broadly rounded distally

16. *Antennal club setae* (ci = 1.00; ri = 1.00)

0: palmately divided

1: one filament

17. *Female epistoma* (ci = 0.50; ri = 0.50)

0: unarmed

1: median lobe

18. *Female frons* (ci = 0.43; ri = 0.56)

0: flat

1: weakly impressed

2: convex

3: excavated

19. *Armed female frons* (ci = 0.33; ri = 0.0)

0: absent

1: carina

20. *Medial area of female frons* (ci = 0.33; ri = 0.56)

0: flat

1: carina

2: impressed

3: carina and impression

4: groove

21. *Female gena mycangium* (ci = 0.60; ri = 0.91) (Fig 1.6)

0: absent

1: crescent shaped

2: oval shaped

3: triangular shaped

22. *Pars stridens* (ci = 0.14; ri = 0.50)

0: extends to dorsal margin of eye

1: extends to level of scape insertion

### **Pronotum**

23. *Setae on anterior margin of female pronotum between eyes* (ci = 0.25; ri = 0.57)

0: absent

1: scales

2: palmately divided into 3 or 4 filaments

24. *Setae on anterior margin of male pronotum between eyes* (ci = 0.25; ri = 0.70)

0: absent

1: scales

2: single seta

3: bifid/trifid

25. *Male anterior pronotal margin* (ci = 0.75; ri = 0.90) (Fig. 1.7)

0: rounded

1: partially sulcate

2: entirely sulcate

3: transversely impressed

26. *Female anterior pronotal margin* (ci = 1.00; ri = 1.00) (Fig. 1.8)

0: rounded

1: weakly sulcate

2: transversely impressed

27. *Emarginate anterior pronotum* (ci = 0.50; ri = 0.50)

0: straight

1: emarginate

28. *Transverse medial groove on male pronotal base* (ci = 0.50; ri = 0.75)

0: absent

1: present

29. *Male pronotum sculpturing* (ci = 0.67; ri = 0.86)

0: smooth to granulate

1: rugose

2: strigulate

3: aciculate

4: anterior half strigulate, posterior punctate

30. *Lateral margin of pronotum* (ci = 1.00; ri = 1.00) (Fig. 1.9)

0: type A

1: type B

2: type C



3: type D

4: type E

5: type F

6: type G

7: type H

8: type I

31. *Pronotum base* (ci = 0.33; ri = 0.70) (Fig. 1.10)

0: straight

1: recurved

2: bisinuate

3: broadly emarginate along medial half

32. *Pronotum apex* (ci = 0.50; ri = 0.67)

0: narrower than base

1: equal width of base

33. *Pronotum vestiture* (ci = 0.50; ri = 0.47)

0: glabrous

1: anterior and lateral areas

2: anterior margin and angle

3: diagonally extending from anterior margin to median area

4: anterior area

- 5: entire
- 6: anterior third
- 7: anterior margin
- 8: entire except for median section of dorsal area
- 9: margins
- A: lateral margin

### **Abdomen**

#### **34. *Metepisternal setae* (ci = 0.40; ri = 0.79)**

- 0: bifid or trifid
- 1: palmately divided into four or more filaments
- 2: variable (scales, single setae and palmately divided seta)

#### **35. *Metepisternum shape* (ci = 1.00; ri = 1.00) (Fig. 1.11)**

- 0: type A
- 1: type B
- 2: type C
- 3: type D
- 4: type E
- 5: type F
- 6: type G
- 7: type H
- 8: type I

- 9: type J
- A: type K
- B: type L
- C: type M
- D: type N
- E: type O
- F: type P
- G: type Q
- H: type R

36. *Mesosternum shape* (ci = 0.94; ri = 0.93) (Fig. 1.12)

- 0: type A
- 1: type B
- 2: type C
- 3: type D
- 4: type E
- 5: type F
- 6: type G
- 7: type H
- 8: type I
- 9: type J
- A: type K
- B: type L

**C: type M**

**D: type N**

**E: type O**

**F: type P**

**37. *Basal margin of elytra* (ci = 0.27; ri = 0.58) (Fig. 1.13)**

**0: flat**

**1: faint carina**

**2: carina extending to scutellar apex**

**3: crenulations**

**38. *Scutellum shape* (ci = 1.00; ri = 1.00) (Fig. 1.14)**

**0: type A**

**1: type B**

**2: type C**

**3: type D**

**4: type E**

**5: type F**

**6: type G**

**7: type H**

**8: type I**

**9: type J**

**A: type K**

**B: type L**

**C: type M**

**D: type N**

**E: type O**

**F: type P**

**39. *Depressed scutellum* (ci = 0.50; ri = 0.83)**

**0: depressed**

**1: level of elytra**

**40. *Elytral base with a tumescence from seventh to ninth interstriae* (ci = 0.20; ri = 0.56)**

**0: absent**

**1: present**

**41. *Discal interstriae punctures* (ci = 0.10; ri = 0.31)**

**0: normal**

**1: confused**

**42. *Disc sculpturing* (ci = 0.33; ri = 0.63)**

**0: smooth**

**1: rugose**

**2: shallow rugosities**

**3: disc absent**

43. *Discal interstriae 1 and 2 ending in a large spine* (ci = 1.00; ri = 0.0)

0: absent

1: present

44. *Strial punctures* (ci = 0.33; ri = 0.33)

0: larger than interstriae

1: equal to interstriae

2: smaller than interstriae

45. *Carinate costa originating on eighth interstria of male elytra* (ci = 1.00; ri = 1.00)

0: absent

1: present

46. *Carina originating at base of tenth interstria* (ci = 0.50; ri = 0.83)

0: absent

1: shorter than metepisternum

2: longer than metepisternum

3: encompasses elytra

47. *Rugae on interior margin of elytra* (ci = 1.00; ri = 0.00)

0: absent

1: present

48. *Elytra* (ci = 0.50; ri = 0.50)

0: non-metallic

1: metallic

49. *Maximum rows of setae on third discal interstria* (ci = 0.33; ri = 0.65)

0: glabrous

1: one row

2: two rows

3: three rows

4: four rows

50. *Setae of interstriae* (ci = 0.33; ri = 0.63)

0: scales

1: hair-like

2: glabrous

3: scales and hairs

51. *Female strial impression* (ci = 0.20; ri = 0.50)

0: not impressed

1: weakly impressed

2: strongly impressed

52. *Density of elytral setae* (ci = 0.25; ri = 0.61) (Fig. 1.15)

0: glabrous

1: light

2: moderate

3: dense; elytra surface not visible

53. *Elytra vestiture coloration* (ci = 0.50; ri = 0.82)

0: monochrome

1: variegated bicolor

2: vestiture absent

54. *Declivity sculpturing* (ci = 0.33; ri = 0.00)

0: smooth

1: recumbent asperities

55. *Male declivity setae* (ci = 0.29; ri = 0.50)

0: less than 3 times longer than disc

1: greater than 3 times longer than disc

2: absent

56. *Apex of declivital margin* (ci = 1.00; ri = 1.00)

0: smooth

1: serrate



57. *Abdomen profile* (ci = 1.00; ri = 1.00)

0: gradually ascending to elytra

1: abruptly flexed upward at posterior margin of visible segment 2

2: abruptly flexed upward at anterior margin of visible segment 2

58. *Male 2<sup>nd</sup> visible abdominal sternite* (ci = 1.00; ri = 1.00)

0: not different from other sternites

1: convex and protuberant at middle and distally distended (see Fig. 1.66 C)

2: rapidly ascending/vertical

59. *Body coloration pattern (including head and pronotum)* (ci = 0.18; ri = 0.47)

0: monochrome

1: bicolored

2: tricolored

60. *Male stria 1 impression* (ci = 0.25; ri = 0.36)

0: not impressed

1: slightly impressed

2: moderately impressed

3: strongly impressed

## **Male Genitalia**

61. *Apical orifice/ejaculatory canal* (ci = 0.50; ri = 0.67)

0: fleshy pore absent

1: fleshy pore

62. *Sensory claspers* (ci = 0.79; ri = 0.79)

0: scythe shape

1: spatula

2: cactus

3: straight

4: round

5: pointed

6: downward 'V'

7: non-sclerotized

8: flat

9: 'V' shaped

A: tooth

B: square

C: loop

63. *Lateral folds of median lobe* (ci = 0.67; ri = 0.62)

0: folds thick and uniformly arcuate

1: one fold with an apical curved extension that folds under other fold

2: folds almost join on basal third

- 3: forming a broad point on apical third
- 4: thin and arcuate distally on basal half
- 5: folds form an acute point on basal quarter
- 6: narrow, forming a thicker subacute point in middle
- 7: thin and straight
- 8: lateral folds thick nearly touching, broadest and touching on apical third
- 9: broadest and nearly touching on apical third
- A: deep and wrinkled

64. *Apex of median lobe* (ci = 0.31; ri = 0.36)

- 0: flat
- 1: rounded with flat lateral margins
- 2: mushroom shaped
- 3: broadly pointed
- 4: round

65. *Relative length of median strut (length until lateral folds start)* (ci = 0.18; ri = 0.47)

- 0: less than 1/4
- 1: 1/4-1/3
- 2: greater than 1/3

### **Feeding habit**

66. *Feeding habit* (ci = 1.00; ri = 1.00)

0: phloeophagous

1: xylomycetophagous

### **Phylogenetic Analysis**

The phylogeny was reconstructed using the criteria of parsimony implemented in PAUP\* 4.0 b10 PPC (Swofford, 1993). A heuristic search was performed with 1,000 stepwise random additions with tree bisection-reconnection (TBR) for 39 taxa (28 ingroup, 11 outgroup). Characters were equally weighted. Bootstrap values were calculated by performing 1,000 pseudoreplicates with simple additions in PAUP\*. Bremer support values were calculated by creating a constraint tree in TreeRot v.2 (Sorenson, 1999) and analyzed in PAUP\* with a heuristic search using 100 addition-sequence replicates.

### **Species Concept**

Information for 17 of 30 species was restricted to morphological characters. In addition, variation among populations could not be assessed for ten species because they are known from only one locality. Species were defined using the phylogenetic species concept of Wheeler and Platnick (2000) which recognizes species as the smallest aggregation of sexual populations diagnosable by a unique combination of character states. This concept is based on observable (morphological) characters and “is compatible with phylogenetic study because speciation is associated with character transformation” (Wheeler & Platnick, 2000).

## RESULTS

*Camptocerus* was recovered as monophyletic, but is weakly supported with less than 50% bootstrap support and a Bremer support value of 2. Phylogenetic analysis produced 26 most parsimonious trees with a length of 432 steps (Fig. 1.16) and 64 of 66 characters were parsimony informative. There was a moderate amount of homoplasy (CI = 0.488, RI = 0.694) and roughly half the characters were consistent with the cladogram. Moderate support was observed for terminal nodes while most deeper relationships among clades within the genus were poorly supported (Fig. 1.16). Two *Cnemonyx* species, originally described as *Ceratolepsis* (*C. bolivae* (Blackman), and *C. insignis* Wood), formed a clade, and received the strongest support in the phylogeny (99 bootstrap/ 6 Bremer).

## DISCUSSION

Examination of specimens revealed that several characters previously used to delimit *Camptocerus* from *Cnemonyx* are homoplastic (Wood, 1982, 1986, 2007). These characters include a scutellum that is at least 1.5 times wider than long, and suture 1 of antennal club marked internally by a septum. The strength of the *Ceratolepsis* clade and general lack of support for *Cnemonyx* suggest that *Cnemonyx* is in need of revision. *Camptocerus* is comprised of five morphologically distinctive clades (Opacicollis, Auricomus, Latipilis, Aeneipennis, and Costatus).

Members of the “Opacicollis” clade (*Camptocerus annectens*, *C. inoblitus*, *C. major*, *C. opacicollis*, and *C. unicornus* sp. n.) include three former *Loganius* species. All superficially resemble *Cnemomyx* with their small size (2.2 - 3.6 mm), elongate bodies (2.0 - 2.4 times as long as wide) and light brown to black coloration. They are identified by the following characters. Male apical epistomal margin unarmed (large tubercle in *C. unicornus*); basal epistomal margin armed with a strongly developed carina; male frons strongly excavated, ornamented with few erect golden setae lateral to medial line; setae do not form bands (except *C. unicornus*); male antennal scape elongate and narrowly rounded distally. Anterior margin of pronotum rounded in both sexes and the margin between the eyes lined with scales; base weakly bisinuate (broadly emarginate along medial half in *C. unicornus*); lateral margin of pronotum type E (*C. unicornus* type H). Metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Scutellum shape type E (*C. unicornus* type P); elytra base with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than metepisternum (absent in *C. unicornus*); elytra apex serrate. Female frons always flat, often with medial area of frons slightly impressed; unarmed; epistoma weakly impressed; female gena with circular mycangium.

The “Auricomus” clade (*Camptocerus auricomus*, *C. niger*, *C. occidentalis*, *C. orientalis*, and *C. rectus*) is the most distinctive clade in *Camptocerus* with species readily diagnosed by their dense, variegated, spatulate setae or scales on the elytra interstriae, strongly bisinuate pronotum base and by two thick bands of setae on the male frons. Unfortunately, older specimens tend to have abraded vestiture on the elytra and pronotum which makes identification difficult. Males also possess a carina on the basal

epistomal margin; lateral margins of epistoma angled inward; antennal scape elongate and narrowly rounded distally (except elongate and narrow in *C. occidentalis*). They are also diagnosed by the following characters. Anterior margin of pronotum rounded in both sexes and the margin between the eyes lined with scales. Scutellum type C; no carina originating at the base of the tenth interstria; elytral base never with a tumescence from seventh to ninth interstriae; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C. Female frons always flat and unarmed; female gena with triangular mycangium.

The “Latipillis” clade (*Camptocerus charpentierae*, *C. coccoformus* sp. n., *C. dolei* sp. n., *C. igniculus* sp. n., *C. latipilis*, *C. mallopterus* sp. n., and *C. petrovi* sp. n.) contains several closely related and morphologically similar species. All species are stout- 1.6 to 2.0 times as long as wide (except *C. dolei* is elongate 2.1-2.3 times as long as wide) and vary in color from orange to black. They are identified by the following characters. The male apical epistomal margin is armed with a short rectangular carina (short rounded tubercle in *C. dolei*); lateral margin of epistoma with vertical costa; basal epistomal margin tumid at scape insertion; male frons is strongly excavated, with the excavation bordering ocular margin (moderately excavated and excavation not bordering ocular margin in *C. dolei*); ornamented with 2-7 golden setae lateral to medial line; setose lateral edges; frons sparsely to moderately covered by erect setae; male scape elongate and expanded distally. The anterior margin of pronotum rounded in both sexes and the margin between the eyes is glabrous or lined with scales in both sexes; pronotum base recurved; lateral margin type C; smooth to granulate; base weakly recurved (weakly bisinuate in *C. charpentierae*). Scutellum type B (type D in *C. dolei*); elytra base never

with a tumescence from seventh to ninth interstriae; metepisternum type C (type R in *C. dolei*); disc covered with shallow rugosities; mesosternum type E (type D in *C. coccoformus*, *C. mallopterus*); carina originating at base of tenth interstria encompassing elytra; white to yellow scales present on interstria; second visible sternite convex or protuberant at middle, noticeably smaller in female (absent in *C. charpentierae*, *C. doeli* and *C. igniculus*, ). Female frons flat, often with medial area of frons slightly impressed; unarmed; female gena with circular mycangium (triangular in *C. dolei*).

Species of the “Costatus” clade (*Camptocerus costatus*, *C. pilifrons* sp. n., *C. quadridens*, and *C. zucca* sp. n.) share numerous synapomorphies. The clade exhibits remarkable sexual dimorphism of the elytra. Male *C. costatus* and *C. quadridens* possess a carinate costa originating on the eighth interstria. *Camptocerus costatus* also have deeply impressed striae and setae originating from recumbent asperities on the interstriae. *C. quadridens* also has a two spines originating from the first and second discal interstriae that extend over the declivity. These characters are not displayed by females. They are also diagnosed by the following characters. The male apical epistomal margin is unarmed; lateral margin with an arcuate costa pointing inward, entirely lined with setae; basal epistomal margin with a short, rectangular, transverse carina (except *C. zucca*); male frons strongly excavated and covered by long, dense, erect, yellow-white hairs; male scape is elongate and broadly rounded distally. Anterior margin of pronotum rounded with the margin between the eyes in both sexes glabrous; lateral margin type D; pronotum base recurved. Elytra never metallic; scutellum shape type I; basal margin of elytra with a weak carina extending to scutellar apex; elytra base never with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than



metepisternum; declivity intrerstriae setae uniserate; apex of declivity margin smooth.

Female frons always flat and unarmed; short, sparse, setae present only on lateral margin of frons; setae present on epistoma; female gena with circular mycangium.

The “Aeneipennis” clade (*Camptocerus aeneipennis*, *C. angustior*, *C. aterrimus*, *C. distinctus* **sp. n.**, *C. hirtipennis*, *C. mandelshtami*, *C. noel* **sp. n.**, *C. pseudoangustior* **sp. n.**, and *C. suturalis*) is the most speciose clade in the genus. Species are large (3.1 - 7.1mm) and vary in color from metallic bronze, green and blue to black, red and orange. Species possess a sundry of synapomorphies and are identified by the following characters. Male apical epistomal margin unarmed or armed by a medial tubercule; lateral margin of epistoma arcuate costa pointing out (vertical costa in *C. distinctus*); basal epistomal margin armed with a transverse, concave carina (tumid above scape insertion in *C. distinctus*); frons strongly excavated and densely covered with long white to yellow hair-like setae (moderate in *C. distinctus*); male scape elongate and narrow. Pronotum base straight (recurved in *C. distinctus*); lateral margin type B; anterior margin in males partially to entire sulcate (round in *C. distinctus*) and round to partially sulcate in females; margin between the eyes lined with scales or bifid setae in females or with bifid/trifid setae or scales in males (glabrous in both sexes of *C. distinctus*). Elytral base with a tumescence from seventh to ninth interstriae; metepisternum with bifid setae; metepisternum type B; mesosternum type A; scutellum type A (*C. distinctus* type H); elytra metallic (*C. aeneipennis*, *C. angustior*, *C. noel*) or normal; interstriae glabrous (hair-like setae on *C. hirtipennis* and *C. suturalis*); elytra smooth (*C. distinctus* with rugae in the sutural interspace); apex smooth. Female frons always flat; medial area often with an impressed area and with a shallow carina originating on the median line between the

eyes and terminating at the epistoma; ornamented with fewer setae than male; female gena with crescent shaped mycangium (absent in *C. suturalis*).

Several novel characters were used in this study. The presence and type of mycangia, shape of the metepisternum, (including the pleural suture and exposed triangular plate of postepimerum), the lateral margin of the pronotum and process of the mesosternum were informative at the species level. Although, previously noted as a potential reliable character (Hulcr et al., 2007b), this is the first time that presence and type of mycangia have been used for scolytines.

*Camptocerus* mycangia are semi-circular to circular structures on the female gena (nonglandular brush mycangium as in Six, 2003) (Fig 1.6) and enlarged punctures on the female vertex under the anterior margin of the pronotum (nonglandular pit mycangium as in Six, 2003) (Fig. 1. 17). Both structures are present in males, but are greatly reduced in size. Attempts to verify these structures by cross-sectioning of female beetle heads were unsuccessful due the rigidity of the cuticle, despite adherence to softening protocols used for closely related taxa (Livingston & Berryman, 1972). These structures are similar in position to those found on *Scolytus ventralis* (Livingston & Berryman, 1972) and are present on all *Camptocerus* species except *C. suturalis*. Loss of these structures appears associated with its ambrosia fungus-stealing habit, mycoecleptism (Hulcr, 2009.) (Fig.1.18).

There are three types of gena mycangia in *Camptocerus*: crescent shaped (Fig. 1.17 B), oval (Fig. 1.17 C), triangular (Fig. 1.17 D). Crescent-shaped mycangium are found in all species of the Aeneipennis clade, except *C. suturalis*. The mycangium consists of a crescent-shaped groove in the cuticle on the anterior margin the gular

striations extending from the level of the ventral aspect of the mandible to the level of scape insertion. The groove gradually deepens from the anterior margin until it reaches the posterior margin and abruptly ascends. The groove is posterior margin is lined with short, thick setae that cover the groove. This type of mycangium is often obscured by the pronotum and is easily visible when the head either turned or extended. Oval-shaped mycangium are found in all species of the *Opacicollis*, *Latipillis* and *Costatus* clades. The mycangium is an oval-shaped impressed area from the posteroventral margin of the eye and gular striations to a posterior margin lined with dense, short, thick setae. Short setae arise from the eye and gular striation margins and face the center of the impression. Two to three rows of long setae originate in the impression and are directed toward the point where the eye meets the gula striations. In the *Opacicollis* clade, the posterior margin is lined with short, sparse setae. Triangular mycangium are found in all species of the *auricomus* clade and *C. dolei*. The position is identical to that of the oval-shaped mycangium. The gular striation margin and posteroventral margin are lined with four rows of long, thick setae (twice the width of other setae) covering roughly the ventral half of the mycangium. Setae are oriented toward center of the impression. The posteroanterior margin is lined by short, sparse setae. Four rows of long setae originate in the impression and are directed toward the point where the eye meets the gula striations.

The enlarged punctures on the female vertex under the anterior margin of the pronotum are present on all species. Each pit has a short-bristle like seta arising from the posterior margin and pits are 3-5 times the diameter of other punctures and 3-10 times as deep.

Interspecific variation in structures (ex. carinae, tubercles), degree and extent of excavation in the male frons, frons vestiture, elytra vestiture and sculpturing are extremely useful for classification of *Camptocerus*. Characters such as the type of mycangia, shape of the metepisternum, the lateral margin of the pronotum and process of the mesosternum typically diagnose clades within *Camptocerus*.

### Key to the males of the species of *Camptocerus*

This key does not include species solely known from females. If the specimen belongs in the “Opacicollis” clade, examine species diagnoses for *Camptocerus annectens* Wood or *C. major* (Eggers) before making a final determination.

- 1 Metepisternal setae bifid or trifid. ....2
- Metepisternal setae palmately divided into four or more filaments. ....12
  
- 2(1) Elytra metallic or with metallic luster, glabrous. ....3
- Elytra never metallic, may be glabrous or densely covered with setae. ....5
  
- 3(2) Apical epistomal margin armed with a median tubercle; anterior pronotal margin declivous, not sulcate; basal half of pronotum slightly less rugose; pronotal punctures larger, deeper; strial punctures shallow. Elytra metallic bronze. Known from Andes Mountains from Colombia to Bolivia, 1000-3000m; 5.0 – 5.8 mm long. ....*C. angustior* Eggers

- Apical epistomal margin unarmed; anterior pronotal declivity sulcate, especially towards sides.....4
- 4(3) Smaller species; first discal striae weakly impressed; striae punctures deeper, larger; lateral declivities on anterior margin of pronotum extending two-thirds of distance to medial line. Elytra metallic bronze to black with a metallic lustre. Costa Rica to Argentina; 4.4 – 5.9 mm long. ....*C. aeneipennis* (Fabricius)
- Larger species; elytral disk smooth, striae punctures shallow, faint; lateral declivity on the anterior margin of the pronotum extending to median line. Elytra metallic bronze, green or blue. Bolivia and Peru to Colombia and Suriname; 6.0 – 7.1 mm long. ....*C. noel* Smith & Cognato, sp. n.
- 5(2) Elytra glabrous, smooth, shining (some setae may be present laterally); finely sculptured, median tubercle on apical epistomal margin.....6
- Elytra with setae present at least on interstriae. ....8
- 6(5) Body black. .... 7
- Pronotum bicolored (posterior fifth to two-fifth's orange, remainder black), profemur and protibia red orange, remaining legs black; thorax, abdomen and elytra black. Peru and Ecuador; 5.9 – 6.5 mm long..... *C. mandelshtami* Petrov
- 7(6) Smaller size; anterior pronotal declivity weakly sulcate. Peru to French Guiana; 3.1 – 4.5 mm long. ....*C. aterrimus* Eggers

- Larger size; anterior pronotal declivity entirely sulcate. Brazil, Peru and Ecuador; 4.5 – 5.4 mm long. ....*C. pseudoangustior* Smith & Cognato, sp. n.
  
- 8(5) Pronotum base recurved; elytra base with a carina extending to scutellar apex. ....9
- Pronotum base straight; elytra base flat or with a faint carina. ....10
  
- 9(8) Short transverse carina at basal epistomal margin. Each elytron with two discal spines arising from the first to fifth striae, with a sharp spine on the first striae and a blunt spine on the second extending over the declivity, and the declivity originating in the recess formed by the spines. Color red brown. Panama; 3.4 – 3.7 mm long. ....*Camptocerus quadridens* Blackman
- No carina on the basal epistomal margin. Distinct orange and black color pattern, pronotum orange with a black mid-dorsal triangle extending from the apex to the basal third of the pronotum; elytra black with each elytron with an orange oval spot encompassing the area from the basal margin of the disk and to the basal fifth of the elytra and from the sutural interspace to the eighth interstriae; ventral surface of thorax and abdomen black. Ecuador; 4.0 – 4.1 mm long. ....  
.....*Camptocerus zucca* Smith & Cognato, sp. n.
  
- 10(8) Elytra black each elytron with eight rugae on the discal sutural interspace to second interstria, each rugae with a single setae arising from the center. A large median tubercle is present on the apical epistomal margin; vertical carinae on the

- lateral margin of the epistoma; basal epistomal margin tumid above scape  
insertion. Ecuador; 5.3 mm long. ....  
.....*Camptocerus distinctus* Smith & Cognato, sp. n.
- Elytra never with rugae, finely sculptured; long yellow, recumbent setae present  
on both striae and interstriae (often abraded in older specimens). .....11
- 11(10) Larger size; elytra solid black, elytra densely covered with recumbent setae,  
surface barely visible. anterior pronotal declivity densely covered with long  
yellow recumbent setae; anterior margin between eyes lined with bifid setae;  
rugose basal medial area of pronotum; vestiture emarginate at median line; setae  
diagonally extend along the lateral margin from the anterolateral margin. Brazil,  
Ecuador; 4.9 – 5.6 mm long. ....*Camptocerus hirtipennis* Schedl
- Smaller size; head, antennae, thorax, pronotum, legs red-orange to red, abdomen  
black; elytra covered with fewer setae, surface largely visible; anterior pronotum  
margin between eyes lined with setae palmately divided into 3-4 filaments; black  
elytron each with an orange oval spot extending from the lateral margin of the  
elytral interspace to the tenth interstria and from the basal fifth of elytra to the of  
apical four-fifths. Peru, Brazil and the Guianas; 3.6 – 5.0 mm long.  
.....*Camptocerus suturalis* (Fabricius)
- 12(1) Frontal setae in two dense, distinct longitudinal bands near middle of frons,  
sometimes merging distally. Basal setae long, and recumbent over anterior setae.  
.....13

- Frontal setae never in two bands, glabrous, with sparse setae or setae denser or longer towards the sides of frons. ....18
  
- 13(12) Apical epistoma with a median tubercle.....14
- Apical epistoma unarmed, with or without trace of carina on basal epistomal margin. ....15
  
- 14(13) Larger size, body stout. Frontal setae in two thick bands which lie flat against the frons. Apical epistomal tubercle small, rounded; carina on basal epistomal margin weakly developed; pronotum base bisinuate. Elytra covered in variegated spatulate setae (often abraded in older specimens). Mexico to Venezuela and Trinidad; 3.5 – 4.1 mm long.....*Camptocerus auricomus* Blandford
  
- Smaller size, body elongate. Frontal setae in two thin bands arcuate above the frons and combine on the median line between the eyes. Apical epistomal tubercle large and broad, carina on basal epistomal margin strongly developed and connecting medially with tubercule; pronotum base broadly emarginate along medial half. Elytra covered in spatulate setae. Brazil; 2.5 mm long. ....  
.....*Camptocerus unicornus* Smith & Cognato, sp. n.
  
- 15(13) Transverse carina on basal epistoma margin faint or obsolete. Pronotum base bisinuate. Elytra covered in variegated spatulate setae (often abraded in older specimens). Bolivia and Brazil to Colombia and the Guianas; 2.8 – 4.1 mm long.



- .....*Camptocerus niger* (Fabricius)
- Transverse carina on basal epistomal margin moderately to strongly developed.  
.....16
- 16(15) Carina on basal epistomal margin arcuate, height uniform. Elytra covered in variegated spatulate setae (often abraded in older specimens). Brazil and Peru; 3.2 – 3.7 mm long. ....*Camptocerus orientalis* Eggers
- Carina on basal epistomal margin straight, height not uniform. ....17
- 17(16) Basal epistomal carina highest at middle, nearly tuberculate. Elytra covered in small, stout variegated spatulate setae (often abraded in older specimens). Striae distinct, black, interstriae reddish. Ecuador to Venezuela; 3.5 – 4.3 mm long.  
.....*Camptocerus rectus* Wood
- Carina on basal epistomal margin straight, highest above antennal insertion, lowest at middle. Elytra black covered in yellow elongate spatulate setae (often abraded in older specimens). Striae obscured. Bolivia and Peru; 4.0 – 4.5 mm long. ....*Camptocerus occidentalis* Eggers
- 18(12) Basal epistomal margin armed by either a complete transverse or short rectangular carina; apical epistomal margin unarmed; scape elongate and rounded distally.....19

- Basal epistomal margin unarmed without complete carina or short rectangular carina; apical epistomal margin with a medial rectangular carina or unarmed; scape elongate and expanded distally. ....22
  
- 19(18) Basal epistomal margin armed by an arcuate transverse carina; pronotum base straight to weakly bisinuate; elytral smooth at base around scutellum. ....20
- Basal epistomal margin armed by a short rectangular carina; pronotum base recurved; elytra with subbasal transverse carina extending to scutellar apex and transverse rugosities around scutellum .....21
  
- 20(19) Uniserate narrow scales on the elytra interstriae, minute hairs on striae. Strial and interstitial punctures equal size. Argentina and Bolivia to Ecuador to Costa Rica; 2.2 – 3.6 mm long. ....*Camptocerus opacicollis* (Eggers)
- Very fine and minute hairs on both striae and interstriae. Strial punctures 2-3 times larger than interstriae. Argentina and Brazil; 2.4 – 3.4 mm long. ....*Camptocerus inoblitus* (Schedl)
  
- 21(19) Elytral declivity strongly impressed below level of disk, occupying apical 4/5 of elytra; carinate costa on eighth interstriae from basal fifth and extending around apex to sutural margin; striae moderately impressed; and bristling brown setae originating from recumbent asperities on the interstriae. Peru and Ecuador to Brazil, Guyana and Trinidad; 3.5 – 3.9 mm long. ....*Camptocerus costatus* Chapuis

- Elytral declivity and striae unimpressed; carinate costa on the eighth interstria absent; elytra smooth with short scales on interstriae. Ecuador; 2.6 – 3.1 mm long.  
.....*Camptocerus pilifrons* Smith & Cognato, sp. n.

22(18) Second visible abdominal sternite convex and distally distended or protuberant at middle (Fig. 1.66 C).....23

- Second visible abdominal sternite not as above. ....26

23(22) Elytra densely covered in pale recumbent scales, surface largely covered. Head and pronotum orange, elytra and abdomen black. Ecuador; 3.8 – 3.9 mm long.  
.....*Camptocerus mallopterus* Smith & Cognato, sp. n.

- Elytra interstriae with small colorless scales, elytra surface clearly visible. ....24

24(23) Lateral margin of epistoma with tuft of setae on apical third; head dark red, nearly black, pronotum dark red; abdomen and elytra black. Second visible abdominal sternite less strongly convex, scarcely protuberant below level of visible sternite 1. Brazil and Ecuador; 2.7 mm long. ....

.....*Camptocerus coccoformus* Smith & Cognato, sp. n.

- Lateral margin of epistoma with tuft of setae on apical half; black. ....25

25 (24) Smaller species; frontal excavation devoid of setae; 10-12 setae on lateral and

- dorsal margins combined. Second visible abdominal sternite strongly convex and protuberant, height of declivity behind much less than length of sternite 3. Brazil and Ecuador. 2.7 – 3.3 mm long. ....*Camptocerus latipilis* Schedl
- Larger species; frontal excavation with 1-2 setae lateral to median line, 15-20 setae on lateral and dorsal margins combined. Second visible abdominal sternite strongly convex and protuberant, height of declivity behind greater than length of sternite 3. Ecuador; 4.0 mm long. *Camptocerus petrovi* Smith & Cognato, sp. n.
- 26(22) Male frons with 6-7 golden setae lateral to medial line; frontal excavation does not touch ocular margin; elytra base black with an orange patch an orange patch covering basal third of elytra from the suture to eighth interstriae. Ecuador; 3.1 – 3.5 mm long. ....*Camptocerus dolei* Smith & Cognato, sp. n.
- Male frons with 2-3 golden setae lateral to medial line; frontal excavation borders ocular margin; elytra color uniform. ....27
- 27(26) Larger species. Pronotum red or black; elytra black. Elytral interstitial scales semirecumbent, shorter, sparse and pale. Brazil to French Guiana; 3.8 – 4.5 mm long. ....*Camptocerus charpentierae* Schedl
- Smaller species. Body uniformly red. Longer semi-recumbent, overlapping golden scales on the elytral interstriae. Brazil; 2.5 – 2.8 mm long. ....*Camptocerus igniculus* Smith & Cognato, sp. n.

## Taxonomy

### Genus *Camptocerus* Dejean

*Camptocerus* Dejean 1821: 100. Type species: *Hylesinus aeneipennis* Fabricius.

**Diagnosis.** *Camptocerus* is distinguished from other Scolytini genera by the large, circular mycangia present on the female gena (present in all species except *C. suturalis* (Fabricius), xylomycetophagy, gradually ascending abdominal profile, the scutellum flush with the elytral surface, the more strongly excavated male frons, with the excavation bordering ocular margin (except *C. dolei*), and from the epistoma to just below the vertex, the male antennal funicle segments 2-7 ornamented with long setae which forms the appearance of a brush dense brush on the distal edge 1 to 2 times the length of funicle, the absence of crenulations on the elytral base, generally larger body size (2.2 – 7.1 mm long), female frons flat, never convex, and by the lack of supplemental denticles acutely margining the on apical anterior edge of the meso- and metathoracic tibiae.

#### “Opacicollis” Clade

*Camptocerus annectens* Wood

(Figs. 1.23, 1.24)

*Camptocerus annectens* Wood, 2007: 210. Holotype, ♀, BRAZIL: *Serra de Baturite*: Ceara, (*L. Gounelle*); Strohmeyer Collection (DEI).

**Diagnosis.** This species is identified by the strigulate anterior third of the pronotum, basal two thirds shining, punctures small; elytra declivity interstriae with uniseriate stout scales, interstriae punctures as large as striae, and interstriae punctures with their bases weakly to moderately elevated.

**Description.** Male unknown. Female 3.5 mm long ( $\bar{x}$  = 3.5 mm; n = 1); 2.2 times as long as wide. Head, antennae, thorax, abdomen, elytra, black; legs dark brown.

Female epistoma impressed, 2-5 rows of setae lateral to the median line (mostly abraded); frons flat, medial area of frons slightly impressed; frons and epistoma shagreen, punctures large, deep spaced by 1-3 diameters of a puncture; frons and epistoma unarmed; frons glabrous; gena with circular mycangium. Antennal scape elongate and narrowly rounded distally; antennal funicle segments 5-7 with setae on dorsal margin less than length of four funicular segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; apical third strigulate; posterior two-thirds smooth, shining. Pronotum minutely punctate, punctures shallow; stout setae present on apical fourth (mostly abraded); base weakly bisinuate; lateral margin of pronotum type E.

Scutellum shape type E; elytra base with a tumescence from seventh to ninth interstriae; elytra declivity interstriae with uniseriate stout yellow-brown scales (mostly abraded); interstriae punctures as large as striae, and interstriae punctures with their bases weakly to moderately elevated; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Apex serrate.

**Specimens examined.** (0♂, 1♀)

*Type material:* Holotype *Camptocerus annectens*, ♀ (DEI).

**Distribution.** Brazil (Ceara).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus inoblitus* (Schedl)

(Figs. 1.44, 1.45)

*Camptocerus inoblitus* (Schedl) 1939: 722 (*Loganius*). Holotype ♂: Brazil: Santa Catharina; viii.1940, F. Plaumann, Schedl Collection (NHMW).

*Camptocerus morio* (Schedl) 1952: 348 (*Loganius*). Holotype ♂: Brazil: Santa Catharina; Schedl Collection (NHMW). **syn. n.**

**Diagnosis.** This species is diagnosed by the brown color and short, very fine hair-like setae on both striae and interstriae.

**Description.** Male 2.4 – 3.4 mm long ( $\bar{x}$  = 3.1 mm; n = 20); 2.1 – 2.4 times as long as wide. Head, antennae, thorax, abdomen, elytra and legs light to dark brown.

Apical epistomal margin unarmed; epistoma impressed; lateral margin with a vertical sub-acute carina; tufts of 3-4 rows of setae along lateral margin; basal epistomal margin armed with a strongly developed sub-acute arcuate carina; epistoma expanded to greater than quarter length of head; male frons strongly excavated, excavation borders the ocular margin; frons ornamented with 3-4 rows of erect pale setae lateral to medial line; shagreen; scape elongate and narrowly rounded distally; scape with setae on distal third; setae half length of scape; funicular segments 2-7 lined with brushes of setae the length of scape; segments 1-7 with setae on dorsal margin less than length of four segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; anterior third strigulate; smooth, shining. Pronotum minutely punctate, punctures

shallow; stout setae present on apical fourth; base weakly bisinuate; lateral margin of pronotum type E.

Scutellum shape type E; elytra base with a tumescence from seventh to ninth interstriae; elytra interstriae with uniseriate minute pale hairs; striae punctures 2-3 times larger than interstriae; striae punctures 2-3 times deeper than striae; striae with uniseriate rows of minute pale hairs; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Apex serrate.

Female similar to male except epistoma less impressed, three rows of setae lateral to the median line; frons flat, medial area of frons slightly impressed; frons with three rows of setae on lateral margin; frons and epistoma shagreen, punctures small; frons and epistoma unarmed; frons glabrous; antennal funicle segments 5-7 with setae on dorsal margin and 3-7 with setae on ventral margins less than length of five funicular segments; gena with circular mycangium.

**Specimens examined.** (21♂, 33♀)

*Type Material.* Holotype, *Camptocerus inoblitus*, ♂ (NHMW); Allotype *Camptocerus inoblitus*, ♀ (NHMW); Holotype *Camptocerus morio*, ♂ (NHMW).

*Other material.* **BRAZIL:** *Santa Catharina:* Nova Teutonia, [27°11'S, 52°23'W (on most labels)], 300-500 ft, viii.1940, (*F. Plaumann*), 6♂, 5♀ (FMNH); xi.1940, 3♂ (FMNH); 1949, 4♂ (FMNH); ex. Sapindaceae sp. 88, 14.x.1949, 2♀ (FMNH); 4.ii.1950, 3♂, 8♀ (FMNH); ex. 'trockenes Reisig' [= dry brushwood], 7.ii.1950, 3♀ (FMNH); 1.iii.1950, 1♂, 5♀ (FMNH); ex. 'trockenes Reisig' [= dry brushwood], 10.ii.1950, 2♀ (FMNH); 7.iii.1950, 2♂, 7♀ (FMNH).



**Distribution.** Argentina (Misiones), Brazil (Santa Catharina).

**Hosts.** *Myrocarpus frondosus* Fr. Allem, Sapindaceae sp.

**Biology.** Unknown.

*Camptocerus major* (Eggers)

(Figs. 1.49, 1.50)

*Camptocerus major* (Eggers), 1929: 60 (*Loganius*). Holotype ♀: Peru: [Junín]

Chanchamajo; Eggers Collection (NHMW).

**Diagnosis.** The female is diagnosed by the strigulate apical third of pronotum and punctate posterior; short, fine setae on the declivity interstriae and shorter, thinner setae on the striae.

**Description.** Male unknown. Female 3.4 mm long ( $\bar{x} = 3.4$  mm; n = 1); 2.3 times as long as wide. Head, antennae, thorax, abdomen, elytra and legs dark brown, nearly black.

Female epistoma impressed, 4-5 rows of setae; frons flat, medial area of frons slightly impressed; frons with 4-5 rows of setae lateral to median lines; frons and epistoma shagreen, punctures on lateral margins larger, deeper; spaced by 1-3 diameters of a puncture; frons and epistoma unarmed; frons glabrous; gena with circular mycangium. Antennal scape elongate and narrowly rounded distally; antennal funicle segments 5-7 with setae on dorsal margin and 3-7 with setae on ventral margins less than length of five funicular segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; apical third strigulate; posterior two-thirds smooth, shining. Pronotum minutely punctate,

punctures shallow; stout setae present on apical fourth; base weakly bisinuate; lateral margin of pronotum type E.

Scutellum shape type E; elytra base with a tumescence from seventh to ninth interstriae; elytra smooth; elytra interstriae with uniseriate minute pale setae; interstriae punctures smaller than striae; striae punctures 2-3 times deeper than striae; striae with uniseriate rows of minute hairs; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Apex serrate.

**Specimens examined.** (0♂, 1♀)

*Type Material.* Holotype *Loganius major*, ♀ (NHMW).

**Distribution.** Brazil, Peru (Huanuco, Junín).

**Hosts.** Unknown liana.

**Biology.** Unknown.

*Camptocerus opacicollis* (Eggers)

(Figs. 1.61, 1.62)

*Camptocerus opacicollis* (Eggers), 1929: 61 (*Loganius*). Holotype ♂: Bolivia: [Cercado], Cochabamba; Eggers Collection (NHMW).

*Camptocerus aquilus* Wood 1972: 244. Holotype ♂: Brazil: Goiás [=Goiás]: near Aldeia Caraya, on or near the Rio Araguaia: 12°49'S 51°46'W; (BMNH).

Synonymy: Wood 1985: 266.

*Camptocerus infidelis* Wood, 1969: 11. Holotype ♀: Costa Rica: Peralta: Cartago, 1500 ft, 10.iii.1964, S.L. Wood, unknown vine; NMNH. **syn. n.**

*Camptocerus uniseriatus* Schedl, 1972: 54. Holotype ♂: Brazil: Guanabara [=Rio de Janeiro], Corcovado, x.1969, Alvarenga & Seabra (NHMW). **syn. n.**

**Diagnosis.** Both sexes are diagnosed by the larger, deeper punctures on the pronotum, and uniseriate narrow scales on the elytra interstriae.

**Description.** Male 2.2 – 3.6 mm long ( $\bar{x}$  = 2.9 mm; n = 17); 2.0 – 2.4 times as long as wide. Head, antennae, thorax, and elytra dark brown to black. Gena, abdomen and legs light to dark brown.

Apical epistomal margin unarmed; epistoma impressed; lateral margin with a vertical sub-acute carina; 4-5 rows of setae lateral to median line; basal epistomal margin armed with a strongly developed sub-acute arcuate carina; epistoma expanded to greater than quarter length of head; male frons strongly excavated, excavation borders the ocular margin; frons ornamented with 5-6 rows of erect pale setae lateral to medial line; shagreen; scape elongate and narrowly rounded distally; scape with setae on distal two-thirds; setae length of scape; funicular segments 2-7 lined with brushes of setae 1.5 times the length of scape; segments 1-7 with setae on dorsal margin less than length of six segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; anterior third strigulate; smooth, shining. Pronotum densely punctate, punctures shallow; stout setae present on apical fourth; base weakly bisinuate; lateral margin of pronotum type E.

Elytra smooth; scutellum shape type E; elytra base with a tumescence from seventh to ninth interstriae; each strial puncture with a hair-like seta arising from basal margin, covering puncture; interstriae punctures equal size of striae; as deep as striae;

interstriae with uniseriate rows of narrow scales; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Apex serrate.

Female similar to male except epistoma less impressed, three rows of setae lateral to the median line; frons flat, medial area of frons slightly impressed; frons with four rows of setae on lateral margin; frons and epistoma shagreen, punctures small; frons and epistoma unarmed; frons glabrous; antennal funicle segments 4-7 with setae on dorsal margins and segments 5-7 with setae on ventral margins less than length of four funicular segments; gena with circular mycangium.

**Specimens examined.** (33♂, 46♀)

*Type Material.* Holotype *Camptocerus opacicollis*, ♂ (NHMW). Allotype *Camptocerus opacicollis*, ♀ (NHMW) **BOLIVIA:** Cochabamba, (Germain), 1907, (*H. Donckier*).

Holotype *Camptocerus aquilus* ♂ (BMNH). Paratypes *Camptocerus aquilus* **BRAZIL:** [Mato Grosso]: 12° 31'S, 51° 46'W, RS-RGS, 12-18.xi.1968, (*R.A. Beaver*), 1♂, 1♀ (NMNH); Holotype *Camptocerus uniseriatus*, ♂ (NHMW). **COSTA RICA:** Holotype *Camptocerus infidelis*, ♀ (NMNH); Paratype *Camptocerus infidelis* Peralta: Cartago, 1500 ft, ex. unknown vine 10.iii.1964, (*S.L. Wood*), ♀ (NMNH).

Holotype *Camptocerus uniseriatus*, ♂ (NHMW).

*Other material.* **BRAZIL:** Amazonas: 69 km N Manaus, (*G. Stevens*), 7.xii.1979, 3♂, 3♀ (NMNH); Goyas [=Goiás]: Jatahy, ix-xi.1897, 4♀ (DEI); **ECUADOR:** Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 610, 1♀ (NMNH); Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot

2034, 1 ♀ (NMNH); lot 2053, 1 ♂ (NMNH). **PERU:** *Madre de Dios*: Los Amigos Biological Station, -12.56916, -70.100114, 250 m, ex. *Protium amazonicum*, 17-25.v.2008, (*Smith, Hulcr*), 7 ♂; 6 ♀ (MSUC); 26-27.v.2008, 19 ♂; 26 ♀ (MSUC); Tampopata, 15 km NE Puerto Maldonado, Maldonado Reserva Cuzco Amazonico, 12°33'S 69°03'W, 200 m, ex. flight intercept trap, 15.vi.1989, (*J. S. Ashe, A. Leschen*), 1 ♀, (SMEC).

**Distribution.** Argentina, Bolivia (Cercado), Brazil (Amazonas, Goiás, Mato Grosso, Rio de Janeiro), Costa Rica, Ecuador (Napo), Peru (Madre de Dios).

**Hosts.** *Hirtella* sp., *Protium* sp. (“Almesca branca” [Brazil], “Almesca vermelha” [Brazil], “Breu branco” [Brazil]) (Beaver, 1972). *Protium amazonicum* Swart. Unknown 1 cm diameter tree sapling (Wood, 1969)

**Biology.** Beaver (1972) provides a detailed account of life history information for *C. aquilus* and Wood (1969) describes the gallery of *C. infidelis*, both are synonyms for *C. opacicollis*.

*Camptocerus unicornus* Smith & Cognato, sp. n.

(Figs. 1.78, 1.79)

**Type Material.** Holotype, ♂, **BRAZIL:** ‘Estado Amazonas’ 010BR Chplac, km 31, 18.vi.1976, (*E. Rufino*) (NMNH).

**Diagnosis.** The male is diagnosed by the large and broad tubercle on the distal epistomal margin medially connecting with carina on basal epistomal margin, two narrow bands of long yellow setae arising above the dorsolateral margin of the eyes which curve above the

frons and combine on the median line between the eyes; pronotum base broadly emarginate along medial half and uni- and diseriatae spatulate setae on interstriae.

**Description.** Male 2.5 mm long ( $\bar{x} = 2.5$  mm;  $n = 1$ ); 2.1 times as long as wide. Head, antennae, thorax, legs, abdomen and elytra light to dark red brown.

Apical epistoma with a large and broad medial tubercle; lateral epistoma margin with a faint costa angled inward; epistoma with six diagonal rows of setae from proximal epistomal margin to tubercle; proximal epistomal margin armed with a strongly developed carina connecting medially with epistomal tubercle; epistoma weakly excavated; frons strongly excavated, two narrow bands of long yellow setae arise above the dorsolateral margin of the eyes and curve above the frons and combine on the median line between the eyes; frons ornamented with 7-8 rows of small and fine and long thick erect golden setae lateral to medial line; scape elongate and narrowly rounded distally; scape with setae on distal third; setae less than half length of scape; funicular segments 2-7 lined with brushes of setae 1.5 times the length of scape; segment 7 with setae on dorsal margin less than length of two segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; surface minutely, densely punctate; punctures shallow; stout setae present on apical fourth; lateral margin of pronotum type H; base broadly emarginated along medial half.

Scutellum shape type P; interstriae densely covered with uni- and diseriatae spatulate setae; each setae arising from granules on interstria; each stria puncture with a hair-like seta arising from basal margin, covering puncture; elytra base with a tumescence from seventh to ninth interstriae; carina absent at base of tenth interstria shorter than

metepisternum; metepisternum shape type D; metepisternum setae palmately divided into four or more filaments. Apex serrate.

Female unknown.

**Etymology.** *Uni-* (L) = one, *-cornus* (L) = horn. In reference to the large tubercle on the distal epistomal margin.

**Specimens examined.** (1♂, 0♀)

**Distribution.** Brazil (Amazonas)

**Hosts.** Unknown.

**Biology.** Unknown.

#### **“Auricomus” Clade**

The “Auricomus” Clade is the most distinctive clade in *Camptocerus* with species readily diagnosed by their distinctive dense, variegated, spatulate setae or scales on the elytra interstriae, strongly bisinuate pronotum base and by two thick bands of setae on the male frons; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum type G; mesosternum type C.

#### *Camptocerus auricomus* Blandford

(Figs. 1.27, 1.28)

*Camptocerus auricomus* Blandford, 1896: 125. Type locality: Panama: Chiriqui, V. de Chiriqui, below 40000 ft. Champion; Lectotype ♂ (here designated). (BMNH).

*Camptocerus striatulus* Hagedorn, 1903: 547, Type locality: French Guiana: Camopi, 1900, F. Geay; MNHN. Holotype ♀, MNHN. **syn. n.**

**Diagnosis.** The male is diagnosed by its median small rounded tubercle on the apical epistomal margin, an sub-acute recurved carina on the basal epistomal margin, frons strongly excavated with dorsal-lateral margin of the eye on excavated area of the frons, the rounded margins of the frons excavation, two thick bands of setae on the male frons, elytra interstriae covered in 2 to 3 rows of variegated uniseriate scales, and thinner and pointed setae on apical quarter.

Female is distinguished from *C. niger* by and hair-like setae on apical quarter of declivity and from *C. orientalis* by the presence of a circular, weakly impressed region between upper level of eyes.

**Description.** Male 3.5 – 4.1 mm long ( $\bar{x}$  = 3.9 mm; n = 20); 1.8 – 2.0 times as long as wide. Color uniform; head, thorax, abdomen, elytra, antennae and legs light orange to black. Elytra interstriae covered in tan scales with dark brown scales often forming a 'X' shape. Occasionally the sides of the 'X' are filled with brown scales forming a triangle on each elytron.

Apical epistomal margin with a small rounded tubercle; lateral margins of epistoma angled inward, lined with a single row of setae; a sub-acute, transverse recurved carina on the basal epistomal margin; epistoma weakly excavated, expanded to less than quarter length of head; ventral margin of frons elevated above epistoma; frons strongly excavated with dorsolateral margin of the eyes on frons excavation, lateral and dorsal margins are rounded; frons densely covered with two thick bands of long yellow-brown setae, clearly divided between the median line with lateral fifths of frons and medial fifth glabrous; single row of setae lining lateral margins; frons surface shagreen; antennal scape elongate and narrowly rounded distally; scape with a lateral row of setae on ventral



margin, setae less than half length of scape; funicular segments 2-7 lined with brushes of setae 1.5 times the length of scape; segments 5-7 with setae on dorsal margin less than length of four segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; medial area of anterior third of pronotum covered with long bristles on the anterolateral areas; base and disc covered with fine, short hair-like setae; short bristles form two to three rows above lateral carinae; pronotum strigulate on apical third and punctate basally; punctures and vestiture on median line; densely and minutely punctured; punctures deep; carina on lateral margin type F; base strongly bisinuate.

Declivity occupying apical half of elytra; each interstria densely covered with three rows of semi-erect spatulate setae on disc, and two rows on declivity; scales transition to uniseriate thinner and pointed setae on apical quarter; interstriae three times width of striae; interstriae punctures strongly confused; striae weakly impressed; each puncture with a hair-like seta arising from basal margin, covering puncture; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C; apex smooth.

Female similar to male except epistoma less impressed and unarmed; epistoma covered by five rows of setae; frons flat, with a circular, weakly impressed region between upper level of eyes; surface shagreen; 3-4 rows of setae lateral to median line; antennal funicle segments scattered with setae less than length of six funicular segments; gena with triangular mycangium; anterior third of pronotum covered with long, dense

hair-like setae on anterolateral areas; long bristles absent; base and disc covered with fine, short hair-like setae.

**Specimens examined.** (37♂, 27♀)

*Type Material.* Paralectotypes *Camptocerus auricomus* 2♂ 1♀ Panama: Chiriqui, V. de Chiriqui, below 40000 ft. (*Champion*) (BMNH). Paralectotypes here designated.

*Holotype* *Camptocerus striatulus*, ♀ (MNHN).

*Other material.* **COSTA RICA:** *Limon:* Reventazon ebene, Hamburgfarm, 24.ii.1937, (*F. Nevermann*), 3♂ (DEI); *Peralta:* Cartago, 500 m, 4" limb, 10.iii.1964, (*S.L. Wood*), 5♂, 5♀ (MSUC); *Puntatenas:* Gromaco, Rio Colo Brus, 1 quarter" trail cutting, 23.vii.1963, (*S.L. Wood*), 1♂, 1♀ (MSUC); *No specific locality:* 'Rio Damites', 200m, 18.ii.1964, (*S.L. Wood*) 1♂, 1♀ (MSUC). **GUATEMALA:** *Petén:* Tikal, 100m, at light at camp, 10.iv.1956, (*T.H. Hubbell, I.J. Cantrall*), 1♂ (UMMZ). **MEXICO:** *Veracruz:* Uxpanapa (Hidalgotitlan), 27.iv.1982, ex. *Protium copalifera* [likely *Protium copal*], (*T.H. Atkinson*), 1♂, 1♀ (CAS). **PANAMA:** *Canal Zone:* Barro Colorado Island, ex. trap, 17.ii.1978, (*Henk Wolda*), 1♂ (STRI); Madden Forest, 3" limb, 2.i.1964, (*S.L. Wood*) 1♂, 1♀ (MSUC); *Chiriqui,* V. de Chiriqui, below 40000 ft. *Champion* 3♂ (BMNH); *Panama,* Parque Nacional Soberanía, Pipeline Rd, 9.166667, -79.75, 95 m, 3.ix.2008, (*S.M. Smith, A.D. Smith, A.R. Gillogly*), 5♂, 5♀ (MSUC), 5♂, 5♀ (STRI). **VENEZUELA:** *Mérida:* 20 km SW Vigía, 50 m, ex. limb, 21.xi.1970, (*S.L. Wood*), 7♂, 6♀ (MSUC).

**Discussion.** *C. striatulus* is recognized as a synonym of *C. auricomus* due to the presence of thinner and pointed setae on apical third of declivity.

**Distribution.** Costa Rica, French Guiana, Guatemala, Mexico (Veracruz), Nicaragua, Panama, Trinidad, Venezuela (Mérida).

**Hosts.** *Protium copal* (Schltdl. & Cham.) Engl., *Cedrela* sp., *Protium* sp., *Protium glabrum* (Rose) Engl., *Protium panamense* (Rose) I.M. Johnst., *Rheedia edulis* [= *Garcinia intermedia* (Pittier), Hammel].

**Biology.** Atkinson & Equihua Martinez (1986) provide a detailed account of host use and gallery description. *C. auricomus* excavate a short circumferential gallery below the bark on both sides of the entrance tunnel. Males use these galleries and the entrance tunnel to turn around without leaving the gallery (Smith, per. ob.).

*Camptocerus niger* (Fabricius)

(Figs. 1.55, 1.56)

*Camptocerus niger* (Fabricius) 1801: 393 (*Hylesinus*). Lectotype ♂: Essequibo [River] [=Guyana] (UZMC). Lectotype designated Wood 1982: 415.

*Camptocerus squammiger* Chapuis, 1869: 259. Lectotype ♂: Cayenne [French Guiana] (IRSNB). Lectotype here designated. Synonymy: Eggers 1934: 27.

*Camptocerus tectus* Eggers 1943:245. Holotype ♂: Brazil: Pernambuco: Sarra da Bernada, 5.vi.1894, Duhant; Strohmeyer Collection, DEI. **syn. n.**

**Diagnosis.** This species is distinguished by unarmed apical epistomal margin, faintly impressed epistoma, nearly indistinct recurved carina on the basal epistomal margin and by two thick bands of setae on the male frons.

The female is distinguished from *C. auricomus* by the absence of hair-like setae on declivital interstriae and from *C. orientalis* by frons with a circular, weakly impressed region between upper level of eyes.

**Description.** Male 2.8 – 4.1 mm long ( $\bar{x}$  = 3.5 mm; n = 19); 1.8 – 2.1 times as long as wide. Color uniform, head, thorax, abdomen, elytra, antennae and legs light orange to dark brown. Elytra interstriae covered in tan scales with dark brown scales creating a variable pattern, often forming an 'X' shape. Occasionally the sides of the 'X' are filled with brown scales forming a triangle on each elytron.

Apical epistomal margin unarmed; lateral margins of epistoma angled inward, lined with a single row of setae; a weakly developed (nearly indistinct) sub-acute recurved carina on the basal epistomal margin; epistoma faintly excavated; expanded to less than quarter length of head; ventral margin of frons elevated above epistoma; frons strongly excavated with dorsal-lateral margin of the eye lies on excavated area of the frons; lateral and dorsal margins are rounded; densely covered with two thick bands of long yellow setae; setae are clearly divided between the median line; setae touch proximal epistomal margin; lateral fifths of frons glabrous; single row of setae lining lateral margins; frons surface shagreen; antennal scape elongate and narrowly rounded distally; scape with a row of setae on ventral margin; ventral margin of funicle segments 2-7 lined with brushes of setae 1.5 times the length of scape; dorsal margin with setae less than four funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; medial area of anterior third of pronotum covered with long bristles on the anterolateral areas; base and disc covered with fine, short hair-like setae short bristles form two rows above

lateral carinae; antennal funicle segments scattered with setae less than length of six funicular segments; pronotum strigulate on apical third and punctate basally; punctures and vestiture on median line; densely and minutely punctured; punctures deep; carina on lateral margin type F; base strongly bisinuate.

Declivity occupying apical half of elytra; each interstria densely covered with three rows of semi-erect spatulate setae on disc, and one to two rows on declivity; interstriae three times width of striae; interstriae punctures strongly confused; striae weakly impressed; each puncture with a hair-like seta arising from basal margin, covering puncture; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C; apex smooth.

Female similar to male except epistoma less impressed and unarmed; epistoma covered by five rows of setae; frons flat, with a circular, weakly impressed region between upper level of eyes; surface shagreen lateral margins may be strigulate; 3-4 rows of setae lateral to median line; gena with triangular mycangium; anterior third of pronotum covered with long, dense hair-like setae on anterolateral areas; long bristles absent; base and disc covered with fine, short hair-like setae.

**Specimens examined.** (34♂, 24♀, 1 unknown sex)

*Type Material.* Lectotype *Camptocerus niger*, ♂ (MZMC); Paralectotypes *Camptocerus niger*, **NO LOCALITY**: 3♀, 1 unknown sex (MZMC); Paralectotypes *Camptocerus squammiger* ♀ Cayenne [French Guiana] (IRSNB); Holotype *Camptocerus tectus*, ♂ (DEI); Paratypes, *Camptocerus tectus* **BRAZIL: Pernambuco:** Sarra da Bernada, 5.vi.1894, (*Duhant*) 2♂ (DEI).

*Other material.* **BOLIVIA:** Beni: Cosincho Region, (G.L. Harrington), 1♂ (NMNH); *No specific locality* 'Aragua', 1♀ (NHMW). **BRAZIL:** Amazonas, Amazonas Parque, 30 km E Manaus, Amazon River, 110 ft, 17.ii.1981, (Chen-wen Young), 1♂, 1♀ (RJRC) 1♀ (MSUC); AM 010 km 26, Reserva Ducke, ex. malaise trap, 21.ii.1978, (Jorge Arias), 1♂, 1♀ (NMNH); Santa Catharina, Corupa (Hansa Humbolt), xi.1945, (A. Maller), 1♂ (AMNH). **COLOMBIA:** Cauca, 10 km SE Tambo, ex. 'Anime' [= local name of *Protium* sp.], 9.vii.1970, (S.L. Wood), 7♂, 10♀ (MSUC); Putumayo: Mocoa, 26.vi.1974, (M. Cooper), B.M. 1964-548, 1♀ (BMNH). **ECUADOR:** Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1995, (T.L. Erwin et al.), lot 996, 1♂ (NMNH); x.1995, lot 1226, 1♂, 1♀ (NMNH); vii.1995, lot 1548, 1♀ (NMNH); Pastaza: Cononaco, -1.55, -75.583333, ex. malaise trap, 29.v.1976, (J. Cohen), 2♂ (NMNH); **FRENCH GUIANA:** *No specific locality:* 'Cayenne' 1♂ (BMNH); **GUYANA:** *No specific locality:* 'Essequibo' [River [=Guyana], 2♂ (MZMC). **PERU:** Loreto: 1.5 km N Teniente Lopez, -2.583333, -76.1, 210-240 m, ex. flight intercept trap, 9-22.vii.1993, (R. Leschen), 1♀ (NMNH); 70 km SSW from Iquitos to Nauta, 150 m, 5.iii.2008, (A. Petrov) 6♂, (MSUC). **SURINAME:** Commewijne: Akintosoela, 32 km SE Suriname River bridge, road to Redi Doti, 5.271389,-70.2517, 40 m, ex. flight intercept trap, 29.vi.-3.vii.1999, (Z.H. Falin, B. DeDijn, A. Gangagin), 1♂ (SMEC); *No specific locality:* 'Surinam', 4♀ (MZMC); **VENEZUELA:** Aragua: Rancho Grande, 1500-1900m, 8.v.1970 (O'Brien, Marshall) 1♂ (CAS). **NO SPECIFIC LOCALITY:** 'America meridionali' [=South America], 2♂ (IRSNB).

**Discussion.** *Camptocerus tectus* is here designated as a synonym of *C. niger* based on lack of a transverse carinae on the male frons and identical male genitalia. When Eggers described *C. tectus*, only specimens of *C. auricomus* were examined for comparison and not *C. niger* (Eggers, 1943).

**Distribution.** Bolivia (Beni), Brazil (Amazonas, Mato Grosso, Pernambuco, Santa Catharina), Colombia (Cauca, Putumayo), Ecuador (Napó, Pastaza), French Guiana, Guyana, Peru (Loreto), Suriname, Venezuela (Aragua).

**Hosts.** *Hirtella* sp., “Iratinga” (Beaver, 1972), *Licania kunthiana* Hook. f., *Protium* spp. (“Almesca branca” [Brazil], “Almesca vermelha” [Brazil], “Breu branco” [Brazil]) (Beaver, 1972).

**Biology.** Beaver (1972) provides a detailed life history. *C. niger* females excavate a short circumferential gallery below the bark on both sides of the entrance tunnel, identical to those produced by *C. auricomus* and *C. rectus*. *C. niger* was also reported to partially block their entrance tunnels with boring dust, a potential defense against predators (Beaver, 1972), which can cause significant *Camptocerus* mortality (chapter 2).

*Camptocerus occidentalis* Eggers

(Figs. 1.59, 1.60)

*Camptocerus occidentalis* Eggers, 1928: 91. Lectotype ♂: Bolivia (NMNH).

Lectotype designated by Anderson & Anderson 1971: 23.

**Diagnosis.** The male is distinguished by lateral margins of epistoma with an arcuate costa angled distally; basal epistomal margin with a straight carina highest above scape insertion and lowest at the middle, elongate and narrow scape.

The female is diagnosed by the elongate and narrow scape.

**Description.** Male 4.0 – 4.5 mm long ( $\bar{x}$  = 4.3 mm; n = 5); 2.0 – 2.1 times as long as wide. Color variable; head, antennae, pronotum, thorax, abdomen, and legs red-brown to dark brown; elytra orange-red to black. Elytra interstriae covered in variegated tan and dark brown scales forming highly variable patterns.

Apical epistomal margin unarmed; lateral margins of epistoma with an arcuate costa angled outward, lined with 6 rows of setae lateral to median line; basal epistomal margin with a straight carina highest above scape insertion and lowest at the middle; epistoma strongly excavated; expanded to greater than quarter length of head; frons strongly excavated with excavation bordering the ocular margin and the posterior margin of the carina; dorsolateral margin of eyes not impressed; lateral margins sub-acute; frons densely covered with two thick bands of long pale yellow setae; setae are clearly divided between the median line; frons shagreen; setae touch proximal epistomal margin; lateral quarters of frons and medial fifth glabrous two to three rows of long setae lining lateral margins; frons surface shagreen; antennal scape elongate and narrow; scape with a row of long setae on ventral margin; ventral margin of funicular segments 2-7 lined with brushes of setae 2 times the length of funicle; posterior margin of funicle segments with setae less than four segments in length; setae on both ventral and dorsal margin equal thickness; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; medial area of anterior third of pronotum covered with long, slender bristles on the anterolateral areas; base and disc covered with fine, short hair-like setae; short setae form two rows above lateral carina; pronotum strigulate on apical third and punctate basally; median line



devoid of punctures and vestiture; densely and minutely punctured; punctures deep; carina on lateral margin type F; base strongly bisinuate.

Declivity occupying apical half of elytra; each interstria densely covered with three rows of semi-erect thin spatulate setae on disc, and one to two rows on declivity; first interstria with uniseriate spatulate setae on apical third; interstriae three to five times width of striae; interstriae punctures strongly confused; striae weakly impressed; each puncture with a hair-like seta arising from basal margin, covering puncture and terminating at basal margin of apical puncture; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C; apex smooth.

Female similar to male except epistoma unarmed, moderately impressed; covered by four rows of setae; frons flat; surface shagreen; 5-7 rows of setae lateral to median line; unable to examine antennae; gena with triangular mycangium; anterior third of pronotum covered with long, dense slender hair-like setae on anterolateral areas; long bristles absent.

**Specimens examined.** (6♂, 2♀)

*Type Material.* Lectotype *Camptocerus occidentalis*, ♂ (NMNH); Paratypes **BOLIVIA:**

*No specific locality*, 'Bolivia', 1♂ (BMNH) 2♀ (NMNH).

*Other material.* **PERU:** *Junín: Tarma, Utcuyacu & Agua Dulce*, iii.1948, (F.

*Woytkowski*), 1♂ (AMNH); *No specific locality: 'Peru'*, (*W. Muller Vermacht*), 1909, 1♂ (NMNH), 2♂ (SMTD).

**Distribution.** Bolivia, Peru (Junín).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus orientalis* Eggers

(Figs. 1.63, 1.64)

*Camptocerus orientalis* Eggers 1943:244. Holotype ♂: Brazil: Bahia: Salobro, 6.vii.1885, L. Gounelle; Strohmeyer Collection, DEI.

**Diagnosis.** The male is diagnosed by an unarmed median apical epistomal margin; a transverse moderately developed arcuate carina on the basal epistomal margin, and the declivity with spatulate setae to apex.

The female is diagnosed from *C. auricomus* by the declivity with spatulate setae to apex.

**Description.** Male 3.2 – 3.7 mm long ( $\bar{x}$  = 3.6 mm; n = 4); 1.9 times as long as wide.

Color uniform, head, pronotum, thorax, abdomen, elytra, antennae and legs red-brown.

Elytra interstriae covered with variegated tan and dark brown spatulate setae forming highly variable patterns.

Apical epistomal margin unarmed; lateral margins of epistoma angled inward, lined with 1-3 rows of setae; a transverse moderately developed arcuate carina on the basal epistomal margin, ventrally lined with two rows of setae; epistoma weakly excavated; expanded to less than quarter length of head; frons strongly excavated with excavation bordering the ocular margin and the posterior margin of the carina; lateral and dorsal margins are sub-acute; densely covered with two thick bands of long pale yellow setae; single row of lining lateral margins; frons shagreen; antennal scape elongate and narrowly rounded distally; scape with a row of setae on distal half of ventral margin;

funicular segments 2-7 lined with brushes of setae two times the length of scape on ventral margin; dorsal margin glabrous; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; medial area of anterior third of pronotum covered with long bristles on the anterolateral areas; short bristles form three rows above lateral carinae; base and disc covered with fine, short hair-like setae; pronotum strigulate on apical third and punctate basally; punctures and vestiture on median line; densely and minutely punctured; punctures deep; carina on lateral margin type F; base strongly bisinuate.

Declivity occupying apical half of elytra; each interstria densely covered with three rows of semi-erect spatulate setae on disc and one to two rows on declivity; first interstria with uniseriate spatulate setae on apical third; interstriae three times width of striae; interstriae punctures strongly confused; striae weakly impressed; each puncture with a hair-like seta arising from basal margin, covering puncture; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C; apex smooth.

Female similar to male except epistoma unarmed, weakly impressed; covered by five rows of setae; frons flat, faintly impressed between eyes, surface shagreen; 3-4 rows of setae lateral to median line; antennal funicle segments scattered with setae less than length of six funicular segments; gena with triangular mycangium; anterior third of pronotum covered with long, dense hair-like setae on anterolateral areas; long bristles absent; base and disc covered with fine, short hair-like setae.

**Specimens examined.** (4♂, 1♀)

*Type material:* Holotype *Camptocerus orientalis*, ♂ (DEI). Paratypes *Camptocerus orientalis*, **BRAZIL: Bahia:** Salobro, 6.vii.1885, (*L. Gounelle*), 2♂, 1♀ (DEI), 1♂ (NMNH).

**Distribution.** Bolivia, Brazil (Amapá, Bahia).

**Hosts.** *Protium* sp.

**Biology.** Unknown.

*Camptocerus rectus* Wood

(Figs. 1.74, 1.75)

*Camptocerus rectus* Wood, 1972: 245. Holotype ♂: VENEZUELA: Barinas: 40 km E Canton, 70 m, ex. *Protium tenuifolium*, 8.iii.1970, (*S.L. Wood*) (NMNH).

**Diagnosis.** The male is diagnosed by the transverse, moderately developed and straight, sub-acute carina highest at middle, nearly tuberculate.

The female is diagnosed by a faint triangular impression from posterior margin of epistoma to with vertex just below upper level of eyes.

**Description.** Male 3.5 – 4.3 mm long ( $\bar{x}$  = 4.0 mm; n = 20); 1.8 – 2.1 times as long as wide. Color uniform, head, pronotum, thorax, abdomen, elytra, antennae and legs red-brown to dark brown. Elytra interstriae covered with variegated tan and dark brown spatulate setae forming highly variable patterns.

Apical epistomal margin unarmed; lateral margins of epistoma angled inward, lined with 1-3 rows of setae; a straight, sub-acute strongly developed straight carina on the basal epistomal margin highest at middle, nearly tuberculate; carina lined ventrally

with three rows of setae; epistoma weakly excavated; expanded to less than quarter length of head; frons strongly excavated with excavation bordering the ocular margin and the posterior margin of the carina; lateral and dorsal margins are rounded; frons densely covered with two thick bands of long pale yellow setae; single row of spatulate setae lining lateral margins; frons shagreen; antennal scape elongate and narrowly rounded distally; scape with a row of setae on ventral margin; ventral margin of funicular segments 2-7 lined with brushes of setae two times the length of scape; posterior margin of segments 5-7 with setae as thick as ventral margin and less than four funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; medial area of anterior third of pronotum covered with long bristles on the anterolateral areas; short bristles form two rows above lateral carinae; base and disc covered with fine, short hair-like setae pronotum strigulate on apical third and punctate basally; punctures and vestiture on median line; densely and minutely punctured; punctures deep; carina on lateral margin type F; base strongly bisinuate.

Declivity occupying apical half of elytra; each interstria densely covered with three to four rows of semi-erect stout spatulate setae on disc, and one to three rows on declivity; first interstria with uniseriate spatulate setae on apical third; interstriae three to four times width of striae; interstriae punctures strongly confused; striae not impressed; each puncture with a hair-like seta arising from basal margin, covering puncture; scutellum type C; no carina originating at the base of the tenth interstria; metepisternum with setae palmately divided into four or more filaments; metepisternum type G; mesosternum type C; apex smooth.

Female similar to male except epistoma unarmed, weakly impressed; covered by four rows of setae; frons flat, with a faint triangular impression from posterior margin of epistoma to with vertex just below upper level of eyes; surface shagreen; 5 rows of setae lateral to median line; antennal funicle segments 5-7 with setae on dorsal margin less than length of three funicular segments; gena with triangular mycangium; anterior third of pronotum covered with long, dense hair-like setae on anterolateral areas; long bristles absent; base and disc covered with fine, short hair-like setae.

**Specimens examined.** (25♂, 29♀)

*Type Material.* Holotype *Camptocerus rectus*, ♂ (NMNH); Allotype *Camptocerus rectus* ♀ (NMNH); Paratypes **VENEZUELA:** *Barinas*, 40 km E Canton, 70 m, ex. *Protium tenuifolium*, 8.iii.1970, (S.L. Wood), 3♂, 5♀ (NMNH); 9 km S Barrancas, 150 m, ex. *Protium* sp., 2.xii.1969, (S.L. Wood), 2♂, 2♀ (NMNH); 10 km SE Miri, 150 m, ex. *Protium tenuifolium*, 8.ii.1970, (S.L. Wood), 3♂, 1♀ (NMNH); 40 km SE Socopo, 150 m, ex. *Protium* sp., 25.i.1970 (S.L. Wood), 4♂, 8♀ (NMNH).

*Other material.* **ECUADOR:** *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, (T.L. Erwin et al.), lot 1464, i.1996, 1♂ (NMNH); ex. canopy fogging lot 1496, i.1996, 1♂ (NMNH). **VENEZUELA:** *Barinas:* 40 km E Canton, 70 m, ex. *Protium tenuifolium*, 8.iii.1970, (S.L. Wood), 1♂, 3♀ (MSUC); 10 km SE Miri, 150 m, ex. *Protium tenuifolium*, 9.ii.1970, (S.L. Wood), 2♂, 4♀ (MSUC); 40 km SE Socopo, 150 m, ex. *Protium* sp., 22.i.1970, (S.L. Wood), 2♂ (MSUC), 5♂, 5♀ (NMNH).

**Distribution.** Ecuador (Napo), Venezuela (Barinas).

**Hosts.** *Protium* spp., *Protium tenuifolium* [= *Protium tenuifolium* (Engl.) Engl.].

**Biology.** Wood (2007) describes the biology as similar to that of *C. aeneipennis*, although the gallery pattern likely resembles that of *C. auricomus* and *C. niger* based on their close relationship to *C. rectus*. All three species excavate a short circumferential gallery below the bark on both sides of the entrance tunnel. Colonization occurs in tree limbs with a diameter less than 10 cm (Wood, 2007).

### **“Latipilis” Clade**

Species in the “Latipilis” clade are diagnosed by the male lateral epistomal margin with vertical costa; basal epistomal margin tumid above scape insertion; carina originating at base of tenth interstria encompassing elytra; lateral margin of pronotum type C.

#### *Camptocerus charpentierae* Schedl **status n.**

(Figs. 1.29, 1.30)

*Camptocerus charpentierae* Schedl, 1970: 582. Holotype ♂: French Guiana: Massikiri-Haut Oyapock, 18.xi.1969, Balachowsky-Gruner Guyane Mission; Schedl Collection, (NHMW).

**Diagnosis.** Both sexes of *C. charpentierae* are distinguished by the black abdomen, red the normal second visible abdominal sternite and short pale scales on the interstriae.

**Description.** Male 3.8 – 4.5 mm long ( $\bar{x}$  = 4.3 mm; n = 6); 1.7 – 2.0 times as long as wide. Head, antennae dark red brown; abdomen, elytra, and legs black. Pronotum and legs may be red to dark red brown.

Apical epistomal margin armed with a short rectangular carina; lateral margins of epistoma with vertical costae; epistoma impressed; six rows of setae from lateral epistoma margins to median line; basal epistomal margin tumid above scape insertion; epistoma expanded to greater than quarter length of head; male frons is strongly excavated, sparsely ornamented with one erect golden setae lateral to medial line; surface clearly visible; 20-30 on lateral and dorsal margin; surface shagreen. Antennal scape elongate and wider distally, dense setae length of scape on distal three-quarters; funicle segments 2-7 with setae equal to 1.5 times funicle length on ventral margin; setae on dorsal margin less than length of five funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; anterior edge with 2-3 rows of yellow-brown setae; surface minutely granulate-punctate; punctures minute, shallow; lateral margin type C; base weakly recurved.

Scutellum type B; base never with a tumescence from seventh to ninth interstriae; disc shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type C, with setae palmately divided into four or more filaments; mesosternum type E; carina originating at base of tenth interstria encompassing elytra; un- and diseriatic rows of yellow-brown scales on interstriae; second visible abdominal sternite normal. Apex smooth.

Female similar to male except epistoma not expanded, less impressed and unarmed; epistoma with a four rows of hairs on apical margin; frons flat, with medial area of frons slightly impressed, joining with impression of epistoma; punctures small,



shallow, larger and deeper laterally; antennal funicle segments 1-7 with scattered setae on less than length of three funicular segments; gena with circular mycangium. Pronotum margin between the eyes lined with scales.

**Specimens examined.** (9♂, 8♀)

*Type Material.* Holotype *Camptocerus charpentierae*, ♂ (NHMW).

*Other material.* **BRAZIL:** Amazonas: Hwy ZF 2, km 20.7, ca 60km N. Manaus, 2°30'S, 60°15'W, ex. canopy fogging, 16.viii.1979, (*Adis, Erwin, Montgomery et al.*), 2♂, 1♀ (NMNH); 18.viii.1979, 1♂ (NMNH). **ECUADOR:** Napo: Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, x.1998, ex. canopy fogging (*T.L. Erwin et al.*), lot 1947, 1♂ (NMNH); ii.1999, lot 2030, 1♀ (NMNH); ii.1999, lot 2047, 1♀ (NMNH); Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 644, 1♂ (NMNH); i.1995, lot 1000, 1♂ (NMNH); vi.1996, lot 1550, 1♀ (NMNH); vi.1996, lot 1586, 1♀ (NMNH); x.1996, lot 1753, 2♂, 3♀ (NMNH).

**Discussion.** This species was considered a synonym of *Camptocerus cinctus* (Wood, 2007). *Camptocerus cinctus* is a synonym of *C. suturalis*. *Camptocerus charpentierae* is here resurrected based on comparison of the holotype with that of *C. suturalis*.

Phylogenetic analysis revealed the *C. charpentierae* ("latipilis" clade) to be in a separate clade from *C. suturalis* ("Aeneipennis" clade) (Fig. 1.16).

**Distribution.** Brazil (Amazonas), Ecuador (Napo), French Guiana.

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus coccoformus* Smith & Cognato, sp. n.

(Figs. 1.31, 1.32)

**Type Material.** Holotype, ♂, **BRAZIL:** Amazonas: Hwy ZF 2, km 20.7, ca 60 km N. Manaus, 2°30'S, 60°15'W, ex. canopy fogging, 16.viii.1979, (*Adis, Erwin, Montgomery et al.*) (NMNH); *Paratypes*, **BRAZIL:** 1♀, Amazonas: Hwy ZF 2, km 20.7, ca 60 km N. Manaus, 2°30'S, 60°15'W, ex. canopy fogging, 16.viii.1979, (*Adis, Erwin, Montgomery et al.*) (MSUC); 1♀, 69 km N Manaus, 7.xii.1979, (*G. Stevens*) (NMNH); **ECUADOR:** 1♀, *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778,-76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 626, (NMNH).

**Diagnosis.** The male is diagnosed by a tuft of setae on distal third of lateral epistoma margins, red brown head, red pronotum black body, second visible abdominal sternite less convex, scarcely protuberant below level of sternite 1.

Female can be distinguished from *C. latipilis* by the more impressed medial frons.

**Description.** Male 2.7 mm long (n = 1); 1.6 times as long as wide. Frons dark red brown; gena, antennae and pronotum reddish. Abdomen, elytra and coxa black; and legs dark red brown.

Apical epistomal margin armed with a short rectangular carina; lateral margins of epistoma with vertical costae; epistoma impressed tuft of setae on distal third of lateral epistoma margins; basal epistomal margin tumid above scape insertion; epistoma expanded to greater than quarter length of head; male frons is strongly excavated, ornamented with two golden setae lateral to medial line; surface shagreen; setose lateral edges; frons sparsely covered by erect setae, surface clearly visible. Antennal scape elongate and wider distally, four rows of setae half-length of scape on distal two-thirds;

funicle segments 2-7 with setae equal to 1.5 times funicle length on ventral margin; setae on dorsal margin less than length of five funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; anterior edge with 2-3 rows of yellow-brown setae; surface minutely granulate- punctate; punctures minute, shallow; lateral margin type C; base weakly recurved.

Scutellum type B; base never with a tumescence from seventh to ninth interstriae; disc shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type C, with setae palmately divided into four or more filaments; mesosternum type D; carina originating at base of tenth interstria encompassing elytra; uniseriate rows of yellow-brown yellow scales on interstria; second visible abdominal sternite convex, scarcely protuberant below level of sternite 1. Apex smooth.

Female similar to male except epistoma not expanded, less impressed and unarmed; epistoma with a row of hairs on apical margin; frons flat, with medial area of frons slightly impressed, joining with impression of epistoma; antennal funicle segments 3-7 with setae on dorsal margin less than length of three funicular segments; gena with circular mycangium; second visible abdominal sternite ventrally convex and distally distended, noticeably smaller than male.

**Etymology.** *Cocc-* (G) = berry, *-form* (L) = shape. In reference to the species globular and reddish appearance.

**Specimens examined.** (1♂, 3♀)

**Discussion:** This species was identified as *Camptocerus latipilis* by Wood (2007).

**Distribution.** Brazil (Amazonas).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus dolei* Smith & Cognato, **sp. n.**

(Figs. 1.38, 1.39)

**Type Material.** *Holotype*, ♂, **ECUADOR: Napo:** Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 2044, (NMNH held in trust for MECN). *Paratypes*, 2♀, **ECUADOR: Napo:** Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 2044, (MSUC) (NMNH); 1♂, x.1998, lot 1944, (MSUC); 1♂, i.1999, lot 2091 (NMNH).

**Diagnosis.** Both sexes are identified by an elongate body, elytra interstria with uni- and diseriata golden setae on elytra; unique color pattern described below, the carina that encompasses the elytra on the tenth interstria, The male is identified by its moderately excavated frons with the excavation never bordering the eye.

**Description.** Male 3.1 – 3.5 mm long ( $\bar{x}$  = 3.3 mm; n = 3); 2.1 – 2.3 times as long as wide. Head, antennae and thorax orange; legs dark red brown; abdomen black; elytra black with an orange patch covering basal third of elytra from the suture to eighth interstriae.

Apical epistomal margin armed with a short rounded tubercle; lateral margins of epistoma with vertical costa; epistoma weakly impressed; nine rows of setae from lateral

epistoma margins to median line; basal epistomal margin tumid above scape insertion; epistoma expanded to greater than quarter length of head; male frons is weakly excavated, excavation not reaching ocular margin; moderately ornamented with four rows of erect golden setae lateral to medial line; surface mostly visible; setose lateral margins; surface shagreen. Antennal scape elongate and expanded distally, dense setae two-thirds length of scape on distal half; funicle segments 2-7 with setae equal to 1.5 times funicle length of funicle on ventral margin; dorsal margin of 1-5 glabrous, setae on segment 6 less than length of two funicle segments, setae on segment 7 length of funicle; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; lateral margins a row of yellow setae; anterolateral margins with 2-3 rows of yellow setae; surface smooth, minutely punctate; lateral margin type C; base weakly recurved.

Elytra base flat; scutellum type D; base never with a tumescence from seventh to ninth interstriae; disc shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type R, with setae palmately divided into four or more filaments; mesosternum type E; carina originating at base of tenth interstria encompassing elytra; un- and diseriatic rows of pale yellow setae on interstriae; second visible abdominal sternite normal. Apex smooth.

Female similar to male except epistoma not expanded, less impressed and unarmed; epistoma with a four rows of hairs on apical margin; frons flat; nine rows of setae lateral to medial line; punctures small, shallow, larger and deeper laterally; antennal

funicle segments 5-7 with scattered setae on less than length of three funicular segments; gena with triangular mycangium.

**Etymology.** This species is named after our colleague, Stephanie Dole for her gracious mentoring and help throughout my graduate study.

**Specimens examined.** (3♂, 2♀)

**Distribution.** Ecuador (Napó).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus igniculus* Smith & Cognato, sp. n.

(Figs. 1.42, 1.43)

**Type Material.** Holotype, ♂, **BRAZIL:** Amazonas: Hwy ZF 2, km 20.7, ca 60km N. Manaus, 2°30'S, 60°15'W, ex. canopy fogging, 16.viii.1979, (*Adis, Erwin, Montgomery et al.*) (NMNH); *Paratypes*, **BRAZIL:** 3♂, 1♀, Amazonas: Hwy ZF 2, km 20.7, ca 60 km N. Manaus, 2°30'S, 60°15'W, ex. canopy fogging, 16.viii.1979, (*Adis, Erwin, Montgomery et al.*) (MSUC) 6♂, 1♀, (NMNH).

**Diagnosis.** Both sexes of *C. igniculus* have 1- 2 rows of golden scales on the elytral interstitial spaces, a reddish-brown hue and a normal second visible abdominal sternite. Its habitus is distinct from all other *Camptocerus* species.

**Description.** Holotype, Male 2.5 – 2.8 mm long ( $\bar{x}$  = 2.7 mm; n = 10); 1.7 – 2.0 times as long as wide. Head, antennae, thorax, abdomen, elytra, and legs reddish- brown.

Apical epistomal margin armed by a short, transverse rectangular carina; lateral epistomal margin armed with a straight carinae ornamented with cluster of 8-12 setae;

epistoma excavated; expanded to greater than quarter length of head; basal epistomal margin tumid above insertion of scape ; frons strongly excavated from epistoma to anterodorsal margin of the eyes with the excavation bordering the ocular margin, frons shagreen; 2-3 golden setae lateral to medial line; setose lateral edges. Antennal scape elongate and wider distally, four rows of setae half-length of scape on distal two-thirds; funicle segments 1-7 with setae equal to funicle length on ventral margin; setae on dorsal margin less than length of four funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes glabrous; pronotum with 2-3 rows of golden scales on anterior edge; surface minutely granulate- punctate; punctures with fine golden setae; lateral margin type C; base weakly recurved.

Elytral base margined by a weak carina; with shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; striae punctures shallow with a fine golden seta arising from the anterior margin; interstitial golden scales mostly uniseriate but also di- seriate on disk; uniserial on declivity; striae punctures 1.5- twice the size of interstriae. Carinae arising on the basal margin of tenth interstriae extending around elytra; scutellum type B; apex of the declivital margin of each elytron smooth. Metepisternum type C, with setae palmately divided into four or more filaments; process of the mesosternum shape type E. Visible abdominal sternites 2-4 each margined with a row of golden scales, sternite 5 with two rows; second visible abdominal sternite inflated. Apex smooth.

Female similar to male in most features, except epistoma not expanded; frons flat, unarmed; antennal funicle segments scattered with setae less than length of three funicular segments; gena mycangia oval shaped; second abdominal sternite normal.

**Etymology.** *Igniculus* (L) = little flame, spark. Name for its “fiery” appearance (golden setae and reddish-brown color) and in honor of a traditional Cognato family name “Ignatius”.

**Specimens examined.** (10♂, 2♀)

**Distribution.** Brazil (Amazonas).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus latipilis* Schedl

(Figs. 1.46, 1.47, 1.48)

*Camptocerus latipilis* Schedl, 1973:166. Holotype ♂: Brazil: Para: Benfica: Ananindeua; (MZUSP).

**Diagnosis.** The male is diagnosed from *C. petrovi* by its smaller size, black color; second visible abdominal sternite strongly convex and protuberant, height of declivity behind much less than length of sternite 3; dense brush of setae extending halfway on the lateral margin from the epistoma to the level of scape insertion; frontal excavation devoid of setae; 10-12 setae on lateral and dorsal margins.

Female can be distinguished from *C. coccoformus* by the less impressed medial frons.



**Description.** Male 2.7 – 3.3 mm long ( $\bar{x}$  = 3.2 mm; n = 6); 1.7- 1.9 times as long as wide.

Head, antennae, thorax, abdomen, elytra, and legs black.

Apical epistomal margin armed with a short rectangular carina; lateral margins of epistoma with vertical costae; epistoma impressed; dense brush of setae extending halfway on the lateral margin from the epistoma to the level of scape insertion; single seta lateral to median line; basal epistomal margin tumid above scape insertion epistoma expanded to greater than quarter length of head; male frons is strongly excavated, setae absent from excavation; surface shagreen; 10-12 setae on lateral and dorsal margins. Antennal scape elongate and wider distally, five rows of setae length of scape on distal two-thirds; funicle segments 2-7 with setae equal to 1.5 times funicle length on ventral margin; setae on dorsal margin less than length of five funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between the eyes glabrous; anterior edge with 2-3 rows of yellow-brown setae; surface minutely granulate- punctate; punctures minute, shallow; lateral margin type C; base weakly recurved.

Scutellum type B; base never with a tumescence from seventh to ninth interstriae; disc with shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type C, with setae palmately divided into four or more filaments; mesosternum type E; carina originating at base of tenth interstria encompassing elytra; uniseriate rows of yellow-brown scales on interstria; second visible abdominal sternite strongly convex and protuberant, height of declivity behind much less than length of sternite 3. Apex smooth.

Female similar to male except epistoma not expanded, less impressed and unarmed; epistoma with a row of hairs on apical margin; frons flat, with medial area of frons above dorsal margin of eyes slightly impressed; antennal funicle segments 4-7 with scattered setae less than length of three funicular segments; gena with circular mycangium; pronotum anterior margin between the eyes lined with scales; second visible abdominal sternite ventrally convex and distally distended, noticeably smaller than male.

**Specimens examined.** (8♂, 5♀)

*Type Material.* Paratype *Camptocerus latipilis*, **BRAZIL:** Para: Belem, 18.x.1962, (*J. Bechyne*), ♂ (NHMW).

*Other material.* **ECUADOR:** Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778,-76.433333, 220 m, ex. canopy fogging, x.1994, (*T.L. Erwin et al.*), lot 936, 1♀ (NMNH); vii.1996, lot 1546, 1♀ (NMNH); Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, x.1995, (*T.L. Erwin et al.*), lot 1257, 1♂ (NMNH); x.1996, lot 1727, 1♂ (NMNH); vi.1998, lot 1895, 1♂, 1♀ (NMNH); x.1998, lot 1930, 1♀ (NMNH); x.1998, lot 1947, 1♂ (NMNH); x.1998, lot 1953, 1♂ (NMNH); x.1998, lot 1987, 1♂ (NMNH); ii.1999, lot 2044, 1♂ (NMNH); ii.1998, lot 2068, 1♀ (NMNH).

**Distribution.** Brazil (Pará), Ecuador (Napo).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus mallopterus* Smith & Cognato, **sp. n.**

(Figs. 1.51, 1.52)

**Type Material.** *Holotype*, ♂, ECUADOR: Napo: Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 2087, (NMNH held in trust for MECN). *Paratypes*, 1♀, ECUADOR: Napo: Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 2087 (NMNH), 1♂, 1♀, (MSUC).

**Diagnosis.** Both sexes of *C. mallopterus* are diagnosed by the distinctive light orange head, pronotum and black abdomen and elytra, with the elytra densely covered in pale recumbent setae.

**Description.** Male 3.8 – 3.9 mm long ( $\bar{x}$  = 3.85 mm; n = 2); 1.8 – 1.9 times as long as wide. Head, thorax, prolegs and coxae orange; antennae black and orange; meso and metathoracic femora black, orange on distal fifth; tibiae orange; abdomen and elytra, black. Elytra striae and interstriae densely covered with pale recumbent setae.

Apical epistomal margin armed with a short rectangular carina; lateral margins of epistoma with vertical costae; epistoma impressed; five rows of setae from lateral epistoma margins to median line; basal epistomal margin tumid above scape insertion; epistoma expanded to greater than quarter length of head; male frons is strongly excavated, ornamented with eight rows of golden setae lateral to medial line; surface shagreen; setose lateral edges; frons moderately covered by erect setae, surface moderately covered. Antennal scape elongate and wider distally, dense setae length of scape on distal three-quarters; funicle segments 2-7 with setae equal to length on ventral margin; setae on dorsal margin less than length of five funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between the eyes glabrous; anterior edge with 4-5 rows of yellow-brown setae; surface densely covered with short, fine hairs; surface minutely granulate- punctate; punctures minute, shallow; lateral margin type C; base weakly recurved.

Scutellum type B; base never with a tumescence from seventh to ninth interstriae; disk with shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type C, with setae palmately divided into four or more filaments; mesosternum type D; carina originating at base of tenth interstria encompassing elytra; punctures not confused; striae indistinguishable from interstriae; 3-4 rows of uniseriate pale yellow setae on interstria; uniseriate on striae; setae equal size on both striae and interstriae; second visible sternite weakly convex and strongly protuberant, height of declivity behind greater than the length of sternite 3. Apex smooth.

Female similar to male except epistoma not expanded; lateral two-thirds to median line impressed; epistoma unarmed; epistoma with five transverse rows of setae; frons flat, with medial area of frons weakly impressed; frons with four setae lateral to medial line; antennal funicle segments 1-7 with scattered setae less than length of four funicular segments; gena with circular mycangium; second visible abdominal sternite ventrally convex and distally distended, noticeably smaller than male.

**Etymology.** *Mallo-* (G) wool, *-pterus* (G) = wing. In reference to the woolly appearance due to the dense pale setae covering the elytra.

**Specimens examined.** (2♂, 2♀)

**Distribution.** Ecuador (Napó).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus petrovi* Smith & Cognato, sp. n.

(Figs. 1.65, 1.66)

**Type Material.** *Holotype*, ♂, **ECUADOR: Napo:** Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 1930, (NMNH held in trust for MECN). *Paratype*, ♂, **ECUADOR: Napo:** Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, ii.1999, (*T.L. Erwin et al.*), lot 1930 (NMNH).

**Diagnosis.** The male is diagnosed by its large size, black color; strongly convex and protuberant second visible sternite the height of declivity behind greater than length of sternite 3; dense brush of setae extending halfway on the lateral margin from the epistoma to the level of scape insertion and frontal excavation with 1-2 setae lateral to median line, 15-20 setae on lateral and dorsal margins.

**Description.** Male 4.0 mm long ( $\bar{x} = 4.0$  mm;  $n = 2$ ); 1.6 times as long as wide. Head, antennae, thorax, abdomen, elytra, and legs black; apical margin of pronotum dark brown. Teneral individuals with a red pronotum.

Apical epistomal margin armed with a short rectangular carina; lateral margins of epistoma with vertical costae; epistoma impressed; dense brush of setae extending halfway on the lateral margin from the epistoma to the level of scape insertion and frontal excavation; single seta lateral to median line; basal epistomal margin tumid above scape insertion; epistoma expanded to greater than quarter length of head; male frons is

strongly excavated, frontal excavation with 1-2 setae lateral to median line, 15-20 setae on lateral and dorsal margins; surface shagreen. Antennal scape elongate and wider distally, five rows of setae length of scape on distal two-thirds; funicle segments 3-7 with setae equal to 1.5 times funicle length on ventral margin; setae on dorsal margin less than length of five funicle segments; setae on ventral margin twice as thick as those on dorsal margin; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes lined with scales; lateral margin type C; anterior edge with 2-3 rows of yellow-brown setae; surface minutely granulate-punctate; punctures minute, shallow; lateral margin type C; base weakly recurved.

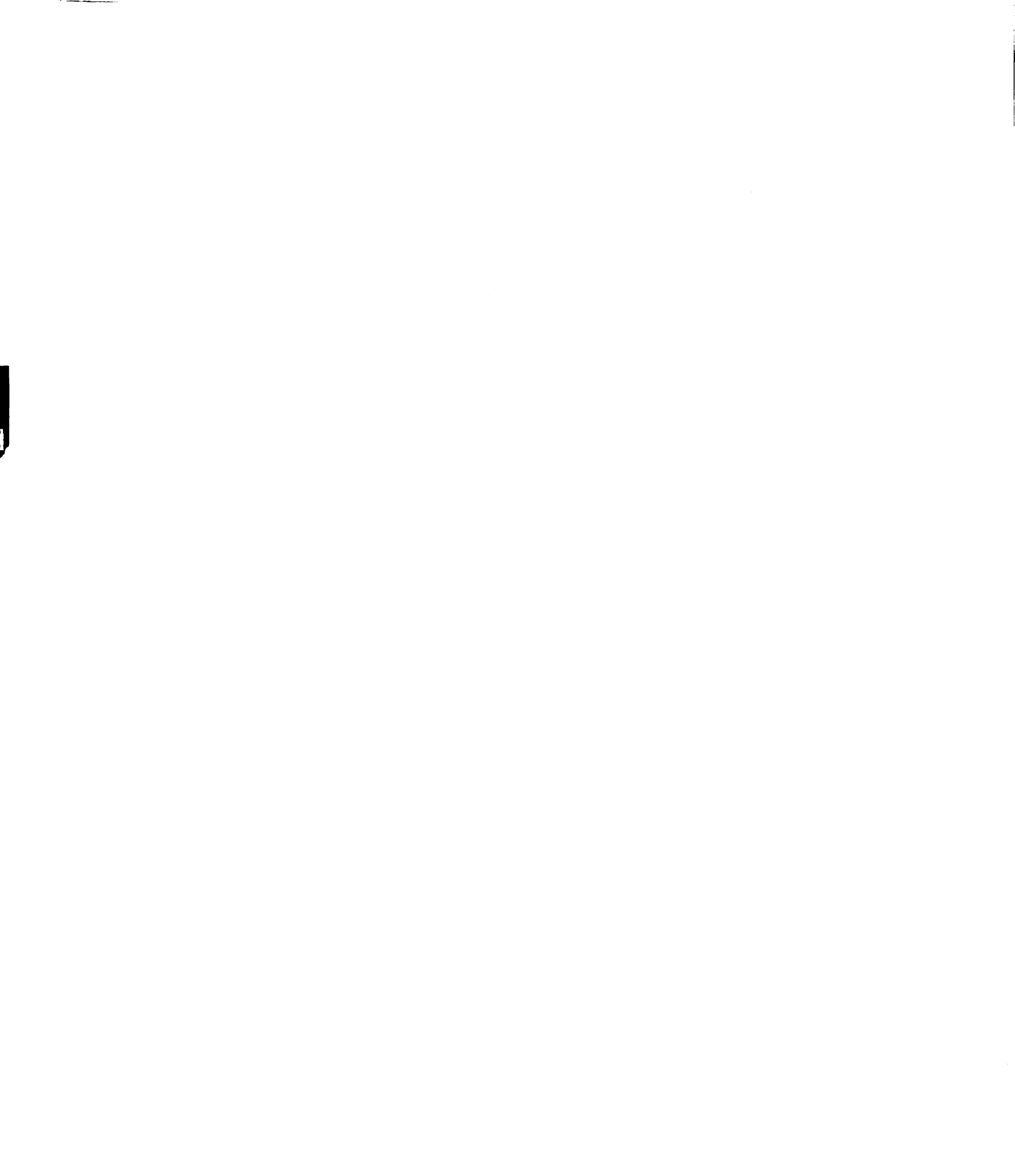
Scutellum type B; base never with a tumescence from seventh to ninth interstriae; disc with shallow rugosities occupying first to fourth striae and interstriae just beyond the scutellum, remaining elytral surface minutely granulate; metepisternum type C, with setae palmately divided into four or more filaments; mesosternum type E; carina originating at base of tenth interstria encompassing elytra; uniseriate rows of yellow-brown yellow scales on interstria; strongly convex and protuberant second visible sternite the height of declivity behind greater than length of sternite 3. Apex smooth.

Female unknown.

**Etymology.** This species is named in honor of our colleague, Alex Petrov who also shares a love of *Camptocerus* and has generously contributed important material for this study.

**Specimens examined.** (2♂, 0♀)

**Distribution.** Ecuador (Napo).



**Hosts.** Unknown.

**Biology.** Unknown.

### “Costatus” Clade

Species in the “Costatus” clade are diagnosed by the pronotum lateral margin type D, recurved pronotum base, scutellum shape type I and basal margin of elytra with a weak subbasal carina extending to scutellar apex.

#### *Camptocerus costatus* Chapuis

(Figs. 1.33, 1.34, 1.35)

*Camptocerus costatus* Chapuis, 1869: 259. Type locality: ‘Brazil, Dejean’. Holotype ♂, (IRSNB).

*Camptocerus seriatus* Eggers 1933:12. Type locality: French Guiana: Les roches de Kourou; Holotype ♀, (MNHN). Synonymy: Wood, 2007: 205.

**Diagnosis.** The male of *C. costatus* is diagnosed by the elytral declivity strongly impressed below level of disk, occupying apical four-fifths of elytra; carinate costa on eighth interstriae from basal fifth and extending around apex to sutural margin; striae deeply impressed; bristling brown setae originating from recumbent asperities on the interstriae.

The female is distinguished from *C. pilifrons* by color, larger size, and more impressed striae.



**Description.** Male 3.5 – 3.9 mm long ( $\bar{x} = 3.7$  mm; n = 6); 1.8 – 2.0 times as long as wide. Head, thorax, abdomen, elytra, antennae and legs red-brown to black. Teneral individuals are orange red.

Apical epistomal margin unarmed; lateral margin with a sub-acute arcuate costa pointing proximally, lined entirely with setae; short, rectangular carina on basal epistomal margin; epistoma excavated; expanded to greater than quarter length of head; male frons strongly excavated and covered by long, dense, erect, dark yellow hairs; two rows on lateral and caudal margin twice the length of other setae on the margins; surface shagreen. Scape is elongate and broadly rounded distally, with a dense brush of setae as long as scape on distal half; funicular segments 2-7 dense brushes of setae 2 times longer than funicle on ventral margin; setae equal width on ventral and dorsal margin; setae on dorsal margin of segments 1-7 less than four segments long; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes glabrous; lateral margin type D; pronotum base procurved; pronotum smooth, densely and minutely punctured, medial line devoid of punctures, 5-6 setae transverse on anterior fourth of pronotum.

Elytra disk short, occupying basal fifth of elytra; interstriae 1-4 rugose, remaining disk smooth. Declivity strongly impressed below level of disk, occupying apical four-fifths of elytra; striae moderately impressed; interstriae on basal fifth with recumbent asperities above punctures, each puncture with a dark yellow, short bristle setae arising from the posterior margin; asperities progressively become smaller in size forming crenulations becoming small tubercles at apical fifth and are obsolete at elytra apex; scutellum type I; basal margin of elytra with a weak carina extending to scutellar apex;

base never with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type M; metepisternum setae palmately divided into more than four filaments; mesosternum shape type B; declivity interstriae twice width of striae, setae uniseriate; apex of declivity margin smooth.

Female similar to male except frons flat and unarmed; shagreen; short, sparse, setae present only on lateral margin of frons; setae present on epistoma; antennal funicle segments 1-7 with setae on dorsal margin less than length of three funicular segments; gena with circular mycangium. Elytra finely sculptured, without indication of spines or carinate costa; disk covered with shallow rugosities to interstria 8; disk covered with shallow rugosities; striae weakly impressed; declivital interstriae with short, bristles of equal length; declivital interstria 1-5 on apical half of declivity with a crenulation at the base of each puncture with short bristle originating; setae of equal length.

**Specimens examined.** (6♂, 5♀)

*Type Material.* Holotype *Camptocerus costatus*, ♂ (IRSNB). Holotype *Camptocerus seriatus*, ♀ (MNHN).

*Other material.* **BRAZIL:** Mato Grosso: Villa Vera, 12°46'S 55°30'W, x.1970, (*M. Alvarenga*), 1♂ (CAS). **ECUADOR:** Napo: Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, vi.1998, ex. canopy fogging (*T.L. Erwin et al.*), lot 1817, 1♂ (NMNH). **GUYANA:** [=Region 8]: Iwokrama Forest, 4.671822, -58.684114, 66 m, ex. *Ocotea oblonga*, 4-9.iii.2007, (*Cognato, Hulcr, Smith, Dole, McCall*), 2♂, 4♀ (MSUC). **PERU:** Loreto: 1.5km N Teniente Lopez, 2°35'S 76°6.92'W, 210-240 m, ex. flight

intercept trap #166, 22.vii.1970, (*Richard Leschen*), 1♀ (SMEC). **TRINIDAD:** Morne Bleu, 2700 ft, 21.viii.1969, (*H & A Howden*), 1♂ (NMNH).

**Distribution.** Brazil (Mato Grosso, Rio de Janeiro, Rondônia), Ecuador (Napo), French Guiana, Guyana, Peru (Loreto), Trinidad.

**Hosts.** *Ocotea oblonga* (Meisn.) Mez.

**Biology.** This species creates galleries in 1 – 2 cm diameter branches.

**Discussion.** Identity of the female and synonymy of *C. seriatus* confirmed when five mated pairs of *C. costatus* were collected from galleries by Cognato et al. in 2007.

*Camptocerus pilifrons* Smith & Cognato, sp. n.

(Figs. 1.67, 1.68)

**Type Material.** *Holotype*, ♂, **ECUADOR:** *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, vii.1995, (*T.L. Erwin et al.*) (NMNH held in trust for MECN). *Paratypes*, **ECUADOR:** 1♂, *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, vii.1994, (*T.L. Erwin et al.*) lot 714 (NMNH); 1♂, vii.1995, lot 1114 (NMNH); 1♂, viii.1995, lot 1115 (MSUC) 1♂ (NMNH); 1♂, 1♀, x.1995, lot 1254 (NMNH); 1♀, x.1995, lot 1256 (NMNH); 1♀, x.1995, lot 1260 (MSUC); 1♂, x.1996, lot 1669 (NMNH).

**Diagnosis.** Both sexes of *C. pilifrons* are diagnosed by its small size and distinctive color pattern described below. The male is distinguished by an elytral disk with setae on interstriae; the absence of a carinate costa on the eighth interstria and by the unimpressed declivity and striae.

The female is distinguished from *C. costatus* by the color, smaller size, and unimpressed striae.

**Description.** Male 2.6 – 3.1 mm long ( $\bar{x}$  = 2.8 mm; n = 7); 1.9 - 2.2 times as long as wide. Head, thorax, abdomen, elytra, antennae and legs red-brown. Pronotum with a black patch extending from the anterior margin of the pronotum and reaching a point to the posterior third of the pronotum along the median line. An oval-shaped black patch is present extending from the elytral base to the posterior margin of the first visible sternite and from the lateral margin to interstria 7.

Apical epistomal margin unarmed; lateral margin with an arcuate costa pointing proximally, lined entirely with setae short rectangular carina on the basal epistomal margin; epistoma excavated; expanded to less than quarter length of head; frons strongly excavated; excavation borders ocular margin; densely covered with white bristles; lateral two rows on frons margin slightly longer than other setae. Scape is elongate and broadly rounded distally, with a dense brush of setae as long as scape on distal half; dorsal margin of funicular segments 2-7 with dense brushes of setae two times longer than funicle; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes glabrous; lateral margin type D; pronotum base recurved; surface punctate, anterior and posterior margins more densely punctured; medial line devoid of punctures; row of setae along lateral margins, 5-6 setae transverse on anterior fourth of pronotum.

Basal margin of elytra with a weak subbasal carina extending to scutellar apex; scutellum shape type I; base never with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than metepisternum; metepisternum

shape type F; metepisternum setae palmately divided into more than four filaments; mesosternum shape type B; elytra smooth; declivity interstriae setae uniseriate, uniform in size; interstriae twice width of striae; strial punctures twice size of interstriae; strial punctures with a setae the length of puncture originating from anterior margin; apex of declivity margin smooth.

Female similar to male except frons flat and unarmed; short, sparse, setae present only on lateral margin of frons; frons shagreen; setae present on epistoma; antennal funicle segments 5-7 with setae on dorsal and ventral margins less than length of three funicular segments; gena with circular mycangium. Elytra finely sculptured; disk covered with shallow rugosities to interstria 8; disk covered with shallow rugosities; declivital interstriae with short, bristles of equal length; declivital interstria 1-5 on anterior half of declivity with a crenulation at the base of each puncture with short bristle originating; setae of equal length.

**Etymology.** *Pili-* (L) = hairy, *-frons* (L) = forehead, brow. In reference to the setose excavation of the frons.

**Specimens examined.** (7♂, 3♀)

**Distribution.** Ecuador (Napó).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus quadridens* Blackman

(Figs. 1.70, 1.71, 1.72, 1.73)

*Camptocerus quadridens* Blackman, 1943: 379. Holotype ♂: Panama: Canal Zone: Cooper's, near source of Rio Aejeta 19.vii.1923, J. Zetek, fallen tree; (NMNH).

**Diagnosis.** The male is diagnosed by the short transverse carina on the basal epistomal margin, each elytron with two discal spines arising from the first to fifth striae, with a sharp spine on the first striae and a blunt spine on the second extending over the declivity, and the red-brown color.

The female is distinguished from *C. costatus* by the color, smaller size, and less impressed striae.

**Description.** Male 3.4 – 3.7 mm long ( $\bar{x}$  = 3.6 mm; n = 4); 1.8 – 1.9 times as long as wide. Head, thorax, abdomen, elytra, antennae and legs orange to red brown.

Apical epistomal margin is unarmed; lateral margin with an arcuate costa pointing proximally, entirely lined with setae; basal epistomal margin with a short, rectangular, transverse carina; epistoma excavated; expanded to less than quarter length of head; male frons strongly excavated and covered by long, dense, erect, pale yellow setae of equal length; excavation borders ocular margin; scape is elongate and broadly rounded distally; distal half of scape covered by hair-like setae the length of scape; ventral margin of funicle segments 2-7 with brushes of setae 1.5 times the length of funicle; dorsal margin of segments 1-7 with hair-like setae half the thickness of ventral margin and three-quarters length of funicle; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between eyes glabrous; lateral margin type D; pronotum base recurved; pronotum smooth, densely and minutely punctured, medial line devoid of punctures, 5-6 setae transverse on anterior fourth of pronotum.

Elytra disk with two spines arising from the first to fifth striae; a sharp spine on the first striae and a blunt rounded spine on the second, spines extend over the declivity, declivity originates in the recess formed by the spines. The declivity under the margin of the spines is moderately depressed until interstria 8, where a carinate costa originates the middle of visible sternite 1 and terminates above the midpoint of visible sternite 5. Scutellum shape type I; basal margin of elytra with a weak subbasal carina extending to scutellar apex; base never with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than metepisternum; interstriae uniseriate, twice width of striae; interstriae punctures indistinct; interstriae 1-4 with thin bristles 2-4 times the length of other bristles arising in the concavity under the spines to the posterior third of declivity; apex smooth.

Female similar to male except frons flat and unarmed; short, sparse, setae present only on lateral margins; frons shagreen; setae present on epistoma; antennal funicle segments 5-7 with setae on dorsal margin less than length of three funicular segments; gena with circular mycangium. Elytra finely sculptured, no indication of spines or carinate costa; disk covered with shallow rugosities from sutural space to interstria 8; declivital interstriae with short bristle of equal length; declivital interstria 1-5 on anterior half of declivity with a crenulation at the base of each puncture with short, bristles; setae of equal length.

**Specimens examined.** (6♂, 1♀)

*Type Material.* Holotype *Camptocerus quadridens*, ♂ (NMNH).

*Other material.* PANAMA: Canal Zone: Barro Colorado Island, ex. trap, 13.ii.1980, (Henk Wolda), 1♂ (UCDC); 21, 24, 26.vii.1986, 1♂ (MSUC); 21, 23, 25.vii.1986, 1♀,

(MSUC), 1-3.vii.1987, 1♂ (UCDC); *Panama*: Cerro Jefe, 19°12'N, 79°21'W, 24.ii.1973, (*H. Stockwell*), 1♂ (NMNH).

**Distribution.** Panama.

**Hosts.** The holotype was collected on the same date and in the same locality as *C.*

*aeneipennis*. These *C. aeneipennis* were collected from *Protium* sp. and since multiple species often colonize the same host, a *Protium* sp. is the probable host (Wood, 1982).

**Biology.** Unknown.

**Discussion.** This is the first time that a female has been identified for this species. It was found in a museum rather than collected in the field, so its identity is hypothesized.

*Camptocerus quadridens* displays marked sexual dimorphism similar to that of its sister taxa, *C. costatus* and *C. pilifrons*.

*Camptocerus zucca* Smith & Cognato, sp. n.

(Figs. 1.80, 1.81)

**Type Material.** Holotype, ♂, **ECUADOR**: *Napo*: Huahua Sumaco, Km 44 on Hollin-Loreto Rd. 16.xii.1989, (*MS & JS Wasbauer, H. Real*) (CSCA). *Paratypes*, **ECUADOR**: 1♀, *Napo*: Huahua Sumaco, Km 44 on Hollin-Loreto Rd. 16.xii.1989, (*MS & JS Wasbauer, H. Real*) (CSCA); 1♂ (MSUC).

**Diagnosis.** This species is closely related to *C. quadridens* and *C. costatus*. It is readily distinguished by its large size, unarmed apical epistomal margin, a distinctive orange and black color pattern of the head, antenna, thorax, abdomen and elytra as described below, absence of a carinate costa on the eighth interstriae and sparse setae on the declivity.



The female is distinguished from other females in the clade by the distinctive color pattern, larger size, and unimpressed striae and the short, fine setae on the interstriae.

**Description.** Male 4.0 – 4.1 mm long ( $\bar{x}$  = 4.05 mm; n = 2); 1.9 times as long as wide.

Antennal scape and club black, funicle orange, epistoma and frons orange, gena black, protibia orange with black margins, profemur and meso- and metalegs black with orange patches, coxae brownish-orange, pronotum orange with a black triangle extending from the apex to the basal third of the pronotum, elytra black with each elytron displaying an orange oval encompassing the area from the basal margin of the disk and to the basal fifth of the elytra and from the sutural interspace to the eighth interstriae; ventral surface of thorax and abdomen black. Teneral adults are pale orange with dark spots.

Apical epistomal margin unarmed; lateral margin with an arcuate costa pointing inward, entirely lined with setae; basal epistomal margin unarmed; epistoma excavated; expanded to greater than quarter length of head; male frons strongly excavated and covered by long, dense, erect, yellow-white hairs; excavation borders ocular margin; male scape is elongate and broadly rounded distally; distal half with patch of setae length of scape; ventral margin of funicle segments 2-7 lined with a brush of hair-like setae 1.5 times the length of funicle; dorsal margin of segments 1-7 lined with hair-like setae half length of ventral margin, anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded, margin between the eyes glabrous; lateral margin type D; pronotum base recurved; pronotum smooth, sparsely covered by very fine, almost indistinguishable punctures.

Elytra disk with shallow rugosities to third interstria; remaining disk smooth, striae not impressed; scutellum type I; basal margin of elytra with a weak subbasal carina extending to scutellar apex; base never with a tumescence from seventh to ninth interstriae; carina originating at base of tenth interstria shorter than metepisternum; metepisternum shape type C; metepisternum setae bifid; mesosternum shape type O; declivity interstriae four times width of striae, setae uniseriate; setae sparse; setae on declivital interstriae 1-5 two to three times as long as those on interstria 6; 2-3 long setae present on each interstria; three lateral rows of short setae present on declivity margin from visible sternite 1 to suture; apex of declivity margin smooth.

Female similar to male except frons flat and unarmed; short, sparse, setae present only on lateral margin of frons; frons shagreen; setae present on epistoma; antennal funicle segments 3-7 with setae on dorsal and ventral margins less than length of four funicular segments; gena with circular mycangium. Elytra finely sculptured, no indication of spines or carinate costa; disk covered with shallow rugosities to interstria 8; disk covered with shallow rugosities; declivital interstriae with short, fine pointed setae of equal length.

**Etymology.** Zucca (Italian) = pumpkin (noun in apposition). In reference to this species jack-o-lantern appearance.

**Specimens examined.** (2♂, 1♀)

**Distribution.** Ecuador (Napo).

**Hosts.** Unknown.

**Biology.** Unknown.

### “Aeneipennis” Clade

Species in the “Aeneipennis” clade are distinguished by elongate and narrow male scape; pronotum lateral margin type B; metepisternum type B; and mesosternum type A.

#### *Camptocerus aeneipennis* (Fabricius)

(Figs. 1.19, 1.20)

*Camptocerus aeneipennis* (Fabricius) 1801: 392 (*Hylesinus*). Lectotype ♂: Essequibo [River] [=Guyana], (UZMC). Lectotype designated Wood, 1982: 412

*Camptocerus gibbus* (Fabricius) 1801: 392 (*Hylesinus*). Type locality: ‘Essequibo’ [River] [=Guyana]; Lectotype ♀ (here designated), (UZMC). Synonymy: Eggers 1933: 17.

**Notes.** Synonymy of *C. gibbus* confirmed by Wood (1972: 243).

**Diagnosis.** This species always has an elytra colored metallic bronze or black with a metallic sheen and is smaller in size than its sister taxa, *C. noel*. The male can and is distinguished by the impressed first discal striae, deeper strial punctures and a moderate pronotum sulcus, encompassing lateral two-thirds of anterior margin.

Females are identified from *C. noel* by their smaller size and deeper strial punctures.

**Description.** Male 4.4 – 5.9 mm long ( $\bar{x}$  = 5.5 mm; n = 20); 1.8 – 2.1 times as long as wide. Head, thorax, antennae and legs red-brown; pronotum dark red-brown; abdomen black; elytra metallic bronze.

Apical epistomal margin is unarmed; lateral margin of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to greater than

quarter length of head; basal epistomal margin armed with a transverse, concave carina; frons strongly excavated and densely covered with long white to yellow hair-like setae; margin of excavation lined with a single row of long hairs; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; frons and epistoma smooth, shining; funicle segments 2-7 with brushes of setae equal of length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Lateral declivities on anterior margin of pronotum extending two-thirds of distance to midline; margin between eyes lined with fine bifid setae; pronotum glabrous, smooth, shining; minutely punctate; lateral margin type B; basal half deeply rugose creating a wrinkled appearance; base straight.

Elytra glabrous; the first discal striae impressed; interstriae punctures strongly confused; elytra smooth; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat with a triangular impressed area originating between the eyes and terminating at the distal and lateral epistoma margins, the triangle is bisected by a shallow carina on the median line; small tubercle at dorsal end; frons ornamented with few short setae; frons shagreen, dorsal and lateral margin reticulate, covered with moderate, deep punctures; antennal funicle segments 5-7 with setae on dorsal margins less than length of two funicular

segments; gena with crescent shaped mycangium. Pronotum anterior margin weakly sulcate, margin between the eyes lined with scales; pronotum, smooth, shining.

**Specimens examined.** (163♂, 109♀)

*Type Material.* Lectotype, ♂, *Camptocerus aeneipennis* (MZMC); Paralectotypes, *Camptocerus aeneipennis*, **NO LOCALITY**, 2♂, 4♀, (MZMC); Lectotype, *Camptocerus gibbus*, ♀ (MZMC).

*Other specimens:* **BOLIVIA:** *Beni:* Cosincho region, (G.L. Harrington), 1♂ (NMNH); Romansos, 1 km N. Junction Rio Itenez & Rio Paragua, 30.vii.1964, (J.K. Bousemen, J. Lussenhop), 1♂, 1♀ (AMNH); *La Paz:* Chuma [dubious locality due to high elevation and biome]: xii.1936 (Y. Mexia), 1♂ (CAS). **BRAZIL:** *Amazonas:* km 60 N Manaus, 18.1 km E Campinas field station, 2° 30'S, 60°15'W, ex. terra firme forest fogged with pyrethrum (Montgomery, Erwin, Schimmel, Krischik, Date, Bacon), sample 6, 22.ii.1979, 1♂ (NMNH); Manaus, 1 km W Taruma Falls, 100m, 12-17.ii.1981, (Ekis, Young), 1♀ (RJRC); *Bahia:* (G. Bondar), 4♂, 1♀ (FMNH); Salobro: 6.vii.1885, (E. Gounelle), 2♂ (DEI); *Parana:* Rolaudia, x.1947, (A. Maller), 1♂ (AMNH); *Pernambuco:* Pery-Pery, 5.vi.1892, (Gounelle), 3♂, 1♀ (DEI); 11.xii.1892, 1♂ (DEI); *Rio de Janeiro:* (Kirsch) 1♂, (SMTD); *Santa Catharina:* Corupa (Hansa Humbolt), xii.1945, (A. Maller), 1♂ (AMNH); 'São Paulo' (Kratz), 1♂ (DEI); *No specific locality:* 'Brazil' (Mearkel), 1♀ (SMTD); 'Brazilien', 1♂ (MZMC); 'Rio Madeira' [river runs through states of Rondônia and Amazonas], 1954, (Mann, Baker), 2♂ (NMNH). **COLOMBIA:** *Cauca:* 10 km SE Tambo, 30 m, ex. 'Anime' [local name of *Protium*], 9.vii.1970, (S.L. Wood), 3♀ (MSUC); *Choco:* Quebrada Docordo, Rio San Juan, (B. Malkin), 4-8.vi.1969, 1♂ (FMNH); *Putumayo:* Santa Rosa (Kofan Indian village), headwaters of Rio San Miguel,

ex. at light, (*B. Malkin, P. Buchard*), 9-12.x.1970, 1♂ (FMNH); *Santa Fe de Bogotá* [=Bogotá D. C.], 4♂ (DEI). **COSTA RICA:** *Peralta*: Cartago, ex. 4" limb, 10.iii.1964, (*S.L. Wood*), 6♂, 4♀ (MSUC); *Santa Clara*: Hamburg Farm, ex. on dry bark, (*F. Nevermann*), 1♂ (NMNH). **ECUADOR:** *Napo*: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, lot 614, 1♀ (NMNH); vii i.1995, lot 1028, 1♂ (NMNH); vii.1995, lot 1110, 1♂ (NMNH); i.1996, (*T.L. Erwin et al.*), lot 1479, 1♂, (NMNH); i.1996, lot 1498, 5♂, 3♀ (NMNH); vii.1996, lot 1530, 1♂ (NMNH); vii.1996, lot 1618, 1♀ (NMNH); Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ii.1999, ex. canopy fogging (*T.L. Erwin et al.*), lot 2056, 1♂ (NMNH); ii.1999, lot 2075, 1♂ (NMNH). **FRENCH GUIANA:** *No specific locality*: 'Cayenne' 2♂ (DEI); 2♂ (MZMC). **GUYANA:** [=Region 8]: Iwokrama Forest, 4.671822, -58.684114, 66m, ex. *Ocotea oblonga*, (*Cognato, Hulcr, Smith, Dole, McCall*), 4-9.iii.2007, 68♂, 42♀ (MSUC). **PANAMA:** *Bocas del Toro*: Corriente Grande, 100 m, 9°17'30"N, 82°32'41"W, 30.iv-5.v.1980, (*H. Wolda*), 1♀; *Canal Zone*: Barro Colorado Island, ex. trap, 9-13.xi.1987, (*H. Wolda*), 3♀ (UCDC); 24.vi.1986, (*H. Wolda*), 1♀ (UCDC); Cooper's nr. source of Rio Ajeta [= along Pipeline Road], 19.viii.1928, (*J. Zetek*), 1♂, 2♀ (NMNH); *Panama*, Parque Nacional Soberanía, Pipeline Rd, 9.166667, -79.75, 95 m, 3.ix.2008, (*S.M. Smith, A.D. Smith, A.R. Gillogly*), 1♂ (MSUC). **PERU:** *Madre de Dios*: Los Amigos Biological Station, -12.56916, -70.100114, 250 m, ex. *Protium amazonicum* (*Smith, Hulcr*) 26.iv.-27.v.2008, 1♂, 2♀ (MSUC). **SURINAME:** *No specific locality*: 'Surinam' 2♂ (MZMC). **VENEZUELA:** *Barinas*: 9 km S Barrancas, ex. *Protium* sp., 6.xii.1970, (*S.L. Wood*), 25♂ 28♀ (MSUC); 40 km E Canton, 100 m, ex. *Protium* sp. 11.iii.1970, (*S.L. Wood*), 2♂, 4♀ (MSUC); 10 km SE Miri, 150



m, ex. *Protium* sp., 9.ii.1970, (S.L. Wood), 4♂, 2♀ (MSUC). **NO SPECIFIC**

**LOCALITY:** ‘Amazons’, 1♂ (MZMC); ‘Cujam’[?] 7♂, 2♀ (DEI).

**Distribution.** Argentina (Chaco), Bolivia (Beni, La Paz), Brazil (Amazonas, Bahia, Brasília, Mato Grosso, Pará, Parana, Pernambuco, Rio de Janeiro, Santa Catharina, São Paulo), Colombia (Bogotá, Cauca, Choco, Putumayo), Costa Rica, Ecuador (Napó), French Guiana, Guyana, Panama, Peru (Loreto, Madre de Dios), Suriname, Venezuela (Barinas).

**Hosts.** Euphorbiaceae, *Ocotea oblonga* (Meisn.) Mez, *Myrocarpus frondosus* Fr. Allem, Myrtaceae, *Protium* sp. (“Almesca branca” [Brazil], “Almesca vermelha” [Brazil], “Breu branco” [Brazil] (Beaver, 1972)), *Protium amazonicum* Swart, *Protium decandrum* (Aubl.) Marchand, *Protium glabrum* (Rose) Engl. *Protium* sp., *Protium tenuifolium* (Engl.) Engl., *Tetragastris altissima* (Aubl.) Swart.

**Biology.** *C. aeneipennis* colonize large branches ranging from 5 cm diameter to more than 30 cm. Wood (2007) offers a detailed description of the gallery system. Beaver (1972) provides a detailed life history. The galleries closely resemble those of *C. noel*. *C. aeneipennis* aggregate in leaves around host trees and perform maturation feeding on leaves (von Winning, 1929; chapter 2).

**Discussion.** *Camptocerus aeneipennis* from Costa Rica and Bolivia exhibited slight variation in the degree of separation was observed in the sensory claspers of the aedeagus.

*Camptocerus angustior* Eggers

(Figs. 1.21, 1.22)



*Camptocerus angustior* Eggers, 1928: 91. Lectotype, ♂, **BOLIVIA**: Yungas: 1000 m (NMNH). Lectotype designated by Anderson & Anderson (1971: 4).

**Diagnosis.** This species has metallic green elytra. The male of the species is diagnosed by a median tubercle on the apical epistomal margin, constricted proximal epistomal margin, nearly sulcate anterior pronotum margin, less rugose basal half of pronotum, larger, deeper punctures on the pronotum and by shallow strial punctures.

The female is diagnosed from *C. aeneipennis* by the unimpressed striae and cannot be distinguished from *C. noel*. This species occurs at higher elevations (1200-3000m) as compared to *C. aeneipennis* or *C. noel*.

**Description.** Male 5.0 – 5.8 mm long ( $\bar{x}$  = 5.5 mm; n = 4); 1.9 – 2.0 times as long as wide. Head, antennae, thorax, abdomen and legs black; elytra metallic bronze to black.

Apical epistomal margin armed with a median tubercle; lateral margin of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to greater than quarter length of head; basal epistomal margin armed with a transverse, concave carina; proximal margin distinctly constricted; frons strongly excavated and densely covered with long white to yellow hair-like setae; margin of excavation lined with a single row of long hairs; frons and epistoma smooth, shining; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; funicle segments 2-7 with brushes of setae equal of length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Pronotum anterior margin declivious, margin between eyes lined with fine bifid setae; pronotum glabrous, smooth, shining; minutely punctate; lateral margin type B;

basal half deeply rugose creating a wrinkled appearance; transverse medial groove on base; base straight.

Elytra glabrous; minutely punctate; elytra smooth; striae not impressed; interstriae punctures strongly confused; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female specimen missing majority of frons. Female similar to male except epistoma with a small median tubercle; antennal funicle segments 4-7 with setae on dorsal margin less than length of two funicular segments; gena with crescent shaped mycangium. Pronotum anterior margin weakly sulcate; margin between the eyes lined with scales; pronotum smooth, shining; transverse medial groove on base absent.

**Specimens examined.** (5♂, 1♀)

*Type material.* Lectotype, *Camptocerus angustior*, ♂ (NMNH); Paratypes, **BOLIVIA:**

*No specific locality:* 'Bolivia', 1♂ (BMNH) 1♀ (NMNH); **COLOMBIA:** *Tolima:* (Natagaima), E. Pehlke S., 1915, (*M. Hagedorn*), 1♂ (NMNH).

*Other material.* **PERU:** *Junin:* Utcuyacu, Tarms, iii.1948, (*F. Woytkowski*), 1♂ (AMNH); 1600–3000 m, 12.iii.1948, (*F. Woytkowski*), 1♂ (AMNH).

**Discussion.** Female is badly damaged and is missing most of head. *Camptocerus pseudoangustior* is commonly identified as *C. angustior* in collections and keys (Wood 2007).

**Distribution.** Bolivia (La Paz), Colombia (Tolima), Peru (Junín).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus aterrimus* Eggers

(Figs. 1.25, 1.26)

*Camptocerus aterrimus* Eggers, 1933: 12. Holotype, ♀, French Guiana: Passoura [=River] (MNHN).

**Diagnosis.** This species is black with dark brown gena and legs. The species is distinguished by its black color; median tubercle on the apical epistomal margin; anterior pronotum margin weakly sulcate (nearly round); groove on pronotum base, and mostly uniseriate discal interstitial punctures.

Females are distinguished from *C. pseudoangustior* by the smaller size and by the larger, deeper punctures on declivital striae.

**Description.** Male 3.1 – 4.5 mm long ( $\bar{x}$  = 3.9 mm; n = 20); 1.7 – 2.2 times as long as wide. Head, antennae, thorax, legs, abdomen and elytra and legs black; gena and coxa red brown.

Apical epistomal margin with a median tubercle; lateral margin of epistoma sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to less than quarter length of head; basal epistomal margin armed with a transverse, concave carina; tuft of thick apically rounded setae above scape insertion; frons strongly excavated and densely covered with long white hair-like setae; margin of excavation lined with a single row of long hairs; hairs near ocular margin with their apex flattened; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; frons and epistoma smooth, shining; funicle segments 2-7 with brushes of setae equal of

length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal declivity weakly sulcate (nearly round), margin between eyes lined with fine bifid setae; pronotum glabrous, smooth, shining; minutely punctate; lateral margin type B; basal half deeply rugose creating a wrinkled appearance; transverse medial groove on base; base straight.

Elytra glabrous; interstriae punctures strongly confused on disk; elytra smooth; striae not impressed; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten longer than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat with a triangular impressed area originating between the eyes and terminating at the distal and lateral epistoma margins, the triangle is bisected by a shallow carina on the median line; frons ornamented with few short setae; frons shagreen, covered with small, deep punctures; dorsal and lateral margins reticulate; antennal funicle segments 4-7 with setae on dorsal margin less than length of two funicular segments; gena with crescent shaped mycangium. Pronotum anterior margin between the eyes lined with scales; pronotum smooth, shining; transverse medial groove on base absent.

**Specimens examined.** (32♂, 93♀)

*Type Material.* FRENCH GUIANA: Passoura [River], vi.1907, (*E. Le Moult*), ♀ (MNHN).

*Other material.* **BRAZIL:** Amazonas: 69 km N Manaus, 7.xii.1979, (*G. Stevens*), 8♂, 7♀ (NMNH); Manaus, 'Corcovado, N.P.' [error?- this park is in Costa Rica], 26.xi.1979, (*G. Stevens*), 1♀, (NMNH); Mato Grosso: 12° 31'S, 51° 46'W, R.S. & R.G.S. Exped, 12-18.xi.1968, ex. dry forest, (*O.W. Richards*) 1♂ (BMNH; [Mato Grosso]: 12° 31'S, 51° 46'W, RS-RGS, 12-18.xi.1968, (*R.A. Beaver*), 6♂, 8♀ (NMNH); Rondônia: BR: 364, km 48, 27.ix.1979, armadilha de malaise [=malaise trap], (*Cecili Blancardi*), 1♂ (NMNH).

**ECUADOR:** Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, vii.1994, (*T.L. Erwin et al.*), lot 744, 2♂, 1♀, (NMNH); x.1994, lot 936, 1♀, (NMNH); i.1995, lot 961, 1♂, (NMNH); x.1995, lot 1265, 3♂, 4♀ (NMNH); x.1995, lot 1495, 1♂ (NMNH); x.1996, lot 1755, 1♂, 2♀ (NMNH).

**GUYANA:** [=Region 8]: Iwokrama Forest, Pakalau hills, 4.748333, -59.026667, 70 m, ex. beating treefall litter, 27.v.2001, (*R. Brooks, Z. Falin*), 1♂, (SMEC); ex. on bark, downed tree, 27.v.2001, (*R. Brooks, Z. Falin*), 1♂, (SMEC).

**PERU:** Madre de Dios: Los Amigos Biological Station, -12.56916, -70.100114, 250 m, 10-16.v.2008, (*Smith, Hulcr*) 2♂, 45♀ (MSUC); 17-25.v.2008, (*Smith, Hulcr*) 3♂, 24♀ (MSUC); Tampopata, 15 km NE Puerto Maldonado, Maldonado Reserva Cuzco Amazonico, Quebrada Mariposa, -12.55, -69.55, 200 m, flight intercept trap, 13-15.vi.1989, (*A. Leschen*), 1♂, (SMEC); *No specific locality:* 'Ibaria' (?), Rio Pachitea, 120 m, 10.xii.1967, (*R. Garcia*), 1♂, (MUSM).

**Distribution.** Brazil (Amazonas, Mato Grosso, Pará, Rondônia), Ecuador (Napo), French Guiana, Guyana, Peru (Madre de Dios).

**Hosts.** *Protium amazonicum*, *Protium* sp. ("Almesca branca" [Brazil], "Almesca vermelha" [Brazil], "Breu branco" [Brazil]) (Beaver, 1972).

**Biology.** *C. aterrimus* infest 2 - 5 cm diameter branches and create a vertical maternal gallery extending above and below the entrance tunnel in the pith of small branches and twigs. Two short radial maternal galleries may also be created in larger stem. Females lay single eggs along the maternal gallery in wide niches cut at right angles to the gallery and plugged with boring dust. Larvae enlarge their cradles parallel to the maternal gallery and parallel to the grain of wood. Beaver (1972) provides a detailed description of the life history.

*Camptocerus distinctus* Smith & Cognato, **sp. n.**

(Figs. 1.36, 1.37)

**Type Material.** *Holotype*, ♂, **ECUADOR: Napo:** Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 613 (NMNH held in trust for MECN). *Paratypes*, **ECUADOR:** 2♀, *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 613 (NMNH) 1♂, 1♀ (MSUC).

**Diagnosis.** This species is solid black. The male of the species is diagnosed by the shining, black elytra, each elytron with eight rugae on the discal sutural interspace to second interstria; each rugae with a single setae arising from the center; large median tubercle on the apical epistomal margin, the vertical carinae on the lateral margins of the epistoma; basal epistomal margin tumid above scape insertion; erect frons setae, and the absence of a groove on the basal margin of pronotum.

The female is diagnosed by the eight rugae on the discal sutural interspace of each elytron, each rugae with a single setae arising from the center and reticulate frons.

**Description.** Male 5.3 mm long ( $\bar{x} = 5.3$  mm;  $n = 2$ ); 1.9 – 2.1 times as long as wide.

The head, antennae, thorax, legs abdomen and elytra are shining black.

Apical epistomal margin with a median tubercle; lateral margin of epistoma with a vertical sub-acute costa; epistoma strongly excavated; expanded to greater than quarter length of head; epistoma covered with a few short setae; basal epistomal margin tumid above scape insertion; frons strongly excavated and moderately covered with erect, fine, long pale hair-like setae; excavation borders the ocular margin; margins of excavation rounded and lined with a single row of long hairs; frons and epistoma reticulate; male scape elongate and expanded distally; glabrous on proximal quarter; setae on ventral half, one third length of scape; funicle segments 2-7 with brushes of setae equal length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin rounded; margin between the eyes glabrous; surface smooth, shining, glabrous; finely punctate; lateral margin type B; base recurved.

Elytra glabrous; eight rugae on the discal sutural interspace to second interstria of each elytron, each rugae with a single setae arising from the center, striae not impressed, punctures small, minute; interstriae punctures strongly confused, minute; base never with a tumescence from seventh to ninth interstriae; scutellum type H; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; epistoma moderately covered with setae; frons flat with a triangular impressed area originating near the vertex and terminating at the distal and lateral epistoma margins, the triangle is

bisected by a shallow carina on the median line; frons ornamented with few short setae; basal epistomal margin tumid above scape insertion; frons sparsely covered with short, fine setae; frons reticulate, covered with moderate, deep punctures; antennal funicle segments 5-7 with setae on ventral and dorsal margins less than the length of two funicular segments; gena with crescent shaped mycangium. Rugae and setae on sutural interspace smaller, nearly indistinct.

**Etymology.** *Distinctus* (L) = distinct. This species possesses numerous distinct apomorphies and is very different from other *Camptocerus* species.

**Specimens examined.** (2♂, 4♀)

**Distribution.** Ecuador (Napo).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus hirtipennis* Schedl **status n.**

(Figs. 1.40, 1.41)

*Camptocerus hirtipennis* Schedl, 1973:165. Holotype, ♂, BRAZIL: Amazonas: Tefe; (MZUSP).

**Diagnosis.** This species has a dark brown pronotum and black elytra. The elytra is densely covered with short, recumbent golden hairs. This species is closely related to *C. suturalis* and the male is distinguished by the larger size, solid black elytra, arcuate costa pointing out on the lateral margin of the epistoma, partially sulcate anterior pronotum margin, rugose basal medial area of pronotum.



The female is diagnosed from *C. suturalis* by the solid black elytra and vestiture as mentioned above, scales on the pronotum anterior margin, groove mycangium on gena and enlarged punctures on vertex.

**Description.** Male 4.9 – 5.6 mm long ( $\bar{x}$  = 5.0 mm; n = 9); 1.9 – 2.2 times as long as wide. Head, antennae, thorax, legs, abdomen and elytra and legs dark black or brown. The body, except pronotum disc, is entirely covered by dense recumbent, hair-like golden setae. Setae are often abraded.

Apical epistomal margin unarmed; lateral margin of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated; expanded to greater than quarter length of head; epistoma covered with a few short setae; basal epistomal margin armed with a glabrous, transverse, concave carina; frons strongly excavated and densely covered with long golden yellow hair-like setae; margin of excavation lined with a single row of long hairs; frons and epistoma shagreen; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; funicle segments 2-7 with brushes of setae 1.5 times the length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal declivity partially sulcate, margin between eyes lined with fine bifid setae; pronotum glabrous, minutely punctate; lateral margin type B; long yellow setae on anterior fifth, vestiture emarginate at median line; setae diagonally extend along the lateral margin from the anterolateral margin; basal margin with a row of short setae, setae twice as long on medial third; basal half deeply rugose creating a wrinkled appearance; base straight.

Elytra densely covered with long recumbent golden hairs on both striae and interstriae; striae not impressed, punctures wide, deep; interstriae punctures strongly confused, minute half as deep at striae; interstriae with 2-4 rows of setae on disc interstriae; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat; with a triangular impressed area originating between the eyes at the ventral end of a weak impression and terminating at the distal and lateral epistoma margins, the triangle is bisected by a shallow carina on the median line; frons ornamented with short, moderately dense setae; frons shagreen, covered with moderate, deep punctures; antennal funicle segments 5-7 with setae on dorsal margin less than length of two funicular segments; gena with crescent shaped mycangium. Anterior pronotal margin rounded, margin between eyes lined with scales; pronotum smooth, shining.

**Specimens examined.** (8♂, 13♀)

*Type material.* Allotype, **BRAZIL: Amazonas:** Tapurucuara am Rio Negro, 29.xi.1962, (C. Lindemann), ♀ (NHMW).

*Other material.* **BRAZIL: Amazonas:** Hwy ZF 2, km 20.7, ca 60km N. Manaus, 2°30'S, 60°15'W, 16.viii.1979, (Adis, Erwin, Montgomery et al.), ex. canopy fogging 1♀ (NMNH); 69 km N Manaus, 7.xii.1979, (G. Stevens), 7♂, 7♀ (NMNH). **ECUADOR:** Napo: Tiputini Biodiversity Station, -0.631944, -76.144167, 220-250 m, ex. canopy fogging, vi.1998, (T.L. Erwin et al.), lot 1853, 1♀ (NMNH); vi.1998, lot 1867, 1♀

(NMNH); vi.1998, lot 1892, 1♂ (NMNH); x.1998, lot 1955, 1♀ (NMNH); x.1998, lot 1988 1♀ (NMNH).

**Discussion.** This species was previously considered a synonym of *Camptocerus suturalis* by Wood (1992). Holotype comparison indicated the resurrection of *C. hirtipennis* based on the solid black color of the elytra, the presence of mycangia on the gena, dense vestiture restricted to the anterior margin of the pronotum, the larger size, and by male genitalia.

**Distribution.** Brazil (Amazonas), Ecuador (Napó).

**Hosts.** Unknown.

**Biology.** Unknown.

*Camptocerus mandelshtami* Petrov

(Figs. 1.53, 1.54)

*Camptocerus mandelshtami* Petrov, 2007:101. Holotype ♂: Peru: Loreto: 68km SW from Iquitos to Itaya river, 4°11'S 73°26'W, 120 m, A. Petrov (ZMMU).

**Diagnosis.** This species is distinguished by a bicolored pronotum (posterior fifth - two fifths orange, anterior black) and other color pattern described below. Elytra glabrous. Males of this species are distinguished a median tubercle on the apical epistoma margin, strongly rugose basal medial region of pronotum, pronotum anterior margin sulcate, and medial groove on pronotum base.

Females are distinguished by the color pattern and by a black frons with an orange area from the vertex to epistoma.

**Description.** Male 5.9 – 6.5 mm long ( $\bar{x}$  = 6.3 mm; n = 6); 1.8 – 2.0 times as long as wide. Head and antennae, dark red brown; pronotum bicolored (anterior fifth to two-fifth's orange remainder black), profemur and protibia red orange, remaining legs black; thorax, abdomen and elytra black.

Apical epistomal margin with a median tubercle; lateral margin of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to less than quarter length of head; basal epistomal margin armed with a transverse, concave carina; tuft of thick apically rounded setae above scape insertion; frons strongly excavated and densely covered with long gold hair-like setae; margin of excavation lined with a single row of long hairs; hairs near ocular margin with their apex flattened; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; frons and epistoma smooth, shining; funicle segments 2-7 with brushes of setae equal of length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal declivity entirely sulcate, margin between eyes lined with fine bifid setae; pronotum glabrous; smooth, shining; minutely punctate; lateral margin type B; basal three-quarters deeply rugose creating a wrinkled appearance; transverse medial groove on base; base straight.

Elytra glabrous, shining; interstriae punctures strongly confused on disk; punctures shallow, minute; elytra smooth; striae not impressed; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat; with a triangular impressed area originating between the eyes and terminating at the distal and lateral epistoma margins, the triangle is bisected by a shallow carina on the median line; medial impressed triangular region orange; frons sparsely covered with short setae; frons shagreen, covered with large, deep punctures; antennal funicle segments 1-7 with setae on dorsal and ventral margins less than length of two funicular segments; gena with crescent shaped mycangium. Anterior pronotal declivity partially sulcate, margin between the eyes lined with scales; pronotum smooth, shining; transverse medial groove on base absent.

**Specimens examined.** (11♂, 13♀)

*Type Material.* Unable to examine type material.

*Other material.* **ECUADOR:** *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778,-76.433333, 220 m, ex. canopy fogging, x.1994, (*T.L. Erwin et al.*), lot 952, 3♂ (NMNH); vii.1995, lot 1082, 2♂, 4♀ (NMNH); x.1995, lot 1222, 1♀ (NMNH); x.1995, lot 1254, 1♂ (NMNH); vii.1996, lot 1604, 1♂, 1♀ (NMNH); x.1996, lot 1712, 2♀ (NMNH); vi.1998, lot 1856, 2♀ (NMNH). **PERU:** *Loreto:* 70km SSW from Iquitos to Nauta, left bank of Amazon River, 140 m, 23.ii.2008, (*A. Petrov*), 3♂, 2♀ (MSUC); 29.ii.2008, 1♂, 1♀ (MSUC).

**Distribution.** Ecuador (Napo), French Guiana, Peru (Loreto).

**Hosts.** *Protium* spp.

**Biology.** Petrov (2007) provides a detailed account of the gallery system, which appears to resemble that of *C. aeneipennis*.

*Camptocerus noel* Smith & Cognato, sp. n.

(Figs. 1.57, 1.58)

**Type Material.** *Holotype*, ♂, **PERU:** Loreto: 1.5km N Teniente Lopez, 2°35'S 76°6.92'W, 210-240m, ex. flight intercept trap #134, 20.vii.1993, (*Richard Leschen*) (SMEC); **BOLIVIA:** La Paz: Chuma [dubious locality due to high elevation and cold climate]: xii.1936 (*Y. Mexia*), 6♂, 4♀ (CAS). **BRAZIL:** Amazonas: AM 010, km 26, Reserva Ducke, ex. malaise trap, 27.ix.1978, (*J. Arias*), 1♀ (NMNH); Manaus, ii.1944, (*Praetorius*), 1♀ (AMNH); Mato Grosso: 12° 50'S, 51° 45'W, Roy. Soc.-Roy. Geogr. Soc. Aavantina-Cachimbo Exped. 1967-1969, coll. 1968 (*B.E. Freeman*) 1♂ (BMNH); [Minas Gerais]: Sete Lagoas, 1♀ (MZMC); Para: Benevides, ii.1895, (*Gounelle*), 2♀ (DEI); Rio de Janeiro: (*Kirsch*), 1♀ (SMTD); Santa Catharina: Joinville, ?.ii.1920, (*Melzer*), 1♀ (DEI); No specific locality: 'São Paulo', 13♀ (DEI); 'Brasil', (*W. Müller*), 2♀ (SMTD); 'Brasilia', 1♀ (MZMC); 'Brazilien', (*Kratz*), 1♀ (DEI); 'Rio Madeira' [river runs through states of Rondônia and Amazonas], Madeira – Mamore R.R. Co Camp 35, (*Mann, Baker*) 2♂ (NMNH). **COLOMBIA:** Santa Fe de Bogotá [=Bogotá D. C.], 1♂ (DEI). **ECUADOR:** [Esmeraldas]: Cachabé: low e., xii[18]96 (*Rosenberg*) 1♂ (BMNH); Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, i.1994, (*T.L. Erwin et al.*), lot 599, 1♀, (NMNH); i.1994, lot 602, 1♀ (MSUC); .1994, lot 751, 1♂ (MSUC); vii.1994, lot 763, 1♂ (NMNH); vii.1994, lot 774, 1♀ (NMNH); vii.1994, lot 776, 1♂ (NMNH); vii.1994, lot 777, 1♀ (NMNH); vii.1994, lot 778, 2♂, 1♀ (NMNH); i.1995, lot 952, 3♂, 1♀ (NMNH); i.1995, lot 1030, 1♀ (NMNH); vii.1995, lot 1082, 1♂ (NMNH); x.1995, lot 1179, 2♀ (NMNH); x.1995, lot 1217, 1♂ (NMNH); i.1996, lot 1452, 1♂, 1♀ (NMNH), 1♀ (MSUC); vii.1996, lot

1572, 1♂ (MSUC); vii.1996, lot 1604, 2♂ (MSUC), 2♀ (NMNH); vii.1996, lot 1618, 1♂ (NMNH); vi.1998, lot 1853, 1♂ (NMNH); vi.1998, lot 1856, 1♂, 1♀ (NMNH); x.1998, lot 1949, 1♂ (NMNH); ii.1999, lot 1856, 1♂ (NMNH); *Pastaza*: Cusuimi, Rio Cusuimi, 150 km SE of Puyo, 320 m, 15-31.v.1971, (*B. Malkin*), 1♀ (FMNH). **FRENCH GUIANA**: *No specific locality*: ‘Cayenne’, 1♀ (MZMC); ‘Cayenne’, 1915, (*Felsche Geschenk*), 1♂, 1♀ (SMTD); ‘French Guiana’, 1♀ (NMNH). **GUYANA**: [=Region 8]: Iwokrama Forest, 4.671822,-58.684114, 66 m, ex. *Ocotea oblonga*, 4-9.iii.2007, (*Cognato, Hulcr, Smith, Dole, McCall*), 6♂, 4♀ (MSUC). **PERU**: [*Huánuco*]: 15 mi NE of Tingo Maria, 700 m, 11.xi.1954, (*E.I. Schlinger, E.S. Ross*), 4♀ (CAS); *Junín*: Satipo, xii.1943, (*Paprzycki*), 1♂ (NMNH); *Loreto*: Iquitos [province not specified, Iquitos is in Loreto], iii-iv.1931, (*R.C. Shannon*), 1♀ (NMNH); *Madre de Dios*: Los Amigos Biological Station, -12.56916, -70.100114, 250 m, ex. *Protium amazonicum*, 26.iv.-27.v.2008, (*Smith, Hulcr*) 36♂, 44♀. **SURINAME**: *Saramacca*: W Suriname Rd, 108 km WSW Zanderij Airport, 5°13’35N, 55°52’54”W, 30 m, ex. flight intercept trap, 8-10.vi.1999, (*Z.H. Falin, B. DeDijn*), 1♂ (SMEC). **VENEZUELA**: *Amazonas*: Cerro de la Neblina, 1 km S Basecamp, 0°50’N, 66°10’W, 140 m, ex. along a small whitewater stream; pools of dead leaves & sticks, 11.ii.1985, (*P.J. & P.M. Spangler, R. Faitoute, W. Steiner*), 1♂ (NMNH).

**Diagnosis.** This species has metallic elytra and is closely related to *C. aeneipennis*. The male is distinguished by larger size, smooth elytral disk, shallow stria punctures and a deep sulcus on the anterior pronotum extending to median line.

The female is diagnosed from *C. aeneipennis* by the larger size and shallow stria punctures.

**Description.** Male 6.0 – 7.1 mm long ( $\bar{x}$  = 6.6 mm; n = 20); 1.8 – 2.0 times as long as wide. Head, thorax, antennae and legs red-brown; pronotum commonly crimson, but may also be black; abdomen black; elytra versicolor, ranging in color from metallic bronze to metallic green; rarely metallic blue in Peru and Bolivia.

Apical epistomal margin is unarmed; lateral margins of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to greater than quarter length of head; basal epistomal margin armed with a transverse, concave carina; frons strongly excavated and densely covered with long white to yellow hair-like setae; margin of excavation lined with a single row of long hairs; frons and epistoma smooth, shining; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; funicle segments 2-7 with brushes of setae equal of length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal margin with a lateral declivity extending to median line, margin between eyes lined with fine bifid setae; pronotum glabrous; finely, minutely punctate; lateral margin type B; basal half minutely punctate; elytra smooth; striae not impressed; interstriae punctures strongly confused; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat with a triangular impressed area originating between the eyes and terminating at the distal and lateral epistoma margins, the triangle is bisected by a shallow carina on the median



line. Frons ornamented short sparse setae; frons rugose, covered with moderate, deep punctures; antennal funicle segments 1-7 with setae on dorsal and ventral margins less than length of two funicular segments; gena with crescent shaped mycangium. Anterior pronotal declivity weakly sulcate, margin between eyes lined with scales; pronotum smooth, shining.

**Etymology.** *noel* (English) = Christmas (used as a noun in apposition). This species commonly display 'Christmas' colors: crimson pronotum and brilliant metallic green elytra.

**Specimens examined.** (77♂, 99♀)

**Distribution.** Bolivia (La Paz), Brazil (Amazonas, Mato Grosso, Minas Gerais, Para, Rondônia?, Rio de Janeiro, Santa Catharina, São Paulo), Colombia (Bogotá), Ecuador (Esmeraldas, Napo, Pastaza), Guyana, Peru (Huánuco, Junín, Loreto, Madre de Dios), Suriname, Venezuela (Amazonas).

**Hosts.** *Ocotea oblonga* (Meisn.) Mez, *Protium amazonicum* Swart.

**Biology.** *C. noel* colonize large branches ranging from 5 cm diameter to more than 20 cm. Females create an entrance tunnel running in a transverse plane toward the center of the stem. From this tunnel, one or two circumferential branches are added creating maternal galleries. The galleries closely resemble those of *C. aeneipennis*. *C. noel* aggregate in leaves around host trees (Chapter 2) and perform maturation feeding on leaves as (von Winning, 1929; chapter 2).

**Discussion.** *Camptocerus noel* has been considered *C. aeneipennis* for many years and is identified as *C. aeneipennis* in collections. However, the male genitalis clearly diagnoses the species. The apex of the median lobe is rounded in *C. noel* (mushroom shaped in *C.*

*aeneipennis*); the sensory claspers are spatulate in *C. noel* (scythe shaped in *C. aeneipennis*). In addition to the morphological characters the validity of this species is supported by molecular characters. The species is differentiated from *C. aeneipennis* by a 12.5% sequence divergence of mitochondrial cytochrome oxidase 1 and has a 5bp insertion in the D2F1-D3R2 region of nuclear ribosomal 28S. Little nucleotide variation is seen within each species (Smith & Cognato, unpublished).

Geographic variation was found in several species, but most notable is the size differences and slight color variation of *C. noel*. The elytra of *C. noel* is a brilliant metallic green in northern South America and the color changes to a metallic bronze in southern Peru and to metallic blue in southern Peru and Bolivia. Color also varies between teneral and mature adults; mature adults are darker colored.

*Camptocerus pseudoangustior* Smith & Cognato, sp. n.

(Figs. 1.69, 1.70)

**Type Material.** *Holotype* ♂, **ECUADOR:** *Pastaza:* Cononaco, ex. malaise trap, 29.iv.1976, (*J. Cohen*) (NMNH). *Paratypes*, **BRAZIL:** *Amazonas:* km 60 N Manaus, 18.1 km E Campinas field station, 2° 30'S, 60°15'W, ex. terra firme forest fogged with pyrethrum, (*Montgomery, Erwin, Schimmel, Krischik, Date, Bacon*), sample 20, 22.ii.1979, 1♀ (NMNH); Manaus, 1 km W Taruma Falls, 100 m, 2.iii.1981, (*C. Young*), 1♀ (RJRC); 69 km N Manaus, 7.xii.1979, (*G. Stevens*) 1♂, 1♀ (NMNH); Teffé (Ega) '7bre-8bre.1879' (*M. de Mathan*), 1♀ (NMHW); *Pará:* Santarém 1♂ (BMNH); 'Par á' 1♀ (BMNH). **ECUADOR:** *Napo:* Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778, -76.433333, 220 m, ex. canopy fogging, vii.1994, (*T.L. Erwin et al.*),

lot 684, 1♂ (NMNH); vii.1995, lot 1125, 1♀ (NMNH); x.1995, lot 1185, 1♂ (NMNH);  
 x.1995, lot 1265, 1♂ (NMNH); vii.1996, lot 1615, 2♂, 1♀ (MSUC), 1♀ (NMNH);  
 x.1996, lot 1755, 1♂ (NMNH); Tiputini Biodiversity Station, -0.631944, -76.144167,  
 220-250 m, ex. canopy fogging, vi.1998, (*T.L. Erwin et al.*), lot 1876, 1♂ (NMNH);  
 x.1998, lot 1927, 1♀ (NMNH); vi.1998, lot 1950, 1♀ (MSUC); *Pastaza*: Cononaco, ex.  
 malaise trap, 29.iv.1976, (*J. Cohen*), 1♂, 2♀ (NMNH); **PERU**: [=Amazonas]: ‘Peru, Rio  
 Santiago’ xi.12.1924, 1♀ (AMNH); [*Huánuco*]: 15 mi NE of Tingo Maria, 700 m  
 11.xi.1954, (*E.I. Schlinger, E.S. Ross*), 1♀ (NMNH); *Loreto*: 58 km SSW from Iquitos to  
 Nauta, Itaya river 120m, 6.ii.2007, (*A. Petrov*) 1♂ (MSUC); *Madre de Dios*: Los Amigos  
 Biological Station, -12.56916, -70.100114, 250 m, ex. *Protium amazonicum*, 10-  
 16.v.2008, (*Smith, Hulcr*) 5♂, 27♀ (MSUC); 7-25.v.2008, (*Smith, Hulcr*) 3♂, 4♀  
 (MSUC); Z.R. Tampopata, 300 m, iv-v.1986, (*I. Bohórquez*), 1♀ (MUSM); **NO**  
**SPECIFIC LOCALITY**: ‘Bassin de l’Amazone’, [Amazon Basin] 1913, (*Guilhermo*  
*Hoffmann*) [Eggers cotype *Camptocerus aterrimus*] 1♂ (NHMW).

**Diagnosis.** This species is black with dark brown gena and legs. Males are distinguished by the generally larger body size, median tubercle on the apical epistoma margin, transversely impressed, groove on pronotum base, basal medial pronotum region strongly rugose disk, elytral interstitial punctures mostly confused.

Females are distinguished from *C. aterrimus* larger size and smaller, shallower punctures on declivital striae.

**Description.** Male 4.5 – 5.4 mm long ( $\bar{x}$  = 5.1 mm; n = 18); 1.7 – 2.0 times as long as wide. Head, antennae, thorax, abdomen and elytra and legs black; gena and legs dark red brown.

Apical epistomal margin with a median tubercle; lateral margin of epistoma with a sub-acute arcuate costa pointing distally; epistoma strongly excavated, expanded to less than quarter length of head; basal epistomal margin armed with a transverse, concave carina; tuft of thick apically rounded setae above scape insertion; frons strongly excavated and densely covered with long white hair-like setae; margin of excavation lined with a single row of long hairs; hairs near ocular margin with their apex flattened; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; frons and epistoma smooth, shining; funicle segments 2-7 with brushes of setae equal of length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal declivity entirely sulcate, margin between the eyes lined with fine bifid setae; pronotum glabrous; smooth, shining; minutely punctate; lateral margin type B; basal half deeply rugose creating a wrinkled appearance; transverse medial groove on base; base straight.

Elytra glabrous; interstriae punctures strongly confused on disk; punctures shallow, minute; elytra smooth; elytra smooth; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten longer than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat; a medial impressed triangular region; a shallow carina originating on the median line between the eyes and terminating at the epistoma; frons ornamented short, sparse setae; frons shagreen, covered with large, deep punctures; antennal funicle segments 1-7 with

setae on dorsal margin less than length of two funicular segments; gena with crescent shaped mycangium. Anterior pronotal declivity partially sulcate, margin between eyes lined with scales; pronotum smooth, shining; transverse medial groove on base absent.

**Etymology.** *Pseudo-* (G) = false, - *angustior* = a *Camptocerus* species.

**Specimens examined.** (20♂, 46♀)

**Distribution.** Brazil (Amazonas; Pará), Ecuador (Napó, Pastaza), Peru (Amazonas, Huánuco, Junín, Loreto, Madre de Dios).

**Hosts.** *Protium amazonicum* Swart, *Protium* sp.

**Biology.** *C. pseudoangustior* infest 2 - 5 cm diameter branches. The maternal gallery extends transversely through the stem to near the opposite side. Females create a vertical maternal gallery extending above and below the entrance tunnel in the pith of small branches and twigs. Two short radial maternal galleries are created in larger stem. Females lay single eggs along the maternal gallery in wide niches cut at right angles to the gallery and plugged with boring dust. Larvae enlarge their cradles parallel to the maternal gallery and parallel to the grain of wood. Galleries strongly resemble those of *C. aterrimus*. Beetles aggregate in leaves around host trees and perform maturation feeding on leaves (Chapter 2).

**Discussion.** Specimens of this species have been commonly identified as *C. angustior* in collections and keys (Wood, 2007).

*Camptocerus suturalis* (Fabricius)

(Figs. 1.76, 1.77)

*Camptocerus suturalis* (Fabricius) 1801: 393 (*Hylesinus*). Type locality: 'Essequibo' [River] [=Guyana]; Lectotype ♂ (here designated), UZMC.

*Camptocerus cinctus* Chapuis 1869: 51. Type locality 'Amerique meridionale' [=South America]; Holotype ♀, IRSNB. **syn. n.**

*Camptocerus fasciatus* (Fabricius) 1801: 392 (*Hylesinus*). Type locality: 'Essequibo' [River] [=Guyana]; Lectotype ♂ (here designated), UZMC. Synonymy: Eggers 1929e: 45.

**Notes.** Synonymy of *C. fasciatus* confirmed by Wood (1972: 243).

**Diagnosis.** Both sexes display a unique color pattern described below. The elytra is moderately covered by short recumbent golden hairs on the striae and interstriae. The male is distinguished from other species in the clade by the vertical costae on the lateral margins of the epistoma, and transverse weakly developed carina on the proximal epistomal margin.

The female is recognized by the anterior pronotal margin with setae palmately divided into 3-4 filaments on between the eyes and by the absence of mycangia on the gena or vertex.

**Description.** Male 3.6 – 5.0 mm ( $\bar{x}$  = 4.3 mm; n = 14); 1.8 – 2.1 times as long as wide.

The head, antennae, thorax, pronotum, legs are red-orange to red. Each elytron black with an orange oval spot extending from the lateral margin of the elytral interspace to the tenth interstria and from the basal fifth of elytra to the of apical four-fifths. Body moderately covered by recumbent, hair-like setae. Setae are often abraded.

Apical epistomal margin unarmed; lateral margin of epistoma with a vertical sub-acute costa pointing distally; epistoma strongly excavated; expanded to greater than

quarter length of head; epistoma covered with a few short setae; basal epistomal margin armed with a glabrous, transverse, concave carina; frons strongly excavated and densely covered with long golden yellow hair-like setae; margin of excavation lined with a single row of long hairs; frons and epistoma shagreen; male scape elongate and narrow; glabrous on proximal quarter, setae on ventral half, one third length of scape; funicle segments 2-7 with brushes of setae 1.5 times the length of scape; dorsal margin with setae less than three funicle segments; anterior face of the club setose with a partial septum.

Anterior pronotal declivity partially sulcate, margin between the eyes lined with fine setae palmately divided into three or four filaments; pronotum smooth, covered with recumbent hairs (often abraded); finely punctate, punctures moderately deep; lateral margin type B; base straight.

Elytra densely covered with long recumbent golden hairs on both striae and interstriae (often abraded); striae weakly impressed, punctures small, shallow; interstriae punctures minute, strongly confused; base never with a tumescence from seventh to ninth interstriae; scutellum type A; carina at base of interstria ten shorter than metepisternum; metepisternum with bifid setae; metepisternum type B; mesosternum type A; apex smooth.

Female similar to male except epistoma with a small median tubercle; frons flat with a shallow carina on the median line originating between the eyes and terminating at the epistoma; frons ornamented short, moderately dense setae; frons shagreen, covered with moderate, deep punctures; antennal funicle segments 1-7 with setae on dorsal margin less than length of two funicular segments; mycangia on the gena and vertex absent. Pronotum anterior margin rounded.

**Specimens examined.** (32♂, 31♀, 3 unknown sex)

**Type Material.** Lectotype *Camptocerus suturalis*, ♂ (UZMC); paralectotypes

*Camptocerus suturalis*, **NO LOCALITY**: 1♂, 3♀ (MZMC); Holotype *Camptocerus cinctus*, ♀ (IRSNB); Lectotype *Camptocerus fasciatus*, **NO LOCALITY**: ♂ (MZMC); Paralectotypes *Camptocerus fasciatus*, **NO LOCALITY**: 1♂, 3♀, 1 unknown sex (MZMC).

**Other material:** **BRAZIL:** Amazonas: 69 km N Manaus, (G. Stevens), 7.xii.1979, 1♂ (NMNH). **ECUADOR:** Napo: Reserva Ethnica Waorani, 1 km S Onkone Gare Camp, -0.652778,-76.433333, 220 m, ex. canopy fogging, (T.L. Erwin et al.), lot 859, x.1994, 1♀ (NMNH); lot 3265, vii.2006, 1♀ (NMNH). **GUYANA:** [=Region 8]: Iwokrama Forest, 4.671822, -58.684114, 66 m, ex. *Ocotea oblonga*, 4-9.iii.2007, (Cognato, Hulcr, Smith, Dole, McCall), 11♂, 10♀ (MSUC). **PERU:** Loreto: 68km SW from Iquitos to Nauta, Nauta River, 120 m, 7.ii.2005, (A. Petrov), 12♂, 7♀, 1 unknown sex (MSUC); Madre de Dios: Los Amigos Biological Station, -12.56916, -70.100114, 250 m, ex. *Protium amazonicum* 26.iv.-27.v.2008, (Smith, Hulcr), 2♂, 3♀ (MSUC). **SURINAME:** No specific locality: 'Surinam', (H. Lund), 1♂ (UZMC). **VENEZUELA:** Amazonas: 'Mt. Duida', 4.xi.1928, 1♂ (AMNH). **NO SPECIFIC LOCALITY:** (2♀, 1 unknown sex; UZMC).

**Distribution.** Brazil (Amazonas, Pará), Ecuador (Napo), French Guiana, Guyana, Peru (Loreto, Madre de Dios), Suriname, Venezuela (Amazonas).

**Hosts.** *Ocotea oblonga* (Meisn.) Mez, *Protium amazonicum* Swart, *Protium* sp.

**Biology.** In Guyana, *Camptocerus suturalis* adults create entrance tunnels within 1 mm of *C. aeneipennis* entrance tunnels. The gallery systems of each species are separated by



a thin septum (less than 1mm), allowing fungal mycelium in *C. aeneipennis* galleries to grow into those of *C. suturalis* indicating that *C. suturalis* is likely mycocleptic (Hulcr, 2009). Females create an entrance tunnel running in a transverse plane toward the center of the stem. From this tunnel, two circumferential branches are added creating maternal galleries. Galleries follow those of the ambrosia fungus host and the thin septum is maintained. Females lay single eggs along the maternal gallery in wide niches cut at right angles to the gallery and plugged with boring dust. Niches are only created on the surface opposite to the host gallery. Larvae enlarge their cradles with the grain of the wood. Mycocleptism was also observed in Peru with *Camptocerus suturalis* parasitizing fungus from galleries of *C. noel*, *C. pseudoangustior*, *C. aeneipennis* (Smith, per. ob.) and *C. mandelshtami* (A. Petrov, per. comm.). This species has also been observed aggregating in leaves around host trees (A. Petrov, per. comm.) in the same manner as described in chapter 2.

**Discussion.** Due to its mycocleptic habit and position within *Camptocerus*, *C. suturalis* has likely lost its mycangia.

**Table 1.1:** Biogeographic distribution of *Camptocerus* species:

| Species                        | NA     |        | Central America |          |             |           |            |        |          |          | South America |        |          |               |        |         |      |         |           |          |         |       |  |
|--------------------------------|--------|--------|-----------------|----------|-------------|-----------|------------|--------|----------|----------|---------------|--------|----------|---------------|--------|---------|------|---------|-----------|----------|---------|-------|--|
|                                | Mexico | Belize | Guatemala       | Honduras | El Salvador | Nicaragua | Costa Rica | Panama | Trinidad | Colombia | Venezuela     | Guyana | Suriname | French Guiana | Brazil | Ecuador | Peru | Bolivia | Argentina | Paraguay | Uruguay | Chile |  |
| <i>Camptocerus aeneipennis</i> |        |        |                 |          |             |           | ●          |        |          | ●        |               |        |          |               | ●      |         |      | ●       | ●         |          |         |       |  |
| <i>C. angustior</i>            |        |        |                 |          |             |           |            |        | ●        |          |               |        |          |               |        |         | ●    | ●       |           |          |         |       |  |
| <i>C. annectens</i>            |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. aterrimus</i>            |        |        |                 |          |             |           |            |        |          |          | ●             |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. auricomus</i>            | ●      |        | ●               |          |             | ●         |            | ●      | ●        |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. charpentierae</i>        |        |        |                 |          |             |           |            |        |          |          |               |        |          | ●             | ●      |         |      |         |           |          |         |       |  |
| <i>C. coccoformus</i>          |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. costatus</i>             |        |        |                 |          |             |           |            |        | ●        |          |               | ●      |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. distinctus</i>           |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      | ●       |      |         |           |          |         |       |  |
| <i>C. dolei</i>                |        |        |                 |          |             |           |            |        |          |          |               |        |          |               |        | ●       |      |         |           |          |         |       |  |
| <i>C. hirtipennis</i>          |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      | ●       |      |         |           |          |         |       |  |
| <i>C. igniculus</i>            |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. inoblitus</i>            |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           | ●        |         |       |  |
| <i>C. latipilis</i>            |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |
| <i>C. major</i>                |        |        |                 |          |             |           |            |        |          |          |               |        |          |               | ●      |         |      |         |           |          |         |       |  |

● = present

Table 1.1(cont.): Biogeographic distribution of *Camptocerus* species:

| Species                   | South America |         |          |           |         |      |         |        |               |          |        |           |          | Central America |        |            |           |             |          |           | NA     |        |  |
|---------------------------|---------------|---------|----------|-----------|---------|------|---------|--------|---------------|----------|--------|-----------|----------|-----------------|--------|------------|-----------|-------------|----------|-----------|--------|--------|--|
|                           | Chile         | Uruguay | Paraguay | Argentina | Bolivia | Peru | Ecuador | Brazil | French Guiana | Suriname | Guyana | Venezuela | Colombia | Trinidad        | Panama | Costa Rica | Nicaragua | El Salvador | Honduras | Guatemala | Belize | Mexico |  |
| <i>C. mallopterus</i>     |               |         |          |           |         |      |         |        |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. mandelstami</i>     |               |         |          |           |         | ●    | ●       | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. niger</i>           |               |         |          |           | ●       | ●    | ●       | ●      | ●             | ●        | ●      | ●         | ●        |                 |        |            |           |             |          |           |        |        |  |
| <i>C. noeli</i>           |               |         |          |           | ●       | ●    | ●       | ●      | ●             | ●        | ●      | ●         | ●        |                 |        |            |           |             |          |           |        |        |  |
| <i>C. occidentalis</i>    |               |         |          | ●         | ●       | ●    | ●       | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. opacicollis</i>     |               |         |          |           | ●       | ●    | ●       | ●      |               |          |        |           |          |                 |        | ●          |           |             |          |           |        |        |  |
| <i>C. orientalis</i>      |               |         |          |           | ●       |      |         | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. petrovi</i>         |               |         |          |           |         |      | ●       |        |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. pilifrons</i>       |               |         |          |           |         |      | ●       | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. pseudoangustior</i> |               |         |          |           |         | ●    |         | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. quadridens</i>      |               |         |          |           |         |      |         | ●      |               |          |        |           |          |                 | ●      |            |           |             |          |           |        |        |  |
| <i>C. rectus</i>          |               |         |          |           |         |      | ●       |        |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. suturalis</i>       |               |         |          |           |         |      | ●       | ●      | ●             |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. unicornus</i>       |               |         |          |           |         |      |         | ●      |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |
| <i>C. zuccus</i>          |               |         |          |           |         |      | ●       |        |               |          |        |           |          |                 |        |            |           |             |          |           |        |        |  |

● = present

**Table 1.2: Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

| Species                        | Characters |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |    |
|--------------------------------|------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|
|                                | 1          | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
| <i>Campiocerus aeneipennis</i> | 1          | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 0  | 3  | 1  | 0  |
| <i>C. angustior</i>            | 1          | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 0  | 3  | 1  | 0  |
| <i>C. annectens</i>            | 1          | 0 | ? | ? | ? | ? | ? | ? | ? | ?  | ?  | ?  | ?  | ?  | ?  | 1  | 0  | 2  | 0  | 2  | 2  | 0  |
| <i>C. aterrimus</i>            | 1          | 0 | 0 | 0 | 2 | 2 | 0 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 2  | 0  | 3  | 1  | 0  |
| <i>C. auricomus</i>            | 1          | 0 | 0 | 0 | 0 | 2 | 3 | 1 | 0 | 3  | 1  | 0  | 1  | 3  | 0  | 1  | 0  | 0  | 0  | 2  | 3  | 0  |
| <i>C. charpentierae</i>        | 1          | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2  | 1  | 0  | 0  | 1  | 2  | 1  | 0  | 0  | 0  | 2  | 2  | 0  |
| <i>C. coccoformus</i>          | 1          | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 2  | 1  | 0  | 0  | 0  | 2  | 1  | 0  | 0  | 0  | 2  | 2  | 0  |
| <i>C. costatus</i>             | 1          | 0 | 0 | 1 | 0 | 0 | 6 | 1 | 0 | 1  | 1  | 0  | 0  | 3  | 4  | 1  | 0  | 0  | 0  | 0  | 2  | 0  |
| <i>C. distinctus</i>           | 1          | 0 | 0 | 1 | 0 | 2 | 1 | 1 | 0 | 2  | 1  | 0  | 0  | 2  | 2  | 1  | 0  | 0  | 1  | 3  | 1  | 1  |
| <i>C. dolei</i>                | 1          | 0 | 0 | 1 | 0 | 2 | 1 | 0 | 1 | 2  | 0  | 0  | 0  | 2  | 2  | 1  | 0  | 0  | 0  | 0  | 3  | 0  |
| <i>C. hirtipennis</i>          | 1          | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 1  | 2  | 1  | 0  |
| <i>C. igniculus</i>            | 1          | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 1 | 2  | 1  | 0  | 0  | 1  | 2  | 1  | 0  | 0  | 1  | 2  | 2  | 0  |
| <i>C. inoblitus</i>            | 1          | 0 | 0 | 1 | 0 | 0 | 2 | 1 | 1 | 2  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 2  | 1  |
| <i>C. latipilis</i>            | 1          | 0 | 0 | 1 | 2 | 1 | 1 | 1 | 0 | 2  | 1  | 0  | 0  | 0  | 2  | 1  | 0  | 0  | 0  | 2  | 2  | 1  |
| <i>C. major</i>                | 1          | 0 | ? | ? | ? | ? | ? | ? | ? | ?  | ?  | ?  | ?  | ?  | ?  | 1  | 0  | 0  | 1  | 0  | 2  | 0  |
| <i>C. mallopterus</i>          | 1          | 0 | 0 | 1 | 0 | 1 | 1 | 1 | 0 | 2  | 1  | 0  | 0  | 2  | 2  | 1  | 0  | 0  | 0  | 2  | 2  | 0  |
| <i>C. mandelshtami</i>         | 1          | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 0  | 3  | 1  | 0  |
| <i>C. niger</i>                | 1          | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 3  | 1  | 0  | 1  | 3  | 0  | 1  | 0  | 0  | 0  | 2  | 3  | 1  |
| <i>C. noeli</i>                | 1          | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 2  | 0  | 3  | 1  | 0  |
| <i>C. occidentalis</i>         | 1          | 0 | 0 | 1 | 0 | 0 | 5 | 1 | 0 | 0  | 1  | 0  | 1  | 3  | 1  | 1  | 0  | 0  | 0  | 2  | 3  | 1  |
| <i>C. opacicollis</i>          | 1          | 0 | 0 | 1 | 2 | 0 | 2 | 1 | 1 | 2  | 1  | 0  | 0  | 1  | 0  | 1  | 0  | 2  | 0  | 2  | 2  | 1  |

**Table 1.2 (cont.): Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

| Species                     | Characters |   |   |   |   |   |   |   |   |    |    |    |    |    |    |    |    |    |    |    |    |    |
|-----------------------------|------------|---|---|---|---|---|---|---|---|----|----|----|----|----|----|----|----|----|----|----|----|----|
|                             | 1          | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 | 21 | 22 |
| <i>C. orientalis</i>        | 1          | 0 | 0 | 0 | 0 | 0 | 3 | 1 | 0 | 3  | 1  | 0  | 1  | 3  | 0  | 1  | 0  | 0  | 0  | 2  | 3  | 0  |
| <i>C. petrovi</i>           | 1          | 0 | 0 | 1 | 1 | 1 | 4 | 1 | 1 | 2  | 1  | 0  | 0  | 1  | 2  | 1  | ?  | ?  | ?  | ?  | ?  | 1  |
| <i>C. pilifrons</i>         | 1          | 0 | 0 | 0 | 0 | 0 | 6 | 1 | 0 | 1  | 1  | 0  | 0  | 3  | 4  | 1  | 0  | 0  | 0  | 0  | 2  | 0  |
| <i>C. pseudoangustior</i>   | 1          | 0 | 0 | 0 | 0 | 2 | 0 | 1 | 0 | 0  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 0  | 3  | 1  | 0  |
| <i>C. quadridens</i>        | 1          | 0 | 0 | 0 | 0 | 0 | 6 | 1 | 0 | 1  | 1  | 0  | 0  | 3  | 4  | 1  | 0  | 0  | 0  | 0  | 2  | 0  |
| <i>C. rectus</i>            | 1          | 0 | 0 | 0 | 0 | 0 | 2 | 1 | 0 | 3  | 1  | 0  | 1  | 3  | 0  | 1  | 0  | 0  | 0  | 0  | 3  | 1  |
| <i>C. suturalis</i>         | 1          | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 2  | 1  | 0  | 0  | 3  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  |
| <i>C. unicolornus</i>       | 1          | ? | 0 | 0 | 0 | 3 | 2 | 1 | 0 | 3  | 1  | 0  | 1  | 1  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | 1  |
| <i>C. zuccus</i>            | 1          | 0 | 0 | 1 | 0 | 0 | 4 | 1 | 1 | 1  | 1  | 0  | 0  | 3  | 4  | 1  | 0  | 0  | 0  | 0  | 2  | 1  |
| <i>Chemomyx boliviae</i>    | 0          | 0 | ? | ? | ? | ? | ? | ? | ? | ?  | ?  | ?  | ?  | ?  | 0  | 0  | 1  | 1  | 0  | 2  | 0  | 1  |
| <i>C. errans</i>            | 1          | 0 | 0 | 0 | 3 | 0 | 4 | 1 | 0 | 4  | 0  | 0  | 0  | 3  | 0  | 1  | 0  | 2  | 0  | 0  | 0  | 0  |
| <i>C. insignis</i>          | 0          | 0 | 0 | 0 | 0 | 4 | 4 | 0 | 0 | 4  | 0  | 0  | 0  | 3  | 0  | 0  | 1  | 1  | 0  | 2  | 0  | 1  |
| <i>C. rugulosus</i>         | 1          | 0 | 0 | 1 | 0 | 0 | 2 | 0 | 0 | 4  | 0  | 0  | 1  | 3  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 1  |
| <i>C. vestitus</i>          | 1          | ? | 0 | 1 | 0 | 0 | 3 | 1 | 0 | 4  | 0  | 0  | 0  | 3  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | 0  |
| <i>Scolytopsis peruanus</i> | 2          | 0 | 0 | 0 | 0 | 0 | 4 | 2 | 0 | 4  | 2  | 0  | 1  | 3  | 3  | 1  | 1  | 2  | 0  | 3  | 0  | 0  |
| <i>Scolytus excavatus</i>   | 2          | 1 | 1 | 0 | 0 | 0 | 4 | 0 | 0 | 3  | 0  | 1  | 0  | 0  | 3  | 1  | 0  | 3  | 0  | 4  | 0  | 0  |
| <i>S. multistriatus</i>     | 2          | 0 | 1 | 0 | 0 | 0 | 4 | 2 | 0 | 4  | 2  | 0  | 0  | ?  | 3  | 1  | 0  | 2  | 0  | 0  | 0  | 0  |
| <i>S. propinquus</i>        | 2          | 1 | 1 | 0 | 0 | 0 | 4 | 2 | 0 | 4  | 2  | 1  | 0  | 1  | 3  | 1  | 0  | 1  | 0  | 2  | 0  | 0  |
| <i>S. schevyrewi</i>        | 3          | 0 | 1 | 0 | 0 | 0 | 4 | 2 | 0 | 4  | 0  | 0  | 0  | 2  | 3  | 1  | 0  | 2  | 0  | 0  | 0  | 0  |
| <i>S. ventralis</i>         | 2          | 0 | 1 | 0 | 0 | 0 | 4 | 2 | 0 | 4  | 2  | 0  | 0  | 2  | 3  | 1  | 0  | 2  | 0  | 0  | 0  | 0  |

**Table 1.2 (cont.): Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

| Species                       | Characters |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|-------------------------------|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
|                               | 23         | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Campocerus aeneipennis</i> | 1          | 3  | 1  | 1  | 1  | 0  | 1  | 1  | 0  | 1  | 2  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. angustior</i>           | 1          | 3  | 1  | 1  | 0  | 1  | 1  | 1  | 0  | 1  | 2  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. anneiens</i>            | 0          | ?  | ?  | 0  | 0  | ?  | ?  | 4  | 2  | 1  | 1  | 1  | 3  | ?  | 0  | 4  | 1  | 1  | 1  | 1  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. aterrimus</i>           | 1          | 3  | 1  | 1  | 0  | 1  | 1  | 1  | 0  | 1  | A  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. auricomus</i>           | 1          | 1  | 0  | 0  | 0  | 0  | 2  | 5  | 2  | 1  | 5  | 1  | 6  | 2  | 0  | 2  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. charpentierae</i>       | 1          | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 2  | 1  | 4  | 1  | 2  | 4  | 1  | 1  | 1  | 0  | 0  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. coccoformus</i>         | 1          | 1  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | 2  | 1  | 2  | 3  | 1  | 1  | 1  | 0  | 1  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. costatus</i>            | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 1  | 1  | 4  | 1  | C  | 1  | 2  | 8  | 1  | 0  | 1  | 1  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. distinctus</i>          | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 7  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. dolei</i>               | 1          | 1  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | A  | 1  | H  | 4  | 0  | 3  | 1  | 0  | 1  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. hirtipennis</i>         | 1          | 3  | 1  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 3  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. igniculus</i>           | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | 2  | 1  | 2  | 4  | 1  | 1  | 1  | 0  | 0  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. inoblitus</i>           | 1          | 0  | 0  | 0  | 0  | 0  | 2  | 4  | 2  | 1  | 6  | 1  | 3  | 2  | 1  | 4  | 1  | 1  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. latipilis</i>           | 1          | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | 7  | 1  | 2  | 4  | 0  | 1  | 1  | 0  | 0  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. major</i>               | 1          | ?  | ?  | 0  | 0  | ?  | ?  | 4  | 0  | 1  | 1  | 1  | 3  | ?  | 1  | 4  | 1  | 1  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. mallopterus</i>         | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | 5  | 1  | 2  | 3  | 1  | 1  | 1  | 0  | 1  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. mandelshtami</i>        | 1          | 3  | 2  | 1  | 0  | 1  | 1  | 1  | 0  | 1  | 2  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. niger</i>               | 1          | 1  | 0  | 0  | 0  | 0  | 4  | 5  | 2  | 1  | 5  | 1  | 6  | 2  | 0  | 2  | 1  | 0  | 0  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. noeli</i>               | 1          | 3  | 1  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 1  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. occidentalis</i>        | 1          | 1  | 0  | 0  | 0  | 1  | 4  | 5  | 2  | 1  | 5  | 1  | 6  | 2  | 0  | 2  | 1  | 0  | 1  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. opacicollis</i>         | 1          | 1  | 0  | 0  | 0  | 0  | 2  | 4  | 2  | 1  | 1  | 1  | 3  | 2  | 0  | 4  | 1  | 1  | 0  | 1  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

**Table 1.2 (cont.): Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

| Species                     | Characters |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|-----------------------------|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
|                             | 23         | 24 | 25 | 26 | 27 | 28 | 29 | 30 | 31 | 32 | 33 | 34 | 35 | 36 | 37 | 38 | 39 | 40 | 41 | 42 | 43 | 44 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. orientalis</i>        | 1          | 1  | 0  | 0  | 0  | 0  | 4  | 5  | 2  | 1  | 5  | 1  | 6  | ?  | 0  | 2  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. petrovi</i>           | ?          | 0  | 0  | ?  | 0  | 0  | 0  | 2  | 1  | 1  | 7  | 1  | 2  | 4  | 1  | 1  | 1  | 0  | 1  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. pilifrons</i>         | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 1  | 1  | 1  | 1  | 5  | 1  | 2  | 8  | 1  | 0  | 0  | 2  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. pseudoangustior</i>   | 1          | 3  | 2  | 1  | 0  | 1  | 1  | 1  | 0  | 1  | 7  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 1  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. quadridens</i>        | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 1  | 1  | 1  | 0  | 8  | 1  | 2  | 8  | 1  | 0  | 0  | 2  | 1  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. rectus</i>            | 1          | 1  | 0  | 0  | 0  | 0  | 4  | 5  | 2  | 1  | 5  | 1  | 6  | 2  | 0  | 2  | 1  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. suturalis</i>         | 2          | 3  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 1  | 5  | 0  | 1  | 0  | 0  | 0  | 1  | 0  | 1  | 1  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. unicornus</i>         | ?          | 1  | 0  | ?  | 0  | 0  | 0  | 7  | 3  | 1  | 1  | 1  | G  | F  | 0  | F  | 1  | 1  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. zuccus</i>            | 0          | 0  | 0  | 0  | 0  | 0  | 0  | 3  | 1  | 1  | 1  | 0  | C  | E  | 2  | 8  | 1  | 0  | 0  | 2  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Nemonyx boliviae</i>     | 0          | ?  | ?  | 0  | 0  | ?  | ?  | 6  | 1  | 0  | 9  | 1  | A  | 6  | 0  | 5  | 1  | 1  | 1  | 3  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. errans</i>            | 0          | 1  | 0  | 0  | 0  | 0  | 2  | 6  | 2  | 0  | 0  | 1  | 7  | B  | 3  | B  | 0  | 0  | 0  | 1  | 0  | 2  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. insignis</i>          | 0          | 0  | 0  | 0  | 0  | 0  | 3  | 6  | 1  | 0  | 0  | 1  | B  | 6  | 1  | A  | 1  | 1  | 1  | 1  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. rugulosus</i>         | 0          | 1  | 0  | 0  | 0  | 0  | 2  | 4  | 0  | 1  | 3  | 1  | 4  | 5  | 0  | 6  | 1  | 1  | 0  | 2  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. vestitus</i>          | ?          | 0  | 0  | ?  | 0  | 0  | 2  | 6  | 0  | 1  | 8  | 1  | 4  | 5  | 1  | D  | 1  | 0  | 1  | 2  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Scolytopsis peruanus</i> | 0          | 1  | 0  | 0  | 0  | 0  | 0  | 8  | 1  | 1  | 0  | 2  | F  | 7  | 1  | E  | 0  | 1  | 0  | 0  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Scolytus excavatus</i>   | 1          | 1  | 3  | 2  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 2  | D  | D  | 0  | C  | 0  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. multistriatus</i>     | 0          | 1  | 3  | 2  | 1  | 0  | 0  | 0  | 2  | 1  | 1  | 2  | 0  | A  | 0  | 9  | 0  | 0  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. propinquus</i>        | 0          | 1  | 3  | 2  | 1  | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 9  | 8  | 1  | C  | 0  | 1  | 0  | 0  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. scheyrewi</i>         | 0          | 0  | 3  | 2  | 0  | 0  | 0  | 0  | 2  | 1  | 1  | 2  | E  | C  | 0  | 9  | 0  | 1  | 0  | 0  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. ventralis</i>         | 1          | 1  | 3  | 2  | 1  | 0  | 0  | 0  | 2  | 0  | 1  | 2  | 0  | 9  | 0  | 9  | 0  | 1  | 0  | 0  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |

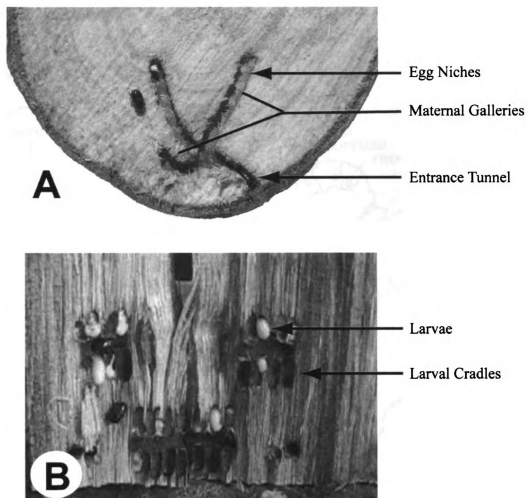
**Table 1.2 (cont.): Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

| Species                       | Characters |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|-------------------------------|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|---|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
|                               | 45         | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Campocerus aeneipennis</i> | 0          | 1  | 0  | 1  | 0  | 2  | 0  | 0  | 2  | 0  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 2  | 1  | 1 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. angustior</i>           | 0          | 1  | 0  | 1  | 0  | 2  | 0  | 0  | 2  | 0  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 3  | 6  | 1  | 2  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. annectens</i>           | ?          | 1  | 0  | 0  | 1  | 0  | 1  | 1  | 0  | 0  | ?  | 1  | 0  | 0  | 0  | ?  | ?  | ?  | ?  | ?  | ?  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. aterrimus</i>           | 0          | 2  | 0  | 0  | 0  | 2  | 0  | 0  | 2  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. auricomus</i>           | 0          | 0  | 0  | 0  | 3  | 0  | 0  | 3  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 6  | 1  | 3  | 0  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. charpentierae</i>       | 0          | 3  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 5  | 4  | 4  | 1  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. coccoformus</i>         | 0          | 3  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 1  | 0  | 1  | 5  | 5  | 4  | 0  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. costatus</i>            | 1          | 1  | 0  | 0  | 1  | 0  | 1  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 1  | 2  | 0  | 4  | 0  | 4  | 1  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. distinctus</i>          | 0          | 1  | 1  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 4  | 3  | 0  | 2  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. dolei</i>               | 0          | 3  | 0  | 0  | 2  | 0  | 0  | 3  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 5  | 3  | 4  | 0  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. hirtipennis</i>         | 0          | 1  | 0  | 0  | 3  | 1  | 0  | 3  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. igniculus</i>           | 0          | 3  | 0  | 0  | 2  | 0  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 5  | 4  | 4  | 1  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. inoblitus</i>           | 0          | 0  | 0  | 0  | 1  | 1  | 1  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 7  | 3  | 4  | 1  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. latipilis</i>           | 0          | 0  | 0  | 0  | 2  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 5  | 2  | 1  | 0  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. major</i>               | ?          | 1  | 0  | 0  | 1  | 1  | 1  | 1  | 0  | ?  | 0  | 1  | 0  | 0  | 0  | ?  | ?  | ?  | ?  | ?  | ?  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. mallopterus</i>         | 0          | 3  | 0  | 0  | 3  | 1  | 0  | 3  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 5  | 4  | 4  | 1  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. mandelshami</i>         | 0          | 1  | 0  | 0  | 0  | 2  | 0  | 0  | 2  | 0  | 2  | 0  | 0  | 0  | 1  | 1  | 0  | 0  | 6  | 2  | 1  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. niger</i>               | 0          | 0  | 0  | 0  | 3  | 0  | 0  | 3  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 6  | 1  | 3  | 0  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. noeli</i>               | 0          | 1  | 0  | 1  | 0  | 2  | 0  | 0  | 2  | 0  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | 1  | 1  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. occidentalis</i>        | 0          | 0  | 0  | 0  | 3  | 0  | 1  | 3  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 8  | 3  | 4  | 1  | ?  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. opacicollis</i>         | 0          | 0  | 0  | 0  | 1  | 0  | 1  | 1  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 1  | 0  | 7  | 3  | 4  | 2  | 1  |   |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |



**Table 1.2 (cont.): Morphological character matrix of 66 characters for 41 species. Characters and states are described in Materials and Methods**

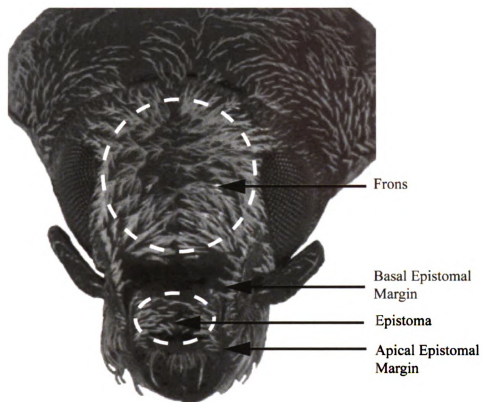
| Species                     | Characters |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |    |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|-----------------------------|------------|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|----|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
|                             | 45         | 46 | 47 | 48 | 49 | 50 | 51 | 52 | 53 | 54 | 55 | 56 | 57 | 58 | 59 | 60 | 61 | 62 | 63 | 64 | 65 | 66 |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. orientalis</i>        | 0          | 0  | 0  | 0  | 3  | 0  | 0  | 3  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. petrovi</i>           | 0          | 3  | 0  | 0  | 2  | 0  | 1  | 1  | 0  | 0  | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 5  | 2  | 4  | 0  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. pilifrons</i>         | 0          | 1  | 0  | 0  | 2  | 0  | 1  | 2  | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 1  | A  | 7  | 0  | 0  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. pseudoangustior</i>   | 0          | 2  | 0  | 0  | 0  | 2  | 0  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 1  | 1  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. quadridens</i>        | 1          | 1  | 0  | 0  | 1  | 3  | 1  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 1  | 0  | 4  | 4  | 4  | 1  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. rectus</i>            | 0          | 0  | 0  | 0  | 3  | 0  | 1  | 3  | 1  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 3  | 1  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. suturalis</i>         | 0          | 1  | 0  | 0  | 2  | 1  | 0  | 2  | 0  | 0  | 0  | 0  | 0  | 0  | 2  | 1  | 0  | 0  | 0  | 2  | 0  | 1  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. unicornus</i>         | 0          | 0  | 0  | 0  | 2  | 0  | ?  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. zuccus</i>            | 0          | 1  | 0  | 0  | 2  | 1  | 0  | 1  | 0  | 0  | 1  | 0  | 0  | 0  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Chemonyx boliviae</i>    | 0          | 0  | 0  | 0  | 0  | 1  | 2  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 3  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. errans</i>            | 0          | 1  | 0  | 0  | 1  | 0  | 2  | 2  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 3  | 0  | 4  | 0  | 3  | 0  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. insignis</i>          | 0          | 0  | 0  | 0  | 0  | 0  | 2  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 3  | 0  | 7  | 0  | 0  | 2  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. rugulosus</i>         | 0          | 1  | 0  | 0  | 1  | 0  | 0  | 2  | 0  | 0  | 0  | 1  | 0  | 0  | 0  | 0  | 0  | 5  | 3  | 4  | 0  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>C. vestitus</i>          | 0          | 0  | 0  | 0  | 4  | 0  | ?  | 3  | 1  | 0  | 0  | 1  | 0  | 0  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Scolytopsis peruanae</i> | 0          | 0  | 0  | 0  | 1  | 0  | 1  | 2  | 0  | 0  | 0  | 1  | 1  | 2  | 1  | 1  | 0  | B  | A  | 3  | 2  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>Scolytus excavatus</i>   | 0          | 0  | 0  | 0  | 0  | 2  | 1  | 0  | 2  | 0  | 2  | 1  | 2  | 2  | 0  | 1  | 0  | 7  | 0  | 4  | 2  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. multistriatus</i>     | 0          | 0  | 0  | 0  | 1  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 2  | 2  | 1  | 0  | ?  | ?  | ?  | ?  | ?  | ?  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. propinquus</i>        | 0          | 0  | 0  | 0  | 0  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 2  | 2  | 0  | 0  | 0  | 4  | 4  | 4  | 2  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. schevyrewi</i>        | 0          | 0  | 0  | 0  | 1  | 1  | 0  | 1  | 0  | 0  | 1  | 1  | 2  | 2  | 1  | 0  | 0  | 7  | 9  | 0  | 1  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
| <i>S. ventralis</i>         | 0          | 0  | 0  | 0  | 0  | 1  | 1  | 1  | 0  | 0  | 0  | 1  | 2  | 2  | 0  | 0  | 0  | 9  | 8  | 4  | 4  | 0  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |



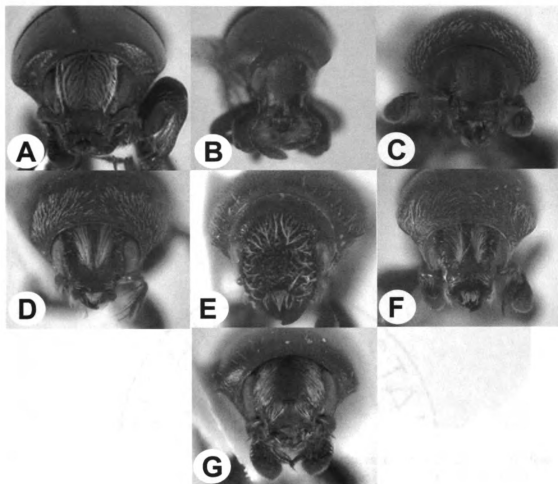
**FIGURE 1.1:** Horizontal cross section (A); vertical cross section (B) of *Camptocerus aeneipennis* galleries.



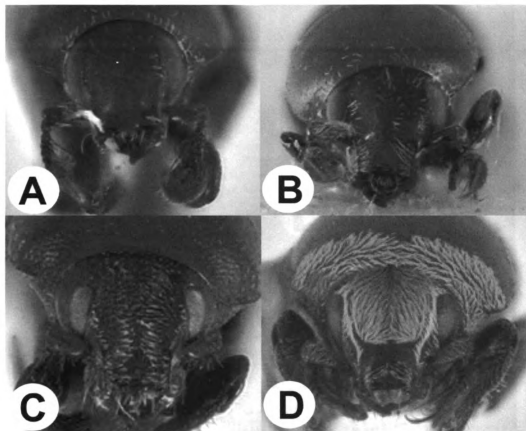
**FIGURE 1.2:** Distribution map illustrating the number of *Camptocerus* species reported for each country in the Neotropics. Countries without numbers lack records. *Camptocerus* species range from Veracruz, Mexico (Atkinson & Equihua- Martinez, 1986) to Chaco, Argentina (Bruch, 1914).



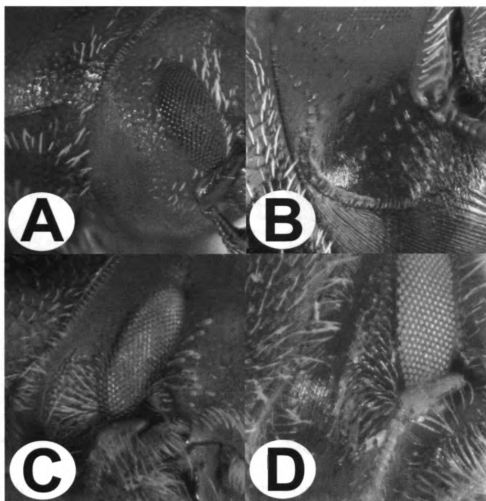
**FIGURE 1.3:** *Camptocerus suturalis* male head illustrating terminology used for the epistoma and frons.



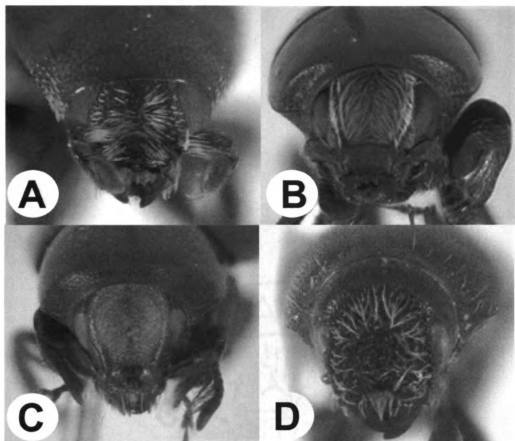
**FIGURE 1.4:** Character 7: Male proximal epistomal margin (A) transverse, concave carina; (B) tumid above scape insertion; (C) strongly developed transverse carina; (D) weakly developed transverse carina; (E) no demarcation; (F) transverse carina with strongly developed lateral areas; (G) short transverse carina.



**FIGURE 1.5:** Character 14: Male frons vestiture on impressed area (A) absent; (B) few setae, less than 20 on impressed area, frons clearly visible; (C) moderate setae; frons largely covered by setae, but surface visible; (D) dense, frons surface not visible.

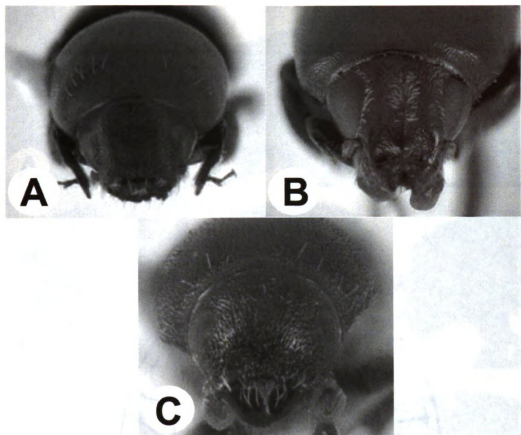


**FIGURE 1.6:** Character 21: Mycangia on female gena: (A) absent; (B) crescent shaped; (C) oval; (D) triangular.

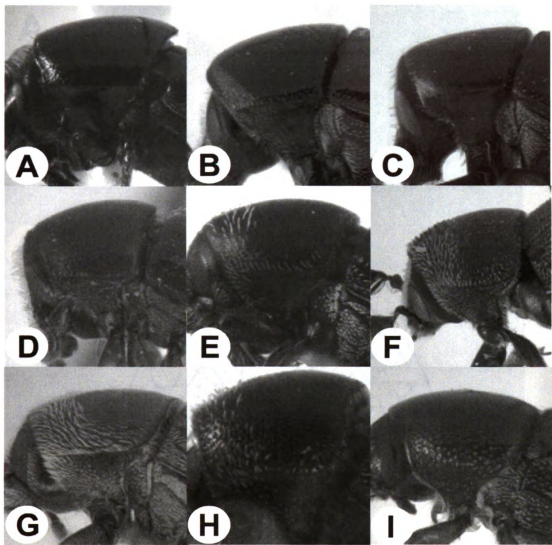


**FIGURE 1.7:** Character 25: Male anterior pronotal margin (A) rounded; (B) partially sulcate; (C) entirely sulcate; (D) transversely impressed.

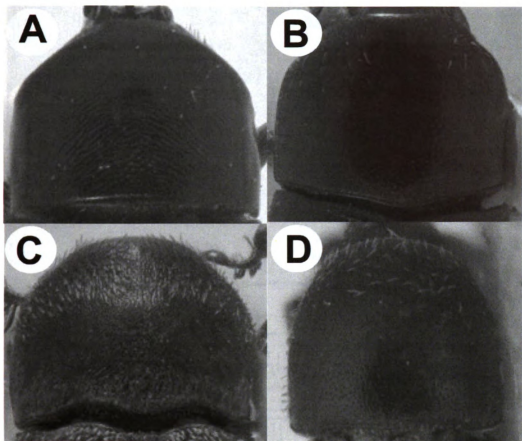




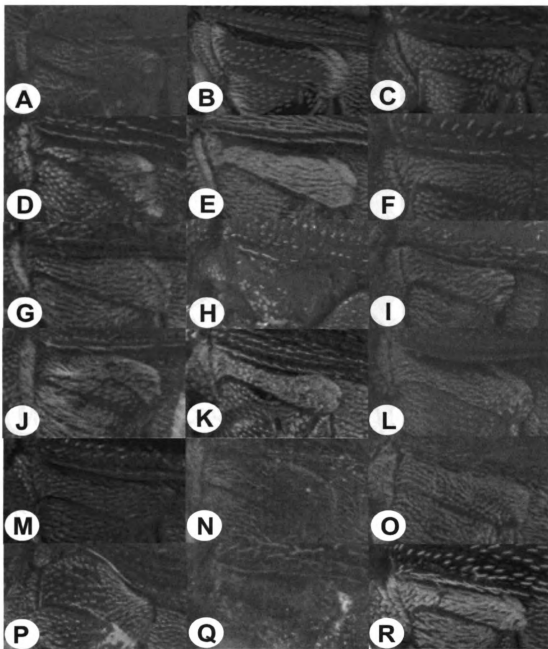
**FIGURE 1.8:** Character 26: Female anterior pronotum margin (A) rounded; (B) partially sulcate; (C) transversely impressed.



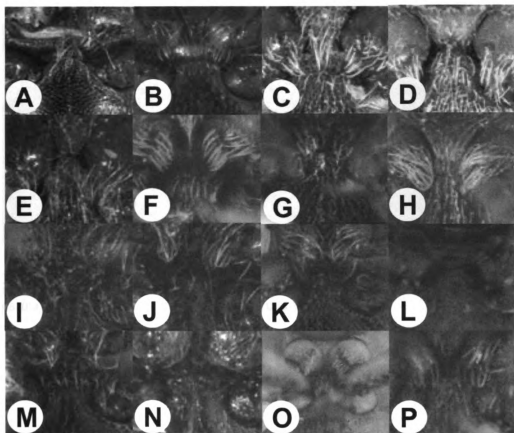
**FIGURE 1.9:** Character 30: Lateral margin of pronotum (A) type A; (B) type B; (C) type C; (D) type D; (E) type E; (F) type F; (G) type G; (H) type H; (I) type I.



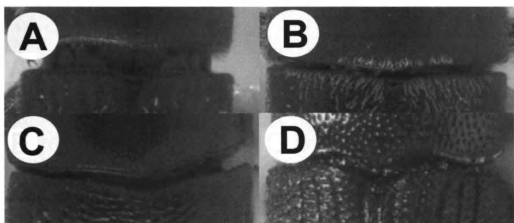
**FIGURE 1.10:** Character 31: Pronotum base (A) straight; (B) recurved; (C) bisinuate; (D) broadly emarginated along medial half.



**FIGURE 1.11:** Character 35: Metepisternum shape (A) type A; (B) type B; (C) type C; (D) type D; (E) type E; (F) type F; (G) type G; (H) type H; (I) type I; (J) type J; (K) type K; (L) type L; (M) type M; (N) type N; (O) type O; (P) type P; (Q) type Q; (R) type R.



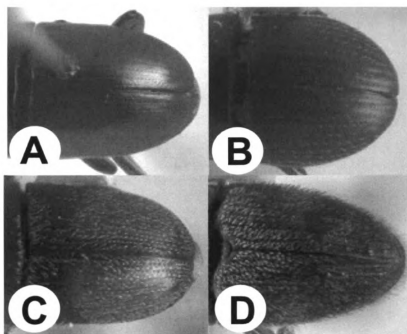
**FIGURE 1.12:** Character 36: Mesosternum (A) type A; (B) type B; (C) type C; (D) type D; (E) type E; (F) type F; (G) type G; (H) type H; (I) type I; (J) type J; (K) type K; (L) type L; (M) type M; (N) type N; (O) type O; (P) type P.



**FIGURE 1.13:** Character 37: Basal margin of elytra (A) flat; (B) faint carina; (C) faint carina extending to scutellar apex (D) crenulations.



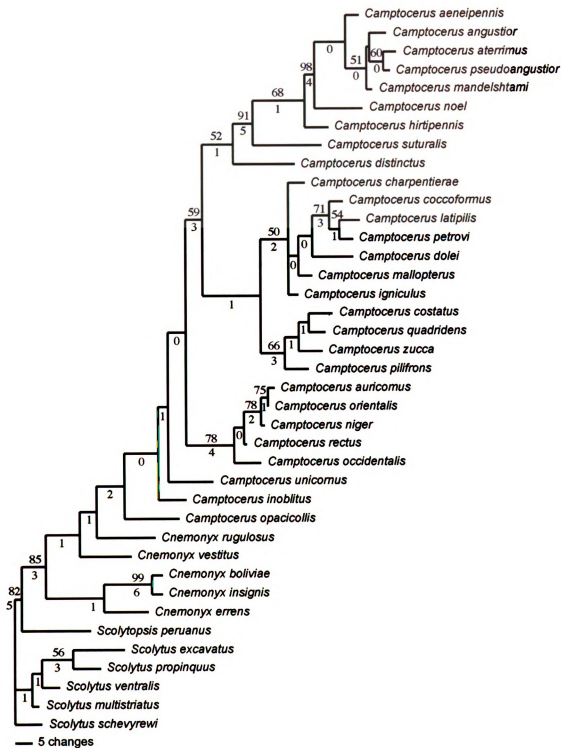
**FIGURE 1.14:** Character 38: Scutellum shape (A) type A; (B) type B; (C) type C; (D) type D; (E) type E; (F) type F; (G) type G; (H) type H; (I) type I; (J) type J; (K) type K; (L) type L; (M) type M; (N) type N; (O) type O; (P) type P.

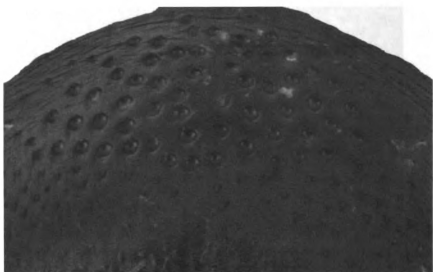


**FIGURE 1.15:** Character 52: Density of elytral setae (A) glabrous; (B) light; (C) moderate; (D) dense, elytral surface not visible.

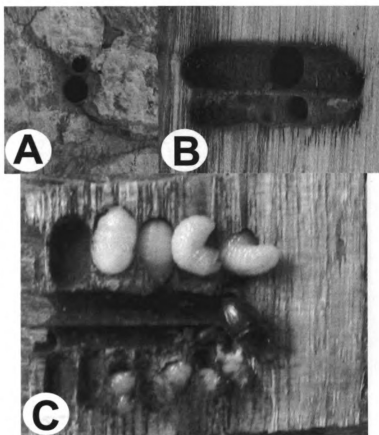


**FIGURE 1.16:** Phylogeny of *Camptocerus*. Phylogram of one of 26 most parsimonious trees (432 steps; consistency index, 0.488; retention index, 0.694) generated for 39 taxa with 66 characters from a heuristic search of 1000 stepwise random additions with TBR in PAUP\*. Numbers above the node indicate bootstrap values (>50) based on 1000 pseudoreplicates. Bremer support values are generated from a heuristic search of 100 random addition sequence replicates.

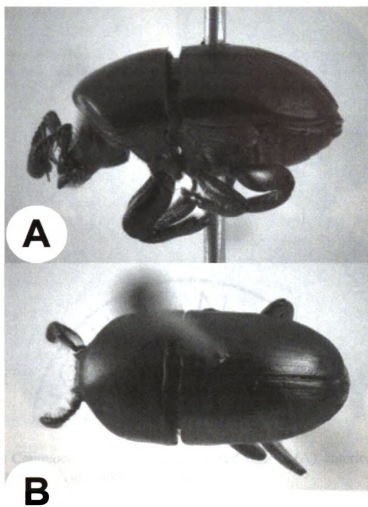




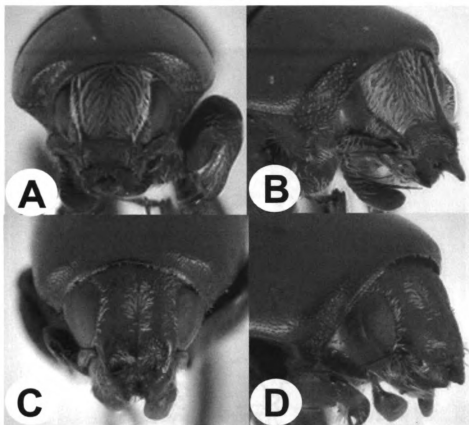
**FIGURE 1.17:** Pit mycangia on female *C. aeneipennis* vertex. Pits are 3-5 times the diameter of other punctures and 3-10 times as deep.



**FIGURE 1.18:** *Camptocerus suturalis* stealing fungus from a *C. aeneipennis* gallery: (A) close proximity of entrance holes, with the smaller *C. suturalis* on top; (B) entrance tunnel and two maternal galleries, *C. suturalis* created the bottom gallery; (C) maternal galleries separated by a thin septum, within the region of fungal staining, *C. suturalis* is in the bottom gallery.



**FIGURE 1.19:** Lateral (A) and dorsal (B) views of *Camptocerus aeneipennis*, 4.4 – 5.9 mm, male.



**FIGURE 1.20:** *Camptocerus aeneipennis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

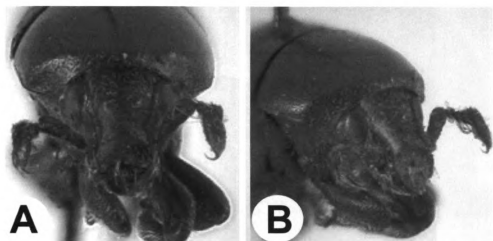


**A**



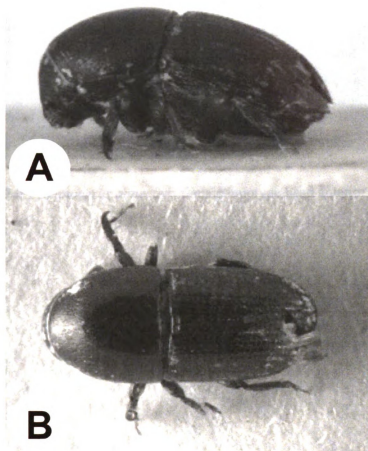
**B**

**FIGURE 1.21:** Lateral (A) and dorsal (B) views of *Camptocerus angustior*, 5.0 – 5.8 mm, male.

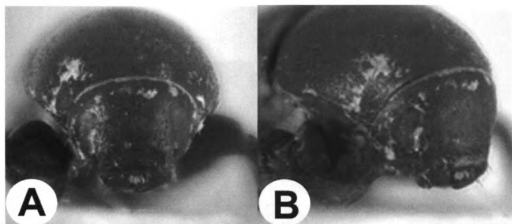


**FIGURE 1.22:** *Camptocerus angustior* male head anterior (A), anterior oblique (B).

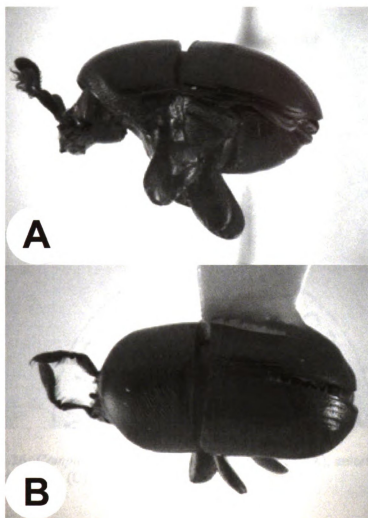




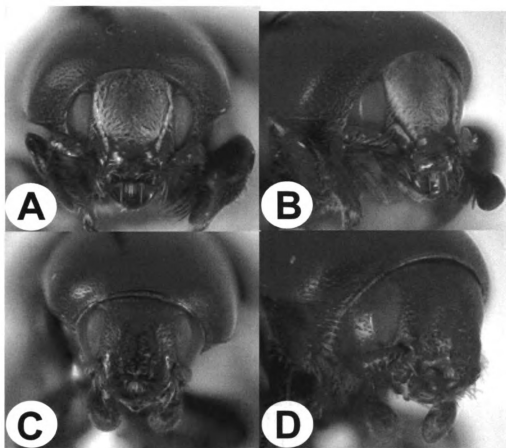
**FIGURE 1.23:** Lateral (A) and dorsal (B) views of *Camptocerus annectens*, 3.5 mm, female holotype.



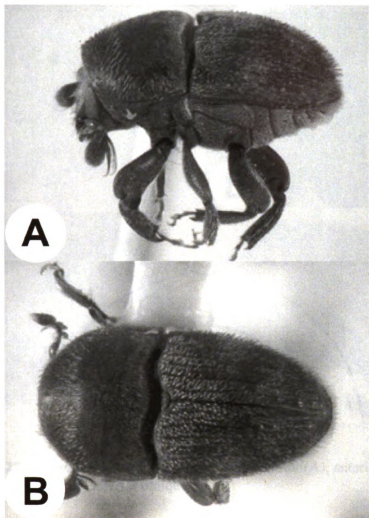
**FIGURE 1.24:** *Camptocerus annectens* female holotype head anterior (A), anterior oblique (B).



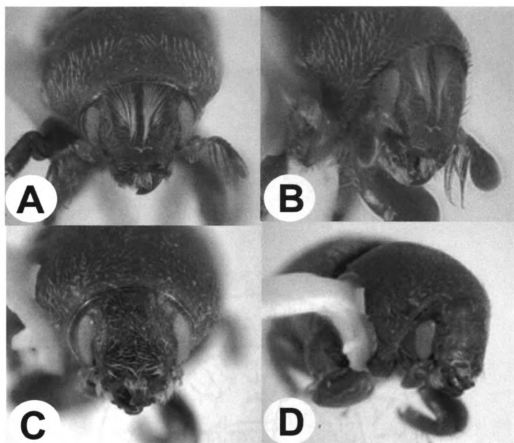
**FIGURE 1.25:** Lateral (A) and dorsal (B) views of *Camptocerus aterrimus*, 3.1 – 4.5 mm, male.



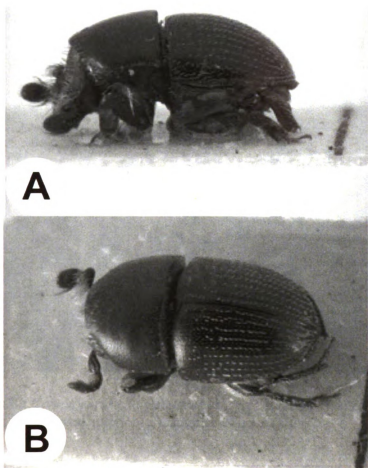
**FIGURE 1.26:** *Camptocerus aterrimus* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



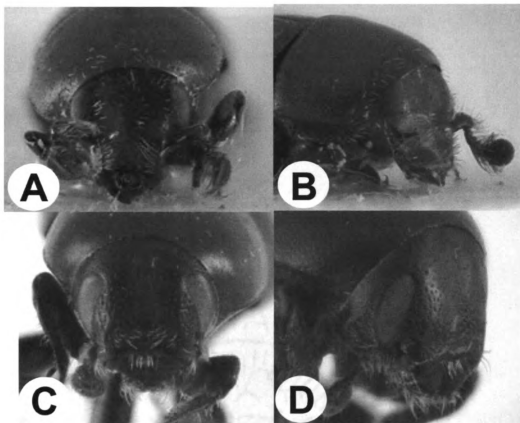
**FIGURE 1.27:** Lateral (A) and dorsal (B) views of *Camptocerus auricomus*, 3.5 – 4.1 mm, male.



**FIGURE 1.28:** *Camptocerus auricomus* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

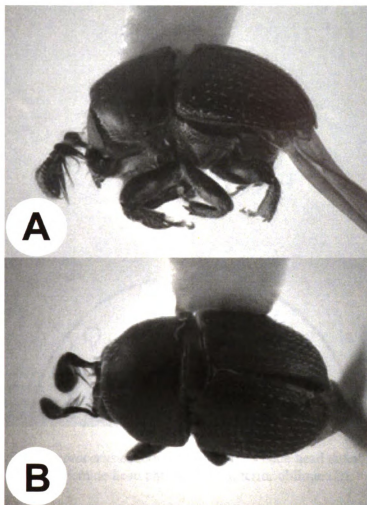


**FIGURE 1.29:** Lateral (A) and dorsal (B) views of *Camptocerus charpentierae*, 3.8 – 4.5 mm, holotype male.

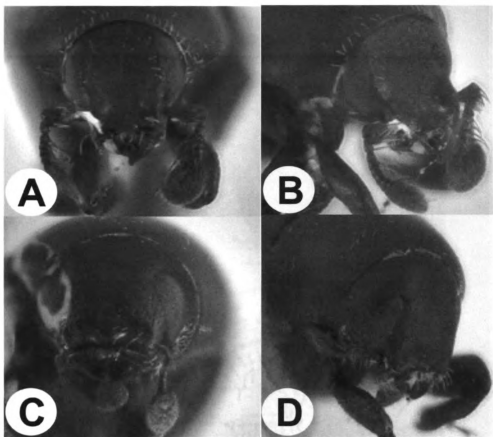


**FIGURE 1.30:** *Camptocerus charpentierae* holotype male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

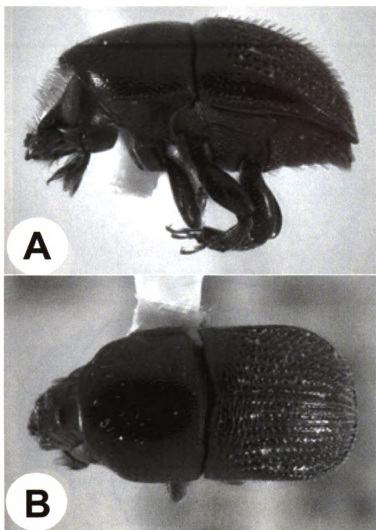




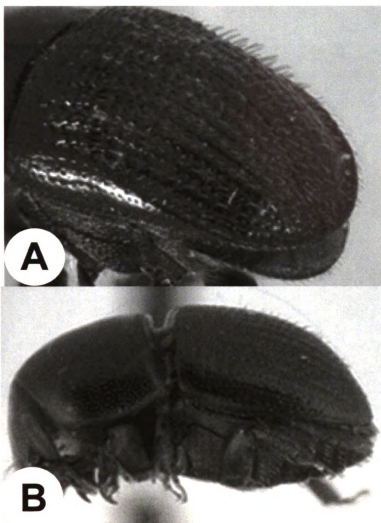
**FIGURE 1.31:** Lateral (A) and dorsal (B) views of *Camptocerus coccoformus*, 2.7 mm, holotype male.



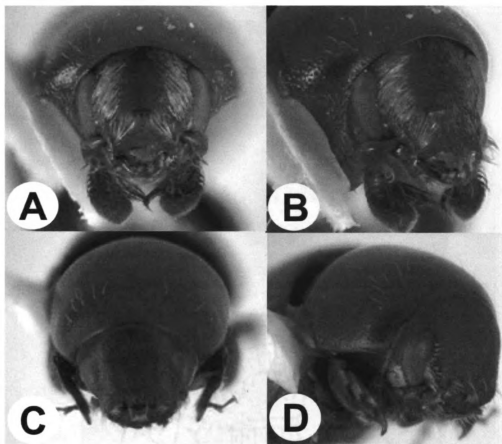
**FIGURE 1.32:** *Camptocerus coccoformis* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).



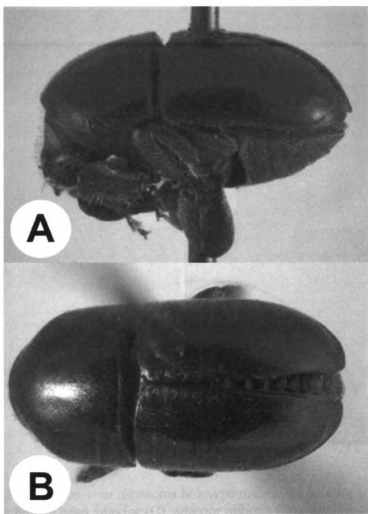
**FIGURE 1.33:** Lateral (A) and dorsal (B) views of *Camptocerus costatus*, 3.5 – 3.9 mm, male.



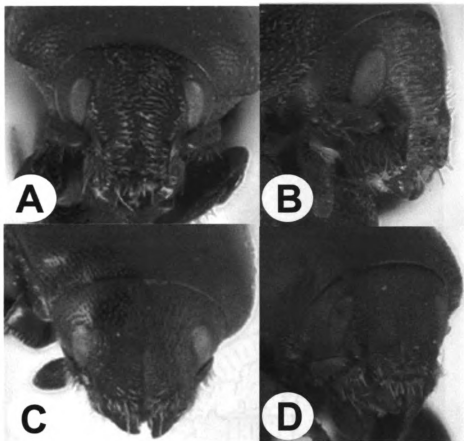
**FIGURE 1.34:** Male declivity (A) and female lateral (B) views of *Camptocerus costatus*.



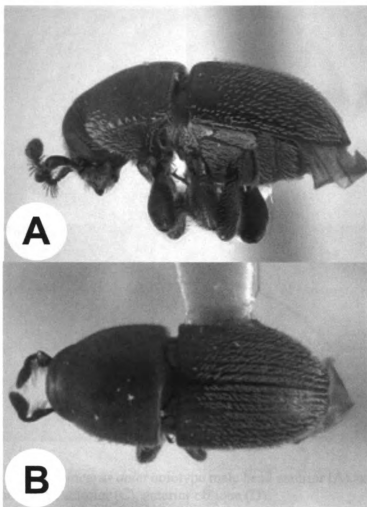
**FIGURE 1.35:** *Camptocerus costatus* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



**FIGURE 1.36:** Lateral (A) and dorsal (B) views of *Camptocerus distinctus*, 5.3 mm, holotype male.

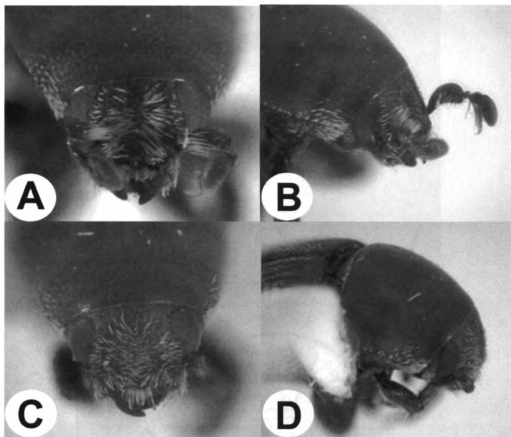


**FIGURE 1.37:** *Camptocerus distinctus* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).

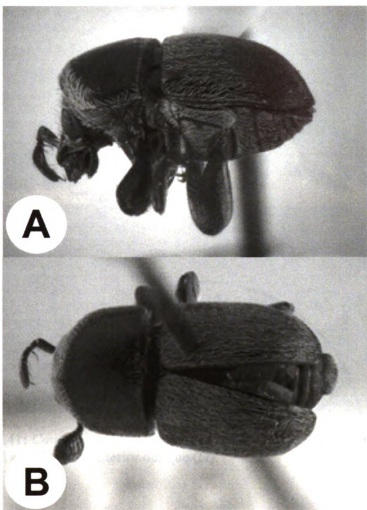


**FIGURE 1.38:** Lateral (A) and dorsal (B) views of *Camptocerus dolei*, 3.1 – 3.5 mm, holotype male.

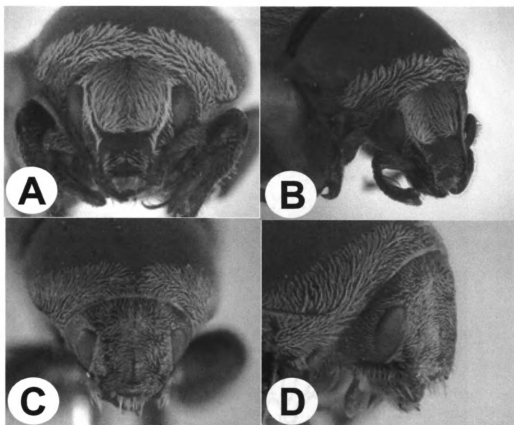




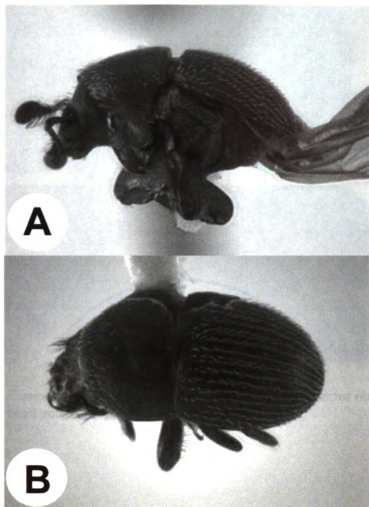
**FIGURE 1.39:** *Camptocerus dolei* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).



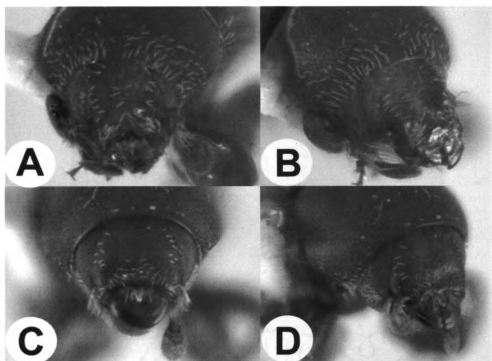
**FIGURE 1.40:** Lateral (A) and dorsal (B) views of *Camptocerus hirtipennis*, 4.9 – 5.6 mm, male.



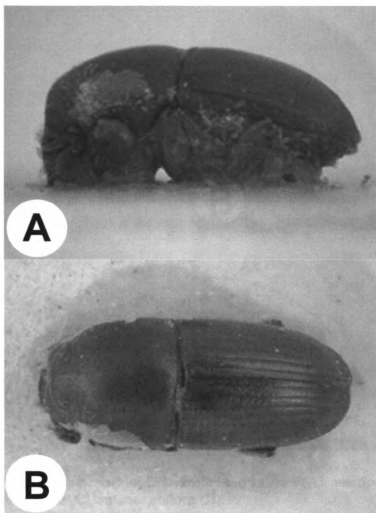
**FIGURE 1.41:** *Camptocerus hirtipennis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



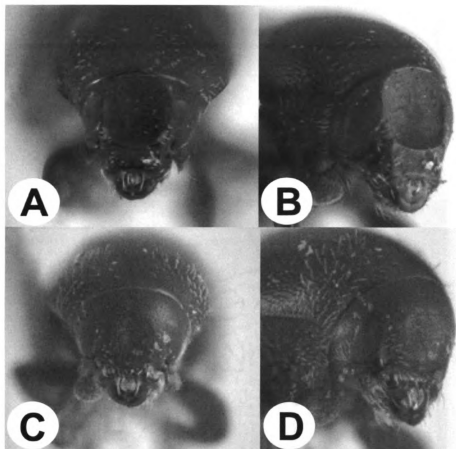
**FIGURE 1.42:** Lateral (A) and dorsal (B) views of *Camptocerus igniculus*, 2.5 – 2.8 mm, male.



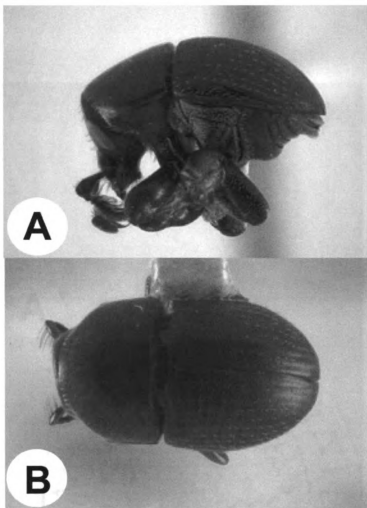
**FIGURE 1.43:** *Camptocerus igniculus* male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).



**FIGURE 1.44:** Lateral (A) and dorsal (B) views of *Camptocerus inoblitus*, 2.4 – 3.4 mm, male.

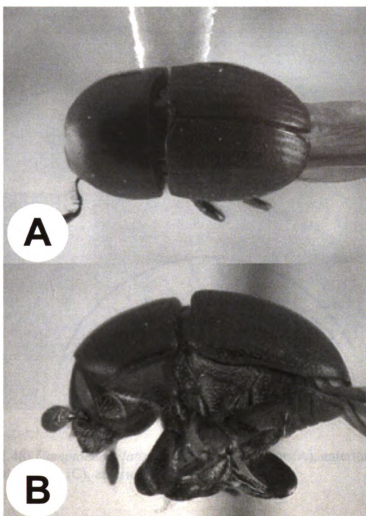


**FIGURE 1.45:** *Camptocerus inoblitus* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

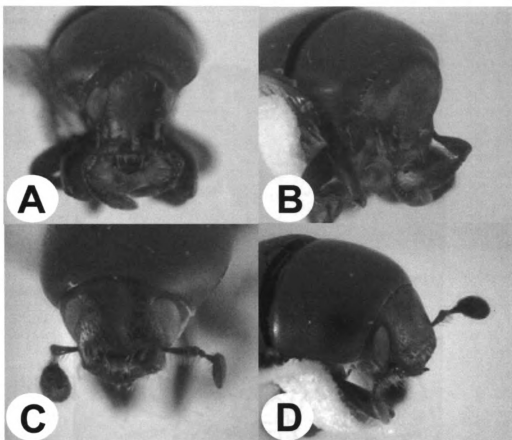


**FIGURE 1.46:** Lateral (A) and dorsal (B) views of *Camptocerus latipilis*, 2.7 – 3.3 mm, male.

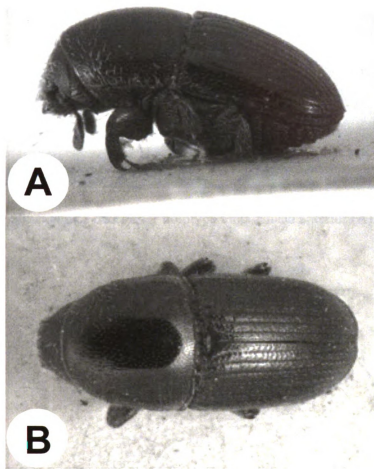




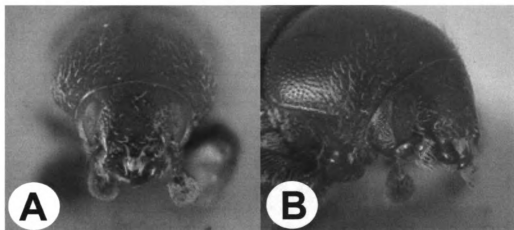
**FIGURE 1.47:** Lateral (A) and dorsal (B) views of *Camptocerus latipilis*, 2.7 – 3.3 mm, female.



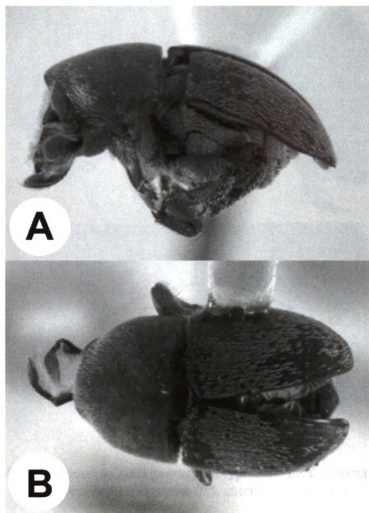
**FIGURE 1.48:** *Camptocerus latipilis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



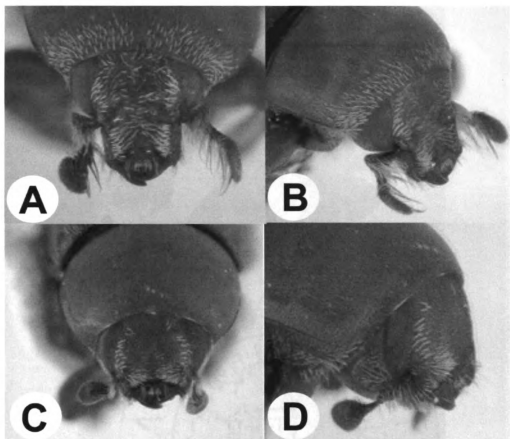
**FIGURE 1.49:** Lateral (A) and dorsal (B) views of *Camptocerus major*, 3.4 mm, holotype female.



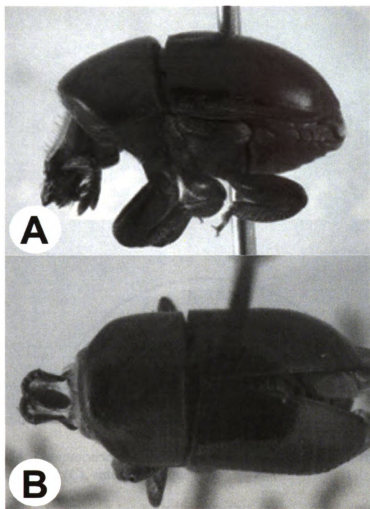
**FIGURE 1.50:** *Camptocerus major* holotype female head anterior (A), anterior oblique (B).



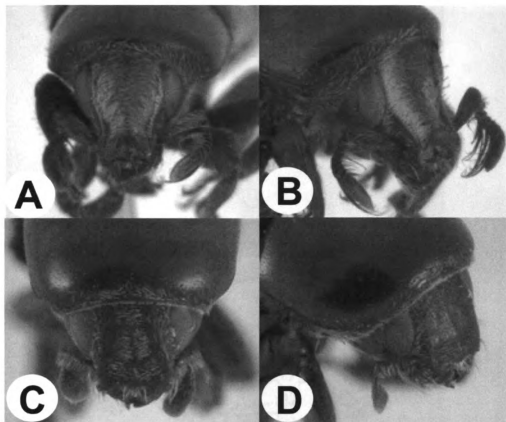
**FIGURE 1.51:** Lateral (A) and dorsal (B) views of *Camptocerus mallopterus*, 3.8 – 3.9 mm, holotype male.



**FIGURE 1.52:** *Camptocerus mallopterus* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).

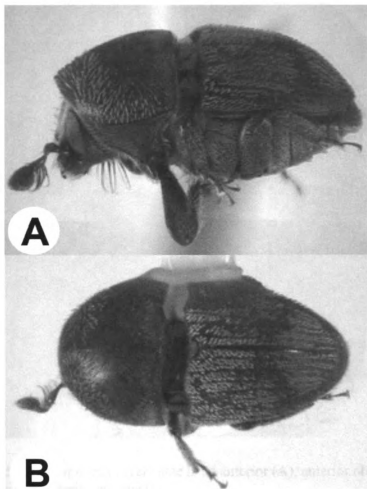


**FIGURE 1.53:** Lateral (A) and dorsal (B) views of *Camptocerus mandelshtami*, 5.9 – 6.5 mm, male.

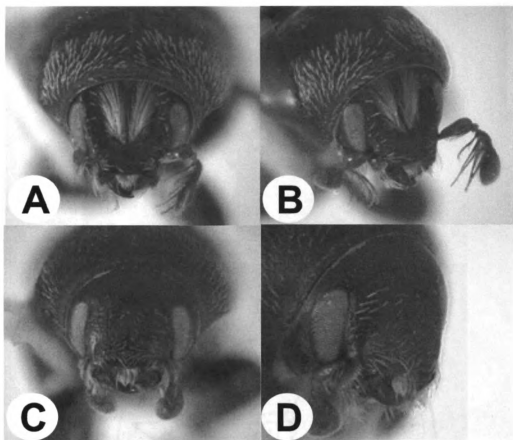


**FIGURE 1.54:** *Camptocerus mandelshtami* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

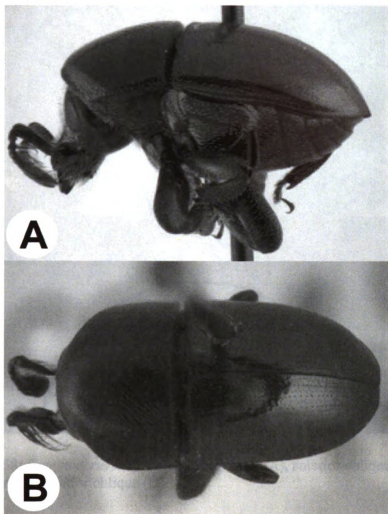




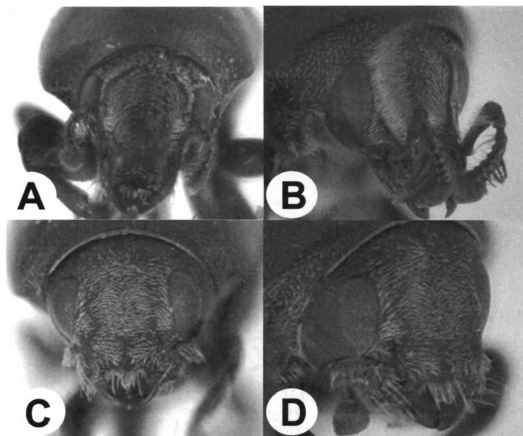
**FIGURE 1.55:** Lateral (A) and dorsal (B) views of *Camptocerus niger*, 2.8 – 4.1 mm, male.



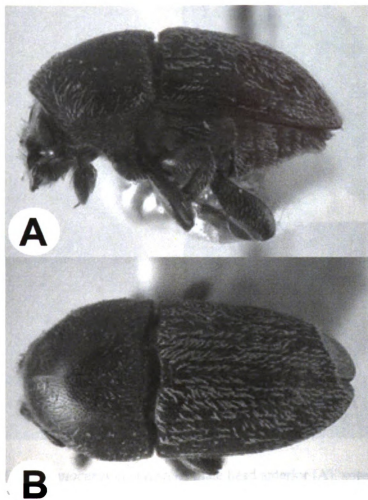
**FIGURE 1.56:** *Camptocerus niger* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



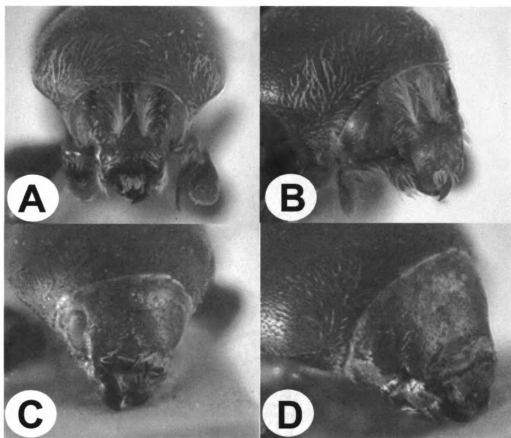
**FIGURE 1.57:** Lateral (A) and dorsal (B) views of *Camptocerus noel*, 6.0–7.1 mm, male.



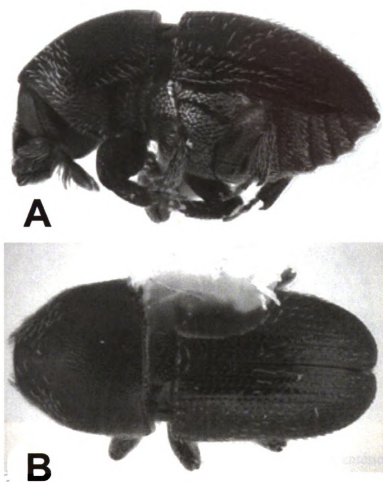
**FIGURE 1.58:** *Camptocerus noel* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



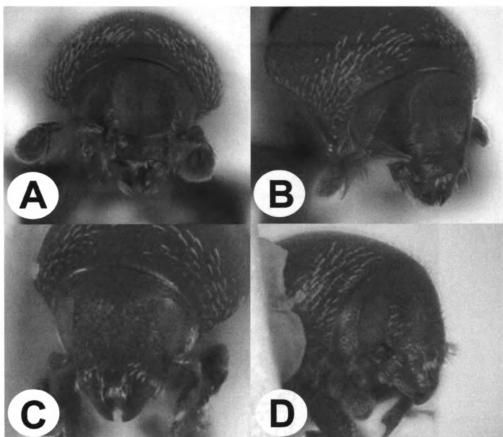
**FIGURE 1.59:** Lateral (A) and dorsal (B) views of *Campocerus occidentalis*, 4.0–4.5 mm, male.



**FIGURE 1.60:** *Camptocerus occidentalis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

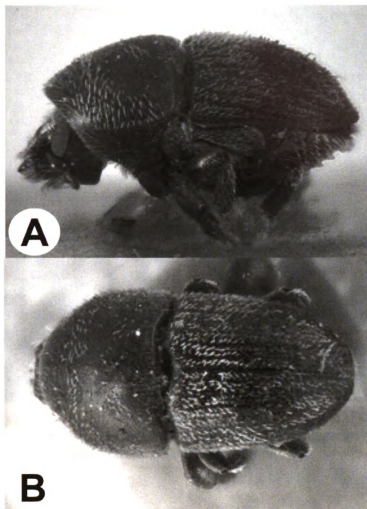


**FIGURE 1.61:** Lateral (A) and dorsal (B) views of *Camptocerus opacicollis*, 2.2 – 3.6 mm, male.

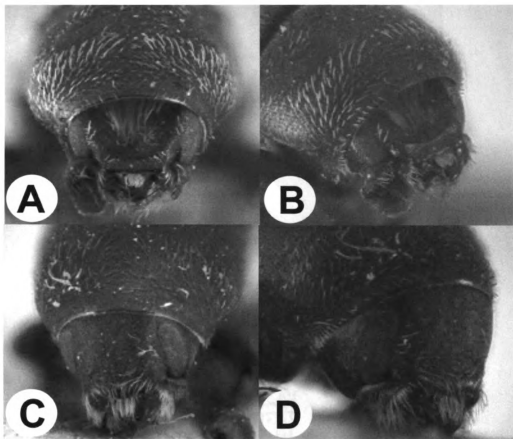


**FIGURE 1.62:** *Camptocerus opacicollis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

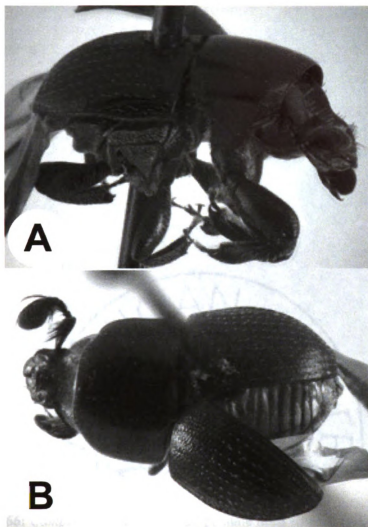




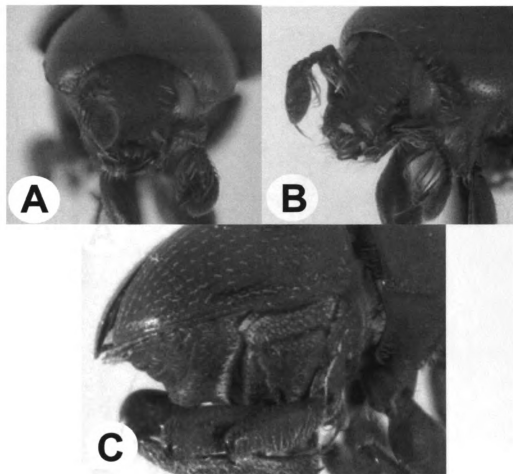
**FIGURE 1.63:** Lateral (A) and dorsal (B) views of *Camptocerus orientalis*, 3.2 – 3.7 mm, holotype male.



**FIGURE 1.64:** *Camptocerus orientalis* holotype male head anterior (A), anterior oblique (B); paratype female head anterior (C), anterior oblique (D).

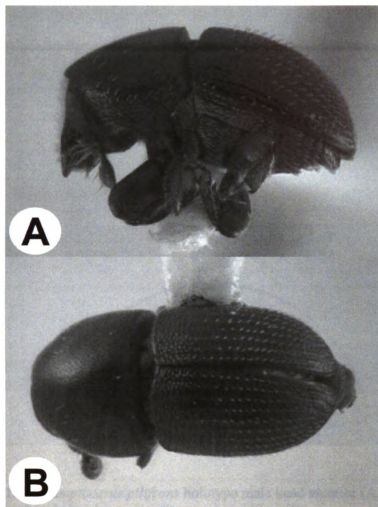


**FIGURE 1.65:** Lateral (A) and dorsal (B) views of *Camptocerus petrovi*, 4.0 mm, holotype male.

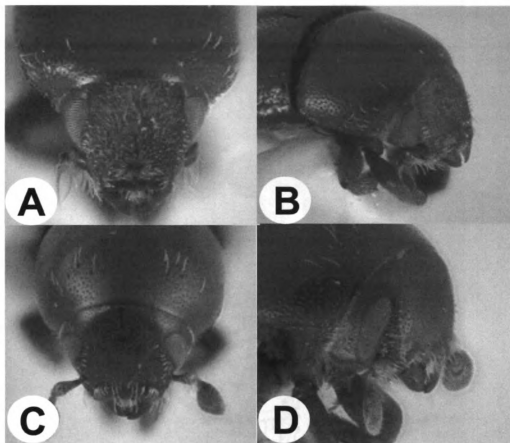


**FIGURE 1.66:** *Camptocerus petrovi* holotype male head anterior (A), anterior oblique (B); abdomen posterior oblique (C).

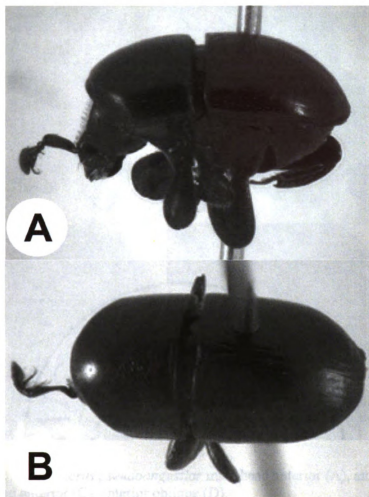




**FIGURE 1.67:** Lateral (A) and dorsal (B) views of *Camptocerus pilifrons*, 2.6 – 3.1 mm, holotype male.

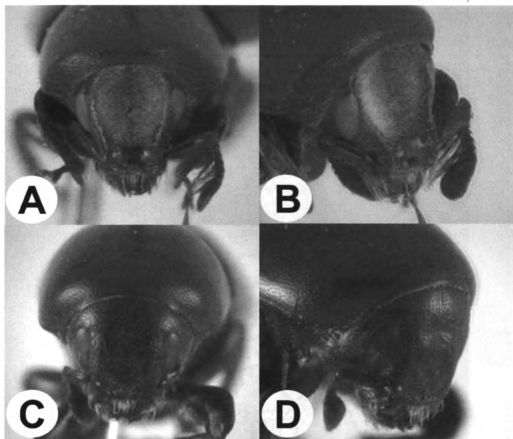


**FIGURE 1.68:** *Camptocerus pilifrons* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).

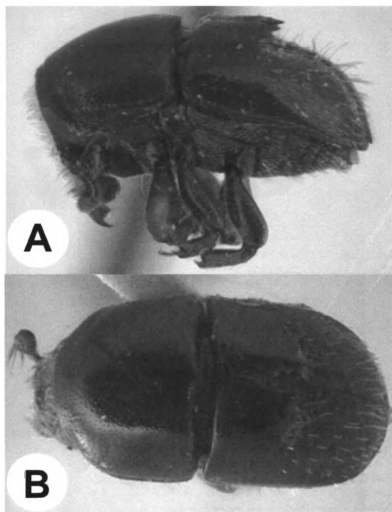


**FIGURE 1.69:** Lateral (A) and dorsal (B) views of *Camptocerus pseudoangustior*, 4.5 – 5.4 mm, male.

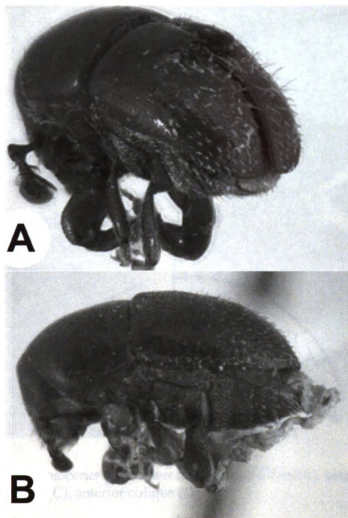




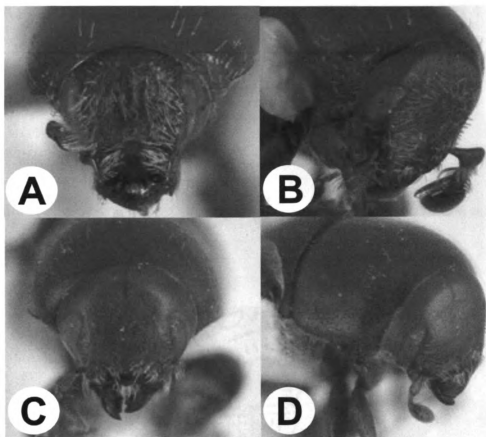
**FIGURE 1.70:** *Camptocerus pseudoangustior* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



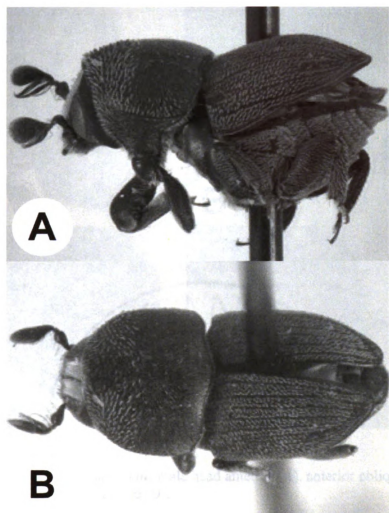
**FIGURE 1.71:** Lateral (A) and dorsal (B) views of *Camptocerus quadridens*, 3.4 – 3.7 mm, male.



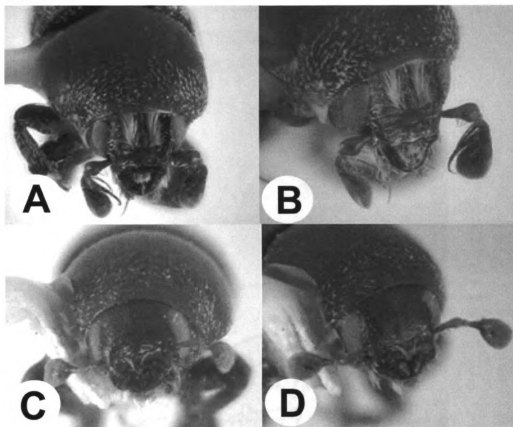
**FIGURE 1.72:** Posterior oblique (A) view of *Camptocerus quadridens* male. Lateral (B) view of female.



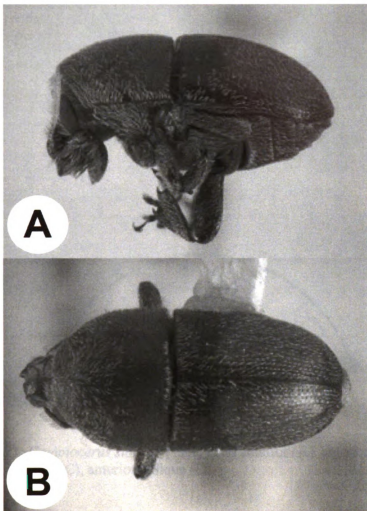
**FIGURE 1.73:** *Camptocerus quadridens* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



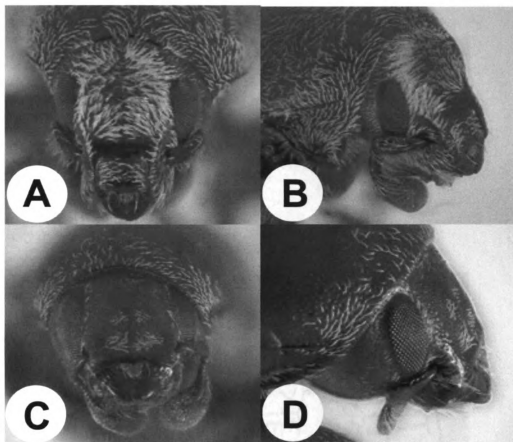
**FIGURE 1.74:** Lateral (A) and dorsal (B) views of *Camptocerus rectus*, 3.5 – 4.3 mm, male.



**FIGURE 1.75:** *Camptocerus rectus* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).



**FIGURE 1.76:** Lateral (A) and dorsal (B) views of *Camptocerus suturalis*, 3.6 – 5.0 mm, male.

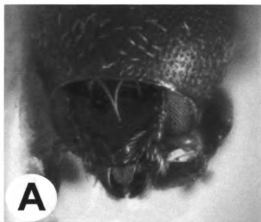


**FIGURE 1.77:** *Camptocerus suturalis* male head anterior (A), anterior oblique (B); female head anterior (C), anterior oblique (D).

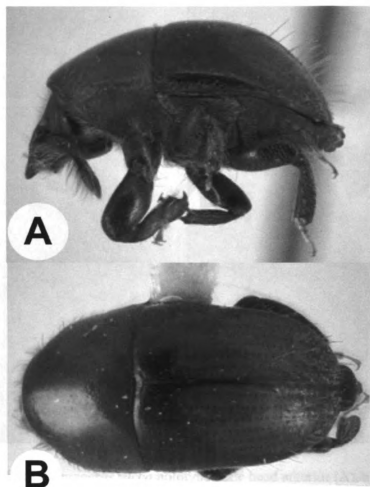




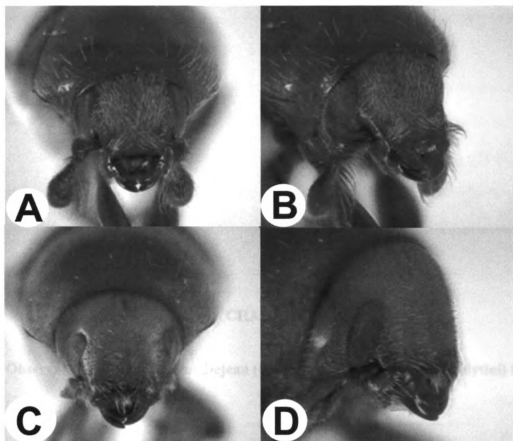
**FIGURE 1.78:** Lateral (A) and dorsal (B) views of *Camptocerus unicornus*, 2.5 mm, holotype male.



**FIGURE 1.79:** *Camptocerus unicornus* holotype male head anterior (A).



**FIGURE 1.80:** Lateral (A) and dorsal (B) views of *Camptocerus zucca*, 4.0 – 4.1 mm, holotype male.



**FIGURE 1.81:** *Camptocerus zucca* holotype male head anterior (A), anterior oblique (B); allotype female head anterior (C), anterior oblique (D).

## **CHAPTER TWO**

**Observations of *Camptocerus* Dejean (Coleoptera: Curculionidae: Scolytini) in Peru.**

## **ABSTRACT**

I report observations of *Camptocerus* attracted to felled *Protium amazonicum* Swart in southeastern Peru and the behavior of four species. An unusual behavior for scolytines was observed as three species aggregated to leaves surrounding potential hosts, bored into leaves and fed, a rare behavior for Scolytines. Males competed for mates with physical contact. Ant predation killed ~50% of colonizing individuals for one species.

## INTRODUCTION

Neotropical scolytines represent a relatively unknown fauna. It is been estimated that only two-thirds of South American species have been described (Wood, 2007) and very little is known about their biology (Beaver, 1972; Wood, 2007). One poorly known xylomycetophagous genus is *Camptocerus* Dejean (Coleoptera: Curculionidae: Scolytinae), despite being among the first described American scolytines (Blandford, 1896; Illiger, 1807). However, certain aspects of its biology have been documented. Like other ambrosia beetles, *Camptocerus* have specialized mycangia that carry fungal spores. Females bore into the xylem and sapwood and create 'galleries.' The symbiotic fungus grows in the galleries where eggs are laid. Larvae enlarge their own galleries and feed on both xylem and fungal mycelia. Some species demonstrate some level of host specificity, but, less than half of *Camptocerus* species have been associated with a host tree (Wood & Bright, 1992). *Camptocerus aeneipennis* (Fabricius) and *Cnemonyx vismiae* Eggers have been observed to chew holes as wide as their pronotum in leaves and lodge themselves in them. Feeding behavior around this hole was reported from the Panama Canal Zone for both species (von Winning, 1930). *Camptocerus aeneipennis* were observed to simply rest or pass through these holes in Venezuela (Wood, 2007). It has been presumed that this behavior is maturation feeding (Wood, 2007). Beaver (1972) presented the first study of *Camptocerus* biology and provided a detailed account of host use and life-history information for four species in Brazil. Beaver cut trees in the Brazilian Amazon, north of Manaus and allowed them to rest *in situ* for 1 to 2 months before dissecting beetles out of infested trees. *Camptocerus aeneipennis*, *C. aterrimus* Eggers *C. niger* (Fabricius), *C.*

*aquilus* Wood (= *C. opacicollis* (Eggers)) were collected and studied. He also provided the first summary of hosts for the genus.

An ecological study to assess ambrosia beetle (Coleoptera: Curculionidae: Scolytine and Platypodine) diversity undertaken in Peru provided an unexpected opportunity to further describe the biology of *Camptocerus*. Four species were found and monitored during the study: *C. opacicollis* (Eggers), *C. suturalis* (Fabricius) and two new to science *Camptocerus noel* Smith & Cognato and *Camptocerus pseudoangustior* Smith & Cognato. Observations of life-history aggregation, leaf-feeding, courtship and mating were observed and are reported herein.

## MATERIALS AND METHODS

The study was performed at Centro de Investigación y Capacitación Río Los Amigos in Madre de Dios, Peru (S12°34'9" W70°6'0.04", 248 m elevation). Species of *Protium* (Burseraceae) are the most frequently documented hosts for *Camptocerus* species (Beaver, 1972; Wood, 2007). The species *Protium amazonicum* Swart was chosen as a bait tree because of its wide range throughout Peru (Paul Fine, per. com.). Preparation of the trees followed the protocol of Hulcr et al. (2008). Six 10-15cm DBH trees were used in the study. Three trees were killed standing by girdling at 1.5m removing 30cm circumferential strips of bark with multiple cuts on 27 April, and then burned at the base on 29 April 2008. These trees ("A"-“C”), a fourth “D” which was girdled but not burned and a fifth ungirdled tree (“E”) were felled on 29 April. A sixth *P. amazonicum* tree (“F”) was felled and then girdled on 11 May. All trees were felled in



secondary forest and left *in situ* to attract ambrosia beetles. Trees were examined approximately every other day throughout the duration of the ecological study and observations were recorded.

## RESULTS

### Colonization

Initial galleries were created 1-2 days after girdling (28-29 April) by *Camptocerus noel* females, however additional galleries were not observed until seven days after girdling (4 May). The five initial attacks were restricted to the girdle and occurred before the trees were felled. Attacks rapidly became more frequent with 40 after nine days (6 May), 80 after 11 days (8 May) and continued until 15 days after girdling (12 May), when they started to diminish but continued on all trees until 26 days after girdling (23 May) when the study was terminated. *Camptocerus noel* was the first species to arrive on 28 April, followed by *Camptocerus pseudoangustior* on 4 May, *C. suturalis* on 10 May and *C. opacicollis* on 16 May. *Camptocerus suturalis* galleries were constructed next to larger galleries created by *Camptocerus noel* and *Camptocerus pseudoangustior* that were 3-6 days old. *Protium* specimen "D" was not girdled prior to cutting and colonization did not begin until 4 May and *Protium* specimen "E" received its first attacks on 6 May. There did not appear to be a difference between girdled and ungirdled trees for the start of colonization. Each tree was colonized by all four species.

### Aggregation

*Camptocerus* were first observed 2 May, three days after the trees were cut and five days after girdling. *Camptocerus noel* and *Camptocerus pseudoangustior* were initially found within 1m of two of the *P. amazonicum* trees. *Camptocerus opacicollis* were observed aggregating 19 days after the trees were cut and corresponded to the start of gallery creation by the species. All species except *C. suturalis* aggregated in leaves of nearly every plant located within 2 m of the felled *P. amazonicum* trees. Host leaves were utilized approximately 10% of total aggregation observations. Leaves with aggregating beetles ranged from thick and waxy to new and thin, living and dead leaves, and leaves with and without latex. Leaves represented 18 families and encompassed trees, shrubs, grasses, climbers and ferns with the exception of leaves with large trichomes and included the following taxa: *Aspidosperma parvifolium* (Apocynaceae), *Bactris* spp. (Arecaceae), *Geonoma* sp. (Arecaceae), *Matisia ochrocalyx* (Bombaceae), *Protium amazonicum* (Burseraceae), Chrysobalanaceae, *Symphonia globulifera* (Clusiaceae), *Bauhinia* sp. (Fabaceae), *Inga* spp. (Fabaceae), *Eschweilera coriacea* (Lecythidaceae), *Carpotroche longifolia* (Flacourtiaceae), *Lomariopsis japurensis* (Lomariopsidaceae), *Calathea* spp. (Marantaceae), Marantaceae, *Olyra* sp. (Poaceae), *Petrea maynensis* (Polygonaceae), Polygonaceae, *Polybotrya* sp. (Pteridophyta), Rubiaceae, *Leonia glyxicarpa* (Verbenaceae), *Costus* sp. (Violaceae), Zingiberaceae. Leaves were selected regardless of their spatial orientation to the forest floor. Holes always touched at least one vein and frequently touched the midrib and a secondary vein. This was not true in grasses where veins are abundant. No differences were observed between the sexes. There was always a pile of dried leaf pieces near the beetles on the leaves (Fig. 2.1) and frass was

never observed. Leaves on three occasions contained two beetles at a time, once in the case of *Camptocerus noel* and twice by *Camptocerus pseudoangustior*.

Beetles were observed with their abdomen above the leaf surface and the head facing the ground in 3 of 113 observations. The pronotum was divided between the two surfaces and the head was pushed tightly against the pronotum. The meso- and metathoracic legs rested against one leaf surface and the prothoracic legs were held tightly against the other leaf surface. Beetles were not observed to move and maintained their grip on the leaf in observed situations, such as movements caused by wind and when the leaf was brushed by an animal. The beetles tucked their legs in, dropped to the ground and hid in the leaf litter when covered by shadows or perturbed by a predator. Empty holes were frequently observed and the beetles did not seem to return to the same hole after a disturbance.

*Camptocerus* beetles were also observed in leaves around an unidentified fallen tree (15 cm DBH) that produced thick, white latex from cuts in the bark. More than 20 *Camptocerus noel* were found in leaves around this fallen tree, but none had attacked it. There were over 100 holes in leaves around this tree.

### **Leaf Feeding**

Feeding on the leaf surface near the hole was observed. Holes were identical to those used for aggregation and were always placed adjacent to a rib. Leaf feeding was observed for all species except *C. suturalis*. Feeding was restricted to leaves of the host (*P. amazonicum*) and *Carpotroche longifolia* (Poepp.) Benth. (Flacourtiaceae). All species were observed in leaves of *P. amazonicum*, but *Camptocerus noel* was found

feeding on *Carpotroche longifolia* approximately 90% of the time. Frass was always present on the leaf surface near a beetle after 6 May. When beetles were present, the leaves had evidence of window feeding on the upper side of the leaf in close proximity to the hole (Fig. 2.2). Over time, feeding damage progressed to skeletonizing. Four *Camptocerus noel* beetles were each observed once performing window feeding on the upper leaf surface within 2 cm of their hole. When disturbed, they quickly retreated to their hole with their abdomens on the upper leaf surface. Observation of leaf damage by feeding was observed in one *Camptocerus noel* five days after girdling (2 May) and became more common as time progressed with twenty *Camptocerus noel* observed after nine days (6 May). Three *Camptocerus pseudoangustior* were first observed after 11 days (8 May) and three *C. opacicollis* after 19 days (16 May). Aggregation was observed in equal frequency by both sexes.

*Protium amzaonicum* "F" was closely observed for the presence of beetles beginning the day after felling. Forty-eight hours after felling, six beetles were observed in leaves and one leaf had fresh signs of feeding. Feeding created skeletonizing damage and both leaf surfaces were eaten with veins left intact. Eight days after felling, leaves commonly showed window-feeding on the upper leaf surface. Dissections of aggregating beetles revealed an empty gut, while dissections of feeding beetles yielded a full digestive tract, confirming the observations. Leaf and beetle vouchers are stored in the A.J. Cook Arthropod Research Collection, Michigan State University (MSUC).

### **Courtship and Mating**

Courtship was observed ten times and mating was observed four times in *Camptocerus noel*. Mating was observed three times in *Camptocerus pseudoangustior*. *Camptocerus noel* females stayed in the entrance tunnel with their abdomens above the bark surface. Males walked the bark in presumed search of females. Two to three males gathered around a female and males fought for access to the female. Fighting consisted of charging at the opponent and pushing him away from the female's vicinity by placing his frons against the abdomen of the opposing male. The male brushed his antennal funicle setae over the female abdomen in a fluttering motion producing a whirling sound. He then repeatedly placed his frons against her abdomen, which corresponded to the concavity of his frons. The male periodically produced chirps using his elytra-abdominal stridulatory mechanism, rather than the gula-prosternum stridulatory mechanism on his head. While the female constructed the gallery, he waited outside and used his brush-like antennae to sweep away boring-dust and frass. In both species, females stayed in the entrance tunnel and copulated with the male as he stood on the bark surface. The beetles mated at a 90-degree angle with the male perpendicular to the female elytra. Two digital movies of these behaviors can be found at [www.scolytid.msu.edu/Camptocerus\\_biology.html](http://www.scolytid.msu.edu/Camptocerus_biology.html).

### **Predation**

Three bullet ants, *Paraponera clavata* (F.), were observed trying to pry *Camptocerus noel* and *pseudoangustior* out of their entrance tunnels with their mandibles. Ants were also seen twice carrying *Camptocerus pseudoangustior* females in their mandibles on the trunk of one tree.

A *Dolichoderus* sp. worker was observed to hunt *Camptocerus* on leaves. A *Camptocerus noel* adult was standing on a leaf and the ant lunged for it. The beetle tucked its legs in and rolled off the leaf on to the forest floor where it buried itself in leaf litter.

Workers of a *Crematogaster* species were observed on two *P. amazonicum* trees performing engaging in behaviors that at first did not resemble predation. Ants were clustered around gallery entrances in excess of twenty individuals. As the male swept frass and sawdust from the gallery and outside the tree, the ants came forward, grabbed any residual frass or sawdust, removed it from the gallery, and dropped it to the ground. Beetles were observed beating their abdomens against the sides of the gallery to block the ant's entry and attempted to push them out of their galleries. However predation became evident when *Crematogaster* were also observed clustering around a *Camptocerus noel* male on a branch. The ants frequently attacked and engulfed beetles on the tree surface. These beetles were likely paralyzed by the ants and were moribund or dead.

*Crematogaster* were observed to bite *Camptocerus* and kill 54 of 110 females creating their galleries as well as numerous males blocking gallery entrances. The ants separated the 7<sup>th</sup> sternite from the 8<sup>th</sup> tergite and hollowed out the beetles through the genital opening. Ant predation was a significant problem for *Camptocerus pseudoangustior* (50% predation in one tree), but was observed to a lesser degree on *Camptocerus noel* and *C. opacicollis*. No predation was observed on *C. suturalis*. A digital movie of *Crematogaster* predation is available at [www.scolytid.msu.edu/Camptocerus\\_biology.html](http://www.scolytid.msu.edu/Camptocerus_biology.html).

## DISCUSSION

Colonization duration was longer than previously documented. This minimal 25-day period was substantially longer than the 3-10 days that had been reported from Brazil (Beaver, 1972). Observations of maturation feeding were identical to those reported by von Winning (1930). Maturation feeding, first observed by von Winning to account for the behavior of *C. aeneipennis*, has now been documented for *Camptocerus noel*, *Camptocerus pseudoangustior* and *C. opacicollis*. Only nine *C. suturalis* individuals were collected during this study compared to a minimum of 200 for other species. *C. suturalis* has also been observed perform aggregation and maturation feeding behaviors in Loreto province, Peru (A. Petrov, per. com.). Similar observations were made with *C. aeneipennis* and *C. auricomus* Blandford in Panama (Smith, per. obs.). However, observations at Los Amigos suggest this behavior is actually two different behaviors in *Camptocerus*: aggregation and maturation feeding. The pile of dried, unconsumed leaf material next to aggregating beetles suggests the beetles were creating a place in which to aggregate around the potential host. Beetles were also observed aggregating around a tree that produced thick latex when bark was removed. It was apparent that the beetles had been there for some time due to the large number of holes and maturation feeding observed. It is possible the beetles were waiting for the latex to subside before colonization.

The biology of *Camptocerus* is similar to the other genera in the tribe Scolytini (*Cnemonyx* Eichhoff, *Scolytus* Geoffroy and *Scolytopsis* Blandford). Species of the Scolytini are known to colonize moribund material in masse (Wood, 1982). Multiple

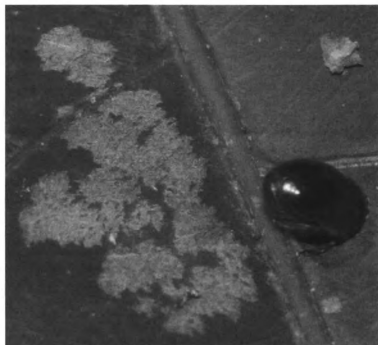
*Camptocerus* species were observed to colonize individual hosts in Brazil (Beaver, 1972), Colombia and Venezuela (Wood, 2007), Guyana and Panama (Smith, per. ob.), and Peru. When multiple *Camptocerus* species colonized a single host, the species segregated by size, as previously reported (Beaver, 1972; Wood 2007). Large numbers of beetles of a single species or of several species of *Cnemonyx* are common in the same host (Wood, 2007; Smith per. ob.). *Camptocerus* mating behavior differs from that of *Scolytus multistriatus* (Marsham). Male *S. multistriatus* also place their frons against the female abdomen, but copulation occurs end-to-end inside the gallery (Collins et al., 1936).

Prior to this study, limited information existed on predation of *Camptocerus*. Beaver (1972) reported larval parasitism by an unidentified species of Braconidae and predation by an unidentified Coleoptera larva. Ants such as species of *Crematogaster*, are commonly known to prey upon ambrosia beetles (Browne, 1961), bark beetles (Moeck & Safranyik, 1984; González & Campos, 1990) and fruit boring scolytines (Philpott & Armbrrecht, 2006). Thus, ant predation on *Camptocerus* is unsurprising given the abundance of ants in the tropics. Beetles attempted to defend themselves by thrashing their abdomens against the sides of their galleries and pushing ants out of their holes as observed in Beaver (1972).





**FIGURE 2.1:** (A) Males of *Camptocerus noel* aggregating and resting in a leaf near a felled *Protium amazonicum* tree. They made the holes in which they rest. (B) Female *Camptocerus noel* resting in a leaf and (C) boring through the leaf with undigested leaf cuttings.



**FIGURE 2.2:** Damage caused by feeding male of *Camptocerus noel* to a *P. amazonicum* leaflet.

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