

# The genus *Callistethus* (Coleoptera: Scarabaeidae: Rutelinae) in the Neotropics: new data and new species from Costa Rica

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## Abstract

The species *Callistethus carbo* sp.n., *C. flavodorsalis* sp.n., *C. fuscrobens* sp.n., *C. lativittis* sp.n., *C. levigatus* sp.n., *C. macroxantholeus* sp.n., *C. microxantholeus* sp.n., *C. multiplicatus* sp.n., *C. parapulcher* sp.n., *C. pseudocollaris* sp.n. and *C. stannibractea* sp.n. from Costa Rica are described. Synonymy of *Callistethus kolbei* (Ohaus, 1897) with *Callistethus specularis* (Bates, 1888) is proposed. A phylogenetic analysis based on the genes 16S, COI and 28S is carried out for Costa Rican species and diagnostic morphological features for the genus are tested on it for phylogenetic signal. An identification key for *Callistethus* species of Costa Rica is provided. The distribution patterns of *Callistethus* species in Costa Rica are discussed.

## Resumen

Se describen las especies *Callistethus carbo* sp.n., *C. flavodorsalis* sp.n., *C. fuscrobens* sp.n., *C. lativittis* sp.n., *C. levigatus* sp.n., *C. macroxantholeus* sp.n., *C. microxantholeus* sp.n., *C. multiplicatus* sp.n., *C. parapulcher* sp.n., *C. pseudocollaris* sp.n. y *C. stannibractea* sp.n. de Costa Rica. Se propone una nueva sinonimia de *Callistethus kolbei* (Ohaus, 1897) con *Callistethus specularis* (Bates, 1888). Se realiza un análisis filogenético basado en los genes 16S, COI y 28S con especies de Costa Rica y sobre el árbol resultante se comprueba la señal filogenética de los caracteres morfológicos diagnósticos del género. Se proporciona una clave para las especies de *Callistethus* de Costa Rica. Se discuten los patrones de distribución del género en Costa Rica.

## Key words

Aedeagus, *Anomala*, distribution, endophallus, identification key, morphology, molecular analysis, phylogeny.

## 1. Introduction

The tribe Anomalini (Coleoptera: Scarabaeidae: Rutelinae) is a heterogeneous group composed by 65 genera, 70% of which have less than 10 species (KRAJCIK 2007). The most speciose genus in the tribe is *Anomala* Samouelle, with more than 1000 species distributed worldwide. In the Neotropics 15 genera are present, of which 5 can be found in Costa Rica: *Anomala*, *Anomalorhina*, *Callistethus*, *Epectinaspis* and *Strigoderma*.

Based on the checklist by KRAJCIK (2007), the genus *Callistethus* Blanchard comprises 142 species distributed in Asia (85 species) and America (57 species), although their real diversity is probably much higher. The life history of this genus is similar to that of other Anomalini and Rutelini genera: larvae feed on roots and organic material, adults on leaves, floral parts and fruits of angiosperms and gymnosperms. Adults of some species are

readily attracted to light at night, while others are diurnal and are found on flowers and foliage. Adult body length ranges from 11 to 23 mm (JAMESON et al. 2003). Rutelinae are considered an useful group to be used in forestry biodiversity groups, due to its richness, wide distribution, standardized collection methods and presence of different trophic habits. However, the implement of the Anomalini tribe is hindered by their poorly known taxonomy (MORÓN 1997; GARCÍA-LÓPEZ et al. 2011, 2012).

The diagnostic features for *Callistethus* are a mesosternal process that is produced beyond the apex of the mesocoxae (often produced to the procoxae), concealed mesepimeron, clypeus not reflexed, maxilla with six teeth (JAMESON et al. 2003), pronotum without bead on the posterior margin, sutural apex of elytron spiniform, and male genitalia with parameres and aedeagal ventral plate fused (MORÓN & RAMÍREZ-PONCE 2012). The nearest genera in America are thought to be *Anomala* and *Yaaxkumukia* Morón & Nogueira (Mexico), which share the features of mesoepimeron, clypeus and maxilla; *Yaaxkumukia* also shares the features of pronotum and the presence of a mesosternal process.

The monophyly of the genus *Callistethus* and its definition in relation to the genus *Anomala* have been widely questioned, but no consensus has been reached (JAMESON et al. 2003). The genus assignment for Neotropical species used by modern authors follows the lists from MACHATSCHKE (1957, 1972) and KRAJCIK (2007).

BATES (1888), BLACKWELDER (1944) and POTTS (1974) considered *Callistethus* as a synonym of *Anomala* when working on Neotropical Anomalini. MORÓN & NOGUEIRA (2002) considered the taxon valid, but with reservations. They suggested that a study including more Neotropical species could possibly identify a natural Neotropical group separated from *Callistethus* and *Anomala*. JAMESON et al. (2003) saw a sign of the probable paraphyly of the genus in these contrasting treatments. RAMÍREZ-PONCE & MORÓN (2009) grouped together species of *Anomala* and *Callistethus* (with short mesosternal process – more or less at same level of apex of mesocoxae –, as *C. cupricollis* (Chevrolat, 1834) and *C. marginicollis* (Bates, 1888)) in a new genus, revalidating the name *Paranomala* Casey, 1915, and considered *Callistethus* a valid genus for the Neotropics, which includes only species with long (reaching procoxae) and acute mesosternal process (also in MORÓN & RAMÍREZ-PONCE 2012). Table 1 presents an overview of the different taxonomical treatments by these authors for the species considered here.

The diagnostic features that separate *Callistethus* from *Anomala* are: mesosternal process produced beyond the apex of the mesocoxae, consequently with a wider space between the mesocoxae, pronotum without bead on the posterior margin, sutural apex of elytron spiniform, male genitalia with parameres and aedeagal ventral plate fused. The same pool of features is also present in oriental species of *Callistethus* (RAMÍREZ-PONCE & MORÓN 2009), including the type species for the genus, *C. auronitens* (Hope, 1835) (except for the ventral plate of the aedeagus, reduced to a narrow strip in this species

and separated from the parameres; personal observation). We therefore agree with the previous authors on the validity of the genus *Callistethus* in the Neotropics, and its testing was not object of the present work.

There are however different interpretations regarding the level of development of the mesosternal structure required to include one species in the genus *Callistethus*: while for JAMESON et al. (2003) it seems to include the species with short mesosternal process (for most of which the process is at level of apex of mesocoxae, not beyond it), for RAMÍREZ-PONCE & MORÓN (2009) and MORÓN & RAMÍREZ-PONCE (2012) only species with mesosternal process reaching procoxae are included.

Apart from these different interpretations, the current classification still does not reflect this definition, due to the lack of any comprehensive revision. Some species of *Anomala* present a well developed mesosternal process and would therefore be better placed in *Callistethus*, as is the case of *A. lepida* (Burmeister, 1844), reported by MORÓN & NOGUEIRA (2002), and species currently in *Callistethus* that have a poorly developed mesosternal process should be placed in *Anomala*.

However, the assignment is still unclear for species with short mesosternal process and pronotum with bead on the posterior margin, parameres not fused with ventral plate (as in *validus* group sensu MACHATSCHKE 1957); for species with short mesosternal process, pronotum with bead on the posterior margin, parameres fused with ventral plate (as *C. biolleyi* (Ohaus, 1902), *C. buchwaldianus* (Ohaus, 1908), *C. nicoya* (Ohaus, 1928) and *C. sulcans* (Bates, 1888)); for species with short mesosternal process, pronotum without bead on the posterior margin, parameres usually fused with ventral plate (as *C. chontalensis* (Bates, 1888), *C. schneideri* (Ohaus, 1905), *C. granulipygus* (Bates, 1888)); all these do not fit clearly in any definition given in MORÓN & RAMÍREZ-PONCE (2012).

Due to these uncertainties, in this paper we will follow the classification found in KRAJCIK (2007), even if not updated, as starting point to verify the different interpretations.

In this paper we do a phylogenetic analysis of *Callistethus* and *Anomala* species from Costa Rica, based on sequences of one nuclear (a fragment of 28S) and two mitochondrial (16S and COI) genes, and we test the phylogenetic signal of diagnostic characters on the resulting trees.

Other phylogenetic works on Anomalini are scarce: based on morphological characters PAUCAR-CABRERA (2003) on *Epectinaspis* and RAMÍREZ-PONCE & MORÓN (2009) on *Anomala*; based on molecular data only broader studies not focused on Anomalini (GARCÍA-LÓPEZ et al. 2013; AHRENS et al. 2014). We also describe 11 new species from the revision of the genus *Callistethus* from Costa Rica and propose a new synonym and new combinations.

**Table 1.** Overview of the taxonomical treatment for the species of *Callistethus* considered here, from the present publication and the main past lists including Neotropical species. The genus used for the species list follows KRAJCIK (2007). The symbol ‘—’ is used for species absent in the corresponding publication. Note: the species *C. schneideri* is absent in BLACKWELDER (1944) and *C. fulvopiceus* and *C. nicoya* are absent in OHAUS (1918).

(KRAJCIK 2007)	FILIPPINI et al.	MORÓN & RAMÍREZ-PONCE 2012	RAMÍREZ-PONCE & MORÓN 2009	MACHATSKHKE 1957, 1972	OHAUS 1918; BLACKWELDER 1944	BATES 1888
<i>C. cupricollis</i> (Chevrolat, 1834)	ANOMALA	PARANOMALA	PARANOMALA	CALLISTETHUS validus group	ANOMALA	ANOMALA I.2
<i>C. validus</i> (Burmeister, 1844)				ANOMALA binotata gr.		
<i>C. megalis</i> (Bates, 1888)				CALLISTETHUS marginatus group		
<i>A. praecellens</i> Bates, 1888				— (B)		
<i>C. chontalensis</i> (Bates, 1888)	CALLISTETHUS	undefined	CALLISTETHUS	CALLISTETHUS marginatus group	— (B)	—
<i>C. schneideri</i> Ohaus, 1905						—
<i>C. granulipygus</i> (Bates, 1888)						ANOMALA I.3
<i>C. valdecostatus</i> (Bates, 1888)						—
<i>C. vanpatteni</i> (Bates, 1888)						—
<i>C. calonotus</i> (Bates, 1888)						—
<i>C. chlorotooides</i> (Bates, 1888)						—
<i>C. specularis</i> (Bates, 1888)						—
<i>A. chrysanthe</i> Bates, 1888						ANOMALA chrysanthe group
<i>A. jordani</i> Ohaus, 1902						—
<i>A. xiphostetha</i> Bates, 1888						—
<i>A. phosphora</i> Bates, 1888						ANOMALA no group
<i>A. lepida</i> Burmeister, 1844						—
<i>A. mimeloides</i> Ohaus, 1902						—
<i>A. xantholea</i> Bates, 1888	—					
<i>A. micans</i> Burmeister, 1844	ANOMALA lucicola gr.	ANOMALA I.5				
<i>C. jansoni</i> (Ohaus, 1897)	ANOMALA	PARANOMALA	PARANOMALA	CALLISTETHUS jansoni gr.	— (0)	—
<i>C. fulvopiceus</i> (Ohaus, 1928)				CALLISTETHUS microcephalus gr.		—
<i>C. biolleyi</i> (Ohaus, 1902)	<i>incertae sedis</i>	undefined	PARANOMALA	CALLISTETHUS sulcans gr.	— (0)	—
<i>C. buchwaldianus</i> (Ohaus, 1908)				—		
<i>C. nicoyus</i> (Ohaus, 1928)				—		
<i>C. sulcans</i> (Bates, 1888)				ANOMALA I.2		
				—		

## 2. Material and methods

### 2.1. Specimens examined

A total of 29 species of *Callistethus* have been studied morphologically: the 11 new species here described and 18 species present in Costa Rica (through specimens in CEUA and INBio collection, and type material) and 7 species of *Anomala* (through specimens in CEUA and INBio collection).

Type material for 38 additional species of *Callistethus* not present in Costa Rica was consulted for identification and to avoid possible synonymy (listed in Appendix with additional specimen information and a brief description).

Distribution data for the Costa Rican species have been compiled through locality labels associated with re-examined specimens and INBio's ATTA Database (<http://atta.inbio.ac.cr>) for species described prior to this work, and for which correct separation was verified personally.

### 2.2. Endophallus preparation procedure

The aedeagus was washed in a 10% hot KOH solution for 5–10 minutes and then rinsed in distilled water. It was then kept in lactic acid for a minimum of 48 hours, until the structures of the aedeagus and endophallus became translucent. The endophallus was then softened in warm water and everted injecting water from the base of the aedeagus with a syringe equipped with a suitable needle, or with microforceps (WPI Dumont #5) when the length of the internal sac made the syringe method inefficient. The dissection was transferred to a microvial containing glycerine, which was attached to the insect pin.

### 2.3. Line drawings

Line drawings were done with the aid of a camera lucida attached to a stereo microscope (Leica M80). The pencil drawings were then traced with technical ink pens. The sacculi are drawn more separated from each other than their natural position to allow a clearer illustration

of shapes and structures in the drawings of the endophallus of some species, when their shape or proximity would hide some portions; these cases are indicated in the caption of the corresponding illustration.

## 2.4. Feature standards

Measurements taken are as explained in FILIPPINI et al. (2013). When measurements among specimens differed by less than 0.03 units they were not included in the 'Variation' paragraph of descriptions. Width of space between the mesocoxae was measured at level of apex of trochanters. Enumeration of elytral striae was as illustrated and discussed in ZORN (2007). Endophallus and aedeagus terminology follows FILIPPINI et al. (2013). Surface sculpturing terminology follows HARRIS (1979).

## 2.5. Molecular-based phylogenetic analysis

The 36 Anomalini specimens from Costa Rica, belonging to 28 species, used for the analysis were conserved either dried or fixed in 100% ethanol and stored at  $-80^{\circ}\text{C}$ . Collection data are provided in Table 2. Of these, 20 species belongs to *Callistethus*, more than 60% of the known species for Costa Rica. As outgroup taxon a species belonging to another Anomalini genus was selected, *Anomalorhina turrialbana* (Ohaus, 1928), also present in Costa Rica, in order to facilitate analysis convergence. Regarding the risk of *Anomalorhina* being an aberrant clade of *Anomala*, this should not affect our aim focused on the genus *Callistethus*.

DNA was extracted from entire or grounded meta-femora using the DNeasy Blood and Tissue Kit (Qiagen, Hilden, Germany) following the manufacturer's protocol. Two mitochondrial (cytochrome c oxidase subunit I, 658–814 bp; 16S rRNA, 518 bp) and one nuclear (a continuous ca. 2267 bp section of 28S rRNA) genes were amplified and sequenced using primers 16Sa and 16Sb for 16S, LCO1490 and HCOoutout or HCO2190 for COI. Partial 28S rRNA was amplified in three fragments, using the primers 28Srd1a–28Srd4b for the first fragment, 28Sa–28Srd5b for the second fragment and 28Srd4.8a–28Srd7b1 for the third fragment. PCRs were carried out in 25  $\mu\text{l}$  reaction volumes according to standard protocols for GoTaq<sup>®</sup> DNA Polymerase (Promega, Madison, WI, USA). The PCR product was purified through enzymatic reaction with ExoSAP-IT (USB Corp., Cleveland, OH, USA). Sequencing was performed with the Big Dye<sup>®</sup> Terminator v3.1 Cycle Sequencing Kit (AppliedBiosystems, Foster City, CA, USA). Chromatograms obtained from the automatic sequencer were read and sequences assembled using the sequence editing software Sequencher<sup>™</sup> 4.7 (Gene Codes Corporation, Ann Arbor, MI, USA) and annealed in Geneious 6.0.5 (Biomatters Ltd., Auckland, New Zealand). The sequence identity for each PCR product was checked

using the basic local alignment search tool (BLAST). The sequences have been deposited in GenBank under the accession numbers shown in Table 2.

First we used PartitionFinder 1.1.1 (LANFEAR et al. 2012) to determine the best-fitting partition and substitution models for the phylogenetic analysis. Alternative partitions and models were also tested with a stepping-stone analysis in MrBayes 3.1.1 (RONQUIST & HUELSENBECK 2003). The best-fitting partition and substitution models chosen for Bayesian analysis were 16S + COI 1st codon position (GTR+I+G), COI 3rd codon position (HKY+G) and 28S + COI 2nd codon position (GTR+I). We analysed the concatenated data set (3831 bp) in MrBayes 3.1.1 (RONQUIST & HUELSENBECK 2003), with unlinked gamma shape and branch lengths, and variable rate prior for each partition. We ran two independent runs with 4 chains each for seven million generations, sampling every 500 generations. AWTY (WILGENBUSCH et al. 2004) and Tracer 1.6 (RAMBAUT et al. 2013) were used to assess convergence. Posterior probabilities are given as statistical branch support.

The best-fitting partition and substitution models for Maximum likelihood was 16S (HKY+I+G), COI 1st codon position (HKY+I+G), COI 2nd codon position (TrN+I+G), COI 3rd codon position (F81), 28S (GTR+I+G). Tree searches were conducted in GARLI (ZWICKL 2006), running eight independent searches.

Bootstrap values were calculated in PAUP\* 4.0 (SWOFFORD 1998) from 100 trees built in GARLI. Mr Bayes and Garli were run through CIPRES Science Gateway (MILLER et al. 2010).

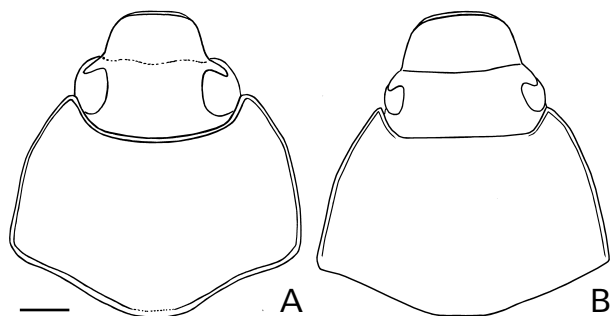
## 2.6. Phylogenetic signal of morphological characters

Morphological characters were adapted from the literature (MORÓN & RAMÍREZ-PONCE 2012), and additional characters were implemented from the dissection and morphological study of the specimens. Characters like 'pronotum with incomplete anterior margin' and 'epipleural fold wide' (MORÓN & RAMÍREZ-PONCE 2012) were not included for lack of definition that would make the coding subjective. The characters and character states analyzed are the following:

1. Interocular distance (based on a dorsal view): [0] narrow, 2–4 eye diameters (Fig. 1A); [1] wide, > 4 eye diameters (Fig. 1B).
2. Presence of basal bead on the posterior margin of pronotum: [0] present (Fig. 1A); [1] absent (Fig. 1B).
3. Shape of the posterior margin of pronotum in correspondence of scutellum: [0] convex (Fig. 1A); [1] straight or slightly concave (Fig. 1B).
4. Distance between mesocoxae: [0] narrow, about 1/4 the height of coxae or less; [1] wide, half the height of coxae; [2] very large, similar to the height of coxae.
5. Development of mesosternal process: [0] not developed, area between mesocoxae flat or slightly convex; [1] reaching apex of mesocoxae, apex connected

**Table 2.** Collection data and GenBank accession numbers for specimens used in phylogenetic analysis. Medium D: dry specimen; E: ethanol.

Species	Medium	Voucher	Locality (Costa Rica)	Date	28S	COI	16S
<i>Anomala eucoma</i> Bates, 1888	D	CEUA00105271	Amubri, A.C. Amistad, Limón	4-21-Dec-1993	KF737953	KF738020	KF737989
<i>Callistethus stannibractea</i> sp.n.	D	CEUA00105277	Estación Barva, P.N. Braulio Carrillo, Heredia	Feb-1990	KF737954	KF738021	
<i>Callistethus specularis</i> (Bates, 1888)	D	CEUA00105278	Isia Bonita, Alajuela	9-Sep-2007	KF737955	KF738022	KF737990
<i>Callistethus levigatus</i> sp.n.	D	CEUA00105281	Volcán Tenorio, Alajuela	3-Jun-2008	KF737956	KF738023	KF737991
<i>Callistethus</i> sp.304	D	CEUA00105801	Cerro Bitáikara, Limón	11-Aug-2007	KF737957	KF738024	KF737992
<i>Callistethus multiplicatus</i> sp.n.	D	CEUA00105283	Cabanga, finca J.Martínez, Alajuela	20-Jul-2010	KF737958	KF738025	KF757331
<i>Callistethus fuscrobens</i> sp.n.	D	CEUA00105284	Estación Altamira, Cerro Biotley, Puntarenas	23-30-Oct-1995	KF737959	KF738026	KF737993
<i>Callistethus parapulcher</i> sp.n.	D	CEUA00105287	Alto Jalisco, Buenos Aires, Puntarenas	22-26-Feb-2009	KF737960	KF738027	KF737994
<i>Callistethus carbo</i> sp.n.	D	CEUA00105294	Río San Lorenzo, Z.P. Tenorio, Guanacaste	23-Mar-21-Apr-1992	KF737961	KF738028	KF737995
<i>Callistethus macroxantholeus</i> sp.n.	D	CEUA00105293	Sector Cerro Cocori, Limón	Apr-1992	KF737962	KF738029	
<i>Anomala subridens</i> Filippini, Micó, Galante 2015	D	CEUA00105802	La Esperanza, Cartago	29-Aug-2008	KF737963	KF738030	KF737996
<i>Anomala calligrapha</i> Bates, 1888	D	CEUA00105803	Albergue Heliconias, Alajuela	13-Sep-2007	KF737964		KF737997
<i>Anomala subusta</i> Filippini, Micó, Galante 2015	D	CEUA105804	Volcán Tenorio, Alajuela	04-Jun-2008	KF737965	KF738031	KF737998
<i>Callistethus jordani</i> Ohaus, 1902	D	INBIOCR1000909339	Estación Biológica Las Alturas, Coto Brus, Puntarenas	23-Mar-2-May-1992	KF737966	KF738032	
<i>Callistethus valdecastatus</i> (Bates, 1888)	D	INBIOCR1001926964	Alto de las Moras, Buenos Aires, Puntarenas	24-Mar-1993	KF737967	KF738033	KF737999
<i>Callistethus megalis</i> (Bates, 1888)	D	INBIOCR1000988672	Manzanillo, Limón	22-Oct-11-Nov-1992	KF737968	KF738034	KF738000
<i>Callistethus validus</i> (Burmeister, 1844)	D	CEUA00003281	Horquetas	12-Feb-2006	KF737969	KF738035	KF738001
<i>Anomala balzapambae</i> Ohaus, 1897	D	CEUA00105805	Volcán Tenorio, Alajuela	20-Jun-2009	KF737970	KF738036	KF738002
<i>Anomala estrella</i> Filippini, Galante, Micó, 2015	D	CEUA00105806	Los Almendros, P.N. Guanacaste, Guanacaste	28-Mar-24-Apr-1992	KF737971	KF738037	KF738003
<i>Anomalorhina turriabana</i> (Ohaus, 1928)	D	CEUA00105807	Cabanga, finca J.Martínez, Alajuela	13-Apr-2010	KF737972	KF738038	KF738004
<i>Callistethus mimeioides</i> Ohaus, 1902	E	CEUA00105808	Catarata Río Buenavista, P.N. Volcán Tenorio, Alajuela	14-Apr-2010	KF737973		KF738005
<i>Callistethus cupricollis</i> (Chevrolat, 1834)	E	CEUA00105809	Cabanga, finca J.Robles, Alajuela	15-Apr-2010	KF737974	KF738039	KF738006
<i>Callistethus cupricollis</i> (Chevrolat, 1834)	E	CEUA00105810	Cabanga, finca J.Martínez, Alajuela	15-Apr-2010	KF737975	KF738040	KF738007
<i>Callistethus chontalensis</i> (Bates, 1888)	E	CEUA00105811	Catarata Río Buenavista, P.N. Volcán Tenorio, Alajuela	15-Apr-2010	KF737976	KF738041	KF738008
<i>Callistethus chontalensis</i> (Bates, 1888)	E	CEUA00105812	Cabanga, finca J.Robles, Alajuela	15-Apr-2010	KF737977	KF738042	KF738009
<i>Callistethus granulipygus</i> (Bates, 1888)	E	CEUA00105813	Cabanga, finca J.Robles, Alajuela	15-Apr-2010	KF737978	KF738043	KF738010
<i>Callistethus lativittis</i> sp.n.	E	CEUA00105814	Cabanga, finca J.Martínez, Alajuela	15-Apr-2010	KF737979	KF738044	KF738011
<i>Callistethus lativittis</i> sp.n.	E	CEUA00105815	Cabanga, finca J.Robles, Alajuela	14-Apr-2010	KF737980	KF738045	KF738012
<i>Callistethus schneideri</i> Ohaus, 1905	E	CEUA00105816	Catarata Río Buenavista, P.N. Volcán Tenorio, Alajuela	13-Apr-2010	KF737981	KF738046	KF738013
<i>Callistethus schneideri</i> Ohaus, 1905	E	CEUA00105817	Catarata Río Buenavista, P.N. Volcán Tenorio, Alajuela	13-Apr-2010	KF737982	KF738047	KF738014
<i>Callistethus macroxantholeus</i> sp.n.	E	CEUA00105818	Catarata Río Buenavista, P.N. Volcán Tenorio, Alajuela	14-Apr-2010	KF737983	KF738048	KF738015
<i>Callistethus microxantholeus</i> sp.n.	E	CEUA00105819	Cabanga, finca J.Robles, Alajuela	12-Feb-2010	KF737984	KF738049	KF757332
<i>Anomala discoidalis</i> Bates, 1888	E	CEUA00105820	Cabanga, finca J.Robles, Alajuela	19-Oct-2009	KF737985		KF738016
<i>Anomala discoidalis</i> Bates, 1888	E	CEUA00105821	Cabanga, finca J.Robles, Alajuela	19-Oct-2009	KF737986	KF738050	KF738017
<i>Callistethus microxantholeus</i> sp.n.	E	CEUA00105822	Cabanga, finca J.Robles, Alajuela	11-Feb-2010	KF737987	KF738051	KF738018
<i>Callistethus microxantholeus</i> sp.n.	E	CEUA00105823	Cabanga, finca J.Robles, Alajuela	11-Feb-2010	KF737988	KF738052	KF738019



**Fig. 1.** Head and pronotum in dorsal view of **A:** *Anomala arara* (male, Estación Cabro Muco, Costa Rica); **B:** *Callistethus flavo-dorsalis* (male, Finca Cafrosa, Costa Rica). Scale = 1 mm.

to mesoventrite; [2] produced beyond mesocoxae for at least half the height of coxae, with apex separated from level of mesoventrite.

6. Definition of mesometasternal suture: [0] well defined; [1] poorly defined or absent.
7. Position of mesometasternal suture: [0] at the same level as posterior margin of mesotrochanter; [1] at the same level as anterior margin of mesotrochanter.
8. Shape of apex of elytral suture: [0] curved; [1] spini-form.
9. Fusion of parameres to aedeagal ventral plate: [0] absent; [1] present.

The scorings of these characters for species of interest are listed in Table 3.

Characters 1, 3, 6 and 7 were added for different states of characters being present in the species studied from Costa Rica and in the type species of the genus.

Characters 4 and 5 are treated as multistate to account for the variability seen in these structures.

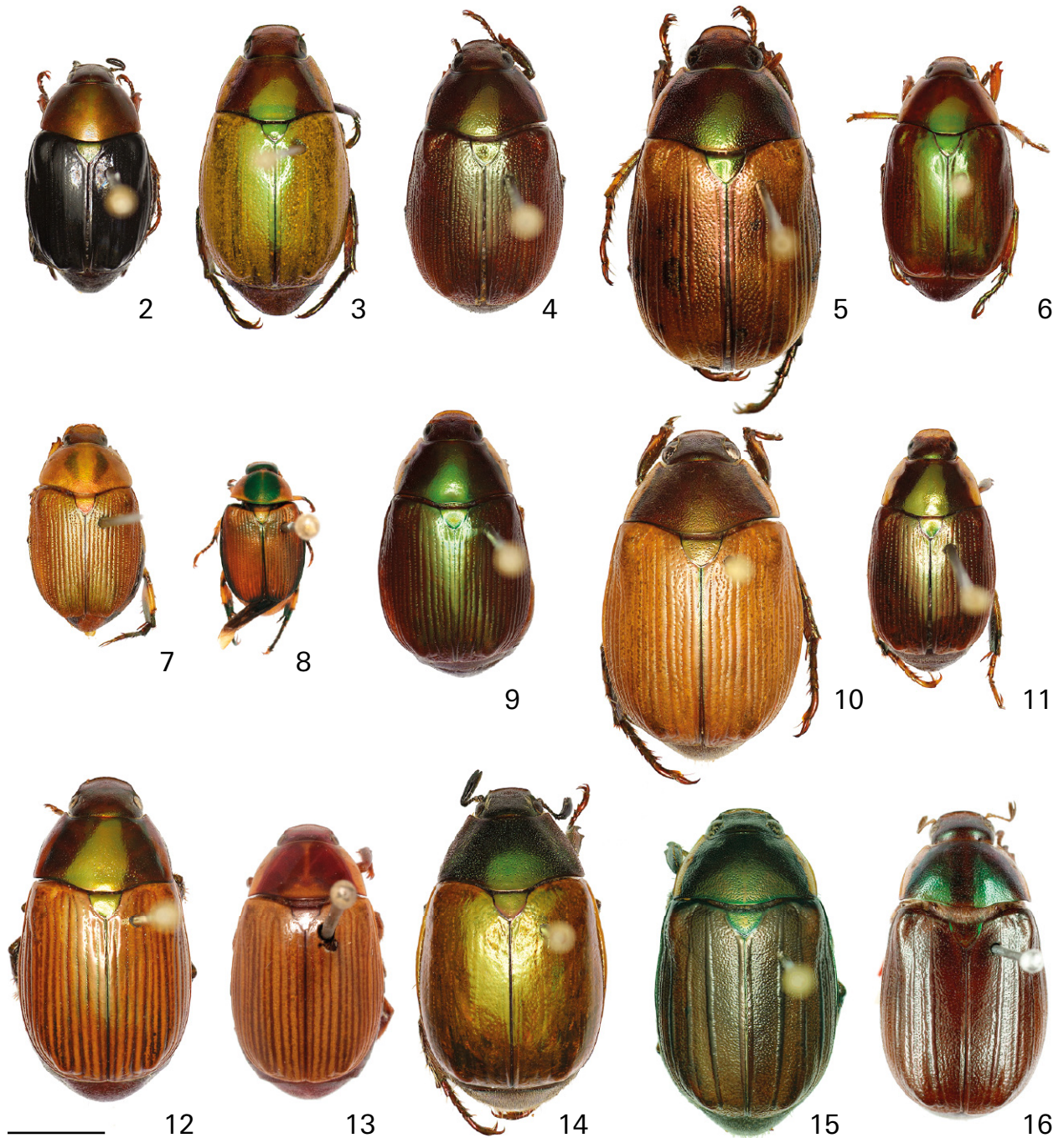
Phylogenetic signal of morphological characters of male genitalia was calculated with the *K* statistics (BLOMBERG et al. 2003), using the R packages *picante* (KEMBEL et al. 2010). *K* values closer to zero correspond to a random, i.e. highly homoplasious, pattern of evolution, while *K* values greater than 1 indicate low homoplasy and thus strong phylogenetic signal.

### 3. Abbreviations

**BMNH** Natural History Museum, London, United Kingdom;  
**CEUA** Colección Entomológica de la Universidad Alicante, Spain;  
**INBIOCRI** Instituto Nacional de Biodiversidad, Costa Rica;  
**MNHN** Muséum National d’Histoire Naturelle, Paris, France;  
**MNHUB** Museum für Naturkunde der Humboldt-Universität zu Berlin, Germany.

**Table 3.** Character scoring for the species treated.

Species	1	2	3	4	5	6	7	8	9
<i>Anomala balzapambae</i> Ohaus, 1897	0	0	0	0	0	0	0	0	0
<i>Anomala calligrapha</i> Bates, 1888	0	0	0	0	0	0	0	0	0
<i>Anomala discoidalis</i> Bates, 1888	0	0	0	0	0	0	0	0	0
<i>Anomala estrella</i> Filippini, Galante, Micó 2015	0	0	0	0	0	0	0	0	0
<i>Anomala eucoma</i> Bates, 1888	0	0	0	0	0	0	0	0	0
<i>Anomala subridens</i> Filippini, Micó, Galante, 2015	0	0	0	0	0	0	0	0	0
<i>Anomala subusta</i> Filippini, Micó, Galante, 2015	0	0	0	0	0	0	0	0	0
<i>Anomalorhina turrialbana</i> (Ohaus, 1928)	0	1	0	0	0	0	0	0	0
<i>Callistethus antis</i> (Ohaus, 1902)	0	0	0	2	0	0	1	?	0
<i>Callistethus bimaculatus</i> (Blanchard, 1851)	0	0	0	1	0	1	0	?	?
<i>Callistethus biolleyi</i> (Ohaus, 1902)	0	0	1	0	0	0	0	1	1
<i>Callistethus buchwaldianus</i> (Ohaus, 1908)	0	0	0	0	1	0	0	?	1
<i>Callistethus calonotus</i> (Bates, 1888)	1	1	1	2	2	1	1	0	1
<i>Callistethus carbo</i> sp.n.	1	1	1	1	1	1	1	1	1
<i>Callistethus chlorotoides</i> (Bates, 1888)	1	1	1	2	2	1	1	1	1
<i>Callistethus chontalensis</i> (Bates, 1888)	0	1	1	0	1	0	1	0	1
<i>Callistethus cicatricosus</i> (Perty, 1832)	0	0	0	1	0	0	0	?	0
<i>Callistethus cupricollis</i> (Chevrolat, 1834)	0	0	0	0	1	1	0	0	0
<i>Callistethus eckhardti</i> (Ohaus, 1897)	0	0	0	1	1	1	1	?	0
<i>Callistethus flavodorsalis</i> sp.n.	1	1	1	2	2	1	1	0	0
<i>Callistethus fulvopiceus</i> (Ohaus, 1928)	0	0	0	1	0	0	0	?	?
<i>Callistethus fusciorubens</i> sp.n.	0	1	1	1	1	1	1	0	1
<i>Callistethus granulipygus</i> (Bates, 1888)	0	1	1	1	1	1	1	0	1
<i>Callistethus jansoni</i> (Ohaus, 1897)	0	0	0	0	0	0	0	?	0
<i>Callistethus jordani</i> Ohaus, 1902	1	1	1	1	2	1	1	0	0
<i>Callistethus lativittis</i> sp.n.	0	1	1	1	1	1	1	0	1
<i>Callistethus lepidus</i> (Burmeister, 1844)	1	1	1	2	2	1	1	?	1
<i>Callistethus levigatus</i> sp.n.	1	1	1	2	2	1	1	0	0
<i>Callistethus macroxantholeus</i> sp.n.	1	1	1	1	1	1	0	1	0
<i>Callistethus megalis</i> (Bates, 1888)	0	0	1	1	0	1	1	0	0
<i>Callistethus microxantholeus</i> sp.n.	1	1	1	1	1	1	0	1	0
<i>Callistethus mimeloides</i> Ohaus, 1902	0	1	1	2	2	1	1	0	1
<i>Callistethus multiplicatus</i> sp.n.	1	1	1	2	2	1	1	1	1
<i>Callistethus nicoyus</i> (Ohaus, 1928)	0	0	0	0	1	0	0	1	1
<i>Callistethus ochrogastrus</i> (Bates, 1888)	0	0	0	0	0	0	0	0	0
<i>Callistethus panamensis</i> (Ohaus, 1902)	0	0	0	1	0	1	1	?	0
<i>Callistethus parapulcher</i> sp.n.	0	1	1	1	2	1	1	0	1
<i>Callistethus plagiatus</i> (Nonfried, 1894)	0	0	0	1	1	1	0	?	?
<i>Callistethus pseudocollaris</i> sp.n.	1	1	1	2	2	0	1	0	1
<i>Callistethus pupillatus</i> (Burmeister, 1844)	0	0	0	0	0	0	0	?	0
<i>Callistethus schneideri</i> Ohaus, 1905	0	1	1	0	1	1	1	0	1
<i>Callistethus ruteloides</i> Filippini, Galante, Micó 2015	0	0	0	2	2	1	1	0	0
<i>Callistethus yalizo</i> Filippini, Galante, Micó 2015	0	1	1	1	1	0	1	0	1
<i>Callistethus</i> sp304	1	1	1	1	2	1	1	1	1
<i>Callistethus specularis</i> (Bates, 1888)	1	1	1	2	2	1	1	0	1
<i>Callistethus stannibractea</i> sp.n.	1	1	1	1	2	1	1	0	0
<i>Callistethus sulcans</i> (Bates, 1888)	0	0	0	0	1	0	0	1	1
<i>Callistethus valdecostatus</i> (Bates, 1888)	0	1	1	0	1	1	1	0	1
<i>Callistethus validus</i> (Burmeister, 1844)	0	0	0	0	0	1	0	0	0
<i>Callistethus vanpatteni</i> (Bates, 1888)	0	1	1	1	1	0	1	0	1
<i>Callistethus xantholeus</i> (Bates, 1888)	1	1	1	1	1	0	0	?	0
<i>Callistethus xiphostethus</i> (Bates, 1888)	1	1	1	2	2	1	1	0	0



**Figs. 2–16.** Habitus. **2:** *Callistethus carbo* (Holotype). **3:** *C. flavodorsalis* (Holotype). **4:** *C. fusciorubens* (Holotype). **5:** *C. lativittis* (Holotype). **6:** *C. levigatus* (Holotype). **7:** *C. macroxantholeus* (Holotype). **8:** *C. microxantholeus* (Paratype, Est. Pitilla). **9:** *C. multiplicatus* (Holotype). **10:** *C. parapulcher* (Holotype). **11:** *C. pseudocollaris* (Holotype). **12:** *C. specularis* (Rio San Lorenzo). **13:** *C. kolbei* (Holotype). **14:** *C. stannibractea* (Holotype). **15:** *C. valdecostatus* (Estación Biológica Las Alturas, Puntarenas, INBIO). **16:** *C. marginicollis* (cotype, Mexico, MNHUB). Scale = 5 mm.

## 4. Taxonomy

### 4.1. *Callistethus carbo* sp.n.

**Description.** Male holotype: **Body shape:** Length 11.81 mm; width 6.74 mm. Oval, stout. Elytral disc flattened. **Colouration:** Head, pronotum and scutellum metallic green with

bronze luster; scutellum darker. Elytra glossy bluish black, pygidium black. Venter greenish dark brown, legs dark reddish brown (Fig. 2). **Head:** Clypeus trapezoidal, nearly rectangular; ratio width/length 2.09. Clypeus surface punctate-reticulate with confluent punctures. Frons punctate-reticulate. Vertex punctate. Ocular canthus wide and stout; apex large and rounded. Eyes elongated, interocular ratio (interocular width/width of eye) 4.53. Antennae:

ratio funiculus/club 0.64. **Pronotum:** Basal width  $1.75 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 1/3 of length from anterior. Anterior angles acute and sharp; posterior angles obtuse and rounded. Posterior margin without basal bead, convex, forming a nearly straight line above the scutellum. Surface punctate, with a pair of linear depressions forming a  $45^\circ$  angle, from posterior margin towards lateral margins, without reaching them. **Scutellum:** Shape sub-pentagonal, sharp apex, with sparse punctures on entire surface; ratio width/length 1.36. **Elytra:** Surface with costae defined by rows of shallow and sparse punctures. First interstice with 2–3 secondary striae, following interstices with 1 stria. The surface appears fairly smooth to the naked eye. Apex of elytral suture spiniform. Lateral margin convex and complete, tapering gradually from the base to the apical third. Marginal membrane narrow, extending along the apical half. **Pygidium:** Strigate-imbriate. Medium-length to long setae at margins. Triangular shape, with acute apex. Slightly convex in lateral view. Ratio width/length 1.42. **Metasternum:** Disc slightly sulcate, densely punctate and densely covered with medium-length setae, reaching half of trochanters height, except on the median sulcus. Mesosternal process short, reaching the anterior margin of mesocoxae, width at base 1/2 of femur height, narrowing towards the apex to 1/2 the width at base; in lateral view blunt, rounded; width at base 0.56 (Fig. 17). Mesometasternal suture absent, metasternal sulcus reaching base of trochanters. **Abdominal sternites:** With sparse oblong punctures coalescing at sides; 1–2 rows of medium-length setae per sternite, denser at sides. Last exposed sternite and apical margin with sparse punctures, apical margin at midline 1/3 as long as total length of last sternite; basal suture of the apical bead sinuate, well defined. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 29), slender; apical tooth narrow, long, curved. Proximal tooth triangular, acute, pointing upwards, slightly above the internal apex of protibia. **Metatibia:** stout, fusiform but with negligible subapical constriction. Ratio length/width 2.53. First carina defined by punctures. Surface with dense deep oblong punctures, nearly glabrous. **Claws of fore leg:** External claw curved; ratio length/height: 1.53; internal claw bifurcate, upper branch slightly shorter than and less than 1/2 as wide as the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 41. Parameres slender, slightly sinuate frontally, with a rounded apex in lateral view, ventral part membranous; dorsally flattened. Ventral plate fused with parameres in the proximal half. Endophallus: Fig. 53. Swollen dorsally, with a thin dorsal sacculus with aligned patches of thick sclerotised setae along all length; ejaculatory duct opening frontal, right above the tip of median lobe. Median lobe strongly sclerotised, apex pointed.

Female: antennal club shorter than in male; apical tooth of protibia (Fig. 29) longer and wider; basal tooth above internal apex. First carina of metatibia well defined. Lower branch of internal foreleg claw thinner than in male, inferior margin straight. Last exposed sternite

with oblong punctures, apical smooth margin narrower than in male.

Variation: body length 11.81–12.50 mm; width 6.74–7.31 mm. Clypeus w/l 1.94–2.09. Interocular ratio 4.05–4.74. Male antennae, ratio funiculus/club 0.64–0.93. Pronotum w/l 1.69–1.75. Scutellum w/l 1.35–1.37. Pygidium w/l 1.42–1.53. Width of mesosternal process at base 0.52–0.56 mm. Metatibia w/l 2.53–2.73. Bronze luster on pronotum can be absent; scutellum from dark green to blackish; pygidium purple black to deep black.

**Differential diagnosis.** *C. carbo* is separated from similar species by the combination of the following features: medium size, the combination of green pronotum and black elytra, the membranous ventral portion of parameres, the pointed median lobe and endophallus with narrow sacculus.

**Derivatio nominis.** From the Latin noun ‘carbo, -onis’, coal, treated here as a noun in apposition, for the shiny black colour of elytra, like anthracite coal.

**Distribution.** *C. carbo* is only known from the Z.P. Tenorio, Prov. Guanacaste (Fig. 97).

**Material.** HOLOTYPE: ♂ ‘Río San Lorenzo, 1050m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste Costa Rica. Abr 1992 F. Quesada L–N 287800,427600’, ‘INBIOCRI000930505’. – PARATYPES (4): 2♂ ‘Río San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste Costa Rica. Abr 1992 F. Quesada L–N 287800,427600’, ‘INBIOCRI000930501’ and ‘INBIOCRI000930510’; 1♀ ‘Río San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste Costa Rica. Abr 1992 F. Quesada L–N 287800,427600’, ‘INBIOCRI000930506’; 1♂ ‘Río San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste Costa Rica. A. Marin 23 mar a 21 abr 1992 L–N 287800,427600’, ‘CEUA00105294’.

#### 4.2. *Callistethus flavodorsalis* sp.n.

**Description.** Male holotype: **Body shape:** Length 15.05 mm; width 7.98 mm. Oval, slender. Elytral disc convex. **Colouration:** Head, pronotum, scutellum and pygidium metallic green, light green on clypeus. Margins of pronotum ochre, with green luster. Elytra yellow with green metallic luster. Venter, legs and antennae metallic dark green (Fig. 3). **Head:** Big in relation to pronotum. Clypeus nearly rectangular, ratio width/length 1.92. Clypeus surface densely and deeply punctate, surface reticulate. Frons with slightly less dense punctures. Vertex with sparse punctures. Ocular canthus short and wide; apex rounded. Eyes very small, interocular ratio (interocular width/width of eye) 5.95. Antennae: ratio funiculus/club 0.88. **Pronotum:** Basal width  $1.76 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at nearly 1/2 of length from anterior. Anterior angles acute and sharp; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a straight line above the scutellum. Surface with small, shallow, sparse punctures. **Scutellum:** Shape



subpentagonal, blunt apex, with fine and sparse punctation on entire surface; ratio width/length 1.43. **Elytra:** Surface with costae clearly defined by rows of shallow punctures. Interstices with 3–4 (first interstice) or 1 (second–fifth interstices) rows of sparse shallow punctures. Small horizontal wrinkles are present between second interstice and third costa, at half the length of elytra surface. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical third, disappearing on apex. Marginal membrane narrow and nearly complete. **Pygidium:** Coriarius-striated. Short sparse setae on margins. Triangular shape, with rounded apex. Nearly straight in lateral view. Ratio width/length 1.41. **Metasternum:** Disc slightly concave, smooth; glabrous centrally, with coarse setigerous punctures on sides, bearing short blonde setae. Mesosternal process long, reaching the base of procoxae, width at basal 2/3 as wide as femur height, narrowing moderately towards the apex to 2/3 the width at base; in lateral view slightly curved upwards, tapering towards apex; width at base 0.88 mm (Fig. 18). Mesometasternal suture absent, metasternal sulcus reaching apex of trochanters. **Abdominal sternites:** With sparse shallow punctures, at side forming 1–2 rows near anterior margin and 3–4 rows near posterior one, with a smooth stripe between them; 1 row of short blonde setae per sternite, a little denser on sides (on 2–3 rows). Last exposed sternite with sparse shallow punctures, apical margin nearly smooth, at midline 1/3 as long as total length; basal suture of the apical bead sinuate, well defined. Sixth abdominal spiracle tuberculiform. **Protibia:** With 2 teeth (Fig. 30), stout; apical tooth with wide base, narrowing at apex, quite short (laterally not reaching the level of the basal tooth), oblique in relation to the vertical axis of protibia, nearly quadrate. Proximal tooth small, protruding slightly from the lateral margin, positioned below the internal apex of protibia. **Metatibia:** Quite stout, fusiform. Ratio length/width 3.70. Both carinae well defined. Surface sparsely punctate, nearly glabrous. **Claws of fore leg:** External claw curved; ratio length/height: 1.63; internal claw bifurcate, with branches strongly diverging, upper branch slightly shorter and less than 1/2 as wide as the lower one. Inferior margin sinuate. **Male genitalia:** Aedeagus: Fig. 42. Very long parameres, with sharp apex and sinuate ventral margin. Ventral plate reduced to a couple of small plates. Endophallus: Fig. 54. Globular shape, with frontal wide ejaculatory duct opening. Dorsally a short sacculus with folded apex. Median lobe sclerotised.

Female: protibia (Fig. 30) with apical tooth longer and wider, basal tooth above the internal apex. Foreleg claw: lower branch of internal claw much narrower than in male, similar in width to upper branch; inferior margin straight. Apical smooth margin of last exposed sternite narrower than in male.

Variation: body length 14.02–15.92 mm; width 7.42–8.93 mm. Clypeus w/l 1.83–1.97. Interocular ratio 5.62–5.95. Male antennae, ratio funiculus/club 0.84–0.90. Pronotum w/l 1.75–1.78. Scutellum w/l 1.32–1.56. Py-

gidium w/l 1.41–1.53. Width of mesosternal process at base 0.70–0.88 mm. Metatibia w/l 3.31–3.76. External foreleg claw l/h 1.63–1.69. Abdominal sternites and apical part of legs light green in some specimens.

**Differential diagnosis.** It is distinguished by the combination of the following features: combination of greenish yellow elytra and green pronotum, narrow and long parameres, reduced ventral plate, globose endophallus with a small sacculus at base. *C. chrysanthe* and *C. jansoni*, also with light elytra, have a much larger size. *C. mimeloides* is entirely yellow.

**Derivatio nominis.** From the Latin adjective ‘flavus, -a, -um’, yellow, and adjective indicating possession from noun ‘dorsum, -i’, back, for the yellowish colour of elytra.

**Distribution.** *C. flavodorsalis* is known from two localities in the southern part of the Talamanca mountain range, Pacific slope, near the boundary with Panama. (Fig. 98).

**Material.** HOLOTYPE: ♂ ‘Fca. Cafrosa, Est. Las Mellizas, P.N. Amistad, 1300 m, Prov. Punt. COSTA RICA. M. Ramirez & G. Mora, Oct 1989. L–S 316100–596100’, ‘INBIOCRI000478886’. – PARATYPES (7): 1♀ ‘Est. Biol. Las Alturas, 1500 m, Coto Brus, Prov. Puntarenas, Costa Rica. M.A. Zumbado, Oct 1991 L–S 322500–591300’, ‘INBIOCRI000376991’; 4♂ ‘Fca. Cafrosa, Est. Las Mellizas, P.N. Amistad, 1300 m, Prov. Punt. COSTA RICA. M. Ramirez & G. Mora, Oct 1989. L–S 316100–596100’, ‘INBIOCRI000478885’, ‘CEUA00105279’, ‘INBIOCRI000478896’ and ‘INBIOCRI000478900’; 2♂ ‘Est. Biol. Las Alturas, 1500m, Coto Brus, Prov. Puntarenas, Costa Rica. M.A. Zumbado, Oct 1991 L–S 322500,591300’, ‘CEUA00105280’ and ‘INBIOCRI000632447’.

#### 4.3. *Callistethus fusciorubens* sp.n.

**Description.** Male holotype: **Body shape:** Length 14.21 mm; width 8.12 mm. Oval, stout. Elytral disc convex. **Colouration:** Head, pronotum and scutellum metallic dark green, dark reddish brown under the stereoscope. Pronotum with ochre margins. Elytra dark reddish brown, with greenish hue. Pygidium reddish brown. Venter and legs greenish to reddish dark brown (Fig. 4). **Head:** Clypeus trapezoidal, ratio width/length 1.78. Clypeus surface densely punctate-reticulate. Frons densely punctate, with secondary small punctures on disc, often with a central depression, next to suture with clypeus. Vertex densely punctate as frons. Ocular canthus long and thin; apex rounded. Eyes rounded, interocular ratio (interocular width/width of eye) 3.09. Antennae: ratio funiculus/club 0.76. **Pronotum:** Basal width 1.77 × length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 1/3 of length from anterior. Anterior angles quadrate and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above the scutellum. Surface with sparse punctures. **Scutellum:** Shape subpentagonal, blunt apex, with sparse punctures; ratio width/length 1.28.

**Elytra:** Surface with costae defined by dense and sulcate rows of punctures. Apical part of second costa with a secondary stria. First interstice with 4–5 secondary striae, the external ones being fairly regular, the median ones irregular; second interstice with 2 secondary striae, coalescing on base of elytra; following interstices with 1 secondary stria. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical third, disappearing on apex. Marginal membrane narrow and nearly complete. **Pygidium:** Granulose-imbricate. Short setae on disc, longer on margins. Triangular shape, with rounded apex. Nearly quadrate in lateral view. Ratio width/length 1.55. **Metasternum:** Disc slightly concave, with sparse medium-length setae, very dense on sides. Mesosternal process short, reaching the anterior margin of mesocoxae; with setae at base; width at base 1/2 of femur height, uniform width along all the length; in lateral view narrowing at apex; width at base 0.62 mm (Fig. 19). Mesometasternal suture absent, metasternal sulcus reaching base of process. **Abdominal sternites:** With oblong punctures, sparse in the middle and dense on sides; 1–2 rows of medium-length blonde setae per sternite, denser on sides. Last exposed sternite with sparse oblong punctures, apical margin nearly smooth, at midline 1/3 as long as total length of last sternite; basal suture of the apical bead sinuate, well defined. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 31), slender; apical tooth short, curved, with uniform width. Proximal tooth small, acute, slightly above the internal apex of protibia. **Metatibia:** Fusiform. Ratio length/width 2.96. First carina made by row of punctures. Surface sparsely punctate, setose. **Claws of fore leg:** External claw strongly curved; ratio length/height: 1.51; internal claw deeply bifurcate, upper branch of same length as and more than 1/2 as wide as the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 43. Parameres nearly tubular, in lateral view with a squared shape, anterior margin slightly sinuate; parameres fused to ventral plate. Endophallus: Fig. 55. With 2 long sacculi: a longer dorsal one, thin, with an inflation near the base that bears sclerotised setae; a ventral shorter and wider one, bearing the wide ejaculatory duct opening laterally and with a large pointed sclerotised plate at the apex. Median lobe sclerotised.

Female: apical tooth of protibia (Fig. 31) longer and wider, expanded at apex; basal tooth above internal apex. Upper branch of internal foreleg claw longer than lower one; lower branch thinner than in male and with inferior margin straight. Last exposed sternite punctate, apical smooth margin narrower than in male.

Variation: body length 14.21–15.79 mm; width 8.12–9.58 mm. Clypeus w/l 1.72–1.94. Interocular ratio 3.09–3.40. Pronotum w/l 1.69–1.80. Scutellum w/l 1.28–1.43. Pygidium w/l 1.55–1.76. Width of mesosternal process at base 0.54–0.62 mm. Metatibia w/l 2.93–3.19. External foreleg claw l/h 1.38–1.51. Venter and femurs from ochre to copper to greenish dark brown. Rest of legs usually darker, reddish brown. Scutellum subtriangular to subpentagonal.

**Differential diagnosis.** *C. fusciorubens* can be separated from other dark coloured species of *Callistethus* by the combination of the following features: pattern of punctuation on elytra, mesosternal process with uniform width, parameres nearly squared in lateral view, pointed ventrally, endophallus with a large sclerotised plate. In detail, it can be separated from *C. granulipygus* (Bates, 1888), also present in Costa Rica, as the latter is smaller with a shorter mesosternal process. It is separated from *C. kulzerei* (Frey 1968) (Perú) by having well developed costae on the elytra, and almost no mesosternal process. *C. ladino* (Ohaus, 1902) and *C. rosenbergi* (Ohaus, 1902) (both in Colombia) are the two most similar species, but they both have narrower first interstices, with more or less regular striae, a shorter mesosternum, and differences in the aedeagus: in *C. ladino* (Fig. 65) the parameres are much shorter and squared in lateral view (anterior margin slightly bilobed, but symmetric), slightly wider on the apex than on the base; in *C. rosenbergi* (Fig. 66) the parameres have a sinuous apex, but the upper lobe is curved and protruding, and the ventral margin is shorter than in *C. fusciorubens*.

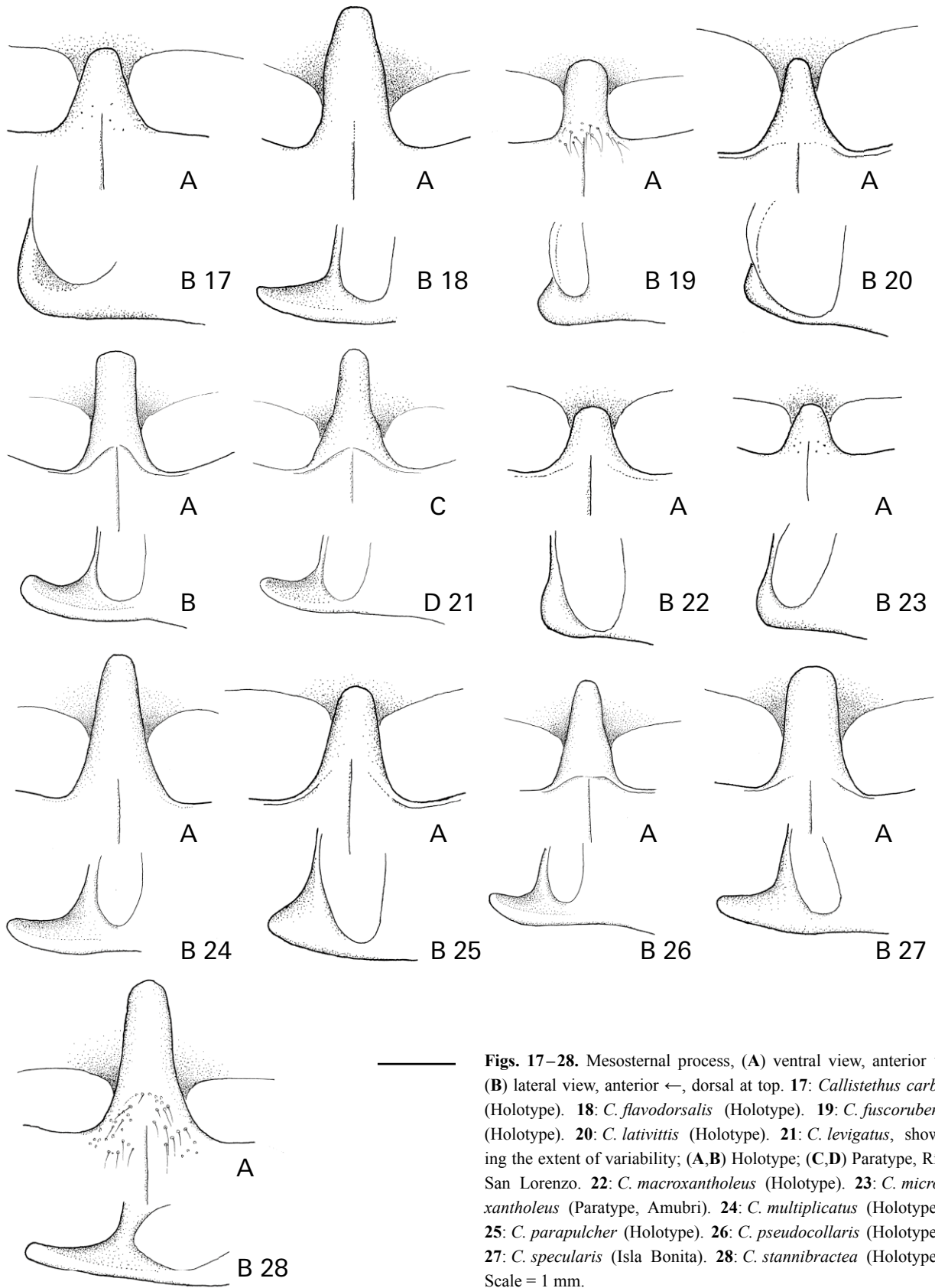
**Derivatio nominis.** from Latin adjectives ‘fuscus, -a, -um’, brown, dark; and ‘rubens, -entis’, reddish, for the dark reddish brown colour of elytra.

**Distribution.** *C. fusciorubens* is widely distributed in the main mountain ranges, the Nicoya and Osa peninsulas, and the Caribbean lowlands, ranging from 0 to 3500 m a.s.l. (Fig. 99).

**Material.** HOLOTYPE: ♂ ‘La Escuadra, P.N. Amistad, Puntarenas, Prov. COSTA RICA. 1340 m. 14 April 1989, M. Ramirez & G. Mora, L–S 326700–581200’, ‘INBIOCRI000010139’. – PARATYPES (4): 1♀ ‘COSTA RICA. Prov. Puntarenas, San Vito Las Cruces. 20 NOV 1988. A. Solis’, ‘INB0003316029’; 1♂ ‘COSTA RICA. Prov. Puntarenas, San Vito Las Cruces. 20 NOV 1988. A. Solis’, ‘INB0003316037’; 1♀ ‘Rancho Quemado, Peninsula de Osa, 200 m. Prov. Punt., COSTA RICA, F. Quesada, Dic 1991, L–S 292500–511000’, ‘INBIOCRI000483196’; 1♂ ‘Est. Altamira, Buenos Aires PILA ACLA, Cerro Biolley, Prov. Punta, COSTA RICA. 1300–1450m. 23–30 OCT 1995. R. Villalobos, L–S 331700–572100 #6347’, ‘CEUA00105284’.

#### 4.4. *Callistethus lativittis* sp.n.

**Description.** Male holotype: **Body shape:** Length 17.47 mm; width 9.61 mm. Oval, stout. Elytral disc convex. **Colouration:** Head, pronotum, scutellum and pygidium metallic green. Pronotum with ochre margins. Elytra light brown, with bronze and green luster. Metasternum greenish yellow, abdominal sternites bronze brown, legs yellowish green to metallic green on extremities, tarsi brownish green (Fig. 5). **Head:** Clypeus trapezoidal, ratio width/length 1.83. Clypeus surface densely punctate-reticulate. Frons punctate-reticulate, with secondary small punctures on disc. Vertex less densely punctate than frons. Ocular canthus long and thin; apex acute. Eyes rounded, interocular ratio (interocular width/width of eye) 3.05.



**Figs. 17–28.** Mesosternal process, (A) ventral view, anterior ↑; (B) lateral view, anterior ←, dorsal at top. **17:** *Callistethus carbo* (Holotype). **18:** *C. flavodorsalis* (Holotype). **19:** *C. fusciorubens* (Holotype). **20:** *C. lativittis* (Holotype). **21:** *C. levigatus*, showing the extent of variability; (A,B) Holotype; (C,D) Paratype, Río San Lorenzo. **22:** *C. macroxantholeus* (Holotype). **23:** *C. microxantholeus* (Paratype, Amubri). **24:** *C. multiplicatus* (Holotype). **25:** *C. parapulcher* (Holotype). **26:** *C. pseudocollaris* (Holotype). **27:** *C. specularis* (Isla Bonita). **28:** *C. stannibractea* (Holotype). Scale = 1 mm.

Antennae: ratio funiculus/club 0.77. **Pronotum:** Basal width  $1.79 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 1/3 of length from

anterior. Anterior angles quadrate and sharp; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above

the scutellum. Surface with sparse punctures. **Scutellum:** Shape subtriangular, blunt apex, with sparse punctures on sides, leaving a smooth stripe along the median longitudinal axis; ratio width/length 1.33. **Elytra:** Surface with costae defined by dense and sulcate rows of punctures. First interstice wide, with irregular punctures; second–fifth interstices with 1 secondary stria, bifurcating at base of elytra for second (into 2 rows) and third (irregular punctures) interstices. Apex of elytral suture rounded. Lateral margin convex, thin along all length, disappearing on apex. Marginal membrane narrow and nearly complete. **Pygidium:** Surface strigate-imbricate. Short setae on disc, longer on margins. Triangular shape, with rounded apex. Convex in lateral view. Ratio width/length 1.58. **Metasternum:** Disc slightly sulcate, nearly glabrous on disc and densely punctate on sides, with long setae. Mesosternal process short, reaching the anterior margin of mesocoxae; width at base 1/2 of femur height, narrowing towards the apex to 2/5 the width at base; in lateral view nearly square; width at base 0.71 mm (Fig. 20). Mesometasternal suture absent, but with a clear change in colour between the metasternum (dark green) and mesosternal process (yellow), metasternal sulcus reaching base of process. **Abdominal sternites:** With sparse shallow oblong punctures; 1–2 rows of sparse medium-length blonde setae per sternite. Last exposed sternite and apical margin with sparse punctures, apical margin at midline 2/5 as long as total length of last sternite; basal suture of the apical bead nearly straight, well defined. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 32), slender; apical tooth less than 1/4 of total length, curved, narrower at apex. Proximal tooth small, acute, at same height as or slightly below the internal apex of protibia. **Metatibia:** Fusiform. Ratio length/width 3.08. First carina made by row of punctures. Surface punctate above second carina, rugose below; glabrous. **Claws of fore leg:** External claw strongly curved; ratio length/height: 1.44; internal claw deeply bifurcate, with branches diverging, upper branch longer and more than 1/2 as wide as the lower one. Inferior margin nearly straight, forming a protruding angle at base. **Male genitalia:** Aedeagus: Fig. 44. Parameres apically deeply sinuate, forming 2 lobes in lateral view; ventral margin curved. Tectum wide. Ventral plate fused to parameres. Basal part with thick margins at the base and apex. Endophallus: Fig. 56. With 2 sacculi: the dorsal one long and narrowing at the apex, with a round ventral flattened inflation near the base, bearing a row of large sclerotised spines with an indented top on its margin, and thick small spines on its ventral side; the ventral sacculus with 2 diverticles at apex, one bearing a flat oval sclerotised plate; ejaculatory duct opening on left side of the shorter sacculus, above 2 small lobes. Medial lobe sclerotised.

Female: apical tooth of protibia (Fig. 32) longer and wider, expanded at apex; basal tooth above internal apex. Lower branch of internal foreleg claw thinner than in male and with inferior margin straight.

Variation: body length 17.47–18.08 mm; width 9.61–10.74 mm. Clypeus w/l 1.82–1.91. Interocular ratio

3.05–3.27. Male club longer than in females. Antennae, ratio funiculus/club 0.77–0.87. Pronotum w/l 1.72–1.79. Scutellum w/l 1.33–1.51. Pygidium w/l 1.56–1.66. Width of mesosternal process at base 0.59–0.71 mm. Metatibia w/l 2.75–3.08. External foreleg claw l/h 1.27–1.44. Pygidium has a bronze luster in some specimens. Elytra ochre to light brown. Venter and legs from ochre to bronze brownish to metallic green. Scutellum subtriangular to subpentagonal.

**Differential diagnosis.** This species is easily distinguished from similar species by the combination of the following features: wide first interstice and the bronze luster on elytra, mesosternal process tapering at apex to less than 1/2 of base width, parameres bilobed, complex endophallus with sclerotised plates and indented spines.

**Derivatio nominis.** From the Latin adjective ‘latus, -a, -um’, wide; and adjective indicating possession from noun ‘vitta, -ae’, band, for the wide and finely punctate first interstice on the elytra.

**Distribution.** *C. lativittis* is found in the Tilarán and Talamanca mountain ranges, from 100 to 1500 m a.s.l. (Fig. 100).

**Material.** HOLOTYPE: ♂ ‘Rio San Lorenzo, Z.P. Tenorio A.C.A. Tilaran, Prov. Guana, COSTA RICA. 1050 m. May 1994, G. Rodriguez, L–N 427600–287800 # 2933’, ‘INBIOCRI001873737’. – PARATYPES (5): 1 ♀ ‘Sect. San Ramon de Dos Rios, Prov. Alaju, COSTA RICA. 620 m. 18 MAR–13 ABR 1995. F. A. Quesada, L–N 318100–381900 #5274’, ‘INBIOCRI002246434’; 1 ♂ ‘Dos de Tilaran (San Ramon), Prov. Guana, COSTA RICA. 1100 m. MAY 1995. G. Rodriguez, L–N 262600–437500 #5891’, ‘INBIOCRI002337541’; 1 ♂ ‘Albergue Heliconias, Bijagua (Costa Rica). 750 m 31-1-2006. T. luz (17:15–21:00). Leg.: Micó, García, Galante.’, ‘Rutelinae *Callistethus* sp.138 Det. Alejandra García’, ‘CEUA00003273’; 1 ♀ ‘Albergue Heliconias, Bijagua (Costa Rica). 750 m 30-1-2006. T. luz (18:45–22:00). Leg.: Micó, García, Galante.’, ‘Rutelinae *Callistethus* sp.138 Det. Alejandra García’, ‘CEUA00003313’; 1 ♀ ‘Estación Cabro Muco, Repr. ICE – Z.P. Miravalles, Guanacaste. Costa Rica. 1000 m 12/06/2010. L. Filipini, Moraga.’, ‘CEUA00105285’.

#### 4.5. *Callistethus levigatus* sp.n.

**Description.** Male holotype: **Body shape:** Length 12.63 mm; width 7.02 mm. Oval, slender. Elytral disc convex. **Colouration:** metallic green, clearer on clypeus and legs. Margins of pronotum ochre, with green luster (Fig. 6). **Head:** Clypeus trapezoidal, ratio width/length 1.88. Clypeus surface densely punctate, with confluent punctures. Frons sparsely punctate. Vertex slightly less densely punctate than frons. Ocular canthus short, wide at base, sharpening at apex. Eyes small and oblong, interocular ratio (interocular width/width of eye) 3.88. Antennae: ratio funiculus/club 0.70. **Pronotum:** Basal width 1.70 × length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 2/5 of length from anterior. Anterior angles quadrate and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinu-

ate, forming a straight line above the scutellum. Surface with small, shallow, sparse punctures. **Scutellum**: Shape subpentagonal, blunt apex, nearly smooth, with very fine and sparse punctation on surface; ratio width/length 1.20. **Elytra**: Surface with costae defined by rows of shallow punctures. Interstices with 3–4 (first interstice) or 1 (second–fifth interstices) rows of sparse shallow punctures. Small horizontal wrinkles are present between second interstice and third costa, almost along entire length. All punctures on pronotum and elytra are very shallow, giving a smooth appearance to the naked eye. Apex of elytral suture rounded. Lateral margin convex and uniform, disappearing at the apex. Marginal membrane narrow and nearly complete. **Pygidium**: Striated, with medium-length sparse setae on margins. Triangular shape, with rounded apex. Nearly straight in lateral view, rounded at apex. Ratio width/length 1.60. **Metasternum**: Disc concave, smooth and glabrous, setigerous punctures on sides, bearing short blonde setae. Mesosternal process long, reaching the base of procoxae; width 2/3 of femur height, uniform width along all the length; in lateral view slightly curved upwards, tapering towards the apex; width at base 0.67 mm (Fig. 21A,B). Mesometasternal suture well marked, reaching the apex of trochanters. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites**: With sparse shallow punctures; 1 (in the middle) to 3 (at the sides) rows of short blonde setae per sternite, borne by oblong punctures, always on apical half of sternites. Last exposed sternite with sparse shallow punctures, apical margin smooth, at midline 1/2 as long as total length of last sternite; basal suture of the apical bead sinuate, well defined. Sixth abdominal spiracle flat. **Protibia**: With 2 teeth (Fig. 33), slender; apical tooth long, with uniform width, oblique in relation to the vertical axis of protibia, curved at apex. Proximal tooth small, acute, at same height as the internal apex of protibia. **Metatibia**: Quite stout, fusiform. Ratio length/width 3.27. First carina defined by punctures. Surface sparsely punctate, with elongate punctures below second carina, nearly glabrous. **Claws of fore leg**: External claw strongly curved; internal claw bifurcate, upper branch slightly shorter and more than 1/2 as wide as the lower one. Inferior margin sinuate. **Male genitalia**: Aedeagus: Fig. 45. Parameres with wide apex pointing downwards in lateral view, ventral margin sinuate. Wide tectum. Ventral plate separated from parameres. Endophallus: Fig. 57. Developed dorsally in relation to medial lobe, leaving a bulge in the frontal part. Frontal sacculus ending in a central pointed inflation, folded dorsally, and 2 diverticles pointed laterally; ejaculatory duct opening at base of right diverticle. Dorsally, a long narrowing sacculus, and on its left side, a short sacculus with lateral inflation. Fine setation is present on these 2 dorsal sacculi. Median lobe horseshoe shaped.

Female: Pygidium densely imbricate-striated. Mesosternal process thinning considerably on apical half. Protibia (Fig. 33): apical tooth wider, basal tooth above the internal apex. Foreleg claw: lower branch of internal claw similar in width to upper branch; inferior margin

straight. Last exposed sternite finely punctate, apical smooth margin narrower than in male.

Variation: body length 12.63–13.12 mm; width 6.93–7.10 mm. Clypeus w/l 1.76–1.88. Interocular ratio 3.88–4.89. Pronotum w/l 1.67–1.70. Scutellum w/l 1.20–1.25. Pygidium w/l 1.60–1.68. Metatibia w/l 3.16–3.41. External foreleg claw l/h 1.32–1.47. Metasternum variable, from uniform width to tapering at apex (Fig. 21).

**Differential diagnosis.** This species is distinguished by the combination of the following features: medium size, homogeneous green colour, smooth surface of elytra, parameres with wide apex pointing ventrally, endophallus with median lobe horseshoe shaped, sacculi and diverticles developing dorsally. It resembles *C. collaris*, *C. multiplicatus* and *C. pseudocollaris*, but the smooth surface of the elytra clearly distinguishes it. The elytra surface of *C. lepidus* is smooth but has a lighter colour, larger size and a slender aedeagus (Fig. 67).

**Derivatio nominis.** From the Latin adjective ‘levigatus, -a, -um’, polished, for the smooth surface of the pronotum and elytra.

**Distribution.** *C. levigatus* is found on the Pacific slope of the Tilarán and Talamanca mountain ranges, from 1000 to 1500 m a.s.l. (Fig. 98).

**Material.** HOLOTYPE: ♂ ‘Quebrada Segunda, P. N. Tapanti, 1250m, Prov. Cartago, Costa Rica, Jul 1992, G. Mora, L–N 194000–560000’, ‘INBIOCRI000712086’. – PARATYPES (4): 1♀ ‘Rio San Lorenzo, 1050 m, Tierras Morenas, Z. P. Tenorio, Prov. Guanacaste, Costa Rica, C. Alvarado, Abr 1992, L–N 287800–427600’, ‘INBIOCRI000415209’; 1♂ ‘Est. La Casona, Res. Biol. Monteverde, 1520m, Prov. Punt. COSTA RICA, N. Obando, Set 1990, L–N 253250–449700’, ‘60’, ‘INBIOCRI000269243’; 1♀ ‘Est. La Casona, 1520 m, Res. Biol. Monteverde, Prov. Punt., COSTA RICA. May 1991, N. Obando. L–N 253250,449700’, ‘INBIOCRI001325937’. 1♂ ‘COSTA RICA Prov. Alajuela. Guatuso. P.N. Volcán Tenorio. Punto 2: Falda N Cerro Montezuma. 1160 m. 3 Jun 2008. J. A. Azofeifa. Tp de Luz 2. L–N 297500–425050 #93851.’, ‘CEUA00105281’.

#### 4.6. *Callistethus macroxantholeus* sp.n.

**Description.** Male holotype: **Body shape**: Length 10.80 mm; width 5.99 mm. Oval, stout. Elytral disc flattened. **Colouration**: Head and scutellum yellow with green luster. Pronotum yellow with green luster and a couple of metallic green vertical bands on disc. Elytra yellowish brown. Pygidium yellow with green luster, lateral sides metallic green. Venter and legs yellow with green luster on sternum and bronze on sternites; tarsi and apical part of metatibiae darker, reddish or green (Fig. 7). **Head**: Clypeus rounded; ratio width/length 1.91. Clypeus surface with confluent punctures. Frons with sparse setae, surface punctate-reticulate. Vertex punctate. Ocular canthus long, stout at the base and acute at the apex. Eyes elongated, interocular ratio (interocular width/width of eye) 4.15. Antennae: ratio funiculus/club 0.64. **Prono-**

**tum:** Basal width  $1.66 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at  $1/3$  of length from anterior. Anterior angles quadrate and sharp; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above the scutellum. Surface punctate, with sparse setae near anterior margin. **Scutellum:** Shape subpentagonal, sharp apex, with fairly dense punctures on entire surface; ratio width/length 1.26. **Elytra:** Surface with 14 costae (excluding lateral margin), defined by dense and sulcate rows of punctures. On second costae a secondary stria is present at the base; the sixth and ninth striae bifurcate at base. Very fine secondary punctures on entire surface. Apex of elytral suture spiniform. Lateral margin convex, tapering gradually from the base to apical third, where it disappears. Marginal membrane narrow, extending along the apical half. **Pygidium:** From oblong punctation to coarsely strigate-imbricate, more or less densely. Long setae at margins. Triangular shape, with rounded apex. Nearly straight in lateral view. Ratio width/length 1.45. **Metasternum:** Disc slightly sulcate, densely punctate, with medium-length setae denser at sides. Mesosternal process short and stout, reaching the anterior margin of mesocoxae, width at base  $1/2$  of femur height, slightly narrower at apex; in lateral view blunt, with dorsal part nearly vertical; width at base 0.49 mm (Fig. 22). Mesometasternal suture poorly defined, reaching half of trochanters height. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites:** With sparse oblong punctures coalescing at sides, 1–2 rows of sparse setae per sternite, denser at sides. Last exposed sternite and apical margin with sparse punctures, apical margin at midline  $1/2$  as long as total length of last sternite; basal suture of the apical bead obliterated at centre, curved. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 34), apical tooth narrow, long, curved. Proximal tooth triangular, acute, at same height as or slightly inferior to the internal apex of protibia. **Metatibia:** Stout, fusiform but with subapical constriction negligible. Ratio length/width 2.64. First carina defined by punctures. Surface with oblong punctures, rugose below second carina, nearly glabrous. **Claws of fore leg:** External claw curved; ratio length/height: 1.57; internal claw bifurcate, upper branch slightly shorter than and  $2/3$  as wide as the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 46. Parameres slender with squared apex in lateral view; ventral margin sinuate. Ventral plate not fused with parameres, ending with a narrow long apex. Endophallus: Fig. 58. With 2 wide sacculi, the ventral one shorter and with ejaculatory duct opening at apex; the dorsal one with microsetae. Median lobe sclerotised.

Female: apical tooth of protibia (Fig. 34) longer and wider; basal tooth above internal apex. Upper branch of internal foreleg claw longer than the lower one, inferior margin straight. Last exposed sternite finely punctate, apical smooth margin narrower than in male.

Variation: body length 9.62–12.33 mm; width 5.81–6.70 mm. Clypeus w/l 1.91–2.04. Interocular ratio 3.88–4.32. Male antennae, ratio funiculus/club

0.57–0.64. Pronotum w/l 1.59–1.72. Scutellum w/l 1.16–1.26. Pygidium w/l 1.40–1.46. Width of mesosternal process at base 0.47–0.59 mm. Metatibia w/l 2.61–2.65. External foreleg claw l/h 1.52–1.60. Head and scutellum from yellow to metallic green; a bronze luster may be present. Pronotum with green or bronze luster. Elytra from yellowish to reddish brown. Pygidium with green or bronze luster. Venter and legs from yellow to reddish brown with green or bronze luster. In males posterior half of the body narrows gradually.

**Differential diagnosis.** Similar to *C. xantholeus* and *C. microxantholeus*, but larger in size, pronotum with more curved sides, narrower apex of parameres and endophallus with 2 long sacculi and no sclerotised setae, in contrast to the globose structure of *C. microxantholeus* and the different sized sacculi of *C. xantholeus* (Fig. 68), one of which bears a patch of sclerotised setae.

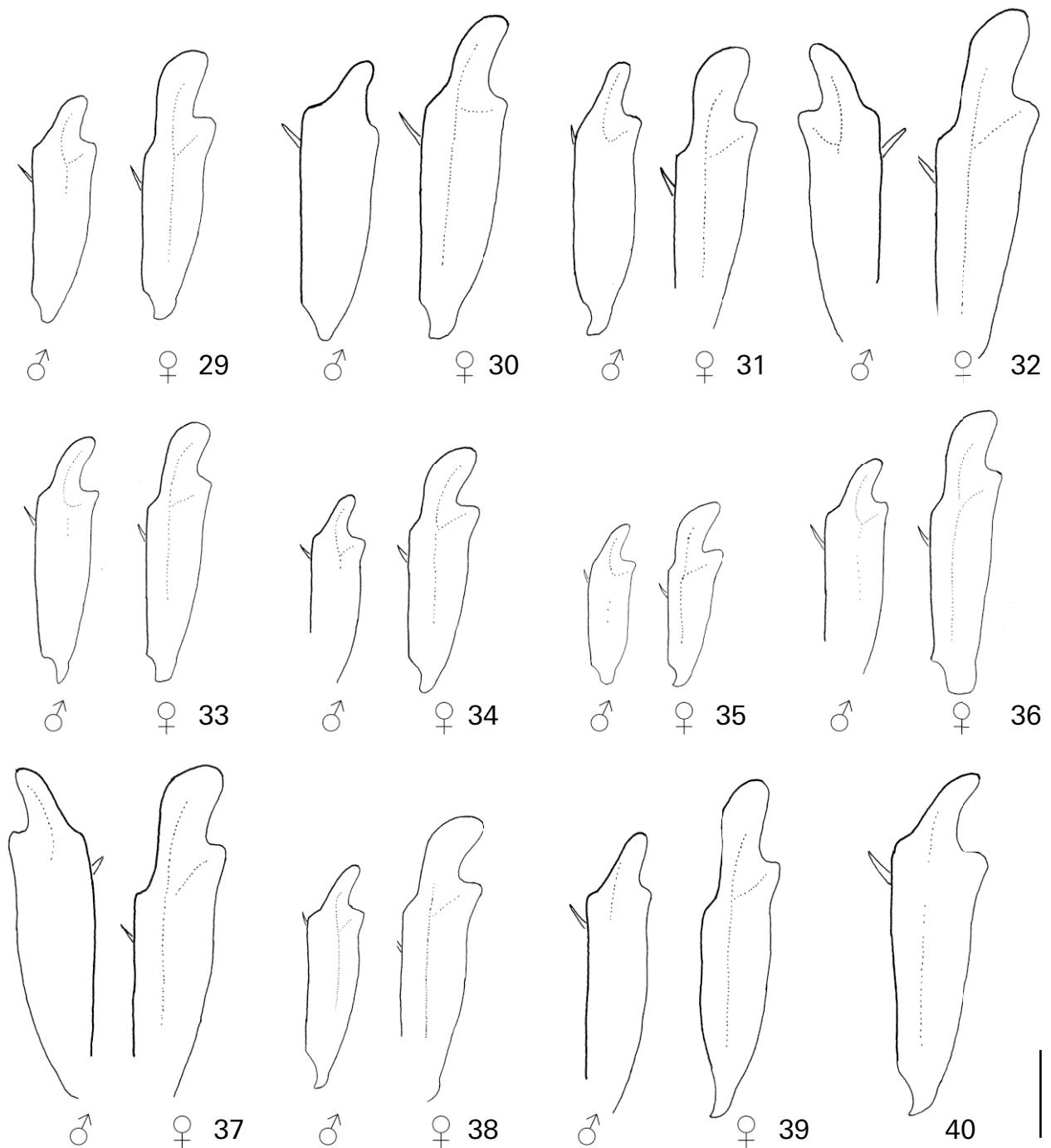
**Derivatio nominis.** From the Greek prefix ‘macro-’, big, and ‘xantholeus’, referring to the species *A. xantholea* Bates, 1888.

**Distribution.** *C. macroxantholeus* distribution almost coincides with that of *C. microxantholeus*, being distributed on both slopes of the Tilarán, Central and Talamanca mountain ranges, Caribbean lowlands and Osa peninsula, but with a narrower altitudinal range, from 700 to 1400 m a.s.l. (Fig. 97).

**Material.** HOLOTYPE: ♂ ‘Est. Pitilla, 700m, 9 km S Sta. Cecilia, P. N. Guanacaste, Prov. Guan., COSTA RICA. 19 May –3 Jun 1993. C. Moraga, L–N 330200\_380200’, ‘INBIOCRI001315235’. – PARATYPES (10): 1♀ ‘P.N.Guanacaste Sector Mengo 15 mayo 1988 Col: D. Janzen’, ‘INBIOCRI001102734’; 1♂ ‘Rio San Lorenzo, 1050 m, Tierras Morenas, Z. P. Tenorio, Prov. Guanacaste, Costa Rica, Abr 1992 F. Quesada L–N 287800–427600’, ‘INBIOCRI000930545’; 2♀ ‘Rio San Lorenzo, 1050 m, Tierras Morenas, Z. P. Tenorio, Prov. Guanacaste, Costa Rica, Abr 1992 F. Quesada L–N 287800–427600’, ‘INBIOCRI000930543’ and ‘INBIOCRI000930553’; 1♀ ‘Est. Cacao, 1000–1400 m, Lado suroeste del Volcan Cacao, Prov. Guan., COSTA RICA, Il curso Parataxon., Jun 1990, L–N 323300–375700’, ‘INBIOCRI000248848’; 1♀ ‘Est. Cacao, 1000–1400m, Lado SO Vol. Cacao, P.N. Guan., Prov. Guanacaste, Costa Rica, R. Vargas 21 a 28 may 1992, L–N 323300–375700’, ‘INBIOCRI000411910’; 1♂ ‘Sector Cerro Cori, Fca. de E. Rojas, 150 m, Prov. Limon, Costa Rica, E. Rojas, Abr 1992, L–N 286000–567500’, ‘CEUA00105293’; 1♀ ‘R. San Lorencito, 900 m, R. F. San Ramón, 5 km N de Colonia Palmareña, Prov. Alaju., COSTA RICA. 13–18 Jun 1993. I Curso Scarabeidae. L–N 244500–470700 #2125’, ‘INBIOCRI001364690’; 1♂ ‘Estac. Pitilla, 700 m, 9 km S Santa Cecilia, Guanac., Pr. COSTA RICA. 21 Mar–21 Abr 1989, GNP Biod. Sur. L–N 330200,380200’, ‘160’, ‘INBIOCRI002517220’; 1♀ ‘Est. Pitilla, 700 m, 9 km S Sta. Cecilia, P. N. Guanacaste, Prov. Guan. COSTA RICA R. W. Flowers, 13 May 1991, L–N 330200–380200’, ‘CEUA00105292’.

#### 4.7. *Callistethus microxantholeus* sp.n.

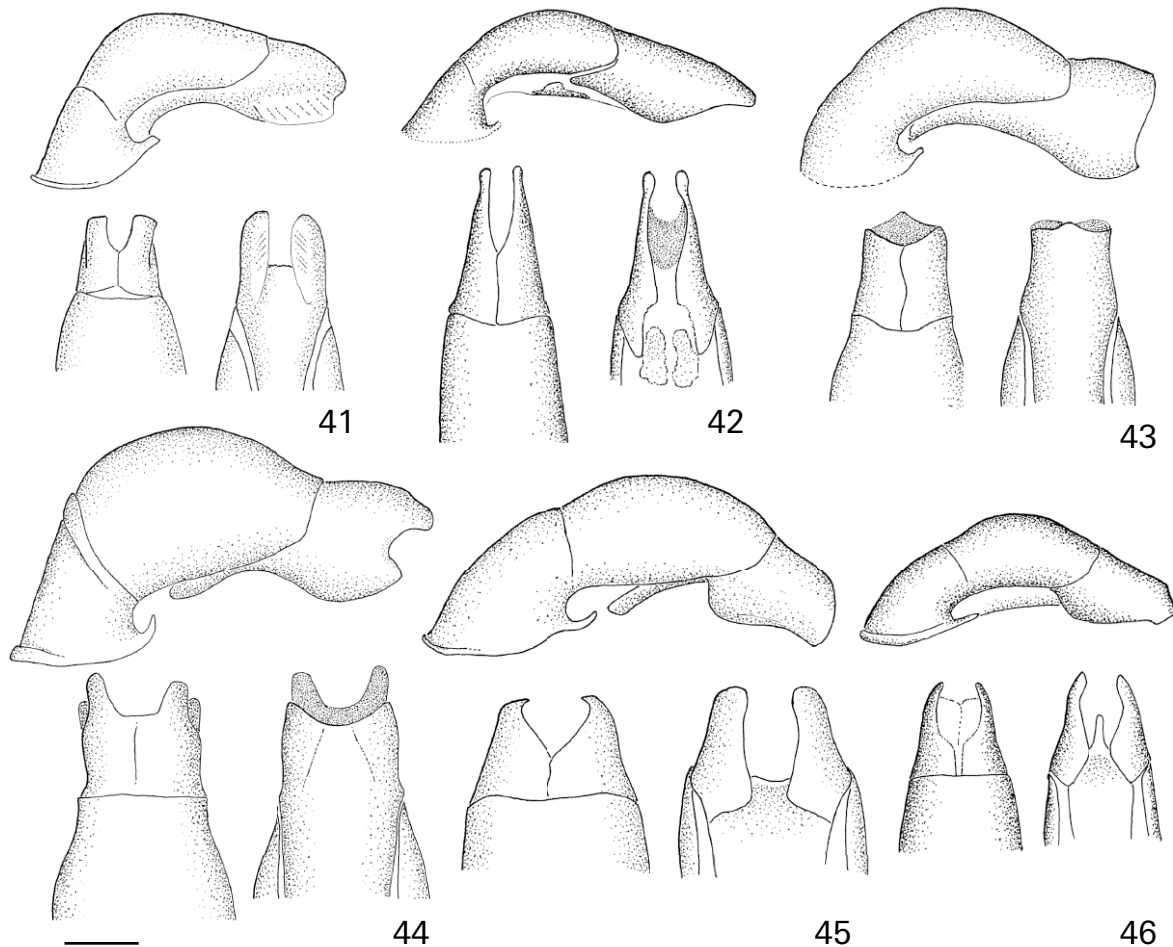
**Description:** Male holotype: **Body shape:** Length 7.02 mm; width 4.22 mm. Oval stout. Elytral disc flattened. **Coloration:** Head and scutellum from yellow to light green.



**Figs. 29–40.** Shape of protibia in dorsal view. Right protibia is shown if not otherwise specified. **29:** *Callistethus carbo*, male: Paratype, Río San Lorenzo; female: Paratype, Río San Lorenzo. **30:** *C. flavodorsalis*, male: Holotype; female: Paratype, Est. Biol. Las Alturas. **31:** *C. fusciorubens*, male: Holotype; female: Paratype, San Vito Las Cruces. **32:** *C. lativittis*, male: Holotype; female: Paratype, Sect. San Ramon de Dos Rios. **33:** *C. levigatus*, male: Holotype, left protibia; female: Paratype, Río San Lorenzo. **34:** *C. macroxantholeus*, male: Holotype; female: Paratype, Estación Pitilla. **35:** *C. microxantholeus*, male: Holotype; female: Paratype, Rancho Quemado. **36:** *C. multiplicatus*, male: Holotype; female: Paratype, Estación Pitilla. **37:** *C. parapulcher*, male: Holotype, right protibia; female: Paratype, Estación Santa Elena. **38:** *C. pseudocollaris*, male: Holotype; female: Paratype, Coto Brus. **39:** *C. specularis*, male: Isla Bonita; female: Río San Lorenzo. **40:** *C. stannibractea* (Holotype). Scale = 1 mm.

Pronotum yellow with a couple of metallic green vertical bands on disc. Elytra reddish brown. Pygidium yellow with green luster. Venter yellow with green luster; antennae blackish, legs yellow with coppery green tarsi

(Fig. 8). **Head:** Clypeus nearly rectangular; ratio width/length 2.18. Clypeus surface with confluent punctures. Frons with sparse setae, surface punctate-reticulate. Vertex with less dense punctures. Ocular canthus long

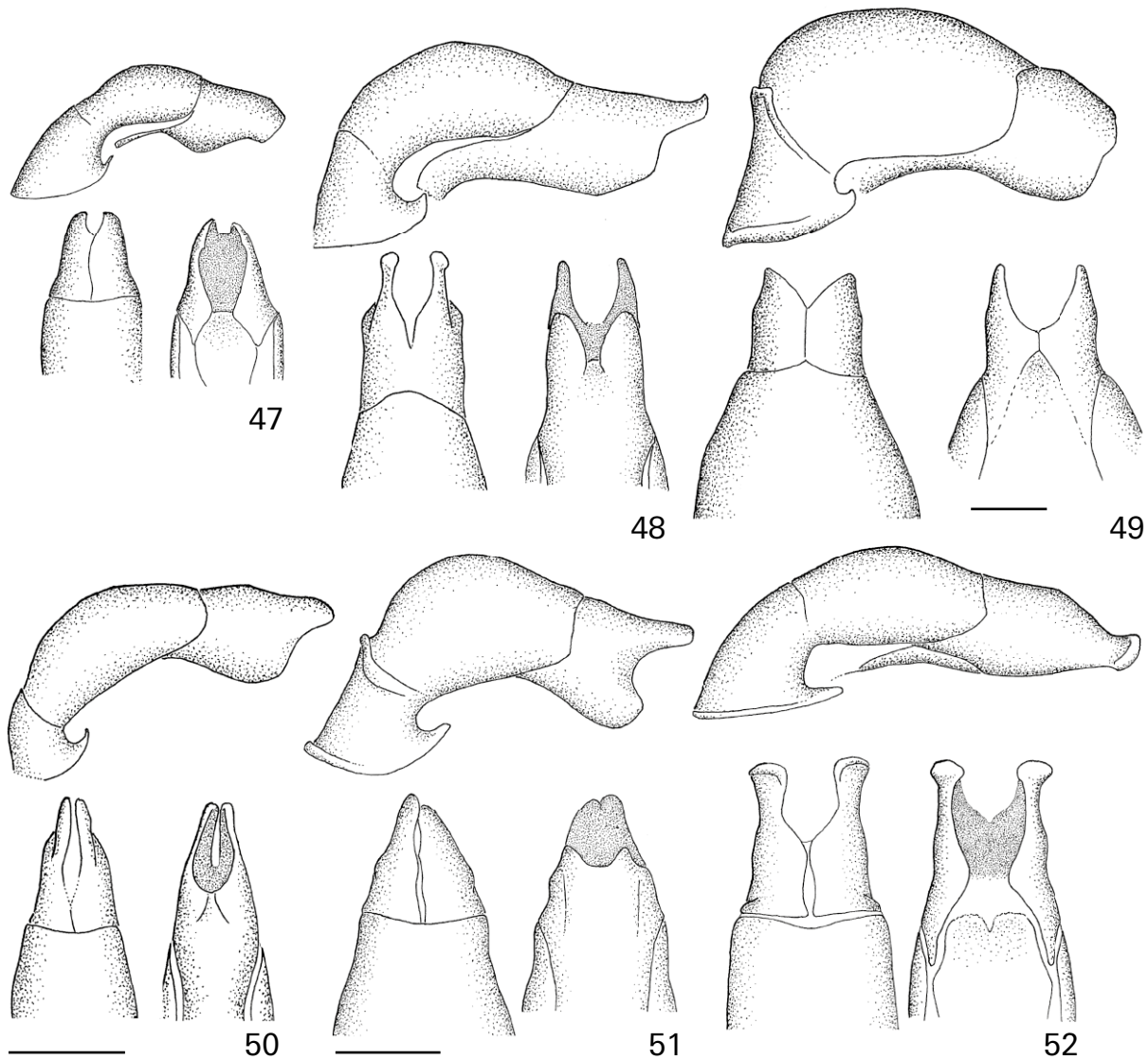


**Figs. 41–52.** Aedeagus, lateral view (top; base at left bottom), dorsal view (bottom left), ventral view (bottom right). **41:** *Callistethus carbo* (Holotype). **42:** *C. flavodorsalis* (Holotype). **43:** *C. fuscorubens* (Holotype). **44:** *C. lativittis* (Paratype, Dos de Tilaran). **45:** *C. levigatus* (Paratype, Est. La Casona). **46:** *C. macroxantholeus* (Paratype, Sector Cerro Cocori). → **47:** *C. microxantholeus* (Paratype, Est. Pitilla). → **48:** *C. multiplicatus* (Holotype). → **49:** *C. parapulcher* (Paratype, Estación Pittier). → **50:** *C. pseudocollaris* (Holotype). → **51:** *C. specularis* (Pittier, Costa Rica, BMNH). → **52:** *C. stannibractea* (Holotype). Scale = 1 mm (general scale bar at left bottom).

and wide; apex rounded. Eyes elongated, interocular ratio (interocular width/width of eye) 4.89. Antennae: ratio funiculus/club 0.67. **Pronotum:** Basal width 1.59 × length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 1/4 of length from anterior. Anterior angles acute and sharp; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above the scutellum. Surface with large, deep punctures, with sparse setae near anterior margin. **Scutellum:** Shape subpentagonal, blunt apex, with sparse punctures on entire surface; ratio width/length 1.07. **Elytra:** Surface with 14 costae (excluding lateral margin), defined by dense and sulcate rows of punctures. Apex of elytral suture spiniform. Lateral margin convex, tapering gradually from base to apical third, disappearing on apex. Marginal membrane narrow and extending along the apical half. **Pygidium:** Coarsely strigate-imbricate, with sparse setae, longer at margins. Triangular shape, with rounded apex. Slightly convex in lateral view. Ratio width/length 1.52. **Metasternum:** Disc slightly concave, coarsely punctate.

Short to medium-length setae on entire surface, denser at sides. Mesosternal process short and stout, reaching the anterior margin of mesocoxae, width at base 1/2 of femur height, narrowing lightly towards the apex; in lateral view blunt, with dorsal part nearly vertical; width at base 0.33 mm (Fig. 23). Mesometasternal suture poorly defined, reaching half of the trochanter height. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites:** With 1–2 rows of sparse setae. Last exposed sternite with large punctures on entire surface; apical margin sparsely punctate, at midline 1/2 as long as total length of last sternite; basal suture of the apical bead poorly defined, curved. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 35), slender, apical tooth narrow, long, curved. Proximal tooth triangular, acute, at same height as the internal apex of protibia. **Metatibia:** Stout, fusiform but with subapical constriction negligible. Ratio length/width 2.35. First carina defined by large punctures. Surface with large punctures, nearly glabrous. **Claws of fore leg:** External claw strongly curved; ratio length/height: 1.51; internal claw bifur-





cate, with branches strongly diverging, upper branch as long as and 2/3 as wide as the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 47. Parameres slender with wide squared apex in lateral view; ventral margin sinuate. Endophallus: Fig. 59. With globular shape, with fine setae at base and a ridge of thick sclerotised setae on top, ventrally; ejaculatory duct opening dorsal. Median lobe sclerotised.

Female: antennal club shorter than in male. Apical tooth of protibia (Fig. 35) longer and wider; basal tooth above internal apex. Inferior margin of internal foreleg claw straight. Last exposed sternite punctate, apical smooth margin narrower than in male.

Variation: body length 7.02–8.58 mm; width 4.20–5.04 mm. Clypeus w/l 1.90–2.18. Interocular ratio 4.32–5.16. Male antennae, ratio funiculus/club 0.54–0.77. Pronotum w/l 1.51–1.59. Scutellum w/l 1.05–1.16. Pygidium w/l 1.27–1.52. Width of mesosternal process at base 0.37–0.50 mm. Metatibia w/l 2.35–2.73. External foreleg claw l/h 1.36–1.51. Pronotum with a couple of vertical bands on disc or 1 large macula. Elytra variable:

from yellow to reddish brown, to bright metallic green; the metallic green colour turns gradually to black in dead specimens, but it only affects elytra. Venter from yellow with green luster to reddish brown and dark metallic green.

**Differential diagnosis.** Similar to *C. xantholeus* and *C. macroxantholeus*, but smaller in size, with nearly straight sides of pronotum, longer parameres in relation to tectum, and globose endophallus, in contrast with the elongated and bifurcated structures of the latter species (Figs. 58, 68).

**Derivatio nominis.** From the Greek prefix ‘micro-’, small, and ‘xantholeus’, referring to the species *A. xantholea* Bates, 1888.

**Distribution.** *C. microxantholeus* is widely distributed on both slopes of the Tilarán, Central and Talamanca mountain ranges, Caribbean lowlands and Osa peninsula, below 1500 m a.s.l. (Fig. 101).

**Material.** HOLOTYPE: ♂ 'Heredia. Costa Rica Pto. Viejo. Finca La Selva 9 setiembre 1986 M.M.Chavarria-Diaz', '63', '63', 'INBIOCRI002517193'. – PARATYPES (16): 2♂ 'Est. Magsasay, P. N. Braulio Carrillo, 200 m, Prov. Here, COSTA RICA R. Aguilar, Oct 1990, L–N 264600–531100', '152', 'INBIOCRI000235712' and 'INBIOCRI000235713'; 1♂ 'Sector Cerro Cocori, Fca. de E. Rojas. 150 m, Prov. Limon, COSTA RICA, E. Rojas, Dic 1991, L–N 286000,567500', 'INBIOCRI000550223'; 1♂ 'Est. Magsasay, 200 m, P. N. Braulio Carrillo, Prov. Here., COSTA RICA. May 1991. A. Fernandez, L–N 264600–531000', 'INBIOCRI001376210'; 1♂ 'Heredia. Costa Rica Puerto Viejo Sarapiquí. Finca La Selva. 35 m. 30 abril 1987 M. M. Chavarria Diaz', '152', 'INBIOCRI002517222'; 1♂ 'Amubri, 70 m, Talamanca, Prov. Limon, Costa Rica, 1 a 22 jul 1992, G. Gallardo, L–S 385500–578050', 'INBIOCRI000757517'; 1♀ 'Rancho Quemado, 200 m, Peninsula de Osa, Prov. Puntarenas, Costa Rica, Ago 1992, M. Segura, L–S 292500–511000', 'INBIOCRI000963755'; 2♀ 'Sector Cerro Cocori, Fca de E. Rojas, 150 m, Prov. Limon, COSTA RICA. Mar 1993. E. Rojas, L–N 286000–567500', 'INBIOCRI001384952' and 'INBIOCRI001385120'; 2♂ 'Est. Pitilla, 700 m, 9 km S Sta. Cecilia, P. N. Guanacaste, Prov. Guan., COSTA RICA. 18 abr a 19 may 1993, P. Rios, L–N 330200–380200', 'INBIOCRI001397208' and 'INBIOCRI001397241'; 1♂ 'Est. Pitilla, 700 m, 9 km S Sta. Cecilia, P. N. Guanacaste, Prov. Guan., COSTA RICA. 19 May–3 Jun 1993. C. Moraga, L–N 330200–380200', 'INBIOCRI001315179'; 1♂ 'Volcán Tenorio. Guanacaste. Costa Rica. 700 m 03/VIII/2009 ex larva F L. 20/VI/2009 L. Filippini, Galante, Marcos.', 'CEUA00105288'; 1♀ 'Cabanga, finca J. Robles. Alajuela, Costa Rica. 500m. 10/II/2010 trampa 2 L.M. Zumbado, J.A.Azofeifa.', 'CEUA00105289'; 1♂ 'Cabanga, finca J.Robles. Alajuela, Costa Rica. 500 m 12/II/2010. Trampa 2 L.M. Zumbado, J.A.Azofeifa.', 'CEUA00105290'; 1♂ 'P.N. Volcán Tenorio. Catarata Río Buenavista. P. Alajuela, Costa Rica. 780 m 15/12/2009. L.M. Zumbado, J.A. Azofeifa.', 'CEUA00105291'.

#### 4.8. *Callistethus multiplicatus* sp.n.

**Description.** Male holotype: **Body shape:** Length 13.86 mm; width 7.75 mm. Oval, slender. Elytral disc convex. **Colouration:** Pronotum metallic green with ochre margins. Elytra metallic green. Rest of body metallic green to yellowish green, lighter on clypeus, legs and mesosternal process (Fig. 9). **Head:** Clypeus nearly rounded, ratio width/length 1.95. Clypeus surface densely punctate, surface reticulate. Frons with less dense punctures than clypeus, longitudinally sulcate on disc. Vertex slightly less densely punctate than frons. Ocular canthus short, wide at base, sharpening at apex. Eyes small and oblong, interocular ratio (interocular width/width of eye) 4.84. Antennae: ratio funiculus/club 0.76. **Pronotum:** Basal width  $1.79 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 2/5 of length from anterior. Anterior angles quadrate and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate on sides, forming a straight line above the scutellum. Entire surface with sparse punctures. **Scutellum:** Shape subpentagonal, blunt apex, with a few shallow punctures on disc; ratio width/length 1.36. **Elytra:** Surface with 14–15 costae (excluding lateral margin), defined by dense and sulcate rows of punctures. Second and third rows (corresponding to first interstice) slightly irregular. Entire surface with very small and fine background punctures. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical

third, disappearing on apex. Marginal membrane narrow and nearly complete. **Pygidium:** Striate in wavy lines, due to confluence on oblong punctures. Short setae on disc, longer on margins. Triangular shape, with rounded apex. Nearly straight in lateral view. Ratio width/length 1.62. **Metasternum:** Disc slightly concave, glabrous, with fine and small punctures. Setigerous punctures on sides, bearing short blonde setae. Mesosternal process long, reaching the base of procoxae; width at base nearly as wide as femur height, narrowing at apex to 1/3 the width at base; in lateral view curved upwards, very thin at the apex; width at base 0.86 mm (Fig. 24). Mesometasternal suture absent, metasternal sulcus reaching the apex of trochanters. **Abdominal sternites:** With oblong punctures, sparse in the middle and dense on sides; 1 row of short setae per sternite at centre, dense at sides. Last exposed sternite with sparse oblong punctures, apical margin finely punctate, at midline 1/3 as long as total length of last sternite; basal suture of the apical bead sinuate, well defined. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 36), slender; apical tooth short, curved, with uniform width. Proximal tooth small, nearly quadrate, at same height of the internal apex of protibia. **Metatibia:** Quite stout, fusiform. Ratio length/width 3.16. First carina defined by punctures. Surface sparsely punctate, glabrous. **Claws of fore leg:** External claw strongly curved; internal claw deeply bifurcate, with branches strongly diverging, upper branch slightly shorter and more than half the width of the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 48. Parameres long, with protruding thin apex slightly turned upwards in lateral view, dorsally widened; ventral margin sinuate, nearly at a right angle. Ventral plate fused to parameres. Endophallus: Fig. 60. A dorsal T-shaped sacculus, with one of the extremes with sclerotised setae in a row. A ventral long and thin sacculus, with a row of sclerotised setae on apex, and 2 lobes placed ventrally at about 1/3 of length, ejaculatory duct opening between them. Medial lobe sclerotised.

Female: protibia (Fig. 36) with apical tooth longer and wider, expanded at apex; basal tooth above the internal apex. Upper branch of internal foreleg claw longer than lower one; inferior margin straight. Last exposed sternite punctate, apical smooth margin narrower than in male, curved.

Variation: body length 13.45–13.86 mm; width 7.07–7.75 mm. Clypeus w/l 1.88–1.95. Interocular ratio 4.84–5.45. Pronotum w/l 1.76–1.86. Scutellum w/l 1.28–1.45. Pygidium w/l 1.56–1.71. Width of mesosternal process at base 0.69–0.86 mm. Metatibia w/l 3.09–3.29. Elytra metallic green to brownish green.

**Differential diagnosis.** This species can be differentiated from similar ones by the combination of the following features: homogeneous green colour, elytra with regular sulcated striae, parameres with thin apex bending dorsally, endophallus with 2 long sacculi, one of which is T shaped. It is very similar to *C. collaris* and *C. pseudocollaris*, and is distinguished by the shape of male genitalia, with parameres with thin apex bending dorsally, whereas

*C. collaris* has a bilobed apex (Fig. 69), and *C. pseudocollaris* a blunt apex (Fig. 50). The endophallus is composed of 2 long sacculi, instead of a short one in *C. pseudocollaris* (Fig. 62).

**Derivatio nominis.** From the Latin adjective ‘multiplicatus, -a, -um’, multiplied, for the high number of species belonging to the *C. collaris* sp. complex

**Distribution.** *C. multiplicatus* is widely distributed on the Caribbean slopes of the Tilarán and Central mountain ranges, and the Caribbean lowlands, from 0 to 800 m a.s.l. (Fig. 102).

**Material.** HOLOTYPE: ♂ ‘Sector Cerro Cocori, Fca. de E. Rojas, 150 m, Prov. Limon, Costa Rica, E. Rojas, 31 ene – 21 feb 1992, L–N 286000–567500’, ‘INBIOCRI000774896’. – PARATYPES (7): 1♀ ‘Estación Pitilla, 700 m, 9 km S Santa Cecilia, Guanac. Pr. COSTA RICA. FEB 1989. GNP Biodiversity Survey. 330200,380200’, ‘INBIOCRI000104897’; 2♂ ‘Sector Cerro Cocori, Fca. de E. Rojas, 150 m, Prov. Limon, Costa Rica. Mar 1992. E. Rojas L–N 286000,567500’, ‘INBIOCRI001331162’ and ‘INBIOCRI001331163’; 1♂ ‘Manzanillo, 0–100m, RNFS Gandoca y Manzanillo, Prov. Limon, Costa Rica, 9 set a 13 oct 1992, K. Taylor, L–S 398100–610600’, ‘INBIOCRI000937526’; 1♂ ‘Limon. Costa Rica Pacuarito Las Brisas 20 julio 1986 M.M. Chavarria Diaz’, ‘?’ ‘5’, ‘5’, ‘INBIOCRI002517475’; 1♂ ‘Cuatro Esquinas, P. N. Tortuguero, Prov. Limon, COSTA RICA. 0m, Set 1989. J. Solano, L–N 280000–590500’, ‘5’, ‘INBIOCRI000086335’; 1♀ ‘Cerro Tortuguero, 0–120 m, P.N. Tortuguero, Prov. Limon, COSTA RICA. Mar 1993, R. Delgado. L–N 285000–588000’, ‘INBIOCRI001353063’.

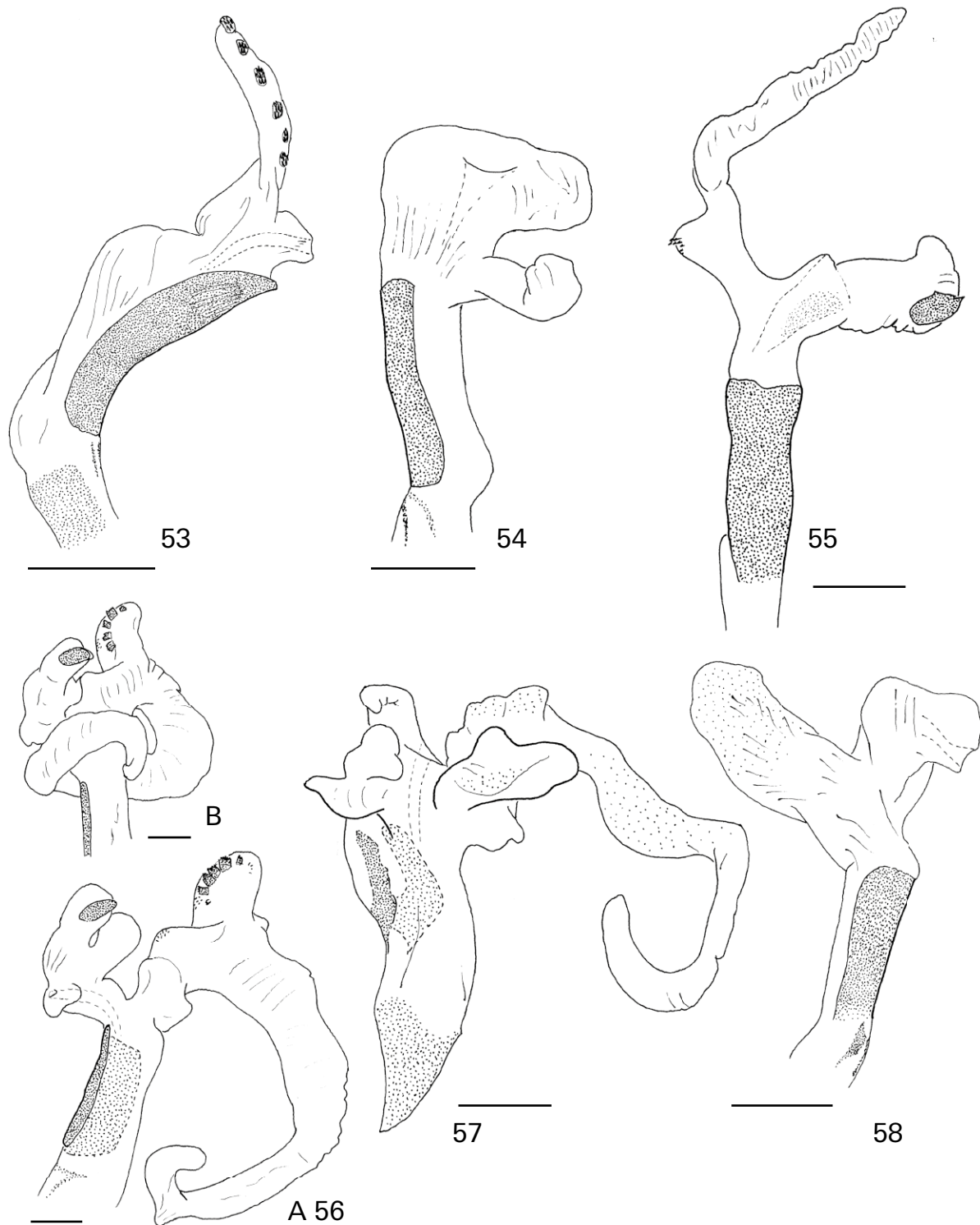
#### 4.9. *Callistethus parapulcher* sp.n.

**Description.** Male holotype: **Body shape:** Length 17.21 mm; width 10.47 mm. Oval, stout. Elytral disc convex. **Colouration:** Head, pronotum and scutellum greenish brown. Pronotum with ochre margins. Elytra light reddish brown. Pygidium dark brown. Abdominal sternites dark green and brown. Sternum and legs yellow to greenish. Tibiae and tarsi darker, metallic green (Fig. 10). **Head:** Clypeus trapezoidal, ratio width/length 1.65. Clypeus surface densely punctate-reticulate. Frons punctate-reticulate, with larger punctures than in clypeus and with secondary small punctuation; sometimes slightly concave on disc. Vertex with same punctuation as frons. Ocular canthus long and narrow, apex rounded. Eyes rounded, interocular ratio (interocular width/width of eye) 2.78. Antennae: ratio funiculus/club 0.61. **Pronotum:** Basal width  $1.88 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, apex of curvature at 1/3 of length from anterior. Anterior angles acute and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above the scutellum. Surface with dense punctures and densely covered with short blonde setae (not evident to the naked eye). **Scutellum:** Shape subtriangular, blunt apex, with sparse punctures, denser at sides; ratio width/length 1.45. **Elytra:** Surface with 14 costae (excluding lateral margin), defined by dense and sulcate rows of punctures. Second

and third striae (defining third costa) somewhat irregular, blending into irregular punctures at the base of the elytra. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical third, disappearing at the apex. Marginal membrane nearly complete. Whole surface covered with microsetae (not evident to the naked eye). **Pygidium:** Strigate-imbricate. Dense short setae on disc, longer on margins. Triangular shape, with rounded apex, with a couple of large deep fossae at sides. Nearly straight in lateral view. Ratio width/length 1.64. **Metasternum:** Disc slightly concave, with sparse medium-length setae, very dense on sides. Mesosternal process short, reaching the anterior margin of mesocoxae; width at base 2/3 of femur height, narrowing at apex to 1/3 or less of femur height; in lateral view with a blunt apex; width at base 0.79 mm (Fig. 25). Mesometasternal suture absent, metasternal sulcus reaching the apex of trochanters. **Abdominal sternites:** With dense punctures, oblong on apical half; 1–2 rows of medium-length setae per sternite, denser on sides. Last exposed sternite with dense punctures, apical margin finely punctate, at midline 1/4 as long as total length of last sternite; basal suture of the apical bead doubled and sinuate, partially obliterated at middle; apically also sinuate. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 37), slender; apical tooth short, curved, acute. Proximal tooth small, quadrate, at same height of internal apex of protibia. **Metatibia:** Slender, fusiform. Ratio length/width 3.33. First carina made by row of punctures. Surface densely punctate above second carina, rugose below, glabrous. **Claws of fore leg:** External claw strongly curved; ratio length/height: 1.41; internal claw thin, deeply bifurcate, with branches strongly diverging, upper branch of same length, nearly as wide as the lower one. Inferior margin straight. **Male genitalia:** Aedeagus: Fig. 49. Parameres short, nearly squared in lateral view; frontal margin slightly sinuated. Ventral plate fused to parameres, but with suture visible. Tectum wide. Basal part with thick margins at the base and apex. Endophallus: Fig. 61. With 2 sacculi: the ventral one short and wide, with ventrally folded apex; at base a long diverticle that end in a thick sclerotised claw-like spine. Dorsal sacculus long, laterally inflated at the base, with a bump near the base bearing 4–5 thick spines (the median fused at base); rest of the sacculus thin and curved in a spiral, with thin setae near the apex; dorsally at the base a long thin sclerotised plate with 2 curved spines at the apex, the spines are partially retracted if the endophallus is not fully inflated. Median lobe sclerotised.

Female: fossae on pygidium not as evident as in male. Apical tooth of protibia (Fig. 37) longer and wider; basal tooth above internal apex.

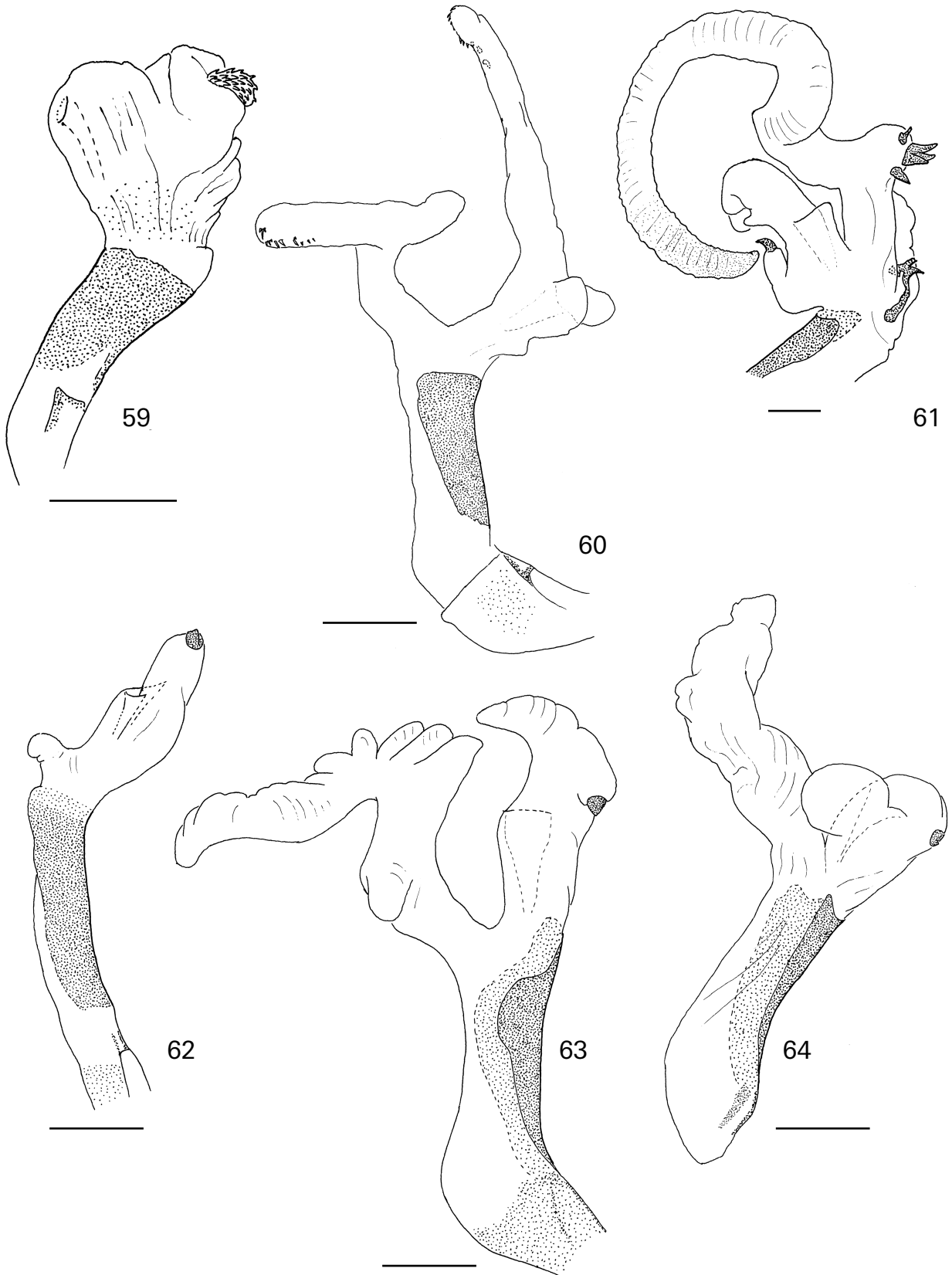
Variation: body length 17.21–18.39 mm; width 10.41–10.98 mm. Clypeus w/l 1.65–1.85. Interocular ratio 2.60–2.78. Male antennae, ratio funiculus/club 0.61–0.69. Club length slightly longer in male. Pronotum w/l 1.81–2.04. Scutellum w/l 1.38–1.45. Pygidium w/l 1.47–1.64. Width of mesosternal process at base 0.73–0.79 mm. Metatibia w/l 3.19–3.40. External foreleg claw l/h 1.41–1.63. Head, pronotum and scutellum metallic dark green



**Figs. 53–64.** Endophallus. **53:** *Callistethus carbo* (Paratype, Río S. Lorenzo). **54:** *C. flavodorsalis* (Paratype, Fca. Cafrosa). **55:** *C. fusc-rubens* (Paratype, Est. Altamira). **56:** *C. lativittis* (Paratype, Albergue Heliconias), **(A)** sacculi artificially separated; **(B)** natural position. **57:** *C. levigatus* (Holotype). **58:** *C. macroxantholeus* (Paratype, Río San Lorencito). → **59:** *C. microxantholeus* (Paratype, Est. Pitilla). → **60:** *C. multiplicatus* (Paratype, Sector Cerro Cocori). → **61:** *C. parapulcher* (Paratype, Est. Pittier). → **62:** *C. pseudocollaris* (Holotype). → **63:** *C. specularis* (Quebrada Segunda), sacculi artificially separated. → **64:** *C. stannibractea* (Paratype, Est. Barva). Scale = 1 mm.

to greenish brown. Pygidium greenish to coppery brown. Mesosternal process variable in width from 1/2 to 2/3 of width of femurs. First carina on metatibiae well defined in some females.

**Differential diagnosis.** *C. parapulcher* can be distinguished from similar species by the combination of the following features: light brown elytra; presence of setae on the pronotum; pointed mesosternal process in lateral



view, wide in ventral view; parameres nearly squared, endophallus with several spines in three different places. In Costa Rica the most similar species is *C. schneideri*, which also presents setation on the body, but the latter is

slightly bigger, with darker elytra and a slender shape, the mesosternal process is narrower in ventral view and blunt in lateral view, and genitalia are different (Figs. 80, 92). The presence of setation and the shape of the genita-

lia distinguish this species from other similar ones, such as *C. cayapo* (Ohaus, 1902) (Brazil), which has pointed parameres, with a sinuate ventral margin (Fig. 70), and also has more irregular striae on elytra, or *C. levii* (Blanchard, 1851) (Ecuador), smaller in size and with slender aedeagus (Fig. 71), and *C. pulcher* (Blanchard, 1851) (Colombia), which has parameres with a sharp point (Fig. 72).

**Derivatio nominis.** From the Greek prefix ‘para-’, side by side, and ‘pulcher’, referring to the species *C. pulcher* (Blanchard, 1851), to which it is very similar.

**Distribution.** *C. parapulcher* is distributed in the Tilarán, Central and Talamanca mountain ranges, from 300 to 1800 m a.s.l. (Fig. 103).

**Material.** HOLOTYPE: ♂ ‘Estacion Altmira, 1 km. S del Cerro Biolley, Sendero Gigantes del Bosque, Puntarenas, Costa Rica. 1300–1450 m. 20–23 NOV 1995. M. Moraga, de Luz L–S 331700–572100’, ‘INBIOCRI002381386’. – PARATYPES (12): 1♀ ‘Estacion Pitilla, 9 km S. Santa Cecilia, P. N. Guanacaste, Prov. Guana, Costa Rica, 700 m. 19–22 Jun 1993, G. Carballo, L–N 330200–380200 # 2199’, ‘INBIOCRI001837034’; 2♂ ‘Est. Pittier, PILA-ACLA, Prov. Punta, COSTA RICA. 1670 m. 5–18 ENE 1995. L. Angulo, L–N 330900–577400 # 4669’, ‘INBIOCRI002199232’ and ‘INBIOCRI002199233’; 1♀ ‘Est. Altamira, Buenos Aires, A. C. Amistad, Prov. Punta, COSTA RICA. 1150–1400 m. Dic 1994, M. Segura, L–S 331700–572100 # 3377’, ‘INBIOCRI002091974’; 1♂ ‘Est. Pittier, PILA-ACLA, Prov. Punta, COSTA RICA. 1670 m. 6–18 ENE 1995. A. Azofeifa, L–N 330900–577400 # 44830’, ‘INBIOCRI002205729’; 1♂ ‘COSTA RICA. Prov. Puntarenas. Buenos Aires. Alto Jalisco. 900–1000 m. 22–26 FEB 2009. E. Ulate, J. A. Azofeifa, M. Moraga. Tp. Luz Mercurio. L–S 327533–523213 # 95832’, ‘CEUA00105287’; 1♀ ‘COSTA RICA. Prov. Puntarenas. Buenos Aires. Alto Jalisco. 900–1000 m. 22–26 FEB 2009. E. Ulate, J. A. Azofeifa, M. Moraga. Tp. Luz Mercurio. L–S 327533–523213 # 95832’, ‘INB0004197431’; 1♀ ‘Fca. Cafrosa, Est. Las Mellizas, P. N. Amistad, 1300 m, Puntarenas COSTA RICA Feb 1990. M. Ramirez, L–S 316100–596100’, ‘INBIOCRI000209842’; 1♂ ‘Puntarenas, Costa Rica San Vito, Las Cruces 20 nov 1988 Col: A. Solis’, ‘INBIOCRI002517067’; 1♀ ‘Est. Santa Elena, Viejo, Santa Elena, Las Nubes, Prov. San J, COSTA RICA. 1210 m. 20–24 NOV 1995. B. Gamboa, de Luz L–S 371750–507800 # 6432’, ‘INBIOCRI002357497’; 1♂ ‘Est. Santa Elena, Viejo, Santa Elena, Las Nubes, Prov. San J, COSTA RICA. 1210 m. 20–24 NOV 1995. B. Gamboa, de Luz L–S 371750–507800 # 6432’, ‘INBIOCRI002357500’; 1♀ ‘La Amistad, Sect. Altamira, Buenos Aires, Prov. Punta, COSTA RICA. 1200 m. 21 Feb–10 Mar 1994, R. Delgado, L–S 572100–331700 # 2691’, ‘CEUA00105286’.

#### 4.10. *Callistethus pseudocollaris* sp.n.

**Description.** Male holotype: **Body shape:** Length 12.64 mm; width 6.66 mm. Oval, slender. Elytral disc convex. **Colouration:** Pronotum metallic green with ochre margins. Elytra brownish green. Rest of body brownish green to yellowish green, lighter on clypeus, legs and mesosternal process (Fig. 11). **Head:** Clypeus trapezoidal, ratio width/length 1.96. Clypeus surface densely punctate, surface with confluent punctures. Frons with sparse punctures, not differentiated from rest of head surface. Ocular canthus short, wide at base, sharpening at apex. Eyes

small and oblong, interocular ratio (interocular width/width of eye) 4.79. Antennae: ratio funiculus/club 0.73. **Pronotum:** Basal width  $1.81 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at 2/5 of length from anterior. Anterior angles quadrate and quite sharp; posterior angles obtuse and quite sharp. Posterior margin without basal bead, sinuate on sides, forming a straight line above the scutellum. Surface with shallow sparse punctures. **Scutellum:** Shape subpentagonal, blunt apex, with a few shallow punctures on disc; ratio width/length 1.22. **Elytra:** Surface with 14 costae (excluding lateral margin), defined by dense and sulcate rows of punctures. Second and third rows (corresponding to first interstice) with more separated punctures. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical third, disappearing on apex. Marginal membrane narrow and nearly complete. **Pygidium:** Punctate-striate in wavy lines, due to confluence of oblong punctures, with sparse short setae on disc, longer on margins. Triangular shape, with rounded apex. Nearly straight in lateral view. Ratio width/length 1.43. **Metasternum:** Disc slightly concave, with sparse short setae on disc, dense at sides. Mesosternal process long, reaching the base of procoxae; width at base nearly as wide as coxae, narrowing at apex to 1/3 the width at base; in lateral view narrowing and curved upwards at apex; width at base 0.72 mm (Fig. 26). Mesometasternal suture shallow, reaching apex of trochanters. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites:** With oblong punctures, sparse in the middle and dense on sides; 1 row of short setae per sternite at centre, dense at sides. Last exposed sternite with sparse shallow punctures, apical margin sparsely punctate, at midline 2/5 as long as total length of last sternite; basal suture of the apical bead curved, partially obliterated in the middle. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 38), slender; apical tooth oblique in relation to vertical axis of protibia, nearly quadrate, with uniform width. Proximal tooth acute, at same height of the internal apex of protibia. **Metatibia:** Stout, fusiform, glabrous. Ratio length/width 2.64. First carina defined by punctures. Surface sparsely punctate, with elongate punctures below second carina. **Claws of fore leg:** External claw strongly curved; internal claw deeply bifurcate, with branches strongly diverging, upper branch of same length and more than 1/2 as wide as the lower one. Inferior margin slightly sinuate. **Male genitalia:** Aedeagus: Fig. 50. Parameres long with protruding wide apex in lateral view; ventral margin angulated and slightly sinuate. Parameres fused with ventral plate. Endophallus: Fig. 62. One short sacculus with a ridged sclerotised plate on apex, ejaculatory duct opening wide, dorsal. A small diverticle at base, dorsal. Median lobe sclerotised, with a weakly sclerotised band on top.

Female: similar to male, protibia (Fig. 38) with apical tooth longer and wider, expanded at apex; basal tooth above the internal apex. Branch of internal foreleg claw similar in width. Last exposed sternite with oblong punctures, apical smooth margin narrower than in male.

Variation: body length 12.64–14.78 mm; width 6.66–7.65 mm. Clypeus w/l 1.84–2.12. Interocular ratio 4.79–6.14. Female antennae, ratio funiculus/club 0.85–0.89. Pronotum w/l 1.73–1.81. Scutellum w/l 1.18–1.36. Pygidium w/l 1.32–1.51. Width of mesosternal process at base 0.72–0.85 mm. Female metatibia w/l 3.14–3.82. Elytra metallic green to brownish green.

**Differential diagnosis.** *C. pseudocollaris* differs from similar species by the combination of the following features: homogeneous green colour, elytra with regular sulcated striae, parameres with wide apex, and endophallus with one short sacculus bearing a sclerotised plate on apex. It is very similar to *C. collaris* and *C. multiplicatus*, and is distinguished by the shape of the male genitalia, with parameres that are long in relation to the tectum, with ventral margin sinuate and a blunt apex, whereas *C. collaris* has a bilobed apex (Fig. 69) and *C. multiplicatus* a thin apex bending dorsally (Fig. 48). The endophallus consists of one short sacculus, instead of the two long ones of *C. multiplicatus* (Fig. 60).

**Derivatio nominis.** From the Greek prefix ‘pseudo-’, false, and ‘collaris’, for its resemblance with *C. collaris* (Burmeister, 1844).

**Distribution.** *C. pseudocollaris* is distributed on the Pacific slopes of the Tilarán and Talamanca mountain ranges, from 1500 to 1700 m a.s.l. (Fig. 102).

**Material.** HOLOTYPE: ♂ ‘Est. La Casona, 1520 m, Res. Biol. Monteverde, Prov. Puntarenas, Costa Rica, Jul 1992, N. Obando, L–N 253250–449700’, ‘INBIOCRI000691543’. – PARATYPES (2): 1 ♀ ‘COSTA RICA, Prov. Puntarenas, A.C.L.A.P. P.I.L.A., Coto Brus, Send Cerro Pittier Estación. 1750 m. 29–30 DIC 1998. M. Moraga. Sombrereta L–S 331250–577150 # 51998’, ‘INBIO0003313790’; 1 ♀ ‘La Escuadra, 1600–1900 m Parque Internac. La Amistad, Prov. Punt., COSTA RICA, M. Zumbado, Ene 1992, L–S 326700–581200’, ‘INBIOCRI000489689’.

#### 4.11. *Callistethus specularis* (Bates, 1888)

*Callistethus kolbei* (Ohaus, 1897) Stettiner Entomologische Zeitung 58: 398. **syn.n.** (Fig. 13).

**Remarks.** OHAUS (1897) described *Anomala kolbei* (now *Callistethus kolbei* sensu MACHATSCHKE 1957) based on a female specimen from Costa Rica. He indicated that this species is similar to *C. calonotus* (Bates, 1888), but with a reddish colour.

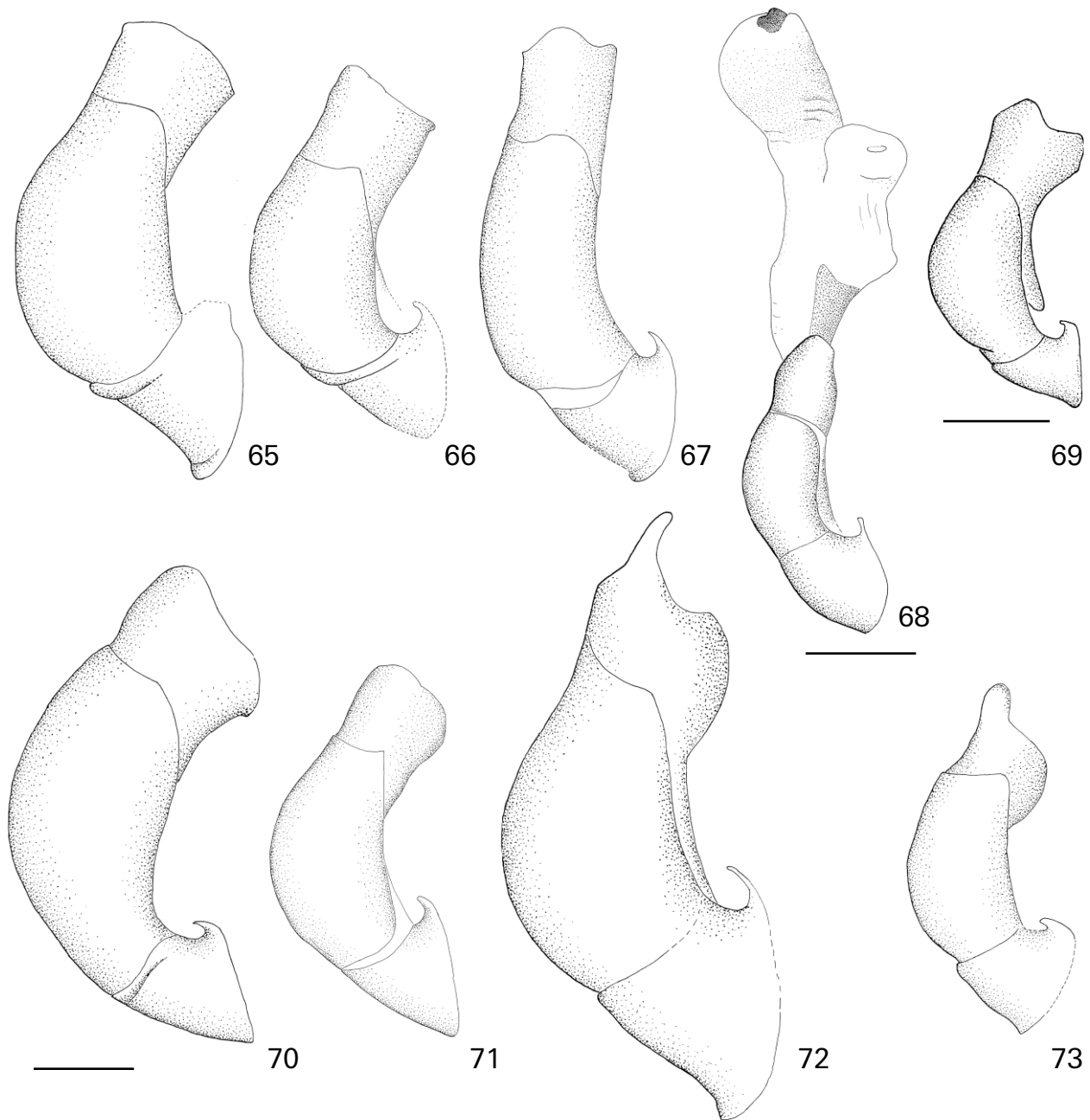
At the Museum für Naturkunde in Berlin, one of the authors (V.F) studied the type of *C. kolbei*, noting its resemblance with *C. specularis* (Bates, 1888), except for its smaller size and reddish colour. The specimen bears a handwritten label ‘A. kolbei type Ohaus’ and coincides with the description: reddish brown colour, glossy, with yellow clypeus, sides of pronotum, basal triangle on pronotum (that is the basal widening of a thin median stripe that runs along all the length of the pronotum), and

metasternal process, except that it was a male. We are confident that this is the actual type of *C. kolbei*, and the error of Ohaus in sex determination was due to wear on the protibial teeth of the specimen, which were therefore not as sharp as males usually show in *Anomalini*.

According to these results, the edeagus of *C. kolbei* coincided in size (despite the smaller body size of the specimen) and shape to that of *C. specularis*. We therefore propose a new synonymy of *C. kolbei* with *C. specularis*.

The reddish colour of *C. kolbei* type is due to the lack of the metallic green luster that is present on all the surface of common *C. specularis* specimens. Among more than 100 specimens of *C. specularis* conserved in the collection of INBio, Costa Rica, there is one from Cariblanco, Alajuela that has a dark reddish colour, but this is ascribed to inadequate conservation conditions of the private collection where it was previously stored (Á. Solís, personal communication). *C. specularis* also was described on a single specimen, that was also illustrated in Bates work (1888). A second specimen in BMNH collection that bears a “typus” label must be considered mislabelled.

**Redescription.** Male holotype: **Body shape:** Length 17.17 mm; width 9.23 mm. Oval, slender. Elytral disc slightly convex. **Colouration:** Head, pronotum and scutellum shiny light green, pronotum with yellowish lateral margins, blended with the main colour by a metallic green luster when seen in natural light. Elytra light brown with metallic green luster, and darker green brownish lines following the rows of punctures. Pygidium, venter, antennae and legs brownish green, with metallic green luster. Mesosternal process yellow, with metallic green luster (Fig. 12). **Head:** Clypeus trapezoidal, ratio width/length 1.98. Clypeus surface densely punctate, with shallow punctures. Frons with less dense punctures, equally shallow. Vertex only slightly less punctate. Ocular canthus subtriangular, with base width 2/3 of the length; apex rounded. Eyes elongates, interocular ratio (interocular width/width of eye) 4.60. Antennae: ratio funiculus/club 0.78. **Pronotum:** Basal width 1.92 × length; in dorsal view broadest at its base. Lateral margins rounded, almost parallel in basal 2/3, curved and convergent in anterior third. Anterior angles nearly right-angled and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate on sides, forming a straight line above the scutellum. Surface with fine, shallow and sparse punctation. **Scutellum:** Shape subpentagonal, sharp apex, with fine and scattered punctures. Ratio width/length 1.36. **Elytra:** Surface with 12 rows of regular punctures, well defined but not deep, leaving the overall surface of ridges flat. The rows are green brownish pigmented, and therefore emphasised. The second row is duplicated at the base; fifth and eighth rows (corresponding to second and third interstices) with slightly more separated punctures, irregular and widened at the beginning. Apex of elytral suture rounded. Lateral margin convex and wide in basal 1/4, thinner until the 3/4,

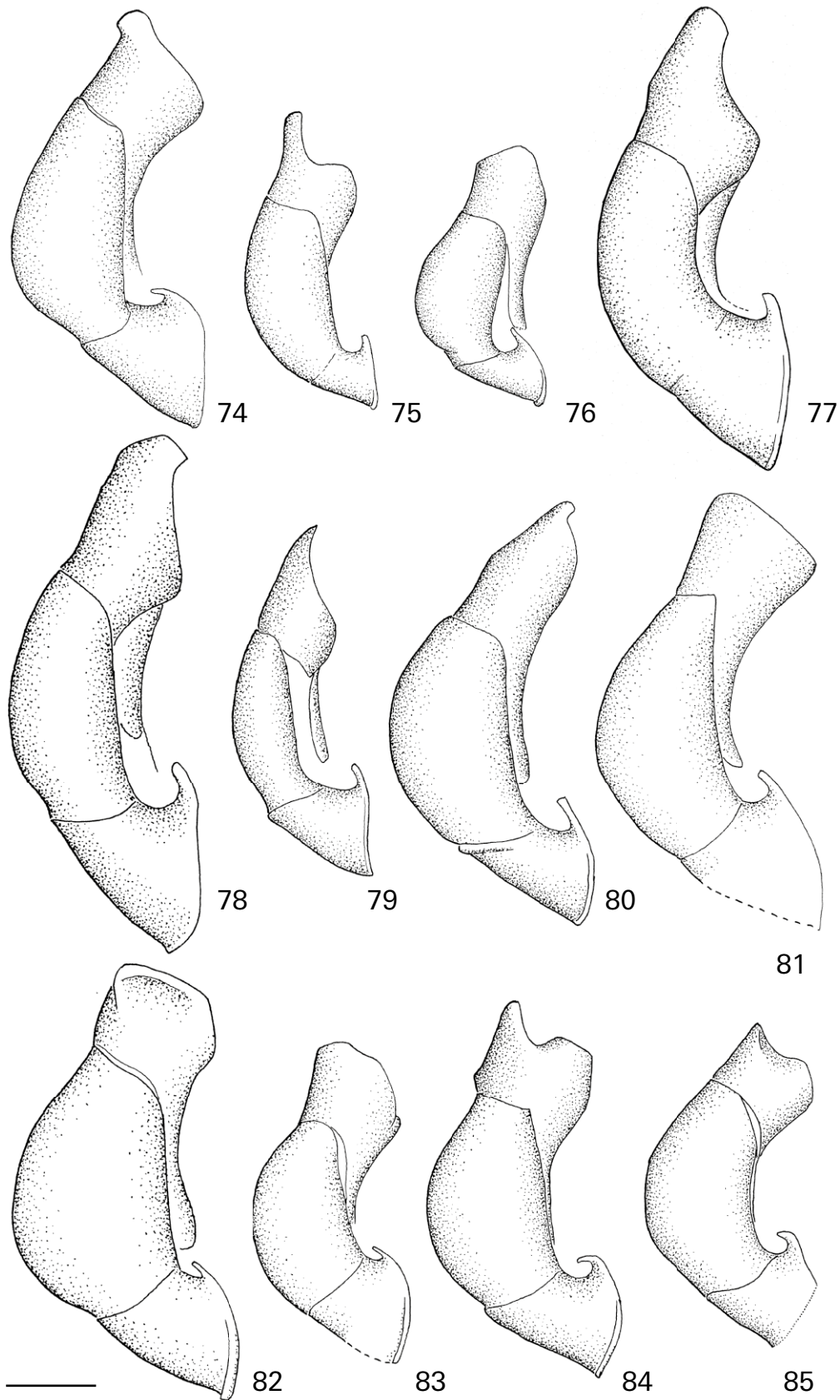


**Figs. 65–73.** Aedeagus of *Callistethus* species not present in Costa Rica, lateral view (base at bottom). **65:** *C. ladino* (Type, Colombia, MNHUB). **66:** *C. rosenbergi* (Type, Colombia, MNHUB). **67:** *C. lepidus* (Guatemala, MNHUB). **68:** *C. xantholeus* (Mexico, INECOL). **69:** *C. collaris* (Holotype). **70:** *C. cayapo* (Type, Brazil, MNHUB). **71:** *C. levii* (Ecuador, MNHUB). **72:** *C. pulcher* (Colombia, MNHUB). **73:** *C. marginicollis* (Cotype, Mexico, MNHUB). Scale = 1 mm (general scale bar at left bottom).

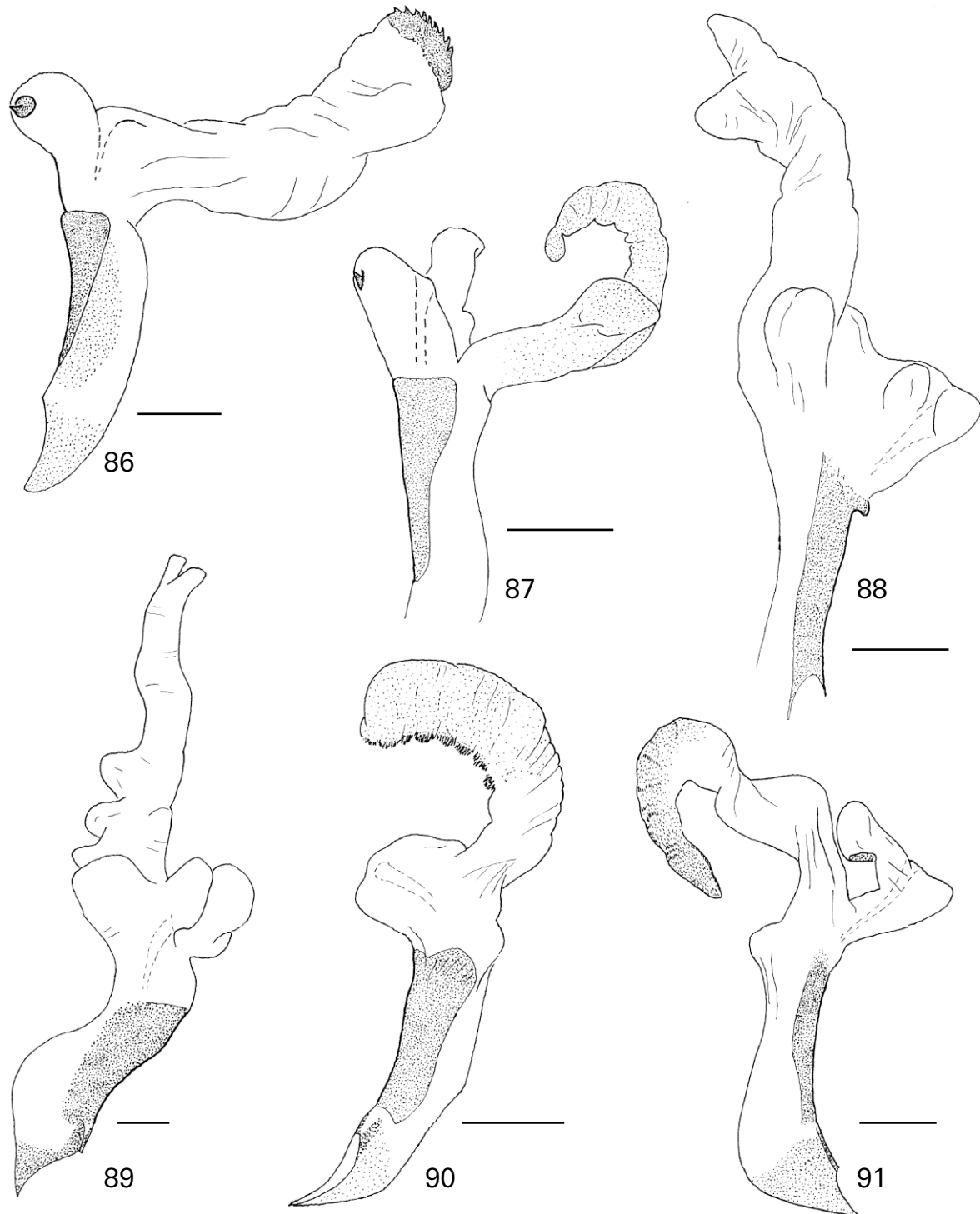
and disappearing at the apex. Marginal membrane narrow, extending along almost the complete margin. **Pygidium:** Coriarious-striated. Covered on entire surface with sparse short blonde setae, longer at margins. Triangular shape, with rounded apex. Nearly straight in lateral view, convex at the apex. Ratio width/length 1.54. **Metasternum:** Disc slightly concave and smooth. Glabrous centrally, with dense setigerous punctures on sides bearing medium-length blonde setae. Mesosternal process long, reaching the procoxae, width 3/4 of coxal height, uniform width along all the length, with rounded apex; in

lateral view slightly curved upwards, and narrowed at the apex; width at base 0.86 mm (Fig. 27). Mesometasternal suture obliterated in the middle, at base of mesosternal process. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites:** Irregularly punctate; punctures denser, deeper and oblong on the sides; presence of short and sparse setae mainly on the sides, arranged in up to 5 rows. Last exposed sternite with shallow sparse punctures, apical margin sparsely punctate, at midline 1/3 as long as total length of last sternite; basal suture of the apical bead sinuate, partially obliterated in the middle





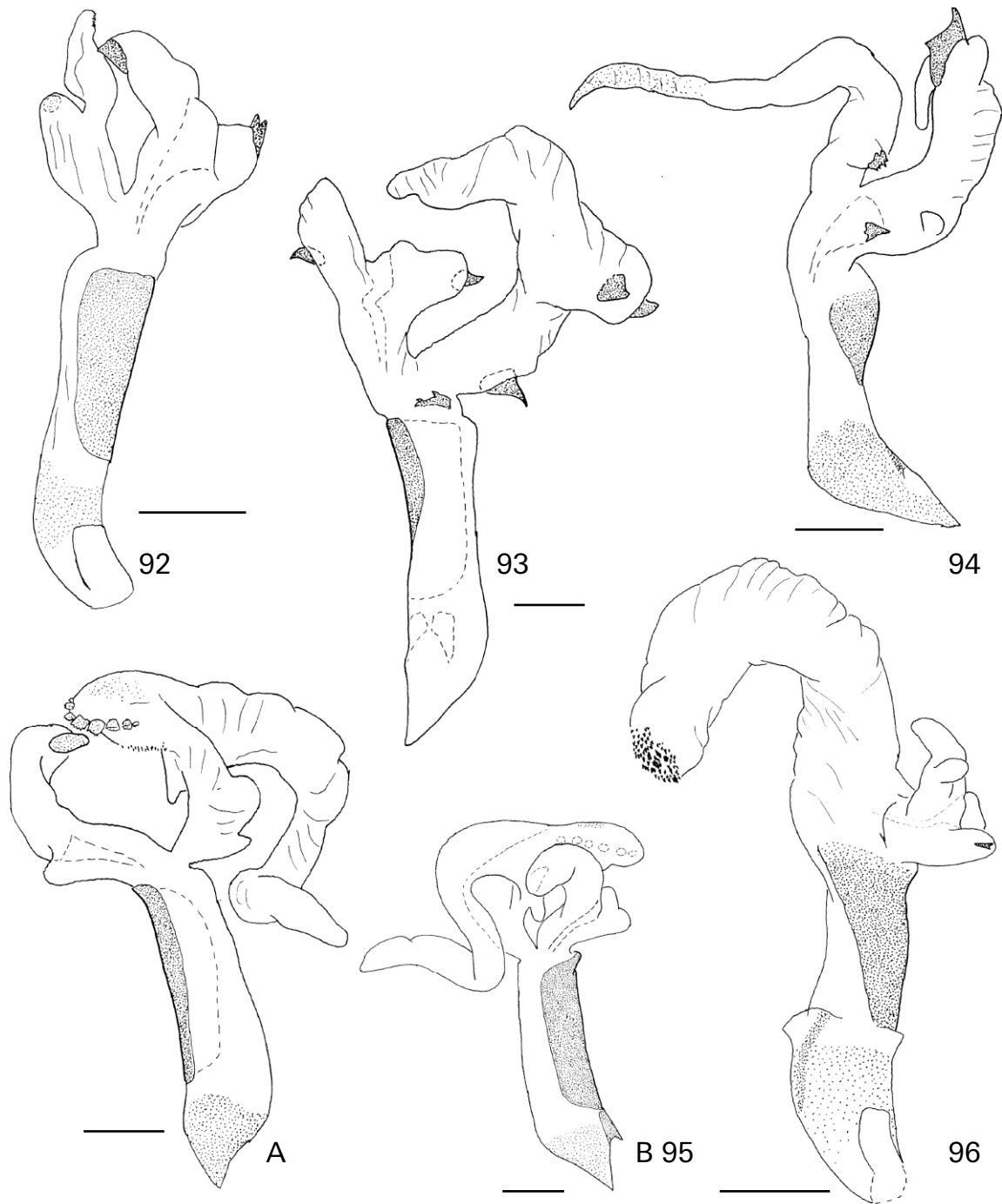
**Figs. 74–85.** Aedeagus of *Callistethus* species, lateral view (base at bottom). **74:** *C. mimeloides* (La Montura, San José, CEUA). **75:** *C. calonotus* (Alto de las Moras, Puntarenas, INBIO). **76:** *C. chlorotoides* (Estación Hitoy Cerere, Limón, INBIO). **77:** *C. chrysanthe* (type, Costa Rica, MNHN). **78:** *C. jordani* (Estación Cacao, Guanacaste, INBIO). **79:** *C. xiphostethus* (Los Angeles, Heredia, INBIO). **80:** *C. schneideri* (Albergue Heliconias, Alajuela, CEUA). **81:** *C. chontalensis* (Cerro Bitárkara, Limón, CEUA). **82:** *C. valdecostatus* (Alto de las Moras, Puntarenas, INBIO). **83:** *C. granulipygus* (Rancho Quemado, Puntarenas, INBIO). **84:** *C. vanpatteni* (Cinco esquinas de Carrizal, Alajuela, INBIO). **85:** *C. sp304* (Cerro Bitárkara). Scale = 1 mm.



**Figs. 86–96.** Endophallus of *Callistethus* species. **86:** *C. mimeloides* (Orosilito, Guanacaste, CEUA). **87:** *C. calonotus* (Alto de las Moras, Puntarenas, INBIO). **88:** *C. chlorotoides* (Reserva Biológica Hitoy Cerere, Limón, INBIO). **89:** *C. jordani* (Estación Cacao, Guanacaste, INBIO). **90:** *C. xiphostethus* (Los Angeles, Heredia, INBIO). **91:** *C. schneideri* (Albergue Heliconias, Alajuela, CEUA). → **92:** *C. chontalensis* (El Copal, Cartago, CEUA). → **93:** *C. valdecostatus* (Las Alturas, Puntarenas, INBIO), number and shape of sclerites is variable. → **94:** *C. granulipygus* (Estación Quebrada Bonita, Puntarenas, INBIO). → **95:** *C. vanpatteni* (Cinco esquinas de Carrizal, Alajuela, INBIO), (A,B) both sides. → **96:** *C. sp304* (Cerro Bitárkara). Scale = 1 mm.

and substituted by a row of punctures. Sixth abdominal spiracle flat. **Protibia:** With 2 teeth (Fig. 39), quite narrow, apical tooth short and blunt, oblique in relation to the vertical axis of the protibia, quadrate. Proximal tooth

small and blunt, at the same height as the internal apex of the protibia. **Metatibia:** Slender, slightly fusiform, glabrous except for carina. Ratio length/width 3.83. Both carinae well defined. Surface sparsely punctate. **Claws**



*of fore leg:* External claw strongly curved; ratio length/height: 1.43; internal claw bifurcate, with branches strongly diverging, upper branch of the same length and more than 1/2 as wide as the lower one. Inferior margin straight. **Male genitalia:** Aedeagus: Fig. 51. Parameres fused to ventral plate; apically deeply sinuate, forming a bilobed apex in lateral view, with wide inferior lobe. Tectum stout, widening from front to rear. Endophallus: Fig. 63. With 2 long sacculi. Ventral sacculus with the ejaculatory duct opening on the left side halfway along its length, situated on the interior of a wide fold; on the opposite side a sclerotised conical spur. Dorsal sacculus longer and with a ridge of small diverticles in the central

part; a wide inflation present near the base. Median lobe sclerotised.

Female: protibia (Fig. 39) wider than in male, apical tooth wider and longer than in male, basal tooth above internal apex. Lower branch of the internal foreleg claw narrower than in male. Last exposed sternite punctate, apical smooth margin narrower than in male.

Variation: body length 16.68–18.04 mm; width 8.77–9.23 mm. Clypeus w/l 1.76–2.04. Interocular ratio 4.60–5.01. Male antennae, ratio funiculus/club 0.70–0.85. Pronotum w/l 1.83–1.98. Scutellum w/l 1.29–1.44. Pygidium w/l 1.46–1.54. Width of mesosternal process at base 0.86–1.08 mm. Metatibia w/l

3.75–3.92. External foreleg claw l/h 1.22–1.43. There is an appreciable variability in the degree of the upward bending and thickness of the mesosternal process seen in lateral view. Scutellum pentagonal to subtriangular.

**Differential diagnosis.** *C. specularis* can be distinguished from other Neotropical *Callistethus* species by the combination of the following features: elytra light brown with green luster, regular flat elytra striation with pigmented striae, parameres deeply sinuate frontally, a row of diverticles on dorsal sacculi of endophallus. The most similar species in colour are *C. chrysanthe* and *C. jordani*, but these are larger, with subtle punctation on elytra, not striated, and different male genitalia (Figs. 77, 78, 89).

**Distribution.** *C. specularis* is widely distributed in Costa Rica, occurring in all the principal mountain ranges from 800 to 2000 m a.s.l. (Fig. 104).

**Material.** Holotype for monotypy: 1♂ 'Type', 'Sp. figured', 'Costa Rica. Van Patten.', 'Anomala specularis Bates', 'B. C. A., Col., II(2) Anomala', 'HOLOTYPE Callistethus specularis (Bates 1888) Labelled by V. Filippini 2012' (BMNH). – *Callistethus kolbei* holotype: 1♂ 'Costa Rica (handwritten)', '23', 'A. Kolbei type Ohaus (handwritten) /Type', '39547', 'HOLOTYPE Callistethus kolbei Ohaus, 1897 labelled by MNHUB 2011', 'Callistethus specularis det. V. Filippini ix.2011'. – Additional material (5): 1♂ 'Anomala specularis Bates', 'Costa Rica. (Pittier) 97–183. L99 La Palma 1100 m 9.96', 'Typus', 'London' (BMNH). 1♂ 'Rio San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste, Costa Rica, Abr 1992 F. Quesada L–N 287800, 427600', 'RUTELINAE Callistethus specularis (Bates 1888) Det. V. Filippini 2013', 'INBIOCRI000930532'. 1♂ 'Rio San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste, Costa Rica. A. Marin 28 mar a 21 abr 1992 L–N 287800, 427600', 'RUTELINAE Callistethus specularis (Bates 1888) Det. V. Filippini 2013', 'INBIOCRI000416015'. 1♀ 'Rio San Lorenzo, 1050 m, Tierras Morenas, Z.P. Tenorio, Prov. Guanacaste, Costa Rica, Abr 1992 F. Quesada L–N 287800, 427600', 'RUTELINAE Callistethus specularis (Bates 1888) Det. V. Filippini 2013', 'INBIOCRI000930529'. 1♂ 'Isla Bonita, Prov. Alajuela, Costa Rica. T. luz 2. 9 sep 2007 Leg. A. García', 'RUTELINAE Anomala sp.37 Det. Alejandra García', 'RUTELINAE Callistethus specularis (Bates 1888) Det. V. Filippini 2013', 'CEUA00105278'.

#### 4.12. *Callistethus stannibractea* sp.n.

**Description.** Male holotype: **Body shape:** Length 16.91 mm; width 10.35 mm. Oval, stout. Elytral disc convex. **Colouration:** Head and pronotum metallic green, with margins of pronotum and central part of clypeus yellow brownish with green luster. Scutellum shiny bronze green. Elytra yellowish light green with metallic luster. Pygidium coppery golden. Venter bronze; antennae, mouth parts and prosternum blackish bronze; legs coppery (Fig. 14). **Head:** Clypeus nearly rectangular, ratio width/length 1.76. Clypeus surface densely and deeply punctate, surface with confluent punctures. Frons with less dense large punctures, like those of the clypeus, and very fine and dense shallow punctures on background. Vertex without larger punctures. Ocular canthus short

and wide; apex rounded. Interocular ratio (interocular width/width of eye) 4.49. Antennae: ratio funiculus/club 0.65. **Pronotum:** Basal width  $1.77 \times$  length; in dorsal view broadest at its base. Lateral margins rounded, angulated at nearly 1/2 of length from anterior. Anterior angles acute and rounded; posterior angles obtuse and rounded. Posterior margin without basal bead, sinuate, forming a nearly straight line above the scutellum. Surface with large, deep, sparse punctures, and very fine, shallow and dense punctures on background, as on frons. Lateral fossae obliterated. **Scutellum:** Shape subpentagonal, blunt apex, with fine and dense punctation on disc; ratio width/length 1.20. **Elytra:** Surface with costae defined by rows of shallow punctures, fairly continuous and sulcated in first and second costae. Interstices with 1 (second–fifth interstices) or 3 (first interstice) rows of sparse shallow punctures. Small horizontal wrinkles present between second interstice and third costa, in the apical half of the elytra surface. Background surface irregular. Apex of elytral suture rounded. Lateral margin convex, tapering gradually from base to apical third, disappearing on the apex. Marginal membrane narrow and extending along the apical half. **Pygidium:** Finely coriarious-striated, densely covered with medium-length blonde setae, longer at margins. Triangular shape, with rounded apex. Nearly straight in lateral view. **Metasternum:** Disc slightly concave, very finely punctate. Glabrous centrally, with dense setigerous punctures on sides, bearing medium-length blonde setae. Mesosternal process long, but not reaching the procoxae; width at base 3/4 of coxal height, narrowing towards the apex to 1/2 the width at base; in lateral view slightly curved upwards at the apex, thin; width at base 0.91 mm (Fig. 28). Mesometasternal suture marked by separate punctures, angulated at the apex where it reaches the apex of trochanters. Metasternal sulcus reaching mesometasternal suture. **Abdominal sternites:** With 2–5 irregular rows of setigerous punctures, more abundant on sides; setae of medium length, blonde colour, dense on sides. Last exposed sternite with shallow dense small punctures on entire surface, apical margin punctate, at midline 2/5 as long as total length of last sternite; basal suture of the apical bead sinuate, obliterated on the sides, due to denser punctures. Sixth abdominal spiracle tuberculiform. **Protibia:** With 2 teeth (Fig. 40), widening gradually from base to lower tooth; apical tooth narrow, long, oblique in relation to the vertical axis of protibia, curved at the apex. Proximal tooth triangular, with wide base, blunt, slightly below the internal apex. **Metatibia:** Slender, nearly conical, subapical constriction negligible. Ratio length/width 4.90. First carina defined by large punctures. Surface sparsely punctate. **Claws of fore leg:** External claw curved; internal claw bifurcate, with branches strongly diverging, upper branch slightly shorter and more than 1/2 as wide as the lower one. Inferior margin straight. **Male genitalia:** Aedeagus: Fig. 52. Parameres long, with thickened apex; ventral margin angulated. Ventral plate separated from parameres, and not well defined on top. Tectum with constant width. En-

dophallus: Fig. 64. A ventral sacculus with a dorsal large diverticle, ejaculatory duct opening situated frontally between both; a sclerotised circular plate with a central spine on right side of the sacculus. A long swollen dorsal sacculus. Median lobe sclerotised.

Female: unknown.

Variation: body length 16.71–16.94 mm; width 9.54–10.35 mm. Clypeus w/l 1.74–1.79. Interocular ratio 3.86–4.49. Male antennae, ratio funiculus/club 0.58–0.65. Pronotum w/l 1.72–1.77. Pygidium w/l 1.71–1.75. Width of mesosternal process at base 0.69–1.02 mm. Metatibia w/l 4.21–4.90. External foreleg claw l/h 1.76–1.80. The yellowish borders of pronotum are more extended in one specimen (INBIOCRI000164337), giving the green part of the disc an ‘M’ form.

**Differential diagnosis.** The large size, colour, abundant ventral setation and particular elytra surface readily separate this species from all congeners. The most similar species in size and colour are *C. chrysanthe* and *C. jordani*, but in these elytra punctation is more evident and regular, and not so green in colour. Also the parameres with thick apex are unique to *C. stannibractea*, whereas are thin and less protruding in *C. chrysanthe* (Fig. 77) and *C. jordani* (Fig. 78).

**Derivatio nominis.** From the Latin noun ‘stanni bractea, -ae’, tin foil, treated here as a noun in apposition, for the irregular and metallic surface of elytra, that looks like it is wrapped in a yellowish green tin foil.

**Distribution.** *C. stannibractea* is known from only one locality in the Braulio Carrillo National Park, Heredia. (Fig. 98).

**Material.** HOLOTYPE: ♂ ‘Estac. Barva, BraulioCarrillo N.P., Pr. Heredia. COSTA RICA. 2500 m. April 1989, M. Zumbado & A. Fernandez’, ‘156’, ‘INBIOCRI002517469’. – PARATYPES (3): 1♂ ‘Estac. Barva, Braulio Carrillo, N.P. 2500 m. Heredia COSTA RICA. Feb 1990. A. Fernandez 233400–523200’, ‘CEUA00105277’; 1♂ ‘Estac. Barva, Braulio Carrillo, N.P. 2500 m. Heredia COSTA RICA. Mar 1990. G. Rivera 233400–523200’, ‘INBIOCRI000164337’; 1♂ ‘Estac. Barva, BraulioCarrillo N.P., Pr. Heredia. COSTA RICA. 2500 m. April 1989 M. Zumbado & A. Fernandez’, ‘156’, ‘INBIOCRI002517467’.

#### 4.13. *Callistethus valdecostatus* stat.n. (Bates, 1888)

**Remarks.** *C. valdecostatus* (Fig. 15) is here elevated to the status of valid species, and not a subspecies of *C. marginicollis* (Bates, 1888) (Fig. 16) (as originally stated by BATES 1888 and listed in KRAJCIK 2007), due to the clear differences in the aedeagus between the two species: the parameres in *C. valdecostatus* are squared frontally (Fig. 82), whereas in *C. marginicollis* the apex is pointed, with sinuate ventral margin (Fig. 73). Moreover, the elytral costae on *C. valdecostatus* are more evident.

**Material.** *C. marginicollis*: 1♂ ‘Misantla Mex.[ico] Höge’, ‘Cotype’, ‘Spilota marginicollis H. Bts.’, ‘Coll. Ohaus | Mus. Berlin’. *C. valdecostatus*: 1♀ ‘♀’, ‘Chiriqui’, ‘Cotype’, ‘S. marginicollis | v. valdecostata | 1a H. Bates’, ‘Coll. Ohaus | Mus. Berlin’; 1♂ ‘Chiriqui’, ‘S. marginicollis | v. valdecostata H. Bates’, ‘Coll. Ohaus | Mus. Berlin’. – Additional material (3): 1♂ ‘Est. Biol. Las Alturas 1500 m, Coto Brus, Prov. Puntarenas, Costa Rica, F. Araya, 23 mar a 2 may 1992, L- S 322500\_591300’, ‘INBIOCRI000915883’; 1♂ ‘COSTA RICA. Prov. Puntarenas. Buenos Aires. R.I. Boruca-Térraba. Alto de las Moras. 800–1000m. 24 MAR 1993. E. Phillips, S. Rojas, M. Solis. L\_S\_326800\_533800 #1977’, ‘INBIOCRI001926965’; 1♀ ‘COSTA RICA. Prov. Puntarenas. Buenos Aires. R.I. Boruca-Térraba. Alto de las Moras. 800–1000m. 24 MAR 1993. E. Phillips, S. Rojas, M. Solis. L-S 326800–533800 # 1977’, ‘INBIOCRI001926964’.

#### 4.14. Distribution patterns

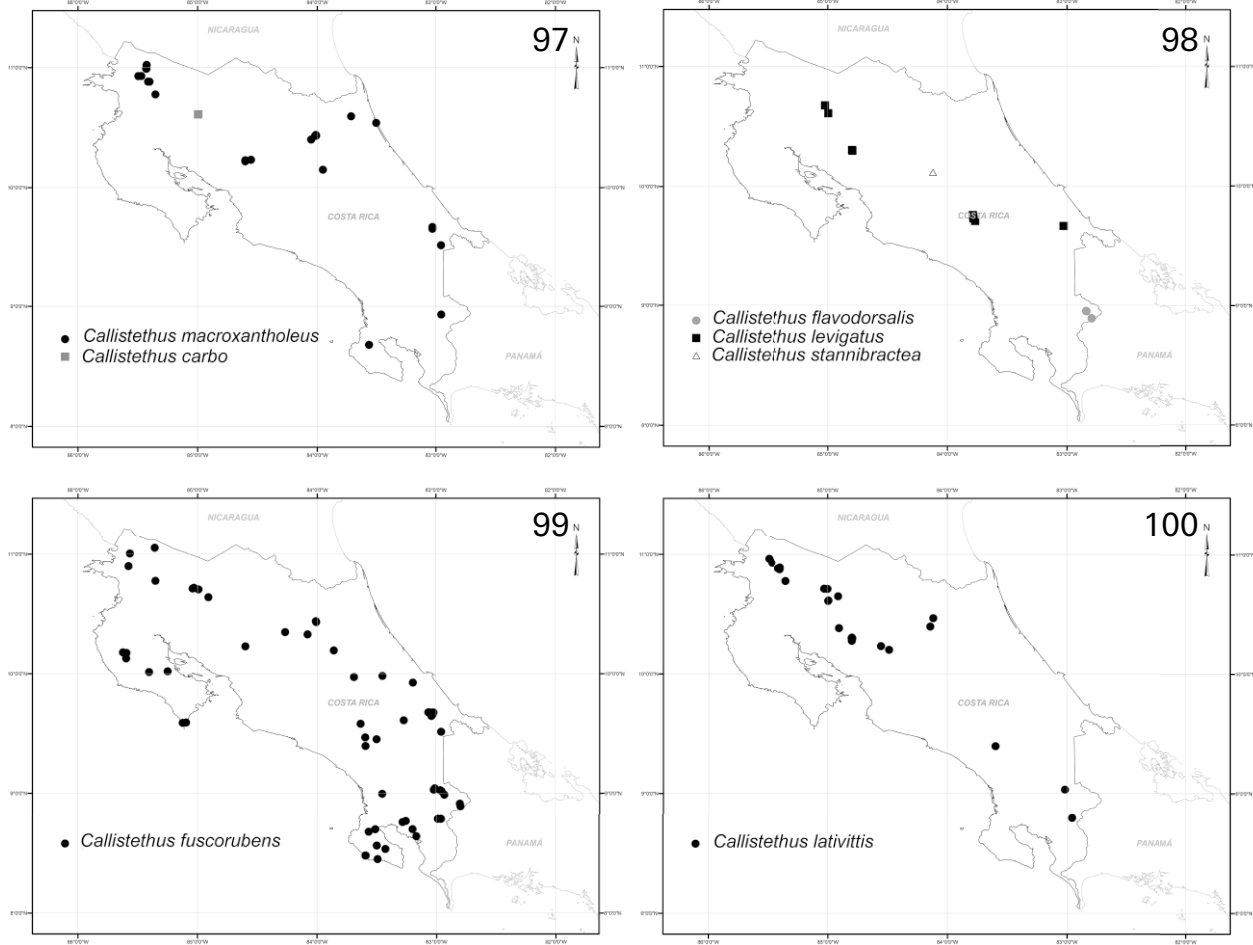
The largest diversity of *Callistethus* in Costa Rica (21 species) is found on the slopes of the main mountain ranges (Guanacaste, Tilarán, Central, Talamanca), approximately between 700 and 1700 m a.s.l. Ten species (*C. chlorotoides*, *C. mimeloides*, *C. chontalensis*, *C. granulipygus*, *C. schneideri*, *C. multiplicatus*, *C. fuscorubens*, *C. lativittis*, *C. parapulcher*, *C. microxantholeus*) were also found at low altitudes (0–700 m a.s.l.), both in Caribbean or Pacific lowlands. Only four species were registered at altitudes above 1800 m a.s.l. These were *C. fuscorubens* (up to 3500 m a.s.l.), *C. specularis* (up to 2000 m.s.l.), *C. stannibractea* (2500 m a.s.l) and *C. xiphostethus* (up to 2400 m a.s.l). All of them, with the exception of *C. stannibractea*, have a wide distribution area and altitudinal range.

Almost all of the species have a wide distribution area, and are found along at least two of the four main mountain ranges and are also commonly present in Caribbean lowlands and Pacific peninsulas. The only species with a narrow distribution range are *C. carbo* (Fig. 101), *C. stannibractea* (Fig. 98) and *C. calonotus* (one locality each, the Tilarán, Central and Coastal Mountain ranges respectively), *C. valdecostatus* (south Talamanca and Coastal) and *C. flavodorsalis* (Fig. 98) (south Talamanca).

The richest habitat is the tropical evergreen broad-leaved lowland and montane forest, where all the species can be found, with the exception of *C. stannibractea*, whose distribution range is limited to the tropical evergreen broad-leaved altimontane forest. The tropical semi-deciduous lowland forest follows in diversity richness, however only 11 species are present in this ecosystem.

The majority of *Callistethus* species in Costa Rica show wide climatic tolerance, as demonstrated by wide altitudinal ranges, and good dispersion ability, with wide distribution areas. This is partly in contrast to other Rutelinae and other scarab families, where the opposite scenario of smaller distribution ranges and high turnover of species among different localities is more common (GARCÍA-LÓPEZ et al. 2013).

The highest richness is found between 700 and 1700 m, a result in line with findings for other insect taxa (dung



**Figs. 97–100.** Distribution of *Callistethus* species in Costa Rica. **97:** *C. carbo* and *C. macroxantholeus*. **98:** *C. flavodorsalis*, *C. levigatus* and *C. stannibractea*. **99:** *C. fusciorubens*. **100:** *C. lativittis*.

beetles and butterflies), as this range presents a higher variety of habitats, and is a transitional-zone for many groups of animals (KOHLMANN et al. 2007).

The number of species registered at lower altitudes (0–700 m) is fairly high, as found for other Rutelinae genera and also for other scarab subfamilies (GARCÍA-LÓPEZ et al. 2012), despite the fact that in these areas the forest is fragmented and subject to the impact of agro-productive land use, which may limit the presence of more species. However, these results are based on the INBio collection, which generally makes more sampling effort in preserved areas (KOHLMANN et al. 2007), so that the perturbation effects could be minimized. The lower richness at higher altitudes is a common pattern in tropical scarab beetles (GARCÍA-LÓPEZ et al. 2012).

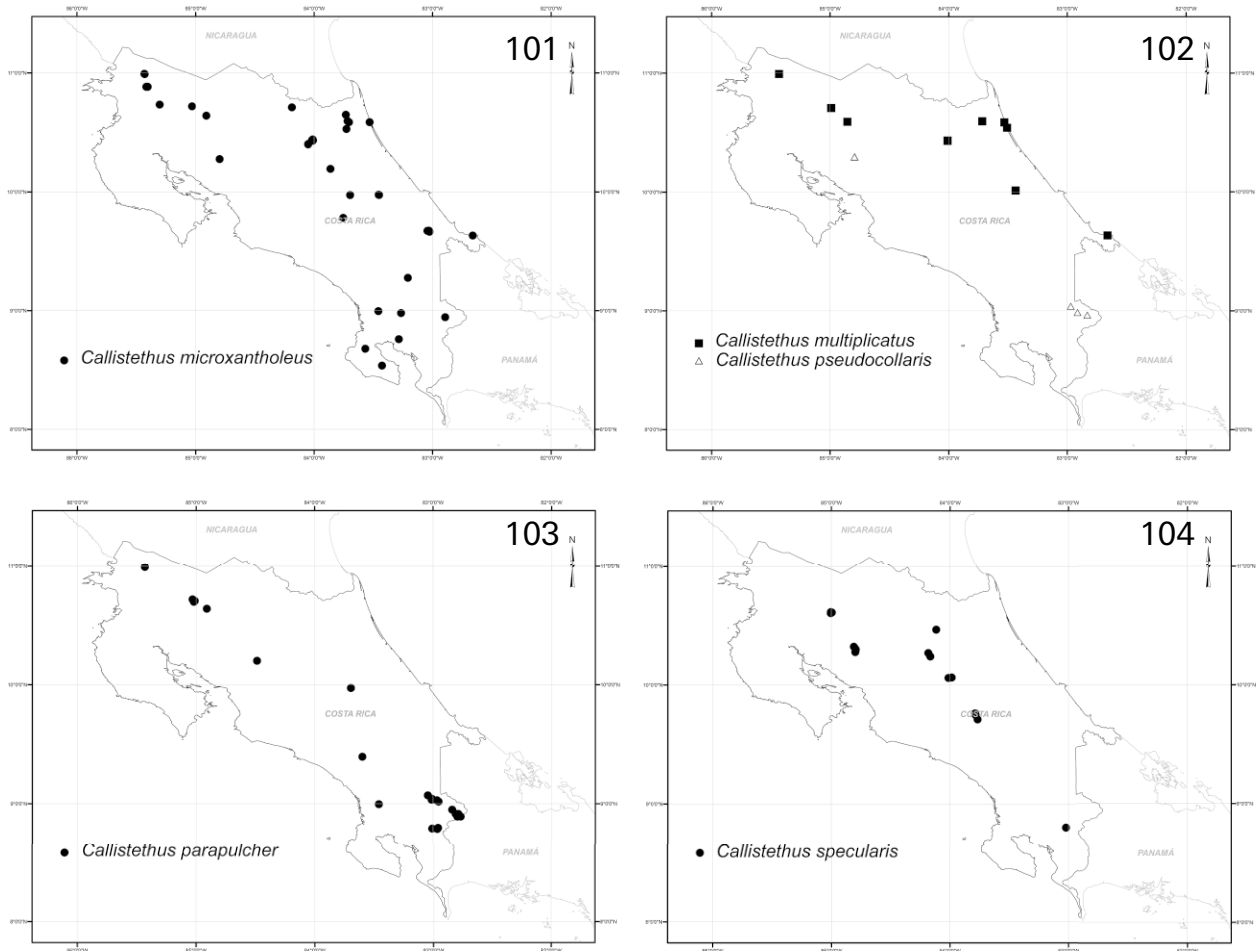
Regarding species with a narrow distributional range, the distribution near the border with Panama suggests a possible wider southern distribution for *C. calonotus* (originally described for northern Panama), *C. valdecostatus* and *C. flavodorsalis* (Fig. 98), whereas *C. carbo* (Fig. 97) and *C. stannibractea* (Fig. 98) probably have a truly restricted distribution, as they have only been collected in one locality each within larger and well sampled

zones, that could be due to ecological factors or influence from deforestations from the 1950s to the late 1970s (ROSETO-BIXBY & PALLONI 1998).

#### 4.15. Key to Costa Rican species of *Callistethus*

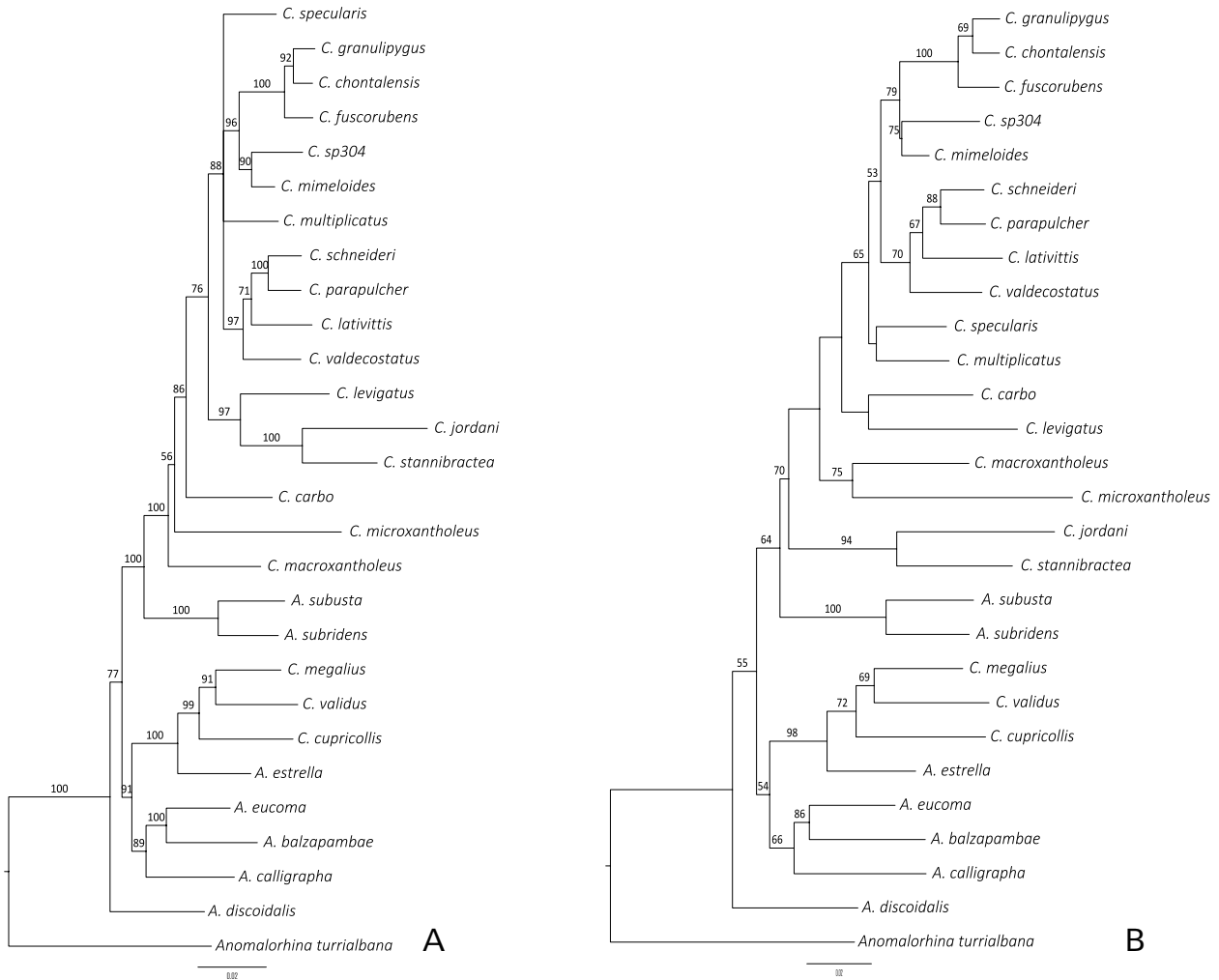
The species *C. ruteloides*, *C. nicoya* and *C. sulcans*, considered *incertae sedis* (see FILIPPINI et al. 2015 and section 5 below) are not included.

- 1** Slender oval body, body surface convex, usually with metallic green colour or luster; wide interocular space (more than  $3.8 \times$  the width of eye), with small and elongated eyes; mesosternal process long (produced anteriorly beyond top of mesocoxae for  $> 2/3 \times$  height of mesocoxae) and with apex separated from level of mesoventrite ..... **2**
- 1'** Mesosternal process short (produced anteriorly beyond top of mesocoxae for  $< 1/2 \times$  height of mesocoxae), laterally seen as a bump, apex connected to mesoventrite ..... **13**

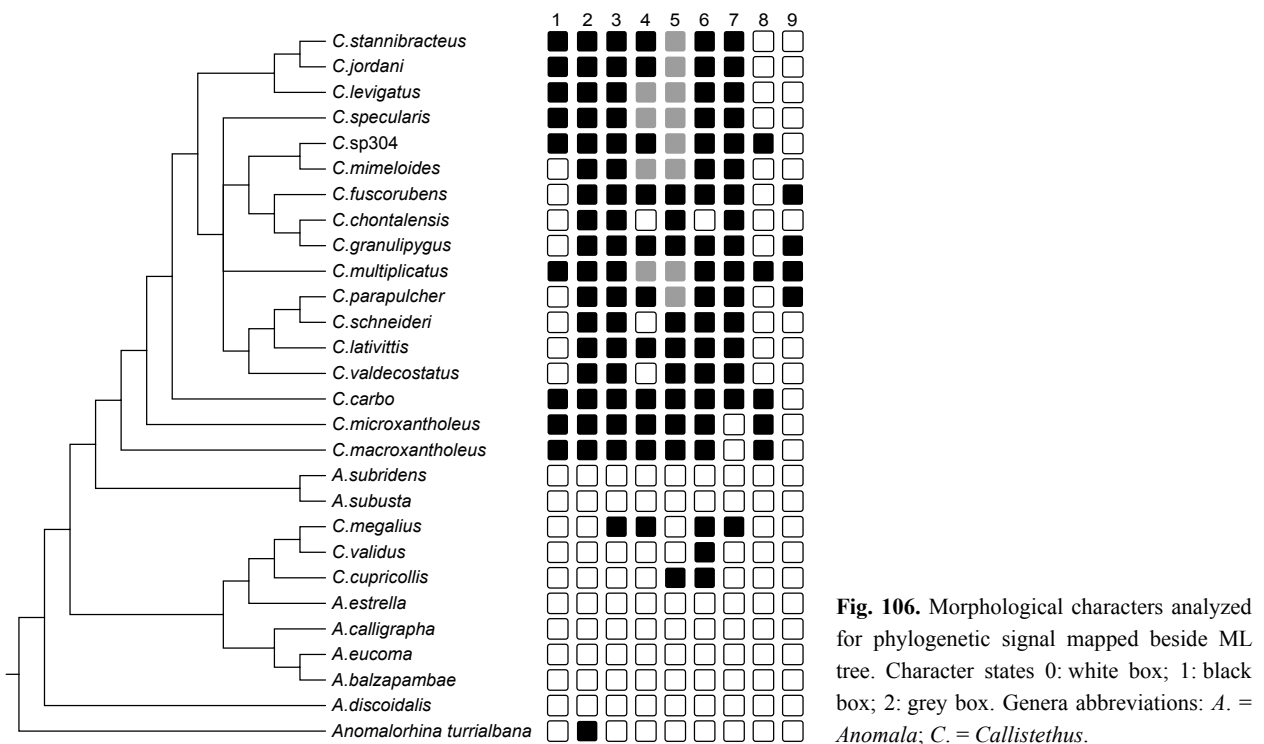


**Figs. 101–104.** Distribution of *Callistethus* species in Costa Rica. **101:** *C. microxantholeus*. **102:** *C. pseudocollaris* and *C. multiplicatus*. **103:** *C. parapulcher*. **104:** *C. specularis*.

- 2 Elytra surface with regular and sulcate striae, normally 14 per side ..... 3
- 2' Elytra surface nearly smooth, or with intercostal spaces with shallow irregular punctures, never forming sulcate striae ..... 7
- 3 Elytra of same colour as pronotum, body length < 16.0 mm ..... 4
- 3' Elytra of lighter colour than pronotum, body length > 16.0 mm ..... *C. specularis* (Bates, 1888)
- 4 Elytra and pronotum yellow; aedeagus Fig. 74, endophallus Fig. 86 ..... *C. mimeloides* (Ohaus, 1902)
- 4' Elytra and pronotum green ..... 5
- 5 Body length > 14.0 mm; ochre margins of pronotum concealed by metallic green luster; bright light green colour with reddish reflex; aedeagus Fig. 75, endophallus Fig. 87 ..... *C. calonotus* (Bates, 1888)
- 5' Body length < 14.0 mm; ochre margins of pronotum wide end evident; dark to brownish metallic green colour ..... 6
- 6 Apex of parameres wide and straight ..... *C. pseudocollaris* sp.n.
- 6' Apex of parameres narrow and bending upwards ..... *C. multiplicatus* sp.n.
- 7 Elytra of same colour as pronotum, green or purple blackish ..... 8
- 7' Elytra of lighter colour than pronotum, yellowish or light green ..... 9
- 8 Elytral surface completely smooth; ventral side brownish, without metallic luster; aedeagus Fig. 76, endophallus Fig. 88 ..... *C. chlorotoides* (Bates, 1888)
- 8' Elytral surface with very shallow punctures, costae visible; ventral side with green metallic luster ..... *C. levigatus* sp.n.
- 9 Body length > 20 mm ..... 10
- 9' Body length < 17 mm ..... 11
- 10 Costae on elytra defined by sulcated rows of punctures; aedeagus Fig. 77 ..... *C. chrysanthe* (Bates, 1888)
- 10' Costae poorly defined, not sulcated; aedeagus Fig. 78, endophallus Fig. 89 ..... *C. jordani* (Ohaus, 1902)
- 11 Elytral surface irregular, with small wrinkles, punctation not clear at bare sight. Body length > 16.5 mm ..... *C. stannibractea* sp.n.
- 11' Elytral surface regular, with clearly visible costae and punctate interstices. Body length < 16 mm ... 12



**Fig. 105.** Trees obtained from (A) Bayesian analysis, (B) Maximum Likelihood. Numbers represent percentage posterior probabilities from the Bayesian analysis in (A), bootstrap values in (B). Genera abbreviations: *A.* = *Anomala*; *C.* = *Callistethus*.



**Fig. 106.** Morphological characters analyzed for phylogenetic signal mapped beside ML tree. Character states 0: white box; 1: black box; 2: grey box. Genera abbreviations: *A.* = *Anomala*; *C.* = *Callistethus*.



**Table 4.** Values of *K* statistics and associated *p* value calculated on the two tree topologies (Bayesian, Fig. 105A, and Maximum Likelihood, Fig. 105B). *K* values closer to zero correspond to a random, i.e. highly homoplasious, pattern of evolution, while *K* values greater than 1 indicate low homoplasy and thus strong phylogenetic signal.

Characters	Bayesian		ML	
	K	p	K	p
1. interocular distance	0.9071399	0.007	0.8833322	0.01
2. posterior margin of pronotum	5.2837439	0.001	4.0408277	0.001
3. shape of posterior margin of pronotum	3.6167561	0.001	3.3997172	0.001
4. distance between mesocoxae	0.8168402	0.098	0.6763212	0.203
5. development of mesosternal process	2.5155903	0.001	2.1363155	0.001
6. definition of mesosternal suture	1.4367777	0.026	1.0989112	0.041
7. position of mesosternal suture	3.11286	0.001	3.2256791	0.001
8. shape of apex of elytral suture	0.5660773	0.138	0.5849185	0.154
9. fusion of parameres to ventral plate	3.0029691	0.001	3.3469446	0.001

- 12 Body length 12–13 mm; deep punctures on elytra; ventral side yellow reddish in colour, or only partially with green luster (not on abdominal sternites or legs); flat sixth spiracle; aedeagus Fig. 79, endophallus Fig. 90 ..... *C. xiphostethus* (Bates, 1888)
- 12' Body length 14–15 mm; shallow punctures on elytra; ventral side completely dark metallic green; tuberculiform sixth spiracle ..... *C. flavodorsalis* sp.n.
- 13 Stout body, wider at 2/3 of elytra length, body surface convex, brown colour but in some species a metallic luster is present; eyes large and rounded, as in *Anomala* species, interocular space < 3.5 × width of eye; elytra with defined costae and punctate interstices; mesosternal process short (produced anteriorly beyond top of mesocoxae for < 1/2 × height of mesocoxae), laterally seen as a bump, apex not free ..... 14
- 13' Body diamond shaped, pronotum long and with anterior margin narrow, end of body narrowing steadily from elytra midlength; body dorsally flattened; wide interocular space (> 3.8 × width of eye), eyes small and elongated; elytra regularly striated or nearly smooth; mesosternal process short (produced anteriorly beyond top of mesocoxae for < 1/2 × height of mesocoxae), laterally seen as a bump, apex not free ..... 22
- 14 Elytra metallic green with brown hues and shallow coalescing punctures  
... *Callistethus yalizo* Filippini, Galante, Micó 2015
- 14' Elytra brown, a metallic luster can be present, costae and punctures well defined ..... 15
- 15 Elytra light brown, lighter colour than pronotum ..... 16
- 15' Elytra dark brown, similar in tone to pronotum ..... 18
- 16 Elytra with bronze luster; first interstice on elytra wide and with dense punctures, pronotum glabrous ..... *C. lativittis* sp.n.
- 16' Elytra without metallic luster; first interstice on elytra narrow, with 1–2 rows of punctures, pronotum covered with setae ..... 17
- 17 Oval shape, mesosternal process pointed in lateral view, large and slightly tapering at apex in ventral view, parameres with squared apex  
..... *C. parapulcher* sp.n.
- 17' Elongated shape, mesosternal process blunt in lateral view, tapering strongly just above base in ventral view, parameres with acute apex; aedeagus Fig. 80, endophallus Fig. 91 ... *C. schneideri* (Ohaus, 1905)
- 18 Pronotum with homogeneous colour, no ochre margins; aedeagus Fig. 81, endophallus Fig. 92  
..... *C. chontalensis* (Bates, 1888)
- 18' Pronotum with ochre margins ..... 19
- 19 Elytral surface with protruding costae, interstices flat with dense irregular punctures; aedeagus Fig. 82, endophallus Fig. 93 .... *C. valdecostatus* (Bates, 1888)
- 19' Costae not protruding in relation to rest of elytral surface, interstices with rows of punctures ..... 20
- 20 Mesosternal process long, slightly beyond mesocoxae. First interstice of elytra with four rows of punctures; other interstices with irregular rows of punctures, flat ..... *C. fusciorubens* sp.n.
- 20' Mesosternal process short, not beyond mesocoxae. First interstice of elytra with three rows of punctures; other interstices with regular rows of punctures forming sulcate striae ..... 21
- 21 Secondary small sparse puncture on all elytra surface; aedeagus Fig. 83, endophallus Fig. 94  
..... *C. granulipygus* (Bates, 1888)
- 21' No secondary punctures on elytra, background surface smooth; aedeagus Fig. 84, endophallus Fig. 95  
..... *C. vanpatteni* (Bates, 1888)
- 22 Elytra clearly striated, of variable colour ..... 23
- 22' Elytra nearly smooth, with very shallow rows of punctures, colour black ..... *C. carbo* sp.n.
- 23 Body length > 9.50 mm. Pygidium yellow with green sides. Head small in relation to pronotum (head width < 0.45 × pronotum width)  
..... *C. macroxantholeus* sp.n.
- 23' Body length < 8.60 mm. Pygidium entirely yellow. Head width > 0.55 × pronotum width  
..... *C. microxantholeus* sp.n.

## 5. Phylogeny and character evolution

The trees obtained with the Bayesian analysis (Fig. 105A) and with the Maximum Likelihood analysis (Fig. 105B) differ in the position of *C. microxantholeus*, *C. carbo* and the clade *C. jordani* + *C. stannibractea* (not supported in the ML) and the resolution for *C. specularis* and *C. multiplicatus*.

Species from the *C. validus* group (*C. cupricollis*, *C. megalius*, *C. validus*) group together with *Anomala* species, while all the other *Callistethus* species form a monophyletic group (*Callistethus* s.str. from now on). The clades within *Callistethus* s.str. are not coincident with morphological features: species with brownish colors, big eyes and short mesosternal process form 2 clades (*C. granulipygus* + *C. chontalensis* + *C. fusciorubens* pp = 100(B)/100(ML) and *C. schneideri* + *C. parapulcher* + *C. lativittis* + *C. valdecostatus* pp = 97/70), mixed with medium sized species with small eye, metallic colors and long mesosternal process (*C. specularis*, *C. mimeloides*, *C. multiplicatus*). Species with short mesosternal process and flattened elytra (*C. carbo*, *C. macroxantholeus* and *C. microxantholeus*) are found at base but do not form a clade. The uncertain position of *C. multiplicatus* must be reassessed, as morphologically it is closer to other species of the *collaris* complex (*C. sp304*), and *C. mimeloides*, who are strongly paired (pp = 90/75). The pairing of *C. jordani* and *C. stannibractea* (pp = 100/94) is not surprising due to their similarities: big size, light colour, small eyes, long mesosternal process.

The genus *Anomala* results paraphyletic, with the clade *A. subridens* + *A. subusta* forming the sister group of *Callistethus*, and *A. discoidalis* being sister to all other ingroup taxa. However, the complicated systematics of *Anomala* is not an object of the present work.

The *K* statistics for the morphological characters analyzed are presented in Table 4, characters have been associated with ML tree in Fig. 106. The analysis has been conducted on both tree topologies, with similar results. Six of the characters have strong phylogenetic signal, with statistical support. The interocular distance (character 1) shows a weak phylogenetic signal, approaching a value of *K* close to 1, probably due to the fact that both states are present inside the *Callistethus* s.str. clade, while characters on the intercoxal distance (character 4) and the shape of apical suture of elytra (character 8) do not have phylogenetic signal, probably due to state distribution inconsistent with the tree.

The characters with strong phylogenetic signal provide states that are suitable as diagnostic features for the genus *Callistethus*: 2[1]. Posterior margin of the pronotum without bead (*K* = 5.28); 3[1]. Posterior margin of the pronotum straight or slightly concave above the scutellum (*K* = 3.62); 5[1,2]. Mesosternal process reaching at least apex of mesocoxae (*K* = 2.55); 6[1] and 7[1]. Mesometasternal suture poorly defined or absent (*K* = 1.44) and at the same level of anterior margin of trochant-

ers (*K* = 3.11); 9[1]. Fusion of the parameres to the aedeagal ventral plate (*K* = 3.00).

The level of development of the mesosternal process then is not a discriminatory feature: both species with short and long mesosternal process are to be considered belonging to the genus *Callistethus*, in contrast to the conclusions of MORÓN & RAMÍREZ-PONCE (2012).

The presence of a mesosternal process is shared also with some species of the *C. validus* group (represented by *C. cupricollis*, *C. megalius*, *C. validus* in the trees), which, however, do not present the other diagnostic features. On the contrary, the length of the process is variable within the *Callistethus* clade, which includes also species with short processes.

According to these diagnostic features, the following Neotropical species that previously belonged to *Anomala* are herewith moved into *Callistethus*: *C. jordani* (Ohaus, 1902) **comb.n.**, *C. mimeloides* (Ohaus, 1902) **comb.n.**, *C. xantholeus* (Bates, 1888) **comb.n.** (Mexico), *C. lepidus* (Burmeister, 1844) **comb.n.** (Guatemala).

*A. jansoni* **comb.n.** Ohaus, 1897, *A. fulvopiceus* **comb.n.** Ohaus, 1928 and *A. ochrogastra* Bates 1888, **comb.n.** *A. penai* Frey 1968 **comb.n.** before included in *Callistethus*, do not present this set of features, and are therefore moved to the genus *Anomala*.

The species of the *C. validus* group (sensu MACHAT-SCHKE 1957), with short mesosternal process, pronotum with bead on the posterior margin, parameres not fused with ventral plate are placed in *Anomala*, waiting for a comprehensive revision of this genus that will elucidate its actual paraphyly: *A. antis* Ohaus, 1902, *A. bimaculata* Blanchard, 1851, *A. cicatricosa* (Perty, 1832) **comb.n.**, *A. cupricollis* Chevrolat, 1834, *A. eckhardti* Ohaus, 1897, *A. megalia* Bates, 1888, *A. panamensis* Ohaus, 1902, *A. plagiata* Nonfried, 1894, *A. pupillata* Burmeister, 1844, *A. valida* Burmeister, 1844.

The species *C. biolleyi*, *C. buchwaldianus*, *C. nicoya*, *C. sulcans* with short and narrow mesosternal process, parameres fused with ventral plate, but pronotum with bead on the posterior margin and mesometasternal suture usually well defined, are considered *incertae sedis*, until a phylogenetic study involving these species resolves their status.

*C. pseudocollaris* and *C. multiplicatus* closely resemble *C. collaris*, and are mainly differentiated from it by the very different shapes of the aedeagus and endophallus. They are supposed to be part of a larger species complex, as from personal experience revising specimens in various European museums, most of the specimens determined as *C. collaris* show a high variety of aedeagus shapes, depending on the locality of the collection. The aedeagus of the type specimen from the Entomological Collection of Martin-Luther-Universität (Halle, Germany) is illustrated in Fig. 69. There is at least one additional species belonging to this species complex in Costa Rica, of which one male from Cerro Bitárkara, Prov. Limón (listed as *C. sp304* on phylogenetic tree) is known, whose aedeagus and endophallus are illustrated in Figs. 85 and 96 respectively.

After the description of the new species presented here, the genus *Callistethus* includes 23 species in Costa Rica. This is almost double the previously known diversity, but this richness remains far from that of the most closely related genus *Anomala*. However, species numbers cannot be directly compared as with the current state of knowledge (Fig. 2) *Callistethus* is subordinate in *Anomala* and thus most likely either *Anomala* has to be split in several genera or *Callistethus* be included in *Anomala* with increasing phylogenetic knowledge. The genus *Callistethus* is a diversified and speciose taxon in the Neotropics, still evolutionarily active as suggested by the presence of species complexes with uniform external morphology (i.e. *C. collaris* species complex), but with strong differences in male genitalia.

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## 8. Appendix

Additional information on *Callistethus* species not present in Costa Rica or not treated in detail in the text. Locality data as retrieved from labels of the species studied, country listed between brackets if not present on original labels.

*C. aequatorialis* (Ohaus 1897) [MNHUB] – Locality data: Loja, Ecuador. – Remarks: body length about 12–13 mm. Dark green pronotum, brownish black elytra, venter dark reddish brown. Dorsal surface smooth. Elytra with regular finely punctured striae, small horizontal wrinkles on fifth stria. Mesosternal process very short, wide with rounded and stout apex. Aedeagus in Fig. 107.

*C. antis* (Ohaus 1902) [MNHUB] – Locality data: Cuzco, Perú. – Remarks: part of *C. validus* group. Body length about 13 mm.

Head, pronotum and scutellum reddish brown, elytra reddish ochre with large pigmented punctures, venter reddish brown. Male protibia wide, with a hint of a third tooth. Posterior margin of pronotum with incomplete bead. Costae defined by regular rows of large punctures, first interstice of elytra with 3–4 irregular rows of punctures, second interstice with 2 irregular rows of punctures. Intermesocoxal distance wide and hairy, slightly convex. Aedeagus in Fig. 108.

*C. benicolus* (Ohaus 1897) [MNHUB] – Locality data: Río Bani, Bolivia. – Remarks: body length about 15–16 mm. Pronotum dark green with ochre lateral margins, elytra dark reddish brown; venter dark brown with metallic luster, coxae and metafemurs yellow, metatibiae metallic green. Pronotum coarsely punctured. Elytra sulcated: costae defined by wide regular punctured sulci, interstices sulcated by slightly irregular rows of wide punctures, first and second interstices with 2 rows, others with 1 row. Small secondary

punctures on all elytral surface. Mesosternal process very short, narrow. Aedeagus in Fig. 109.

*C. bimaculatus* (Blanchard 1851) [MNHN] – Locality data: Mexico. – Remarks: part of *C. validus* group. Female. Body length about 19–20 mm. Head, pronotum and scutellum bronze, elytra ochre with large punctures, often pigmented; venter reddish brown. Posterior margin of pronotum with incomplete bead. First interstice of elytra with 4–5 irregular rows of punctures. Mesosternal process poorly developed, not more than a bump. Presence of two median dark spots on elytral disc. Pygidium strigate.

*C. biolleyi* (Ohaus 1902) [MNHUB] – Locality data: Volcán de Chiriqui, Costa Rica. – Remarks: body length about 16–17 mm. Greenish black color. Posterior margin of pronotum with incomplete bead; venter reddish brown with green luster. Pronotum surface smooth. Elytra regularly sulcated. Mesosternal process not developed, intermesocoxal distance narrow and convex. Median lobe with apical long projection curved to one side. Aedeagus in Fig. 110.

*C. buchwaldianus* (Ohaus 1908) [MNHUB] – Locality data: hacienda Ana María, Quevedo, Ecuador. – Remarks: body length about 16 mm. Pronotum metallic green with copper red luster; elytra emerald green; venter reddish brown with green luster. Pronotum surface smooth. Posterior margin of pronotum with incomplete bead. Elytra regularly sulcated. Mesosternal process poorly developed, narrow. Median lobe with apical projection (probably broken in specimen examined). Aedeagus in Fig. 111.

*C. caucanus* (Ohaus 1897) [MNHUB] – Locality data: Cauca, Colombia / Río Yurumanguí, Colombia. – Remarks: body length about 15 mm. Very dark metallic green color, surface smooth; venter reddish brown. Elytra with regular rows of fine and shallow punctures. Aedeagus in Fig. 112.

*C. cayapo* (Ohaus 1902) [MNHUB] – Locality data: Goyaz, Jatahy [Brasil]. – Remarks: body length about 17 mm. Pronotum metallic green with wide ochre bands on lateral margins; scutellum metallic green; elytra light brown; venter yellow, abdominal sternites reddish brown. Elytra with costae defined by sulcated rows of punctures, first interstice with 2 irregular rows of punctures, other interstices with 1 regular sulcated row of punctures, irregular punctures on apical calli. Mesosternal process very short, tapering at apex. Aedeagus in Fig. 70.

*C. chalcosomus* (Blanchard 1851) [MNHN, MNHUB] – Locality data: S. Lauren, Cayenne. – Remarks: body length about 16 mm. Pronotum dark metallic green, elytra dark reddish brown; venter reddish brown. Posterior margin of pronotum with incomplete bead, nearly straight in correspondence of scutellum. Pronotum with coarse punctures. Elytra regularly sulcated. Mesosternal process weakly developed, narrow.

*C. coeruleus* (Ohaus 1908) [MNHUB] – Locality data: Sto. Domingo [Ecuador]. – Remarks: body length about 17–18 mm. Female. Shiny dark blue color, all surface with very fine and sparse puncture, not evident at bare sight; venter reddish black. Mesosternal process short, barely produced. Elytra with regular rows of fine and shallow punctures.

*C. collaris* (Burmeister 1844) [MLUH] – Locality data: Venezuela. – Remarks: body length about 11.5–13.5 mm. Metallic green color, pronotum with ochre lateral margins; venter yellow to ochre. Elytra regularly striated. Long mesosternal process, with uniform width. Aedeagus in Fig. 69. As mentioned in the text, it belongs to a wide species group of similar species present in Central and South America.

*C. eckhardti* (Ohaus 1897) [MNHUB] – Locality data: Chuchuras, Amazon, Perú. – Remarks: part of *C. validus* group. Body length about 18–22 mm. Head, pronotum and scutellum greenish bronze, elytra reddish ochre, venter reddish brown. Posterior margin of pronotum with incomplete bead. Elytra with large punctures, not pigmented; first interstice with 5–6 irregular rows of punctures. Mesosternal process short. Aedeagus in Fig. 113.

*C. flavofemoratus* (Ohaus 1897) [MNHUB] – Locality data: Río Dagua, Colombia. – Remarks: body length about 12.5–14.5 mm. Pronotum brownish green with ochre lateral margins, elytra reddish brown with green luster, venter dark reddish brown, femurs yellow, tibiae brown with green luster. Pronotum with fine punctures, smooth appearance. Elytra with regular rows of punctures. Mesosternal process short, narrow, with uniform width. Aedeagus in Fig. 114.

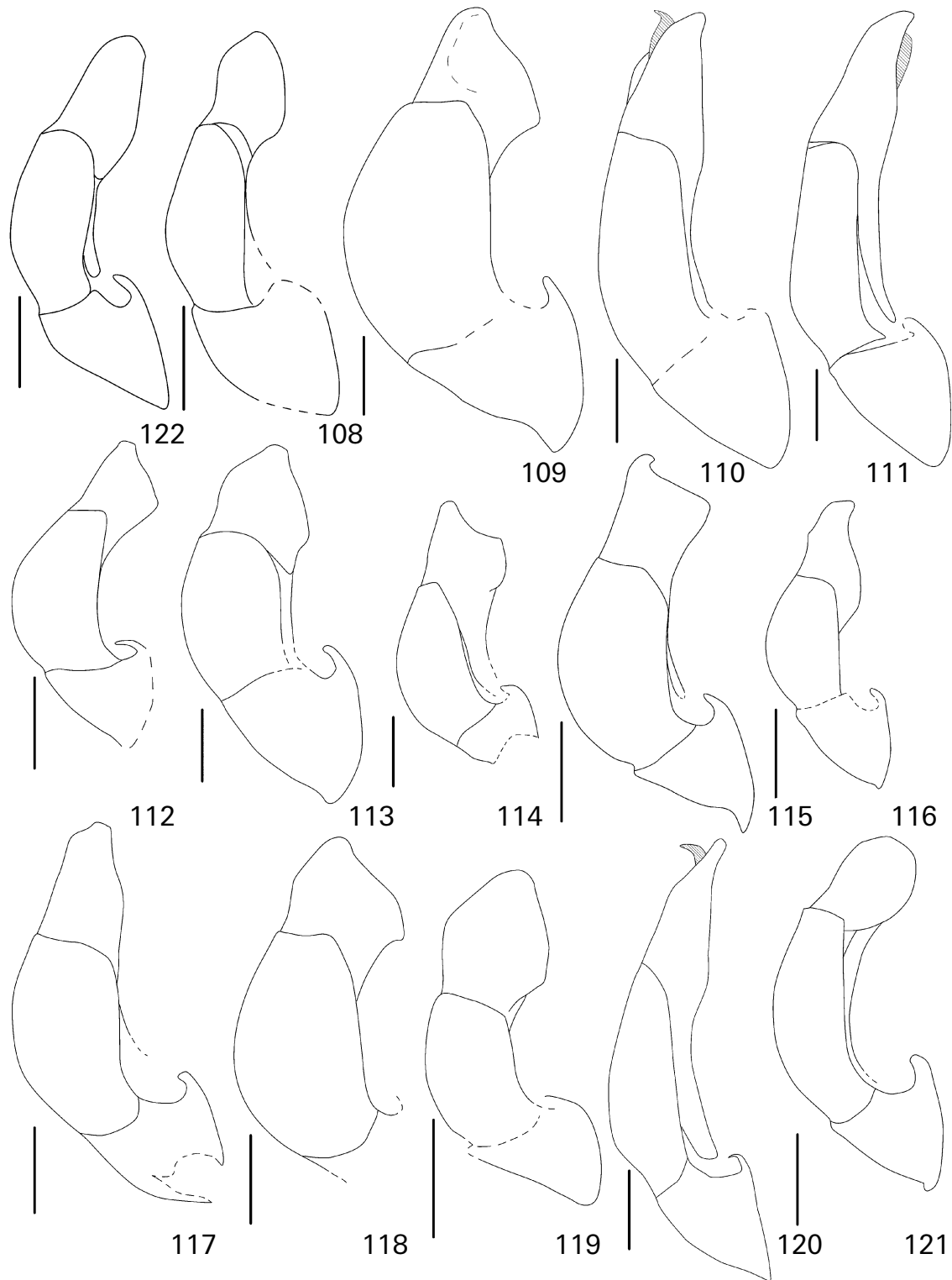
*C. fulvopiceus* (Ohaus 1928) [MNHUB] – Locality data: Cauca, Colombia. – Remarks: body length about 15 mm. Head, pronotum and scutellum reddish black; elytra ochre with suture and lateral margins reddish black; venter blackish brown. Pronotum with coarse and dense coalescing punctures. Elytra sulcated; first striae with punctures sparse on basal half, ribs corresponding to second and third interstices with sparse punctures in a row. Posterior margin of pronotum with complete bead; mesosternal process not produced, intermesocoxal space wide and convex.

*C. hiekei* (Frey 1968) [MNHUB] – Locality data: Cachabé to Paranda, Colombia. – Remarks: body length about 15 mm. Head and pronotum metallic green, pronotum with ochre lateral margins; elytra bronze green; venter yellow. Elytra with costae defined by sulcated rows of punctures; first interstice with 3 irregular rows of punctures on median portion of interstice, leaving the sides smooth as additional costae; other interstices with 1 regular row of punctures. Mesosternal process long, wide, tapering at apex. Aedeagus in Fig. 115.

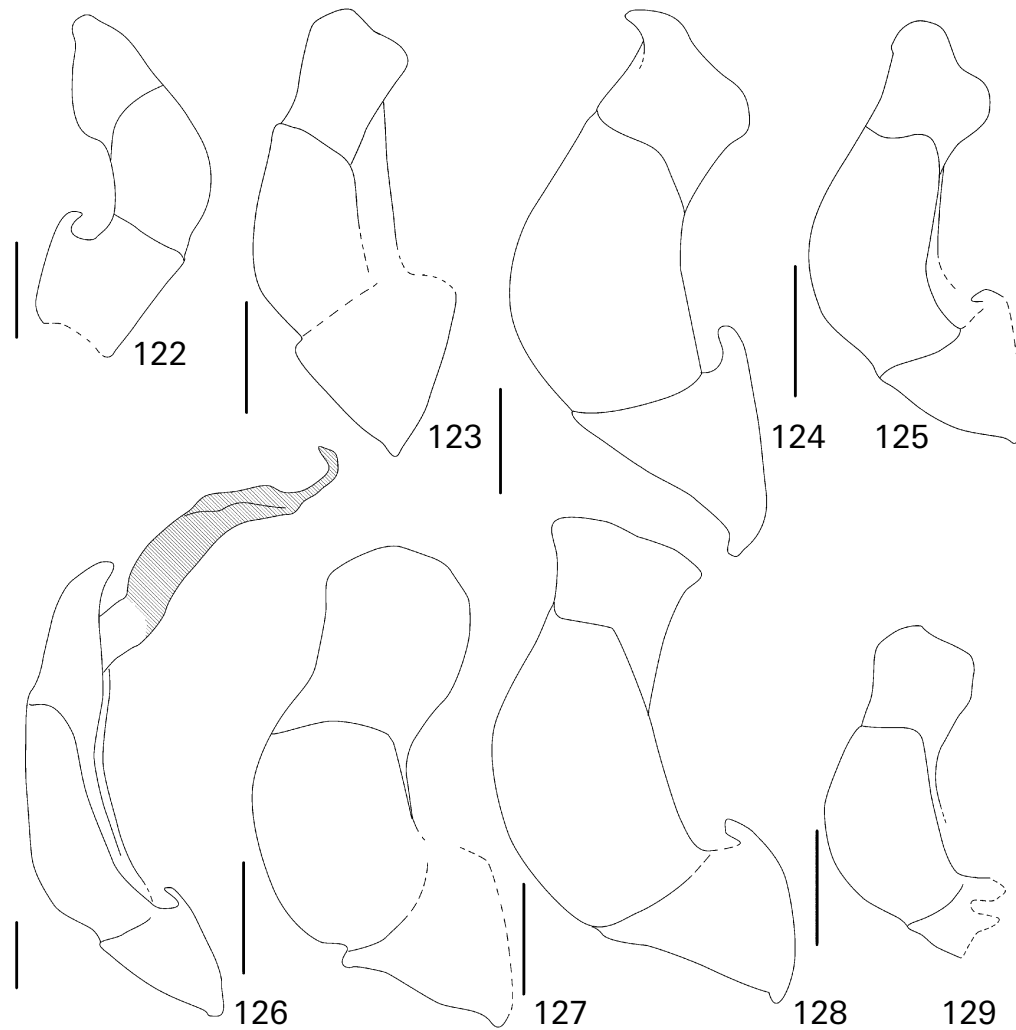
*C. jansoni* (Ohaus 1897) [MNHUB] – Locality data: Monte Rondon, Costa Rica. – Remarks: body length about 15 mm. Head reddish brown, pronotum, elytra and venter ochre yellow, pronotum with 2 irregular dark brown maculae touching anterior margin, elytral suture dark brown. Posterior margin of pronotum with complete bead. Elytra with costae defined by regular rows of punctures, first interstice with 2 irregular rows of punctures. Intermesocoxal distance narrow, mesosternal process not produced. Aedeagus in Filippini et al. 2015.

*C. kulzeri* (Frey 1968) [MNHUB] – Locality data: Avispas, Departamento Madre de Dios, Peru. – Remarks: body length about 18 mm. Pronotum dark metallic green with ochre lateral margins, elytra brown. Elytra with costae defined by sulcated rows of punctures, interstices with sulcated somewhat irregular rows of punctures, first interstice with 2–3 irregular rows of punctures next to each other. Mesosternal process very short, narrow at apex, no more than a bump in lateral view. Pygidium strigate.

*C. ladinus* (Ohaus 1902) [MNHUB] – Locality data: Colombia. – Remarks: Pronotum metallic green with wide ochre bands on lateral margins; scutellum metallic green; elytra dark reddish brown; venter yellow, abdominal sternites reddish brown. Elytra with costae defined by sulcated rows of punctures, first interstice with 2–3 irregular rows of punctures, second interstice with 1 irregular row of punctures bifurcating on apical third, other interstices with 1 regular sulcated row of punctures. Mesosternal process short, tapering at apex. Pygidium granulated. Aedeagus in Fig. 65.



**Figs. 107–129.** Aedeagus of **107:** *C. aequatorialis* (Type, Loja, Ecuador, MNHUB). **108:** *C. antis* (Type, Cuzco, Perú, MNHUB). **109:** *C. benicolus* (Type, Río Bani, Bolivia, MNHUB). **110:** *C. biolleyi* (Type, Chiriqui, Costa Rica, MNHUB). Striped structure is median lobe. **111:** *C. buchwaldianus* (Type, hacienda Ana maría, Quevedo, Ecuador, MNHUB). Striped structure is median lobe. **112:** *C. caucanus* (Type, Cauca, Colombia, MNHUB). **113:** *C. eckhardti* (Type, Chuchuras, Perú, MNHUB). **114:** *C. flavofemoratus* (Type, Río Dagua, Colombia, MNHUB). **115:** *C. hiekei* (Type, Cachabé to Paranda, Colombia, MNHUB). **116:** *C. micans* (Oaxaca, Mexico, MNHUB). **117:** *C. microcephalus* (Pacho, Colombia, MNHUB). **118:** *C. mojo* (Tarapoto, Perú, MNHUB). **119:** *C. naponensis* (Type, Colombia, MNHUB). **120:** *C. nicoya* (Type, Turrialba, Costa Rica, MNHUB). Striped structure is median lobe. **121:** *C. panamensis* (Type, Chiriqui, Panama, MNHUB). **122:** *C. penai* (Type, Avispas, Perú, BMNH). **123:** *C. pupillatus* (Campeche, Mexico, MNHUB). **124:** *C. pyropygus* (Type, Cauca, Colombia, MNHUB). **125:** *C. rufomicans* (Type, Colombia, MNHUB). **126:** *C. sulcans* (Gracias, Honduras, MNHUB). Striped structure is median lobe. **127:** *C. tricostulatus* (Type, Ega, Brasil, MNHUB). **128:** *C. tricostulatus* (Type, Muzo, Colombia, MNHUB). **129:** *C. virescens* (*C. demerarae*) (Type, Georgetown, Guyana, MLUH). Scale = 1 mm.



*C. lepidus* Burmeister 1844 [MLUH] – Locality data: Guatemala. – Remarks: body length about 17 mm. Metallic light green color, reddish legs. Small eyes. Pronotum surface smooth. Elytra regularly striated. Mesosternal process long with rounded apex. Aedeagus in Fig. 67.

*C. levii* (Blanchard 1851) [MNHN] – Locality data: Santa Fe, Bogotá [Colombia]. – Remarks: body length about 14 mm. Head and pronotum metallic green, pronotum with ochre lateral margins, elytra light brown with green luster, venter ochre. Elytra regularly striated. Mesosternal process short, stout, tapering at apex. Pygidium striated–granulated. Aedeagus in Fig. 71.

*C. marginicollis* (Bates 1888) [BMNH] [MNHUB] – Locality data: Misantla, Mexico. – Remarks: body length about 14 mm. Head and pronotum metallic green, pronotum with ochre lateral margins, elytra and venter dark brown, femurs yellow. Elytra with costa defined by sulci, interstices with irregular punctures. Mesosternal process short and narrow. Habitus in Fig. 16, aedeagus in Fig. 73.

*C. micans* Burmeister 1844 [MLUH] – Locality data: Mexico. – Remarks: body length about 8.5 mm. Head metallic green, ochre clypeus, pronotum metallic green with wide ochre bands on lateral margins, elytra and venter reddish brown. Elytra regularly sulcated, surface flattened. Mesosternal process short, tapering at apex. Aedeagus in Fig. 116.

*C. microcephalus* (Burmeister 1844) [MLUH] – Locality data: Río Napo, Colombia. – Remarks: body length about 15–17 mm. Color reddish black, pronotum usually darker than elytra, metallic green luster present in some specimens. Head narrow in respect to pronotum. Elytra with striae defined by sulcated rows of punctures. Mesosternal process very short, slightly narrowing at apex. Aedeagus in Fig. 117.

*C. mojo* (Ohaus 1897) [MNHUB] – Locality data: Tarapoto [Peru] \*not type material. – Remarks: body length about 14 mm. Head and pronotum metallic green, pronotum with ochre lateral margins, elytra reddish brown, venter ochre. Elytra sulcated, except for first interstice, with 2 irregular rows of punctures. Mesosternal process short, tapering at apex. Aedeagus in Fig. 118.

*C. naponensis* (Ohaus 1897) [MNHUB] – Locality data: Río Napo, Colombia. – Remarks: body length about 11 mm. Head and pronotum dark green, elytra blackish green, venter dark brown with green luster. Elytra with costae defined by regular rows of punctures, first interstice with 3–4 irregular rows of punctures, other interstices with 1 row of punctures; small horizontal wrinkles on second interstice. Mesosternal process short, with rounded apex. Aedeagus in Fig. 119.

*C. nicoya* (Ohaus 1928) [MNHUB] – Locality data: Turrialba, Costa Rica. – Remarks: body length about 15.5 mm. Pronotum metallic dark green with copper red luster; bronze brown; venter

blackish brown with green luster. Posterior margin of pronotum with incomplete bead. Elytra with costae defined by sulcated rows of punctures, first interstice 2–3 irregular rows of punctures, following interstices with 1 row; small secondary punctures on entire surface. Mesosternal process not developed, intermesocoxal distance narrow and convex. Median lobe with apical long projection curved to one side. Aedeagus in Fig. 120.

*C. panamensis* (Ohaus 1902) [MNHUB] – Locality data: Chiriqui, [Panama]. – Remarks: part of *C. validus* group. Body length about 16–17 mm. Head, pronotum and scutellum dark brown, elytra ochre with large punctures, often pigmented; venter reddish brown. Posterior margin of pronotum with incomplete bead. Costae poorly defined by rows of sparse large punctures, first interstice with 4–5 irregular rows of smaller punctures. Intermesocoxal distance wide, slightly convex. Aedeagus in Fig. 121.

*C. penai* (Frey 1968) [BMNH, MNHUB] – Locality data: Avispas, Departamento Madre de Dios, Perú / Quincemil, departamento Cusco, Perú. – Remarks: body length about 13 mm. Head, pronotum and venter reddish brown, elytra tan ochre. Large eyes. Elytra with coarse punctures, costae defined by not continuous rows of punctures, first interstice with irregular punctures. Posterior margin of pronotum with incomplete bead. Mesosternal process not produced, intermesocoxal space narrow. Aedeagus in Fig. 122.

*C. plagiatus* (Nonfried 1894) [MNHUB] – Locality data: Honduras. – Remarks: part of *C. validus* group. Body length about 18–18,5 mm. Head, pronotum and scutellum bronze, elytra light ochre with large pigmented punctures, in some specimens with a pair of dark median maculae; venter reddish brown. Posterior margin of pronotum with incomplete bead. Costae poorly defined by rows of sparse large punctures, first interstice with 5–6 irregular rows of smaller punctures. Mesosternal process poorly developed.

*C. porcatus* (Blanchard 1851) [MNHN] – Locality data: Santa Cruz de la Sierra, [Bolivia]. – Remarks: body length about 14–15 mm. Female. Reddish brown color; head, pronotum, scutellum and pygidium with green luster. Posterior margin of pronotum with incomplete bead. Elytra striated, presence of a secondary row of punctures on fifth stria; surface irregular for the presence of secondary small punctures and wrinkles. Pygidium strigate. Mesosternal process not produced, intermesocoxal space wide and convex.

*C. pulcher* (Blanchard 1851) [MNHN] – Locality data: Santa Fe, Bogotá, [Colombia]. – Remarks: body length about 18–19 mm. Head and pronotum dark green, pronotum with ochre lateral margins; elytra light brown with weak green luster, venter reddish brown. Elytra regularly striated, first interstice with irregular striae. Mesosternal process short, tapering at apex, pointed in lateral view. Aedeagus in Fig. 72.

*C. pupillatus* (Burmeister 1844) [BMNH, MLUH, MNHN] – Locality data: Guatemala. Syn *A. smithi* Bates 1888: Teapa, Tabasco, Mexico. – Remarks: part of *C. validus* group. Body length about 15–16 mm. Head, pronotum and scutellum bronze, elytra ochre with large punctures, often pigmented, venter reddish brown. Posterior margin of pronotum with incomplete bead. Pronotum and interstices of elytra very densely punctured, much denser than in other species of the group. First interstices of elytra irregularly punctured, not arranged in rows, containing up to 11 punctures in its width. Intermesocoxal space narrow, slightly convex. Aedeagus in Fig. 123.

*C. pyropygus* (Nonfried 1891) [MNHUB] – Locality data: Cauca Valley [Colombia]. – Remarks: body length about 15–16 mm. Bright metallic dark red color, pronotum with orangish–ochre lateral margins; coxae, femurs and mesosternal process light brown (other specimens – not type material – from Colombia are green in color). Small eyes. Elytra with regular rows of shallow and small punctures. Mesosternal process long, tapering at apex. Aedeagus in Fig. 124.

*C. rosenbergi* (Ohaus 1902) [MNHUB] – Locality data: Río Dagua, Colombia. – Remarks: body length about 15 mm. Head and pronotum dark green, pronotum with ochre lateral margins; elytra reddish brown with weak green luster, venter reddish brown. Elytra regularly striated, but first interstice with 2–3 irregular rows of punctures on basal two thirds. Mesosternal process very short with uniform width and rounded apex. Aedeagus in Fig. 66.

*C. rufomicans* (Ohaus 1897) [MNHUB] – Locality data: Colombia / Perú. – Remarks: body length about 12 mm. Head and pronotum dark green, pronotum with ochre lateral margins; elytra reddish brown, venter greenish ochre. Elytra with sulcated rows of deep oblong punctures, first interstice with 3 irregular rows of punctures. Mesosternal process long with tapering apex. Aedeagus in Fig. 125. Specimen from Perú with different aedeagus: parameres with a notch on the dorsal margin when seen in lateral view.

*C. strigidiodes* (Blanchard 1851) [MNHN] – Locality data: Santa Fé, Bogotá, [Colombia]. – Remarks: body length about 15–16 mm. Head and pronotum dark brown with green luster, elytra dark brown, venter reddish brown with green luster. Pronotum with fine punctures, elytra with regular rows of shallow small punctures. Mesosternal process short, stout, with uniform width. Pygidium finely granulated–striated.

*C. sulcans* (Bates 1888) [BMNH] – Locality data: Chontales, Nicaragua. – Remarks: body length about 17 mm. Purplish black color. Posterior margin of pronotum with incomplete bead. Elytra regularly sulcated. Mesosternal process very short, tapering at apex. Median lobe with apical long projection curved to one side. Aedeagus in Fig. 126.

*C. tricolostatus* (Ohaus 1897) [MNHUB] – Locality data: Ega [Brasil] / Muzo, Nouvelle Grenade [Colombia]. – Remarks: body length about 13 mm. Head and pronotum metallic green, pronotum with ochre lateral margins, elytra dark reddish brown with green luster, venter ochre. Elytra sulcated by slightly irregular rows of deep punctures. Mesosternal process short, slightly tapering at apex. Specimens from Brasil and Colombia with different aedeagi, illustrated in Figs. 127–128.

*C. virescens* (Burmeister 1844), syn: *C. demerarae* (Ohaus 1897) [MLUH] – Locality data: Georgetown, Demerara [Guyana]. – Remarks: body length about 12 mm. Head and pronotum dark brown with green luster, elytra brown with weak green luster, venter reddish brown with green luster. Elytra regularly striated with shallow punctures. Mesosternal process short, with uniform width. Aedeagus in Fig. 129.

*C. xantholeus* Bates 1888 [BMNH, MNHUB] – Locality data: Tuxtla, Mexico / Cordoba, Mexico. – Remarks: body length about 9.5 mm. Head and pronotum yellow, pronotum with 2 elongated green maculae on disc; elytra reddish brown. Eyes small. Elytra regularly sulcated. Mesosternal process very short, tapering at apex. Aedeagus in Fig. 68.



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