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Cladispa Baly: revision, biology and reassignment of the genus to the tribe Spilophorini (Coleoptera: Chrysomelidae: Cassidinae)

LUKÁŠ SEKERKA[1,2], DONALD WINDSOR[3] and GUILLAUME DURY[3,4]

[1]Department of Entomology, National Museum, Prague, Prague, Czech Republic, [2]Department of Zoology, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic, [3]Smithsonian Tropical Research Institute, Panamá, República de Panamá and [4]Department of Plant Science, McGill University, Québec, Canada

Abstract. The genus, *Cladispa* Baly 1858, is transferred from the tribe Imatidiini (= Cephaloleiini Chapuis, 1875) to Spilophorini Chapuis, 1875 based on the review of type material, newly collected specimens and molecular phylogenetic analysis. The type species, *C. quadrimaculata* Baly, 1858, is redescribed, and two new species, *C. amboroensis* **sp.n.** from Bolivia (Santa Cruz Department) and *C. ecuadorica* **sp.n.** from Ecuador (Pastaza Province), are described and figured. The morphology of *C. amboroensis* **sp.n.** immature stages is broadly consistent with other Spilophorini. Field observations document that both *C. quadrimaculata* and *C. amboroensis* **sp.n.** are trophic specialists on Orchideaceae. Keys to *Cladispa* species and Spilophorini genera are provided. Trophic associations of other Cassidinae and Orchideaceae are discussed.

This published work has been registered in ZooBank, http://zoobank.org/urn:lsid:zoobank.org:pub:42A1ECF3-2030-4938-8F3D-FE7EC36F303A

Introduction

Baly (1858) proposed the genus *Cladispa* for a single species, *Cladispa quadrimaculata* Baly, 1858, from 'Demerara' (present-day Guyana). He placed his new genus between *Oediopalpa* Baly and *Octocladiscus* Thompson because of a similarly shaped labium and subserrate antennae. Chapuis (1875) noted that adult *Cladispa* possess antennae resembling those of *Cephaloleia* Chevrolat and palps resembling those of *Oediopalpa*. He placed both genera together with *Octocladiscus* in his group Callispites, whereas he created Cephaloléites for *Cephaloleia* and related genera. Weise (1910) proposed Amplipalpini (now included in Spilophorini) for *Oediopalpa* (= *Amplipalpa* Harold). Later, Weise (1911a,b) transferred *Cladispa* and *Octocladiscus* to Cephaloleiini (recently changed to Imatidiini due to name priority), a system followed for the next century, with *Cladispa* cited mainly only in catalogues (Uhmann, 1957; Seeno & Wilcox, 1982; Staines, 2014).

We examined the holotype of *C. quadrimaculata* and found that it has a long stiff seta in all four pronotal angles, strong evidence that the genus belongs within the tribe Spilophorini not Cephaloleiini, which has a seta only on the anterior angles. We also examined specimens of *Octocladiscus fasciatus* (Guérin-Méneville), finding setae only on the anterior angles, indicating that its placement is correct within the Imatidiini (= Cephaloleiini). We have recently collected a series of adult and associated immature specimens in Bolivia, here described as a new species, adults of which perfectly match the generic concept of *Cladispa* and larvae with characters typical for Spilophorini (exophagous, eruciform larvae with apical shield formed by old exuviae, contrasting clearly with the shieldless, onisciform larvae of Imatidiini). In addition to morphological and natural history information, we used Maximum Likelihood and Bayesian methods to analyse 1418 bp of DNA sequences from the nuclear ribosomal genes *18S* and *28S*, supporting the new placement of genus *Cladispa*.

The newly described species constitute only the second record of leaf beetles in the subfamily Cassidinae associated with the plant family Orchideaceae. The first record of orchid feeding

Correspondence: Lukáš Sekerka, Department of Entomology, National Museum, Golčova 1, CZ-14800 Prague, Czech Republic. E-mail: sagrinae@seznam.cz

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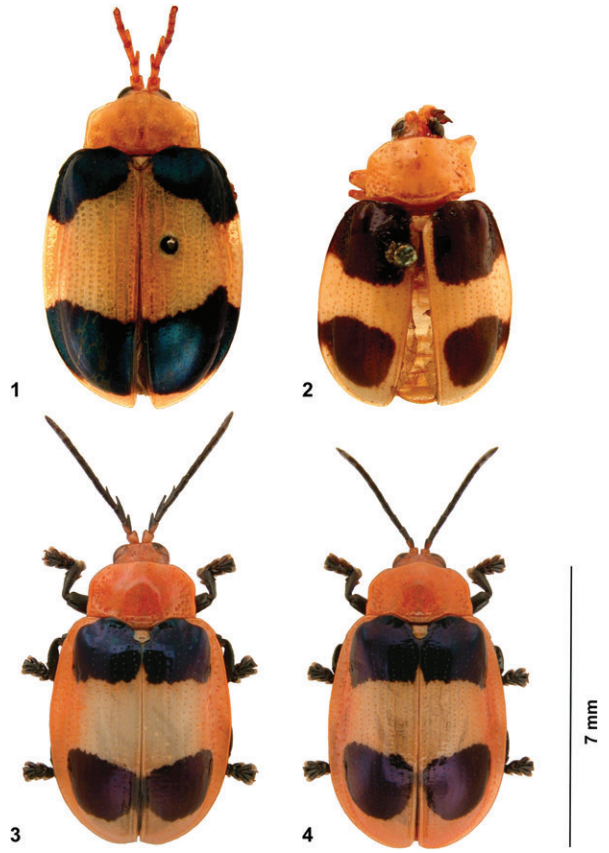


Figs. 1–4. Dorsal aspects of *Cladispa* species. 1, *C. ecuadorica* **sp.n.**, holotype, ♂; 2, *C. quadrimaculata* Baly, holotype, ♂; 3, *C. amboroensis* **sp.n.**, paratype, ♂; 4, *C. amboroensis* **sp.n.**, paratype, ♀.

involved *Cephaloleia orchideivora* Sekerka, Windsor & Staines, 2013, belonging to the tribe Imatidiini (Sekerka *et al.*, 2013), a feeding associate of at least three genera of Orchidaceae in Panamá.

Material and methods

Specimens were compared using standard methods of comparative morphology.

Photos of adult specimens (Figs 1–4) were taken using a Leica S8Apo stereomicroscope with Leica 10447367 0.63× photo tube attached to a Nikon Coolpix 4500 and Nikon MDC Lens as 15–20 separate images and then composed in Helicon Focus software. Images in Figs 5–11 were taken with a Canon G15 digital camera, Figs 12–17 with a Canon S100 digital camera hand held to the objective of a Wild MP5 stereomicroscope, and Figs 18–30 with a Zeiss EVO 40 Scanning Electron microscope.

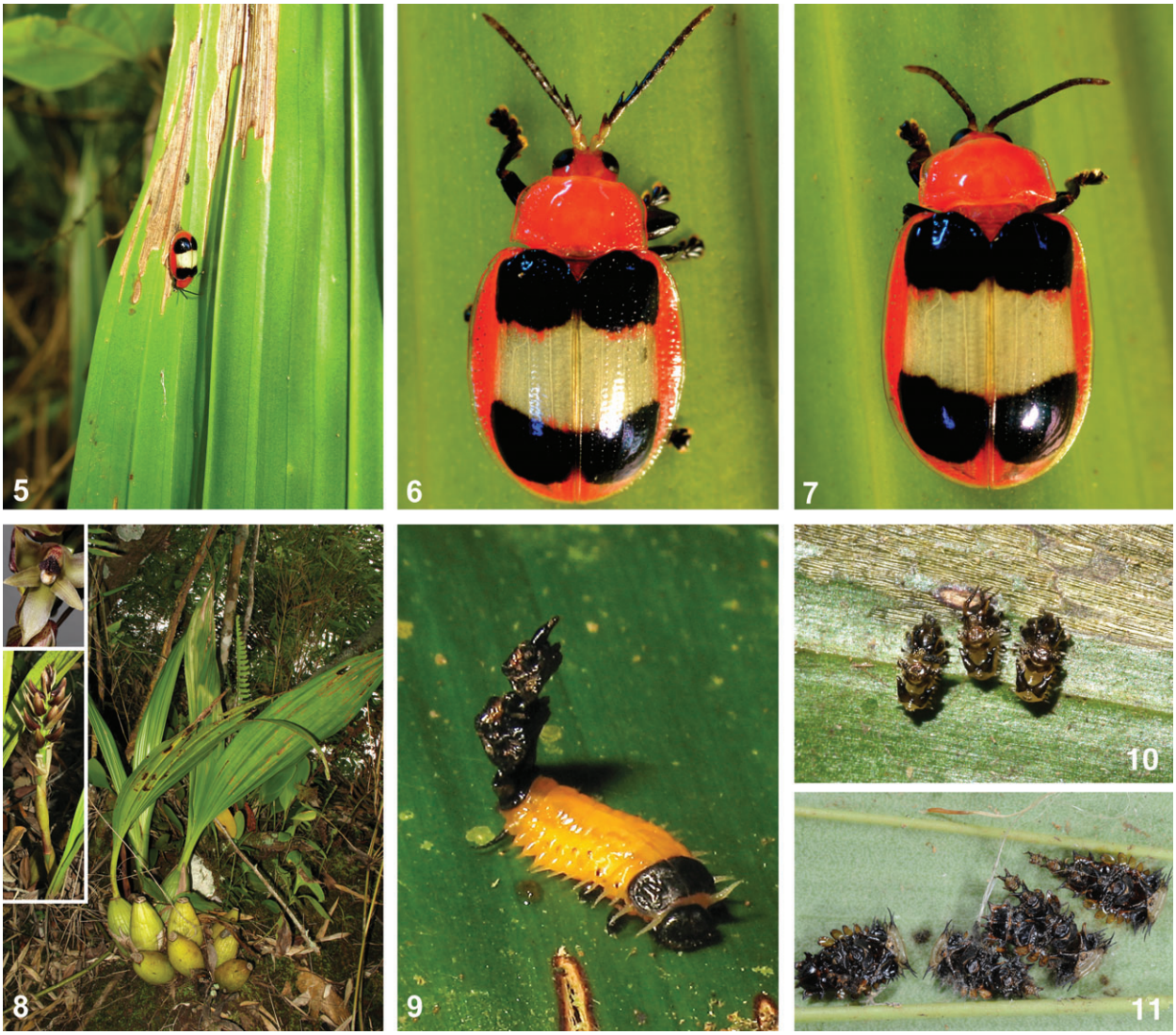
DNA was extracted from muscle tissue of whole insects maintained in absolute ethanol at −80°C and deposited in the collection of Donald Windsor (DWC). Duplicate specimens of dry pinned adults and photographs vouchering each of the 26 taxa included in the phylogenetic analysis (see Figure S1, Table S1) were also kept in DWC. Taxa were sampled primarily to test the traditional placement of *Cladispa* within Imatidiini (i.e. Weise, 1911a; Uhmann, 1957; Staines, 2002), versus an alternative arrangement in Spilophorini as suggested by the adult and larval morphological characters. We compared the sequences from *Cladispa amboroensis*, the only species in the genus from which we obtained DNA, to sequences from seven species of Cephaloleini and eight of Spilophorini. To test the more remote possibility that *Cladispa* is more closely related to hispine tribes other than Cephaloleiini or Spilophorini, we also included one representative of eight other common Neotropical hispine tribes and one important Paleotropical tribe (Hispini). As an outgroup basal to all Hispinae, we used *Platyphora megistomelina* Bechyně, 1954, a broad-shouldered leaf beetle, subfamily Chrysomelinae, as suggested by Gómez-Zurita *et al.* (2008).

All label data are given in their original spelling; a vertical bar (|) separates data on different rows, a double vertical bar (||) separates different labels. Additional information about the label and explanatory notes are given in the square brackets.

Examined specimens are housed in following collections: BMNH, Natural History Museum, London, UK; DBET, Department of Biodiversity and Evolutionary Taxonomy, University of Wrocław, Poland; DWC, working collection of Donald Windsor, Ciudad de Panamá, Panamá; LSC, collection of Lukáš Sekerka, Liberec, Czech Republic; MNKM, Museo de Historia Natural 'Noel Kempff Mercado', Santa Cruz de la Sierra, Bolivia; NMP, National Museum, Prague, Czech Republic; OKC, collection of Ondřej Konvička, Zlín, Czech Republic; USNM, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA.

DNA extraction, sequencing and analysis

Genomic DNA was extracted from flight muscle ground in 180 µL of ATL tissue lysis buffer (Qiagen Inc., Valencia, CA, U.S.A.) and 20 µL proteinase K with a sterile pestle, vortexed for 10 s and incubated overnight at 55°C. Following incubation, we added 200 µL AL lysis buffer (Qiagen Inc.) and heated the sample to 70°C for 10 min, before adding 200 µL molecular grade ethanol to each sample. This mixture was then pipetted into a DNeasy mini spin column and centrifuged at 8000 rpm (~6000 *g*) for 1 min, discarding the flow-through and collection tubes. The DNeasy mini spin column was placed in a new 2-mL collection tube, and 500 µL wash buffer AW1 (Qiagen, Inc.) was added, the sample centrifuged for 1 min at 8000 rpm, subsequently discarding the flow-through and collection tubes. To a new collection tube, 500 µL wash buffer AW2 (Qiagen, Inc.) was added and the sample centrifuged for 3 min at 14 000 rpm (20 000 g); the collection tube was then discarded. The mini column was placed in a 1.5-mL tube and 200 µL AE elution buffer (Qiagen, Inc.) was added, the sample was incubated for 2.5 min at room temperature, and the sample centrifuged for 1 min at 8000 rpm (~6000 g). Extractions were held at −20°C between use, and at −80°C for long-term storage. Partial sequences from the *18S* and *28S* genes were obtained

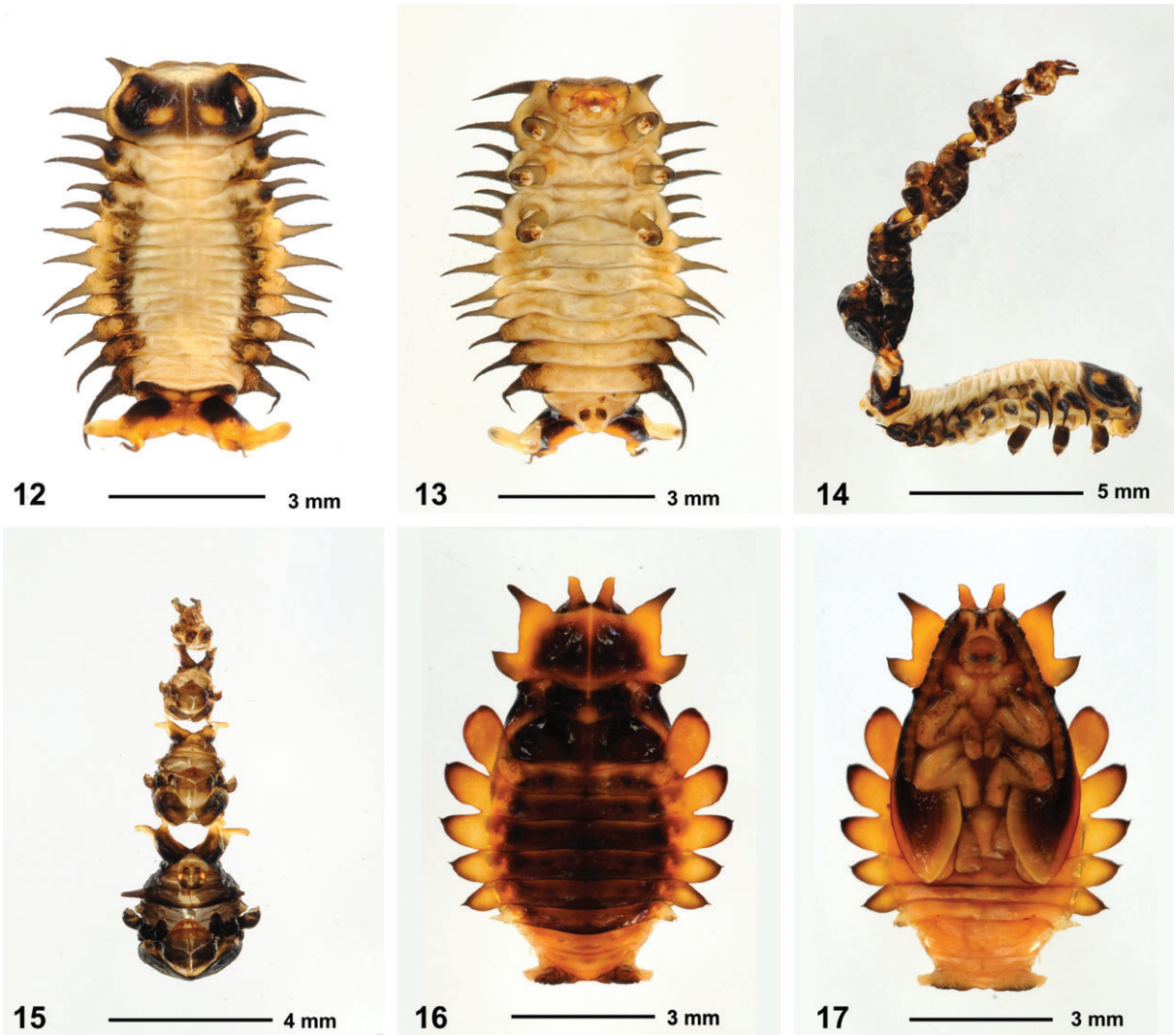


Figs. 5–11. *Cladispa amboroensis* **sp.n.**: appearance in nature. 5, Adult feeding; 6, live adult male; 7, live adult female; 8, the host plant, *Xylobium* sp., Orchidaceae; 9, fourth instar larva; 10, aggregation of three larvae; 11, aggregation of four pupae.

from the resulting genomic DNA using the primer sets given in Prado *et al.* (2012). The PCR cycling conditions were: 94 °C for 2 min, 10 cycles of 94°C for 30 s, 46°C for 30 min, 72°C for 45 min, then 24 cycles of 94°C for 30 s, 48°C for 30 min, 72°C for 45 min, and finally 72°C for 10 min and 10°C for 2 min.

Forward and reverse sequences were combined, reconciled and trimmed in Sequencher v5 (Gene Codes Corporation, Ann Arbor, MI, USA), leaving two segments of *18S*; fragment A of 502 bp and fragment B of 395 bp and one segment of *28S* of 521 bp. The two *18S* fragments were concatenated and treated as a single fragment in analyses (897 bp). Sequences were deposited in GenBank under accession numbers given in Table S1.

Sequences were aligned independently using 10 iterations of MUSCLE (Edgar, 2004). Evolutionary models of single-genes were selected with Modeltest 3.4 (Posada & Crandall, 1998) in Paup* v4.0b10 (Swofford, 2003) using the PaupUP graphical interface (Calendini & Martin, 2005) and Modeltest v3.7 (Posada, 2005). For the concatenated dataset, evolutionary models and partitioning strategy were selected using PartitionFinder v1.0.1 (Lanfear *et al.*, 2012). A single partition was suggested for the concatenated dataset, and both procedures suggested a TVM + I + G model, except for *18S*, for which Modeltest suggested GTR + I + G. This translated into a six-state model in MrBayes. Bayesian inference was done with 5 million generations in MrBayes v3.1.2 (Ronquist *et al.*, 2012). An appropriate burn-in of 10% was determined in MrBayes, and remaining trees were combined into single 50 percent majority rule trees. Maximum Likelihood analysis with 100 bootstrap pseudo-replications was performed on supercomputers of the Cyberinfrastructure for Phylogenetic Research (CIPRES) Science Gateway v3.3 (Miller *et al.*, 2010) using RAxML-HPC



Figs. 12–17. *Cladispa amboroensis* **sp.n.**: immature stages. 12, Dorsal; 13, ventral and; 14, lateral aspects of fifth instar larva; 15, dorsal aspect of exuvial annex from same larva; 16, dorsum and; 17, venter of pupa with larval annex removed.

(Stamatakis, 2006) to yield best-scoring trees. Both analyses were performed on single-gene datasets and on a concatenated dataset (1418 bp).

Results

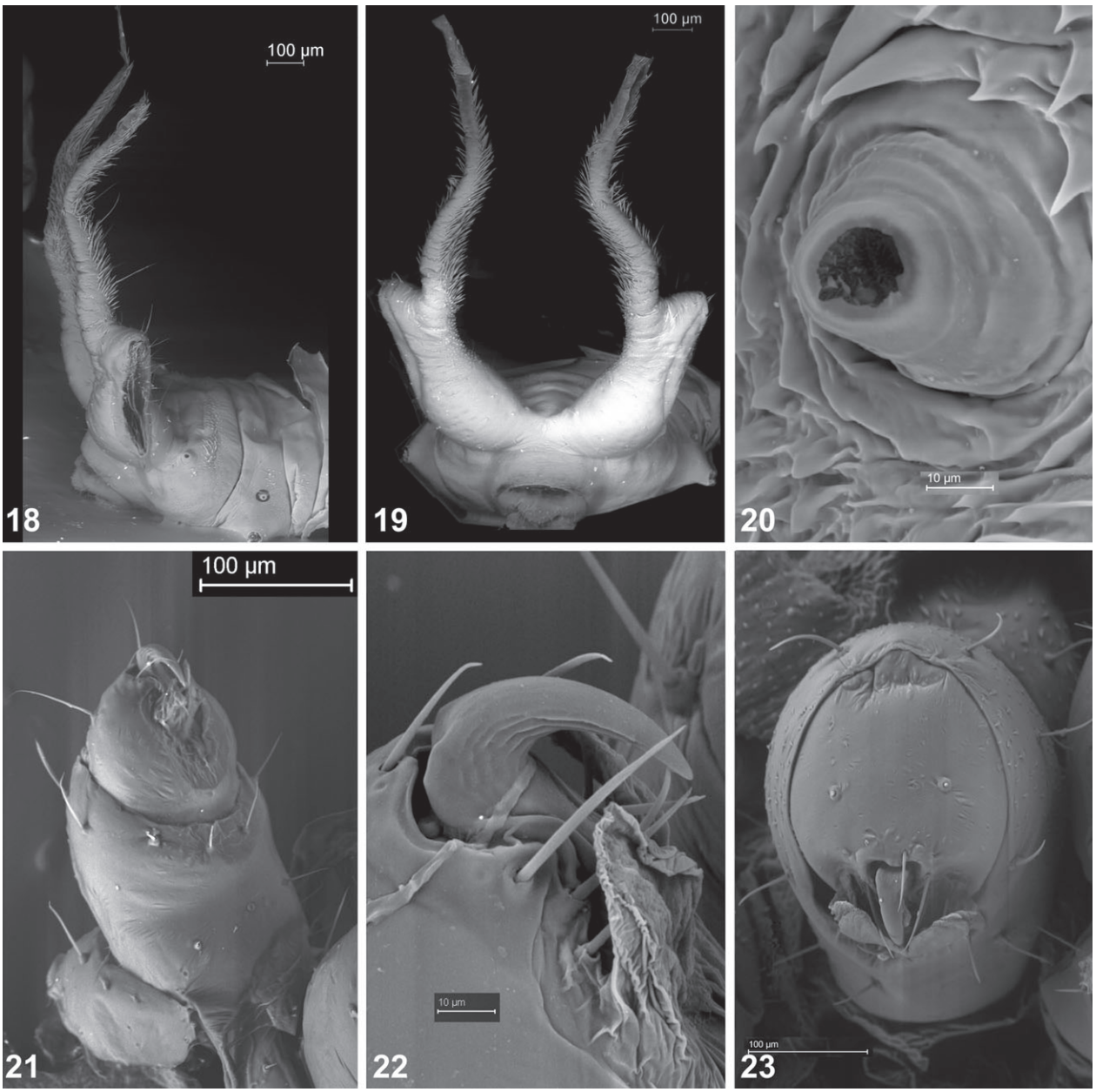
Cladispa Baly, 1858

Cladispa Baly, 1858: 22 (original description).

Type species. Cladispa quadrimaculata Baly, 1858 by monotypy.

Differential diagnosis. Cladispa is differentiated from other genera of Spilophorini by the form of antennae. Males have antennomeres II–IV pectinate, and females have filiform antennae. The only other genus with apparently pectinate antennae is *Spilophora* Boheman. However, males of *Spilophora* have pectinate antennomeres III–VI, and the projecting tooth of each is rather thin and short. *Spilophora* species also have an extremely long third antennomere, which is longer than IV and V combined, and more or less tubular antennae with tightly arranged antennomeres, whereas *Cladispa* has antennomeres III and IV subequal in length and antennae with the antennomeres loosely arranged and more or less constricted at their bases.

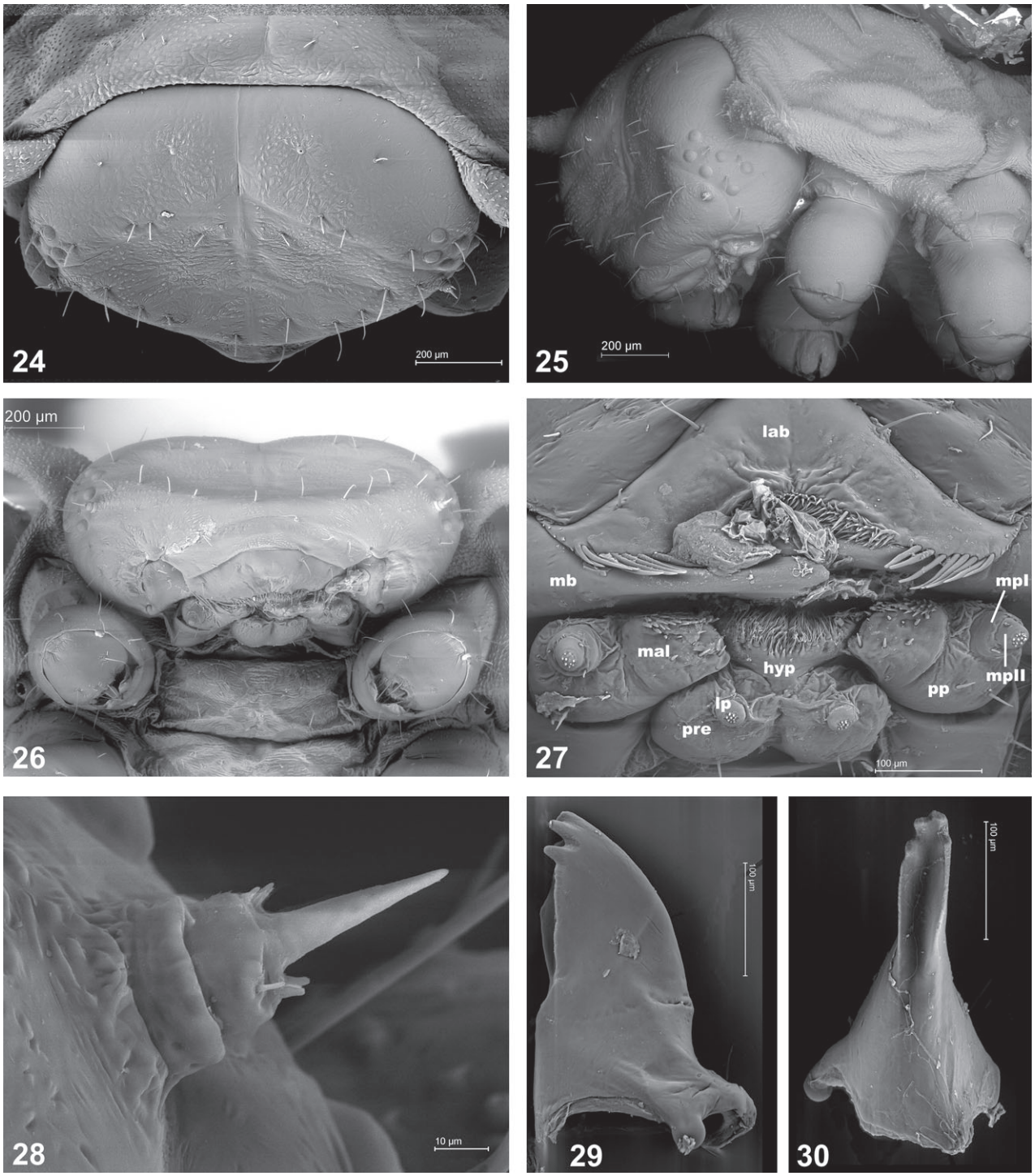
Description. Body broadly oval (Figs 1–4), pronotum subpentagonal, transverse, *c.* 1.6–1.8× wider than long, basal ¾ parallel-sided and apical fourth converging, anterior margin slightly convex.



Figs. 18–23. *Cladispa amboroensis* **sp.n.**: SEM images of first instar larva. 18, Lateral aspect of segments VII–IX; 19, ventral aspect of urogomphus, abdominal segment IX; 20, spiracle, segment VII; 21, right foreleg; 22, tarsal apex with tarsal claw, setae and deflated tarsungulus; 23, apical view of tarsus, claw and setae.

Vertex of head smooth, shiny, impunctate and with soft medial sulcus. Clypeus transverse, *c.* 2× wider than long, smooth and shiny with a few weakly impressed punctures. Labrum large, elliptical, along midlength with sharp carina. Antennae thin, antennomere I subglobose in both sexes. Remaining antennomeres in females filiform. Males with pectinate antennomeres II–IV, process on III longest and truncate, II and IV short and spiniform; V on ventral side slightly expanded. In both sexes antennomeres I–V sparsely pubescent, shiny and microreticulate, VI–VII intermediate, VIII–XI densely pubescent. Antennomere III twice as long as II and slightly shorter than IV. In males, pedicel and scape subequal in length; in females, scape 1.15× longer than pedicel. Remaining antennomeres proportionally similar in length in both sexes.

Pronotum with disc moderately convex, smooth and shiny, lateral margins with 10–30 coarse punctures. Outer margin not explanate but swollen and separated from disc by deep furrow. Disc with basal transverse impression. All four angles of pronotum with small tubercle possessing single long sensillum. Scutellum subpentagonal, smooth and shiny. Base of elytra as



Figs. 24–30. *Cladispa amboroensis* **sp.n.**: SEM images of head of first instar larva. 24, Dorsal; 25, lateral and; 26, ventral aspects; 27, mouthparts: hyp, hypopharynx; lab, labrum; lp, labial palp; mal, mala; mb, mandibula; mpI, fist maxillary palpomere; mpII, second maxillary palpomere; pp, palpiger; pre, prementum; 28, antenna; 29, lateral and; 30, mesal views of mandible.

wide as base of pronotum, straight. Humeral angles broadly rounded, not protruding. Humeral calli distinct, moderately convex, smooth, impunctate and shiny. Base of elytra with short, impressed and transverse row of coarse punctures. Each elytron with ten regular rows of punctures, scutellar row absent. Rows rather fine, not impressed. Punctures fine but distinctly impressed. Intervals broad, smooth and shiny. Outer rows coarser than inner. Marginal row distinct, interrupted below humeral callus, otherwise even. Explanate margin as broad as 1/5 of elytral width, moderately declivous and around midlength subhorizontal. Elytral surface, shiny and coarsely but sparsely punctate. Extreme outer margin moderately swollen, with one small but distinct denticle in posthumeral area, otherwise even, bare, not serrate. Apex conjointly rounded.

Prosternal process broad, moderately expanded towards mouthparts. Apex broadly rounded and slightly expanded. Its surface shiny, and sparsely and coarsely punctate. Outer margins swollen and separated by deep furrow. Remaining parts of thorax smooth, shiny and micro-reticulate. Episterna and epimera with several fine punctures. Legs rather short, robust. Last tarsomere not projecting behind the sole of third tarsomere. Abdominal sterna I–II completely fused, III–V separate.

Sexual dimorphism distinct in shape of antennae. Females also posessing slightly narrower pronotum and somewhat less stout body.

***Cladispa quadrimaculata* Baly, 1858**

(Fig. 2).

Cladispa quadrimaculata Baly, 1858: 23 (original description).

Type locality. 'Demerara'.

Type material. Holotype (by monotypy), ♂, pinned: 'Type | H.T. [white, printed and cardboard circular label with red frame] || Baly coll. [white, printed and cardboard] || Cladispa | quadrimaculata | Baly | Demerara [green, handwritten (by Baly) and cardboard label]' (BMNH). Baly (1858) clearly stated he had only one specimen at disposal. The specimen was provided with an additional red, printed and cardboard label with black frame: 'HOLOTYPUS | Cladispa | quadrimaculata | Baly, 1858 | Sekerka & Windsor des. 2013'. The holotype is damaged and was dissected. It is missing the left antenna from beyond the antennomere I, as well as the right antenna beyond the III. The mouthparts and genitalia were dissected (not by the authors). The aedeagus is inside the microvial pinned under the specimen. Mouthparts were not preserved except for the labrum.

Differential diagnosis. Cladispa quadrimaculata (Fig. 2) is readily characterized by the uniformly yellow ventrites and legs, except for the black tarsi, while the two congeners have meso- and metathorax partly to completely black and legs mostly infuscate to black. *Cladispa quadrimaculata* also has both bands on the elytra broken and the posterior spots rounded, whereas *C. amboroensis* **sp.n.** and *C. ecuadorica* **sp.n.** have at least one of these forming a complete band. Of all the three species, *C. quadrimaculata* is most coarsely punctate, particularly on the pronotum and in the basal row of punctures on the elytra. All punctures are very deep and pit-like, whereas the other two species have these less numerous and much shallower. Also, it has the external intervals with more confused punctures, but the explanate margin has fewer punctures and thus is smoother than in the congeners.

Description. Measurements ($n = 1$): length of body 7.11 mm, width of body 4.02 mm, length/width of body ratio 1.77, length of pronotum 1.56 mm, width of pronotum 2.56 mm, width/length of pronotum ratio 1.64.

Head, pronotum and scutellum yellow. Elytra yellow, each elytron with two large brown spots, one on base reaching from second interval to extreme outer lateral margin of elytra, the other on posteroapical part of the disc and extending laterally to explanate margin as narrow band (Fig. 2). Ventrites and legs yellow with exception of black tarsi. First antennomere yellow, II–III brown.

Pronotum 1.64× wider than long, subpentagonal, basal ¾ parallel-sided and apical fourth converging, anterior margin slightly convex. Disc moderately convex, smooth and shiny, with *c.* 30 coarse punctures on each side and deep transverse basal impression possessing a row of coarse and foveolate punctures. Lateral margins swollen along whole length and separated from disc by deep furrow. Scutellum subpentagonal, smooth and shiny. Base of elytra as wide as base of pronotum, straight. Humeral angles broadly rounded, not protruding. Humeral calli distinct, moderately convex. Basal transverse row formed by 4–6 very coarse and deeply impressed punctures. Punctation of disc regularly arranged in rows. Punctures small with interspaces in rows *c.* 1–3× wider than puncture diameter. Intervals 5 and 7 with a few confused punctures. Explanate margin of each elytron with *c*. 10 coarse punctures.

Remaining characters as in the generic description.

Host plant. Orchideaceae: *Cyrtopodium andersonii* (according to Remillet, 1988).

Distribution. French Guiana (Remillet, 1988) and Guyana (Baly, 1858).

Remarks. Jolivet (1989) published the feeding record of larvae based on Remillet's (1988) thesis (P. Jolivet, personal communication). For an unknown reason, the original source was not cited, and only the genus for both the host plant and the beetle was mentioned in Jolivet (1989). However, Remillet (1988) gave precise information: 'This hispine was observed by Melle Veyret in April 1977 in the ORSTOM orchid collection in Cayenne on *Cyrtopodium andersonii* R. Br. Larvae feeding on leaves. [translated from French]' Remillet also mentioned that the larvae remain attached to the leaf and that exuviae are stacked dorsally upon the caudal appendices, a habit typical for nearly all exophagous Cassidinae. Other works (i.e. Jolivet,

1989) mentioning host plant association of *Cladispa* were based on Remillet's thesis. The pale coloration of the holotype and nonmetallic spots suggest that the specimen was still teneral when captured. Other possibilities are that the specimen was bleached by killing substance or when genitalia were dissected.

***Cladispa ecuadorica* Sekerka & Windsor sp.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:8FAC448F-96C3-4E5A-8E3D-025ACBA9EFC1

(Fig. 1).

Type locality. Ecuador: Pastaza Province, Puyo. Puyo is the capital of Pastaza Province situated circa 01°04′00′′S, 78°00′04′′W at 950 m a.sl. The locality label does not provide any additional information about precise placement of the type locality.

Type material. HOLOTYPE: ♂, pinned: 'ECUADOR,Past. | Puyo | 16 May 1977 | P.J.Spangler& | D.R.Givens#48 [white, printed and cardboard label]' (USNM). The holotype is missing left the antenna from the antennomere VI and right antenna from IX. PARATYPE: ♂, pinned: same data (LSC). The paratype is missing the left antenna from the antennomere II and the right antenna from V. Both specimens were provided with an additional red, printed and cardboard label with black frame: 'HOLOTYPUS [or PARATYPUS respectively] | Cladispa | eduadorica sp. nov. | Sekerka & Windsor des. 2013'.

Differential diagnosis. Cladispa ecuadorica **sp.n.** (Fig. 1) can be easily distinguished by the narrow (*c.* 1/5 of length of elytra) and interrupted basal band on the elytra and the broad and complete posterior band, leaving only the extreme apex of the elytra and the disc yellow. The other two species have basal spots or bands occupying the basal third and apex of the elytra broadly yellow. *Cladispa ecuadorica* is intermediate regarding colour of the underside, as it has the thorax and legs partly infuscate (yellow in *C. quadrimaculata* and mostly black in *C. amboroensis* **sp.n.**). Punctation is similar to *C. amboroensis* but slightly weaker, particularly regarding the pronotal punctures and basal row on the elytra. This row is formed by only 3–4 punctures that do not differ from the others, whereas the two congeners have these distinctly coarser than the remaining. The basal impression on the pronotal disc is almost impunctate (shallowly but distinctly punctate in *C. amboroensis* **sp.n.** and coarsely punctate in *C. quadrimaculata*).

Description. Body measurements ($n = 2$): length 6.95–7.62 mm, width 4.17–4.70 mm, length/width of body ratio 1.62–1.67, length of pronotum 1.39–1.46 mm, width of pronotum 2.46–2.64 mm, width/length of pronotum ratio 1.77–1.81.

Head, pronotum and scutellum yellow. Elytra yellow, with basal and apical metallic blue band. Basal band interrupted by scutellum and sutural interval, otherwise reaching to extreme outer margin of elytra and prolonged on lateral slope and explanate margin. Apical band complete, covering approximately apical 1/4 of elytra, except narrow yellow apical margin (Fig. 1). Prothorax yellow. Meso- and metathorax mostly black, with only areas around trochanters yellow. Abdomen yellow. Coxae and trochanters yellow, femora, tibiae and tarsi irregularly infuscate, brownish-black, only fore femora in basal half yellow. Antennae rusty, first antennomere yellow.

Pronotum *c.* 1.8× wider than long, subpentagonal, basal ¾ parallel-sided and apical fourth converging, anterior margin slightly convex. Disc moderately convex, smooth and shiny, with *c.*15 coarse punctures on each side and deep transverse basal impression. Basal impression with only three punctures on each side. Punctures large but shallow, those in basal impression and towards centre of disc finer than those on sides. Lateral margins swollen and separated from disc by deep furrow, converging parts distinctly less swollen than parallel-sided ones. Scutellum subpentagonal, smooth and shiny. Base of elytra as wide as base of pronotum, straight. Humeral angles broadly rounded, not protruding. Humeral calli distinct, moderately convex. Basal transverse row formed by 3–4 moderate and shallowly impressed punctures that are similar to remaining punctures. Punctation of disc regularly arranged in rows. Intervals 5, 6 and 7 with a few irregularly distributed punctures. Explanate margin of each elytron with *c.* 20 coarse punctures.

Remaining characters as in the generic description.

Length ratio of antennomeres I–VIII (remaining missing): 100:75:138:100:73:88:91:87.

Etymology. Named after Ecuador.

Host plant. Unknown.

Distribution. Ecuador (Pastaza Province).

Remarks. The biology of this species is unknown; however, we predict that it feeds on orchids, as do the two other species in the genus.

***Cladispa amboroensis* Sekerka & Windsor sp.n.**

http://zoobank.org/urn:lsid:zoobank.org:act:376A218E-9147-4DE7-9CDF-F08152551BA5

(Figs 3–30).

Type locality. Bolivia: Santa Cruz Department, Florida Province, Refugio los Volcanes, 18°06′S, 63°36′W, 1045 m a.s.l. The type locality is situated *c.* 5 km north of Bermejo, a small settlement at km 65, Road 7 connecting Santa Cruz de la Sierra and Cochabamba.

Type material. HOLOTYPE: ♂, glued: 'BOLIVIA Santa Cruz dpt. | Florida prov. 9–13.xii.2008 | Refugio los Volcanes | 18°06′S, 63°36′W, 1045 m | D. Windsor, S. Lingafelter | & T. Henry lgt. [green, printed and cardboard label]' (BMNH). PARATYPES: 6♂♂, 4♀♀, glued and 6 in alcohol: same data

(4 LSC, 6 DWC); 4 ♂♂, 4 ♀♀, glued and 4 in alcohol: 'BOLIVIA Santa Cruz dpt. | Florida prov. | Refugio los Volcanes | 18°06′S, 63°36′W, 1045 m | 29–31.v.2009 | D. Windsor & E. Gowin lgt. [green, printed and cardboard label]' (4 DWC, 1 BMNH, 1 DBET, 2 LSC); 15 ♂♂, 5 ♀♀, glued: 'BOLIVIA Santa Cruz dpt. | Florida prov. 1050–1150 m | Refugio los Volcanes | 18°06.3′S, 63°26.0′W | ORCH: Xylobium sp. | L. Sekerka lgt. 10–14.xii.2011 [white, printed and cardboard label]' (13 LSC, 1 DBET, 4 MNKM, 1 NMP, 1 USNM); 1 ♀, glued: 'Bolivia, depart. Santa Cruz | Refugio los Volcanes | Bermejo env. 1–4.5.2012 | 18°6′18″S, 63°35′55″W | lgt. O. Konvička [white, printed and cardboard label]' (OKC); 1 ♀, glued: 'BOLIVIA Santa Cruz dpt. | Florida prov. 1050–1150 m | Refugio los Volcanes | 18°06.3′S, 63°26.0′W| ORCH: Xylobium sp. | L. Sekerka lgt. 10–12.xi.2013 [white, printed and cardboard label]' (LSC); 1 ♂, glued: 'BOLIVIA Santa Cruz dpt. | Florida prov. 1050–1150 m | Refugio los Volcanes | 18°06.3′S, 63°26.0′W| ORCH: ? Oncidium sp. | L. Sekerka lgt. 10–12.xi.2013 [white, printed and cardboard label]' (LSC). All specimens were provided with an additional red, printed and cardboard label with black frame: 'HOLOTYPUS [or PARATYPUS respectively] | Cladispa | amboroensis sp. nov. | Sekerka & Windsor des. 2013'.

Larvae and pupae, collected on same occasions as adults, were preserved in pure ethanol and are deposited in DWC, DBET and LSC.

Differential diagnosis. Cladispa amboroensis **sp.n.** (Figs 3, 4) can be easily distinguished from its congeners (characters given in parentheses) by the uniformly yellow explanate margin of the elytra (elytral spots extending to explanate margin), the mostly black antennae (rusty to brownish), the mostly black legs, meso- and metathorax (yellow in *C. quadrimaculata* and only partly infuscate to black in *C. ecuadorica*), the complete basal metallic blue band on the elytra (interrupted by suture and at least one interval). Regarding punctation, *C. amboroensis* is intermediate between its congeners, but the punctation is generally similar to *C. ecuadorica*, with the basal row of punctures on the elytra more distinct and coarser than the remaining punctures. Punctures in the basal impression on the pronotal disc are more distinct than in *C. ecuadorica*. The explanate margins are similarly punctate to those in *C. ecuadorica*.

Description. Body measurements: males ($n = 14$): length of body 7.05–7.48 mm (mean 7.28 mm), width of body 4.26–4.47 mm (mean 4.35 mm), length/width of body ratio 1.66–1.73 (mean 1.67 mm), length of pronotum 1.43–1.62 mm (mean 1.55), width of pronotum 2.53–2.79 mm (mean 2.71), width/length of pronotum ratio 1.63–1.82 (mean 1.75). Females ($n = 10$): length of body 7.43–8.11 mm (mean 7.81 mm), width of body 4.43–4.79 mm (mean 4.65 mm), length/width of body ratio 1.65–1.70 (mean 1.68 mm), length of pronotum 1.54–1.64 (mean 1.60 mm), width of pronotum 2.65–2.89 mm (mean 2.79), width/length of pronotum ratio 1.69–1.81 (mean 1.74). Females (Fig. 3) slightly larger and stouter than males (Fig. 4).

Head, pronotum and scutellum yellow. Scutellum frequently with narrow metallic blue outer margin. Elytra yellow, with basal and apical metallic blue band. Basal band complete and broad occupying 1/3 of elytra, laterally reaching to marginal row of punctures, only scutellum yellow. Apical band complete or interrupted by suture and one interval, but always constricted in sutural area, sometimes suture only somewhat darkened, laterally reaching to marginal row of punctures and as wide as 1/6 length of elytra. Apical sixth of elytra yellow, as well as explanate margin. Living specimens bright red with metallic blue bands and with central portion of elytra nearly white (Figs 5–7). Prothorax yellow. Meso- and metathorax black. Abdomen yellow. Legs mostly uniformly black, with only part of coxae and basal 1/5 of femora yellow, trochanters black. Antennae black, antennomere I yellow, II and sometimes also III basally and externally yellow. Terminal 2–3 antennomeres slightly paler than the preceding.

Pronotum 1.7–1.8× wider than long, subpentagonal, basal 3/4 more or less parallel-sided but always slightly concave, apical fourth converging, anterior margin convex. Disc moderately convex, smooth and shiny, with *c.* 12–18 coarse punctures on each side and deep transverse basal impression. Basal impression with a row of coarse punctures, laterally coarser than in middle. Pronotal punctures gradually shallower from sides towards centre. Lateral margins swollen and separated from disc by deep furrow. Scutellum subpentagonal, slightly but distinctly constricted in basal 1/3, smooth and shiny. Base of elytra as wide as base of pronotum, straight. Humeral angles broadly rounded, not protruding. Humeral calli distinct, moderately convex. Basal transverse row formed by 2–5 moderately coarse and impressed punctures that are distinctly coarser than remaining punctures. Punctation of disc regularly arranged in rows. Intervals 7 and 8 with a few irregularly distributed punctures. Explanate margin of each elytron with *c.* 20 coarse punctures.

Length ratio of antennomeres: 100:98:128:102:93:77:100:96:86:99:176 (males), 100:114:132:106:93:83:96:93:98:94:171 (females). In males III and IV subequal in length, in females IV slightly longer than III.

Remaining characters as in the generic description.

Etymology. The species is named after its type locality, Amboró National Park in the Santa Cruz Department of Bolivia.

Host plant. Orchideaceae: *Xylobium* sp. (Fig. 8).

Distribution. Bolivia (Santa Cruz Department, Florida Province).

Remarks. Present data indicate that the species may be restricted to the foothills of the eastern Bolivian Cordillera at the so-called 'Elbow of the Andes' where the direction of the Cordillera abruptly changes. This area largely coincides with Amboró National Park, one of the most diverse parks in the World, and the type locality of *C. amboroensis* is near its south-eastern limit. The vegetation of Refugio Los Volcanes (RLV) is lower Yungas forest that can be characterized as humid premontane cloud forest with steep slopes and cliffs, alluvial valleys and

deep gorges. Yungas is generally the typical and most diverse habitat type in Amboró NP. Specimens of *C. amboroensis* were found on five consecutive visits to RLV, occurring on a single species of large orchid growing as a hemi-epiphyte on older forest trees or as a terrestrial plant (Fig. 8) in the understorey of open forests on sandstone hills and cliffs. The orchid was later identified to genus by R. Vásquez based on photographs of sterile mature plants and dry flowering stalks. Two species, *X. flavescens* Schltr. (*Xylobium*) and *X. varicosum* (Rchb.f.) Rolfe, occur on a list of orchid species for RLV (Vásquez *et al.*, 2001). In 2013 we found a single male specimen feeding on a second, as yet unidentified, orchid species. Eggs were laid in strip-like groups of 5–7 along one of the main leaf veins close to the base of the leaf. Freshly emerged larvae feed on the tip of the same leaf. Larvae and adult beetles were mostly found on the underside of middle-aged to old leaves. Feeding damage occurred in the form of narrow strips or broader patches, with feeding grooves running parallel to leaf venation (Fig. 5). Whereas larvae (Fig. 9) and pupae were occasionally found as single individuals, more commonly they occurred in small clusters of 3–6 individuals (Figs 10, 11), this being the first indication of gregarious larval habits in the Spilophorini.

Description of immature stages

Egg

Light ochraceous, membraneous, flat, semitransparent, 4.00–4.25 mm long and 1.5 mm wide ($n = 7$), bearing no maternal adornments. The description is based on older, already hatched eggs, as we never found fresh ones.

Larva

The larva (Figs 9, 12–15) agrees with the eruciform, exophagous larva described for other Spilophorini, including *Oediopalpa negligens* (Weise) by Bruch (1906), *Calyptocephala paralutea* Buzzi & Miyazaki by Buzzi & Miyazaki (1992), *C. gerstaeckeri* Boheman by Córdova-Ballona & Sánchez-Soto (2008), and their synthesis by Świętojańska (2009).

Body elongate, subparallel-sided, widest at abdominal segments I–III; bearing 13 pairs of sparsely setose, conical, lateral scoli, two pairs on each thoracic segment, and one pair on abdominal segments I–VII, but absent on heavily sclerotized segment VIII (Figs 12, 13). Ventral and dorsal surfaces of abdomen flavous in life (Fig. 9), the bases of scoli on segments V–VII and transverse band on dorsum of segment VIII densely covered by asperites. Thoracic and abdominal segments oval in cross-section, flattened, depth approximately one half of width. Prothorax dark brown, distinctly sculpted and plate-like, equal in length to meso- and metathoracic segments combined, bearing two widely spaced scoli on each side. Meso- and metathoracic segments and scoli proportionally similar. Segment IX (urogomphus) with base brown to black, thickened and sclerotized, with ventrally opening anus bordered anteriorly by two sclerotized plates (Fig. 13) covered by fine, equal-spaced setae. Segment IX with two horn-like processes, projecting dorsally (first instar – Figs 18, 19; fifth instar – Figs 12, 13), basal portions greatly thickened and bearing elongate, lateral sulcus sealed by membrane (Fig. 18), terminating apically in thinner and less sclerotized, lyriform extension (Fig. 19), densely covered in setae, which grabs and holds the interior surfaces of the thorax and abdomen of the previous moult, thereby forming a dorsal shield (Figs 14, 15).

Spiracles (Fig. 20) annular, raised, uniforous, with crenulate peritreme on dorsum of abdominal segments I–VIII. Mesothoracic spiracle opening ventrolaterally, partially hidden from laterotergite between fore and middle legs and ventral to thoracic scolus II (Fig. 26).

Legs (Figs 21–23, 25, 26) three-segmented; c-shaped coxa (Fig. 21) bearing three setae on both anterior and posterior surfaces; femur cylindrical with approx. ten stout setae arranged near and parallel to femorotibial joint; tibiotarsus with strong laterally grooved claw (Fig. 22), apex of tibia bearing two prominent setae (Fig. 23), base of claw with three setae, and junction of ventral tibia and pulvinus with 4–6 additional stout setae. Two-lobed fleshy pulvillus attached ventrally to tibiotarsus (Figs 21–23).

Head (Fig. 24) hypognathous, inclined, all but anterior margin covered by prothorax in dorsal view. Epicranial stem long, frontal arms straight, median endocarina extending anteriorly to clypeal suture. Stemmata (Fig. 25) equal-sized, loosely arranged near lower anterior margin of epicranial plate in two lines of three. Clypeus (Fig. 26) subrectangular, width 3–4× length, with three pairs of setae bordering frontoclypeal suture. Labrum (lab, Fig. 27) with two pairs of stout setae parallel and next to clypeolabral suture, lower margin emarginate, bordered by eight stout setae laterally and medially by dense array of finer setae. Antenna (Fig. 28) three-segmented, inserted in frontal plate anterior to lower stemmata, pedicel bearing six sensoria surrounding base of elongate, cone-shaped flagellum, these greater in length than scape and pedicel combined. Mandible (mb, Figs 27, 29) subtriangular, heavily sclerotized, quadridentate, mesal surface (Fig. 30) canaliculate. Maxilla (Fig. 27) consisting of palpifer (pp) bearing two stout setae, circular two-segmented maxillary palp with basal segment bearing two setae (mxI), apical segment with one seta plus a group of 12 short sensillae (mxII). Mala (mal) truncate apically, densely setose, proximally with seven stout setae. Labium densely setose, prementum (pre) attached basally to incompletely divided mentum, each section bearing a single stout seta and a globose single-segmented labial palp (lp) terminating apically with a cluster of nine sensillae. Hypopharynx (hyp) densely covered with numerous spines.

Pupa

Pupa of *C. amboroensis* **sp.n.** broadly resembling description of *Oediopalpa negligens* pupa by Bruch (1906) and summarized by Cox (1996), normally attached to host plant with larval exuvia attached apically. Body (Figs 16, 17) dorsoventrally flattened, widest at abdominal segment III, dorsal surface dark brown grading to flavous laterally, uniformly glabrous. Head bearing pair of conical processes projecting anteriad. Prothorax with two pairs of lateral scoli, meta- and mesothoracic scoli absent,

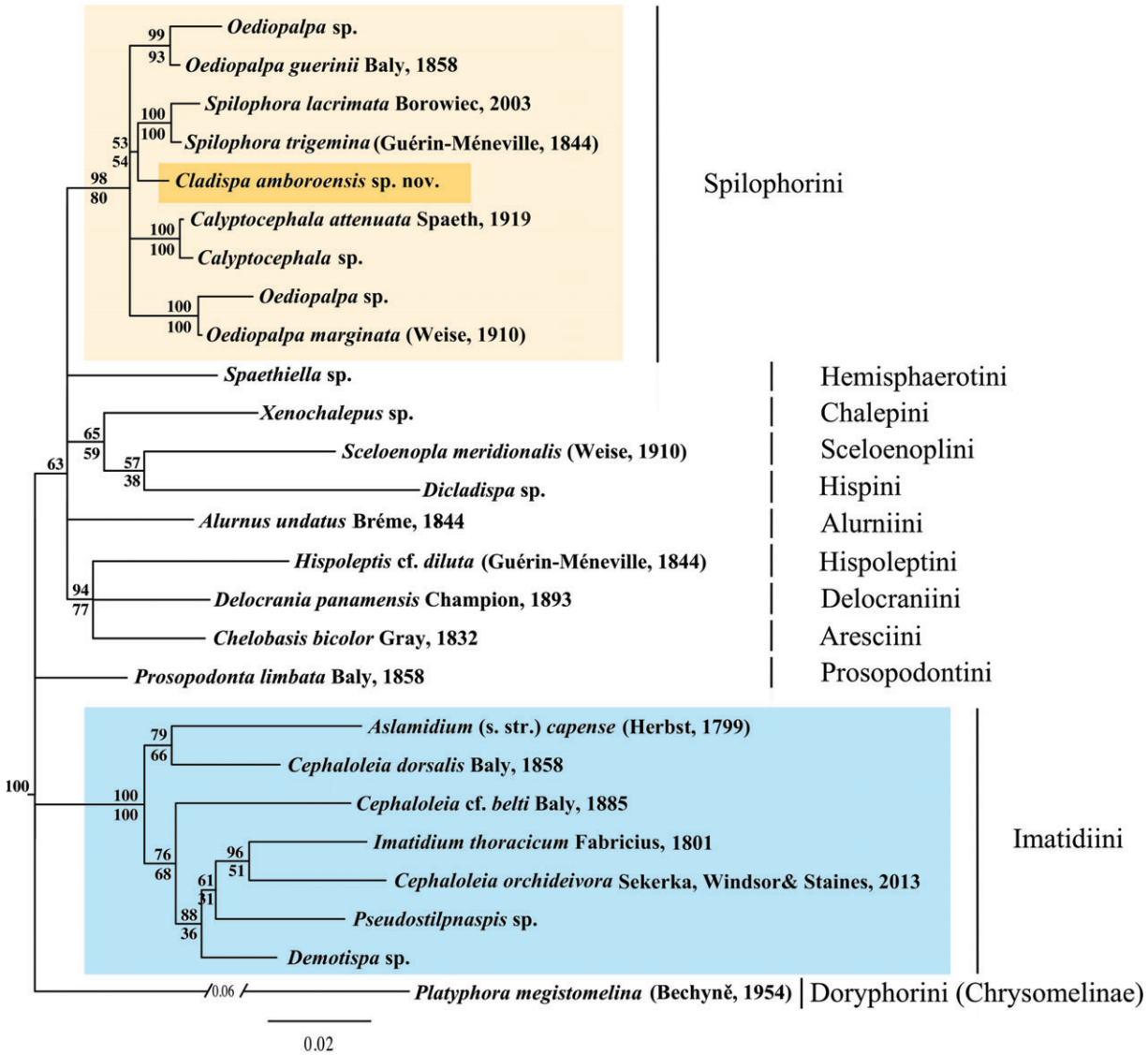


Fig. 31. Phylogenetic relationships among 25 hispine beetle taxa and one outgroup species inferred by Bayesian analysis of three concatenated nuclear ribosomal gene segments (1418 bp); two from *18S* and one from *28S*. Bayesian posterior probabilities are placed above the nodes whereas maximum likelihood (ML) bootstrap values are placed below. Two missing bootstrap values did not have corresponding values in the slightly better resolved ML tree.

abdominal segments I–VI each with one pair. Scoli on prothorax basally flattened and conical towards apex; abdominal scoli flattened with rounded terminals bearing short spines on segments II–VI. Abdominal segments VII–VIII less sclerotized, segments IX–X largely fused, surface wrinkled and expanded laterally into paired, widely separated urogomphi bearing thin vertical lyriform processes (rudimentary furca). Sternite VII laterally possessing pair of sclerotized, toothed processes which grab final larval molt permitting it and older molts to remain attached as a dorsal shield through pupation. Spiracles absent from thoracic segments, annular-uniforous on abdomen, diminishing in size on abdominal segments I through VI, with vestige remaining on VII.

Key to adults of *Cladispa* species

1. Spots on elytra extending to explanate margin; antennae yellow or rusty; legs yellow to infuscate 2
– Explanate margin of elytra uniformly pale; only two basal antennomeres rusty, remaining black; legs mostly black, only bases of femora yellow. Bolivia ..... *C. amboroensis* **sp.n.**
2. Underside uniformly yellow; legs mostly yellow, with only tarsi black; spots on elytra more or less rounded, isolated, posterior spots smaller than basal spots, apex of elytra broadly yellow. Guianas Region. ..... *C. quadrimaculata*
– Meso- and metathorax mostly black; femora and tibia infuscate, partly black; basal and apical spots forming transverse

bands, basal band interrupted in scutellar area, posterior band complete, only extreme outer margin of elytra yellow. Ecuador. . . . . *C. ecuadorica* **sp.n.**

Key to genera of Spilophorini

1. Base of elytra much wider than base of pronotum. 2
– Base of pronotum as wide as or wider than base of elytra. 3
2. Body narrow, elongate, mostly parallel-sided, with narrow margin; lateroapical margin of elytra serrate; antennae in both sexes filiform. . . . . *Oediopalpa*
– Body stout, oval, with broadly explanate margin; lateroapical margin of elytra smooth; antennomeres II–IV serrate in males. . . . . *Cladispa*
3. Third antennomere short, three terminal antennomeres always longer than the third; antennae mostly short (except *C. nigricornis* (Germar)) and filiform in both sexes. . . . . *Calyptocephala*
– Third antennomere very long, three terminal antennomeres always shorther than the third; antennae long, in males antennomeres III–VI serrate. . . . . *Spilophora*

Discussion

Based upon a review of taxonomically useful characters of adult and immature stages and upon phylogenetic analysis, we reassign the genus *Cladispa* to the tribe Spilophorini, and remove it from the tribe Imatidiini. The three species in the genus – two of them described as new – are distributed entirely within South America, one from the Guianas Region, and two from the mid-Andean region. Whereas the feeding habits of *C. ecuadorica* **sp.n.** remain unknown, larvae and adults of the other two species feed exclusively on foliage of Orchidaceae; this is the first report of orchidivory within the Spilophorini and the second known in all Cassidinae (Sekerka *et al.*, 2013). Orchid-feeding is apparently not only limited to *Cladispa* species within Spilophorini, as two of the authors (DW and LS) have independently observed numerous adults of *Spilophora lacrimata* Borowiec feeding on as yet unidentified *Sobralia* sp. at San Rafael, Sucumbíos Province, Ecuador. Because larvae of this species were not observed, it remains unclear whether the association with Orchidaceae is as intimate as it appears to be for species of *Cladispa*. Finally, we report for the first time that *Cladispa amboroensis* **sp.n.** immatures remain aggregated while feeding and pupating, this being the first record of gregarious social behaviour within the Spilophorini.

Bayesian and Maximum Likelihood analyses of partial sequence data from the *18S* and *28S* nuclear ribosomal genes were used to test the monophyly of the hispine genus *Cladispa*, with the analyses including representatives of ten Neotropical tribes and one Paleotropical hispine beetle tribe (Hispini) (see Figure S1, Table S1). Traditionally, the little-known genus *Cladispa* has been placed in the tribe Imatidiini. Neither analysis of the two gene dataset recovers the orchid-feeding species *Cladispa amboroensis* within the well-supported clade containing seven species and five genera of tribe Imatidiini (Fig. 31). Furthermore, Bayesian analysis indicates, with a posterior probability of 98, that *Cladispa* is within the monophyletic clade containing eight species and three genera of Spilophorini, whereas Maximum Likelihood analysis indicates, with bootstrap support of 80, the same pattern of association. Although these reconstructions provide robust support for *Cladispa*'s affiliation with Spilophorini rather than Imatidiini, the assembled taxa and genetic data lack sufficient information to adequately resolve most other hispine tribal relationships. However, moderate levels of support (>50%) are present for a sister taxon arrangement between the genera, *Cladispa* and *Spilophora*. We report for the first time that one of the species (*S. lacrimata*) is also trophically associated with Orchidaceae (*Sobralia* sp.) in Ecuador, as are *Cladispa quadrimaculata* and *C. amboroensis*. Thus, a shared propensity to feed on Orchidaceae appears to underline a close historical relationship between these two genera.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12070

Figure S1. Single gene trees (*18S*, *28S*) computed by Maximum Likelihood (ML) and Bayesian Inference (MB).

Table S1. Specimen voucher codes, names, tribes, country where collected, presence or absence of pronotal setae, cross-section of larva, position of head relative to thorax, ornamentation attached to the eight abdominal segment, larval feeding niche broadly defined, principal host plant family used by adults and larvae, and GenBank accession numbers for deposited DNA sequence data.

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References

Baly, J.S. (1858) *Catalogue of Hispidae in the Collection of the British Museum. Part I*. Printed by Order of the Trustees, London.

Bruch, C. (1906) Metamórfosis y biología de Coleópteros Argentinos. *Revista del Museo de La Plata*, **12**, 207–219.

Buzzi, Z.J. & Miyazaki, R.D. (1992) *Calyptocephala paralutea* sp. n. e descriçao de larva e pupa (Coleoptera, Chrysomelidae, Cassidinae). *Revista Brasileira de Zoologia*, **9**, 157–166.

Calendini, F. & Martin, J.-F. (2005) *PaupUP v1.0.3.1: A Free Graphical Frontend for Paup* Dos Software*. Published by the Authors, Montpellier. (Software).

Chapuis, F. (1875) Tome onzième. Famille des phytophages. In: *Histoire naturelle des insectes. Genera des coléoptères ou exposé méthodique et critique de tous les genres proposés jusqu'ici dans cet ordre d'insectes* (ed. by T. Lacordaire & F. Chapuis), 420 pp. A la Librairie encyclopédique de Roret, Paris.

Córdova-Ballona, L. & Sánchez-Soto, S. (2008) Bionomics data and descriptions of the immatures of *Calyptocephala gerstaeckeri* Boheman (Coleoptera: Chrysomelidae), pest of the oil palm (*Elaeis guineensis* J.) and camedor palm (*Chamaedorea elegans* Mart.) Arecaceae in Jalisco, Mexico. *Neotropical Entomology*, **37**, 674–680.

Cox, M.L. (1996) The pupae of Chrysomeloidea. In: *Chrysomelidae Biology, Vol. 1: The Classification, Phylogeny and Genetics* (ed. by P.H.A. Jolivet & M.L. Cox), pp. 119–265, 452 pp. Academic Publishing, Amsterdam.

Edgar, R.C. (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Research*, **32**, 1792–1797.

Gómez-Zurita, J., Hunt, T. & Vogler, A.P. (2008) Multilocus ribosomal RNA phylogeny of the leaf beetles (Chrysomelidae). *Cladistics*, **24**, 34–50.

Jolivet, P. (1989) Sélection trophique chez les Hispinae (Coleoptera Chrysomelidae Cryptostoma). *Bulletin Mensuel de la Société Linnéenne de Lyon*, **58**, 297–317.

Lanfear, R., Calcott, B., Ho, S.Y.W. & Guindon, S. (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution*, **29**, 1695–1701.

Miller, M.A., Pfeiffer, W. & Schwartz, T. (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. Proceedings of the Gateway Computing Environments Workshop (GCE). New Orleans, 14 November 2010, pp. 1–8.

Posada, D. (2005) *Modeltest v3.7*. Facultad de Biología, Universidad de Vigo, Vigo. (Software).

Posada, D. & Crandall, K.A. (1998) MODELTEST: testing the model of DNA substitution. *Bioinformatics*, **14**, 817–818.

Prado, A., McKenna, D. & Windsor, D. (2012) Molecular evidence of cycad seed predation by an immature Aulacoscelidinae (Coleoptera: Orsodacnidae). *Systematic Entomology*, **37**, 747–757.

Remillet, M. (1988) *Catalogue des insectes ravageus des cultures en Guyane Française*. Institut Française de recherche scietifique pour le développement en coopération. Etudes et Thèses, Éditions de l'ORSTOM, Paris.

Ronquist, F., Teslenko, M., Van der Mark, P. *et al.* (2012) MrBayes 3.2: efficient bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology*, **61**, 539–542.

Seeno, T.N. & Wilcox, J.A. (1982) Leaf beetle genera (Coleoptera: Chrysomelidae). *Entomography*, **1**, 1–221.

Sekerka, L., Windsor, D. & Staines, C.L. (2013) A new species of *Cephaloleia* from Panama with description of larva and first record of orchid-feeding in Cephaloleiini (Coleoptera: Chrysomelidae: Cassidinae). *Acta Entomologica Musei Nationalis Pragae*, **53**, 303–314.

Staines, C.L. (2002) The new world tribes and genera of hispines (Coleoptera: Chrysomelidae: Cassidinae). *Proceedings of the Entomological Society of Washinghton*, **104**, 721–784.

Staines, C.L. (2014) Catalog of the Hispines of the World (Coleoptera: Chrysomelidae: Cassidinae) [WWW document]. URL http://entomology.si.edu/collections_coleoptera-hispines.html [accessed on 5 January 2014].

Stamatakis, A. (2006) RAxML-VI-HPC: maximum likelihood-based phylogenetic analyses with thousands of taxa and mixed models. *Bioinformatics*, **22**, 2688–2690.

Świętojańska, J. (2009) The immatures of tortoise beetles with bibliographic catalogue of all taxa (Coleoptera: Chrysomelidae: Cassidinae). *Polish Taxonomical Monographs*, **16**, 1–157.

Swofford, D.L. (2003) *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4*. Sinauer Associates, Sunderland, MA. (Software).

Uhmann, E. (1957) Chrysomelidae: Hispinae. Hispinae Americanae. In: *Coleopterorum Catalogus Supplementa, Pars 35,1* (ed. by W. D. Hincks), vii + 153 pp. W. Junk, The Hague.

Vásquez, R., Taylor, E. & Drozd, M. (2001) Lista de las especies de orquídeas de Los Volcanes y sus alrededores [WWW document]. URL http://www.refugiovolcanes.net/Lista_Orquideas_Volcanes.pdf [accessed on 14 January 2014].

Weise, J. (1910) Beitrag zur Kenntnis der amerikanischen Hispinen. *Archiv für Naturgeschichte*, **76**, 67–127.

Weise, J. (1911a) Chrysomelidae: Hispinae. In: *Coleopterorum Catalogus, Pars 35* (ed. by S. Schenkling), 94 pp. W. Junk, Berlin.

Weise, J. (1911b) Coleoptera Phytophaga, Fam. Chrysomelidae, Subfam. Hispinae. In: *Genera Insectorum, Fascicule 125* (ed. by P. Wytsman), 124 pp + 4 pl. V. Verteneuil & L. Desmet, Bruxelles.

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