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Taxonomy and biology of the bromeliad-inhabiting genus *Lachnodacnum* (Coleoptera: Hydrophilidae: Sphaeridiinae)

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Abstract. The water scavenger beetle genus Lachnodacnum Orchymont, 1937 sensu HANSEN (1991) is revised. The three species that had previously been placed in the genus, L. luederwaldti Orchymont, 1937 (southern Brazil), L. saundersi Orchymont, 1937 (northern Brazil) and L. urichi (Scott, 1912) (Trinidad and Tobago), are redescribed in detail and illustrated with habitus photographs, line drawings, and SEM micrographs of relevant diagnostic characters. Lachnodacnum urichi is found not to be congeneric with the remaining two species. It is transferred to the genus Phaenostoma Orchymont, 1937 (as P. urichi (Scott, 1912) comb. nov.) and the genus Psilodacnum Orchymont, 1937 previously erected for this species is removed from the synonymy with Lachnodacnum and placed to synonymy with Phaenostoma. The preimaginal stages of Lachnodacnum luederwaldti, including the egg case, all three larval instars and pupa, are described. Basic information on the biology of the species is provided based on field observations and rearing in the laboratory. The species is found to be aquatic, living in water tanks of terrestrial and epiphytic bromeliads. An updated identification key to adults of the Neotropical genera of the Coelostomatini is also provided.

Resumo. Uma revisão taxonômica do gênero de Sphaeridiinae *Lachnodacnum* Orchymont, 1937 sensu HANSEN (1991) é apresentada. As três espécies pertencentes ao gênero, *L. luederwaldti* Orchymont 1937 (parte sul do Brasil), *L. saundersi* Orchymont 1937 (parte norte do Brasil) e *L. urichi* (Scott, 1912) (Trindade e Tobago), são redescritas em detalhe e ilustradas com fotografias do habitus, desenhos e imagens de MEV das características diagnósticas relevantes. *Lachnodacnum urichi* mostra-se não congenérica com as outras duas espécies e é transferida para o gênero *Phaenostoma* Orchymont, 1937 (como *P. urichi* (Scott 1912) comb. nov.). O gênero *Psilodacnum* Orchymont, 1937, anteriormente erigido para essa espécie, é removido da sinonímia com *Lachnodacnum* e colocado como sinônimo de *Phaenostoma*. Os estágios pré-imaginais de *L. luederwaldti*, incluindo o envoltório dos ovos, todos os três estádios larvais e pupa, são descritas. Informações básicas sobre a biologia das espécies são fornecidas baseadas em observações em campo e criação em laboratório. As espécies são encontradas em ambientes aquáticos tais como 'copos' de bromélias terrestres e epífitas. Uma chave atualizada para a identificação de adultos dos gêneros Neotropicais de Coelostomatini é apresentada.

Key words. Coleoptera, Hydrophilidae, Coelostomatini, *Lachnodacnum*, *Phaenostoma*, *Psilodacnum*, new synonymy, new combination, taxonomy, morphology, biology, immature stages, bromelicolous taxa, Atlantic forests, Brazil, Trinidad and Tobago, Neotropical Region

Introduction

The accumulations of water and detritus at the leaf bases of bromeliads are frequently inhabited by a diverse arthropod fauna, including several genera of the hydrophilid subfamily Sphaeridiinae (Orchymont 1937, Richardson 1999, Frank & Loubino 2008). Many of these taxa may be found in a wide variety of habitats and are not specific for bromeliads -e.g.Phaenonotum Sharp, 1882 (e.g., Archangelsky & Durand 1992, Deler-Hernández et al. 2013), Dactylosternum Wollaston, 1854 (ARCHANGELSKY 1994, COSTA et al. 1988; Fikáček, unpubl. data), and Cvclotypus Sharp, 1882 (A. E. Z. Short, pers. comm.; Fikáček, unpubl. data). The coelostomatine genus Lachnodacnum Orchymont, 1937 has seemed to be the only exception: it includes three species, L. luederwaldti Orchymont, 1937 and L. saundersi Orchymont, 1937 from the Atlantic coast of Brazil, and L. urichi (Scott, 1912) from the island of Trinidad. All three species are only known according to very short type series collected in bromeliads. ORCHYMONT (1937) originally erected two genera for these three species - Lachnodacnum for L. saundersi and L. luederwaldti, and Psilodacnum Orchymont, 1937 for P. urichi (Scott, 1912), based on the differences in the pubescence of the mesofemora and the shape of the eyes and pronotum. Both genera were later synonymized by HANSEN (1991) who considered the above characters too weak to justify a distinction on the generic level. None of the three species have been recently reexamined and no recently collected material was known. The preference for bromeliads mentioned in original descriptions (ORCHYMONT 1937, SCOTT 1912) was never reconfirmed for any of the three species.

Recently, long series of *Lachnodacnum* were collected in Brazil during the field excursions of the students of Federal University of Rio de Janeiro and in a project focused on bromeliad faunas in Federal University of Santa Catarina. Additional older material was found in several institutional collections. In addition, the immature stages were observed in the field and also

reared in laboratory. In order to identify this newly accumulated material, we reexamined the type specimens of all three species of the genus. The results of our studies are summarized here: all three species are redescribed and their diagnostic characters illustrated. The immature stages of *L. luederwaldti* are described and notes on its biology are provided. Moreover, the generic status of *Lachnodacnum* is revised and an updated key to adults of the coelostomatine genera of the Neotropical Region is provided.

Material and methods

We examined more than 200 specimens of the genus Lachnodacnum for this study, including the type specimens of all three described species. A portion of the specimens was dissected, genitalia were placed on small piece of glass below the beetle in the alcohol-soluble Euparal resin. Label data of the type specimens are cited verbatim, using a slash (/) for dividing separate rows and a double-slash (//) for dividing separate labels; data on additional specimens are listed in an adapted form. Habitus photographs were taken using Canon EOS 550D digital camera with MP-E 65 mm macrolens. SEM micrographs of uncoated adult specimens were prepared at the Department of Paleontology of the National Museum in Prague using Hitachi S-3700N scanning electron microscope; SEM micrographs of coated immature specimens were prepared at the MZSP laboratory with Carl Zeiss microscope LEO 440 and those of coated adult specimens at Federal University of Santa Catarina (UFSC) in the Central Laboratory of Electronic Microscopy/LCME using JEOL JSM-6390LV microscope. Adult morphological terminology follows Fikáček (2010), Komarek (2004), Kukalová-Peck & Lawrence (1993, 2004) and LAWRENCE et al. (2011). Morphological terminology of immature stages follows MINOSHIMA & HAYASHI (2011), FIKÁČEK et al. (2008), FIKÁČEK et al. (2013) and BYTTEBIER & TORRES (2009). Higher level classification follows Short & FIKÁČEK (2013).

The examined material is deposited in the following collections:

- BMNH Natural History Museum, London, United Kingdom (M. Barclay);
- DZRJ Instituto de Biologia, Universidade Federal do Rio de Janeiro, Brazil (N. Ferreira-Jr);
- IRSN Institut Royal des Sciences Naturelles de Belgique, Brussels (P. Limbourg);
- SEMC Biodiversity Institute, University of Kansas, Lawrence, U.S.A. (A. Short);
- MCZ Museum of Comparative Zoology, Harvard University, Cambridge, U.S.A. (P. Perkins);
- MZSP Museu de Zoologia da Universidade de São Paulo, Brazil (S. A. Casari);
- NMPC National Museum, Prague, Czech Republic (M. Fikáček).

For comparative purposes as well as for the construction of the updated generic key, we have examined the following identified material of the Neotropical Coelostomatini, plus additional material of the genera *Dactylosternum* and *Phaenonotum* not identified to species and deposited in NMPC and SEMC.

Cyclotypus godmani Sharp, 1882: 1 spec. (SEMC): Costa Rica: Cartago, 19.3 km NB, San Rose, 17.v.1993, 1010 m a.s.l., #07, ex. treefall litter, J.S. & A.K.Ashe lgt., det. M. Hansen det.

Dactylosternum cayannum (Mulsant, 1844): 2 spec. (SEMC): Peru, Callanga, lgt. Sataudinger.

Dactylosternum subdepressum striatopunctatum (Castelnau, 1840): 10 spec. (SEMC, NMPC): Ecuador, Napo province, 3.3 km W of Archidona, 00°54'48"S 77°50'15"W, 625 m a.s.l., 19–21.xi.2006, locality 10, plantations of indigenous people: hollow trunk of *Bactris gasipes* palm (very wet decaying leaves & trunk tissues) exposed, M. Fikáček & J. Skuhrovec lgt., det. M. Fikáček.

- *Galapagodacnum darwini* (Blair, 1933): 6 spec. (SEMC): Galapagos Isl., Academy Bay, Santa Cruz Is., 26.i.[19]64, at light, G. Kuschel lgt., det. A.E.Z. Short 2006.
- Hydroglobus puncticollis (Bruch, 1921): 1 syntype (BMNH): Argentina, Prov. B.-Aires, without date, C. Bruch lgt.
- Phaenostoma kontax Gustafson & Short, 2010: 6 paratypes (SEMC): Peru, Loreto department, Campamento San Jacinto, 2°18.75'S 75°51.77'W, 2.vii.1993, 175–215 m a.s.l., #1, ex. Berlese, Richard Leschen lgt.
- Phaenonotum argentinense Bruch, 1915: 5 spec. (SEMC, NMPC): Argentina bor., Chaco province, 97 km NW of Resistencia, 10 km W of Capitan Solari, 3–7.ii.2004, 26°48'32"S 59°36'29"W, without collector data, det. M. Archangelsky.
- Phaenonotum caribense Archangelsky, 1989: 5 spec. (SEMC, NMPC): Ecuador, Pastaza province, 2.8 km S of Santa Clara, 1°17'29"S 77°53'05", 880 m a.s.l., 15–16.xi.2006, secondary *Heliconia + Carludowica* bushes without understory vegetation (sifting of moss and leaf litter on the ground), locality 5c, M. Fikáček & J. Skuhrovec lgt., det. M. Fikáček (compared with holotype by P. Torres).
- Phaenonotum regimbarti Bruch, 1915: 4 spec. (SEMC, NMPC): Argentina bor., Chaco province, 97 km NW of Resistencia, 10 km W of Capitan Solari, 3–7.ii.2004, 26°48'32"S 59°36'29"W, without collector data, det. M. Archangelsky

The data on the biology of *Lachnodacnum luederwaldti* are based on observations in the field and in the laboratory. Larvae of the species were reared in containers partly filled with water extracted from the bromeliads, containing abundant tiny crustaceans (copepods) and dipteran larvae (Chironomidae), as well as decaying detritus. Some larvae were placed separately in Petri dishes with water from the same source and pieces of bromeliad leaves. Some of these larvae were fed with *Enchytraeus* sp. (Annelida: Enchytraeidae).

Morphology and taxonomy

Lachnodacnum Orchymont, 1937

Lachnodacnum Orchymont, 1937: 134.

Type species. Lachnodacnum saundersi Orchymont, 1937, by original designation.

Diagnosis. Eyes small, rounded in dorsal view (Fig. 3); labial palpomere 2 bearing dense brush of long setae on inner face and distal margin; pronotum weakly convex, anterior corners rounded, posterior corners weakly angulate; hypomeron with large pubescent inner portion and moderately wide marginal glabrous portion (Fig. 26); mesoventrite well-divided from anepisternum 2 except sublaterally, anepisternal suture distinct medially and laterally (Figs 27, 34); preepisternal plate widely attaching and as high as anterior portion of metaventral process, forming a mesometaventral keel, constricted at the area where meso- and metaventrite join each other (Figs 24, 33–36); anteromedian pit-like groove large, well developed (Fig. 27); grooves for reception of procoxae not defined (Figs 27, 34); elytron weakly convex, sutural stria very fine but distinct, developed only on elytral apex (Fig. 30); mesofemur pubescent on ventral surface (Fig. 29); metatarsus slightly compressed laterally, metatarsomere 1 about twice as long as metatarsomere 2; aedeagus with rather long and well developed symmetrical phallobase (Figs 15–16); parameres wide throughout; median lobe wide basally, with a pair of short basal projections, more or less gradually narrowing apicad; gonopore distinct, subapical.

Redescription. Body widely oval, weakly convex in lateral view; pronotal and elytral outline continuous in dorsal and lateral views (Figs 1–2, 9–10).

Head. Clypeus wide even anteriorly, only slightly narrowing before eyes, with anteromedian margin truncate (Fig. 3). Frontoclypeal suture conspicuous; lateral portions of frons between



Figs 1–10. General habitus of adults and larvae of *Lachnodacnum* Orchymont, 1937. 1-3 – adults of *L. luederwaldti* Orchymont, 1937 (1 – dorsal view, 2 – lateral view, 3 – dorsal view of the head). 4-8 – larva of *L. luederwaldti* (4 – third instar larva in dorsal view; 5 – same in ventral view; 6 – first instar in dorsal view; 7 – detail of head and thorax of third instar, dorsal view; 8 – same, ventral view). 9-10 – adults of *L. saundersi* Orchymont, 1937 (9 – dorsal view).



Figs 11–14. Morphological details of *Lachnodacnum* Orchymont, 1937 and *Phaenostoma* Orchymont, 1937. 11–12 – hind wings (11 – *Lachnodacnum luederwaldti* Orchymont, 1937; 12 – *Phaenostoma urichi* (Scott, 1912)). 13–14 – detail of spiracular atrium of the third instar larva of *L. luederwaldti*.



Figs 15–17. Aedeagus. 15 – Lachnodacnum luederwaldti Orchymont, 1937; 16 – L. saundersi Orchymont, 1937; 17 – Phaenostoma urichi (Scott, 1912).

anterior margin of eye and frontoclypeal suture lacking punctuation. Eyes small (Fig. 3), not protruding laterad, rounded in dorsal view, surrounded by micropunctures, separated by 7× the width of one eve, distinctly emarginated anteriorly in lateral view. Clypeus and frons with scattered trichobothria. Labrum small, membranous, concealed under clypeus. Maxillary palps with four palpomeres, short and rather stout. Mentum (Fig. 25) $1.4 \times$ as wide as long; lateral margins nearly parallel-sided, each side bearing a row of setae [examined in L. *luederwaldti* only, poorly preserved in available specimens of L. saundersi; anterior margin deeply bisinuate; surface of mentum bearing sparsely distributed long setae. Labial palps with three palpomeres: palpomere 2 longest, strongly widened distally, bearing dense brush of long setae on its inner face and distal margin; palpomere 3 much narrower and about $0.6 \times$ as long as palpomere 2. Submentum pubescent. Gula slightly constricted between tentorial pits, bearing low longitudinal carina in posterior half [examined only for L. luederwaldti] (Fig. 25). Antenna with nine antennomeres (Fig. 28); scapus rather long and thick, its basal portion bent dorsally; pedicel cylindrical; antennomere 3 twice the length of antennomere 4, antennomeres 3–5 narrower than pedicel proximally, slightly widened distally; cupula long and wide, bare, concealing basal portion of antennomere 7; antennal club loosely segmented, depressed dorsoventrally, densely pubescent with few longer and thicker setae on sides and on distal margins of antennomeres.

Prothorax. Pronotum weakly convex, with a bead on anterior and lateral margins including antero- and posterolateral corners; anterior corners rounded, posterior corners weakly angulate;



Figs 18–23. Biology of *Lachnodacnum luederwaldti* Orchymont, 1937. 18 – micropool in the rosette of *Neoregelia* sp., a typical habitat; 19 – egg cases attached at the inner face of a bromeliad leaf; 20 – third instar larva and pupa in the detritus accumulated in the bromeliad rosette; 21–22 – pupa in the broken pupal chamber (21 – dorsal view; 22 – ventral view); 23 – adults staying submerged among bromeliad leaves in the rearing box. Figs 18–19, 23: photo B. Clarkson in Ubatuba Municipality, São Paulo; Figs 20–22: photo by F. F. Albertoni in Florianopolis, Santa Catarina.



Figs 24–28. Adult morphology of *Lachnodacnum luederwaldti* Orchymont, 1937, SEM micrographs. 24 – whole beetle, ventral view; 25 – head, ventral view; 26 – prothorax in ventral view (prosternum and hypomeron); 27 – lateral portion of mesoventrite (arrow indicates the anepisternal suture); 28 – antenna.

posterior margin slightly arcuate; pronotal trichobothria present sublaterally. Prosternum not carinate medially, weakly convex (Fig. 26). Procoxal cavities large, open posteriorly, anterolateral aperture of procoxal cavity open (Fig. 26). Hypomeron with large pubescent inner portion and moderately wide marginal glabrous portion.

Mesothorax. Mesoventrite fused with an episternum 2 sublaterally, an episternal suture deeply concave, distinct medially and laterally (Figs 27, 34); epimeron 2 well delimited, divided from an episternum 2 by a suture, pubescent; anterior collar of mesothorax broad, well



Figs 29–32. Adult morphology of *Lachnodacnum luederwaldti* Orchymont, 1937, SEM micrographs. 29 – mesofemur; 30 – apical portion of elytra; 31 – microsculpture of the clypeus; 32 – trichobothrium on the elytron.

demarcated. Mesoventrite highly elevated medially into preepisternal plate; widely attaching metaventral process (Figs 24, 33–36); mesoventral process as high as metaventral one in lateral view; anteromedian pit-like groove large, well developed. Grooves for reception of procoxae not defined. Elytron weakly convex, without longitudinal series of larger punctures (Figs 1, 9); elytral trichobothria present (Fig. 32); sutural stria very fine but distinct, developed only on elytral apex (Fig. 30). Epipleuron (Fig. 24) wide and strongly inclined throughout, reaching elytral apex; inner pubescent portion (= 'epipleuron') very wide anteriorly, strongly narrowing towards the level of posterior coxae. Mesocoxal cavities transverse, narrowly divided medially by meso-metaventral plate.

Metathorax. Metaventrite with pubescent surface, slightly elevated into narrow, longitudinal bare plate medially; median plate projecting anteriorly into long and narrow metaventral process joining mesoventral plate to form a meso-metaventral keel (Fig. 24), the keel constricted at the area where meso- and metaventrite join each other. Median bare portion of metaventrite with scattered punctures, punctures densely arranged in anterior half and on posterior margin;

punctation of posterior half of the keel sparser than on anterior half, posterior half with weak longitudinal groove. Metepimeron rather large with long posterior projection. Hind wigs (Fig. 11) with R-M loop distally the maximum width of the wing; RA₃₊₄ not attached to RA basally, forming a opened radial cell; radial cell large, subtrapezoidal, pigmented on anteroapical half; r3 absent; r4 developed, connecting RA₃₊₄ to R-M loop; apical field with RA₃ well defined, short, not reaching the margin of the wing apically; RA_4 fused with RP_1 , together forming a pigmented area almost reaching wing margin apically; base of RP1 far of R-M loop; RP2 forming a pigmented area wide on base, almost reaching R-M loop basally but not reaching edge of the wing apically; RP₃₋₄ well defined, narrow and long, arising from R-M loop basally, curved posteriad and reaching wing margin apically; medial field with medial spur rather long, narrow and sharp; MP3+4 present, weakly developed, nearly connected with MP₁₊₂, not attached to MP₃ and MP₄+CuA₁; MP₃ and MP₄+CuA₁ well defined, not connected to basal portions of the veins proximally, reaching wing margin posteriorly; CuA, strongly reduced, without connection with MP₃₊₄, MP₃ and MP₄+CuA₁; CuA₂ present and well defined, reaching the posterior edge of the wing apically; CuA₃₊₄ absent and hence wedge cell missing; AA₃ and AA₄ strongly defined and long, nearly reaching posterior margin of the wing; anal field with venation strongly reduced, composed of a short AP₃₊₄ and nearly inconspicuous AP₁₊₂.

Legs. Procoxa globular, pubescent; profemur with deep tibial groove delimited by low ventral and high dorsal ridges, ventral surface pubescent except for small bare distal area; protibia cylindrical, bearing series of stout spines and irregularly arranged small spines, distal portion bearing "crown" of smaller stout spines and two large spurs. Mesotrochanter slightly sinuate on posterior margin; ventral surface of mesofemur pubescent in basal 0.75 (Fig. 29), reticulate; tibial groove deep, developed throughout, delimited by high ventral and low dorsal ridges; mesotibia flattened, sparsely covered by short and stout spines, bearing longitudinal series of larger spines and a subapical transverse series of larger spines; distal apex with series of short spines and two long spurs on inner margin. Metatrochanter slightly sinuate on posterior margin, pubescent; metafemur large and wide, ventral surface bare except of sparsely arranged setae on extreme anteroproximal portion, surface reticulate with scattered setiferous punctures; tibial groove well developed, deep, delimited by high ventral and low dorsal ridges. Metatibia flattened, bearing scattered short spines and two series of larger spines on outer margin, and a series of larger spines on inner margin on ventral surface; distal portion with transverse series of moderately long spines and two long spurs on inner margin. Tarsi much shorter than tibiae, each tarsomere bearing a dense brush of long setae ventrally, with longer setae sideward and with a single to few long setae dorsally. Metatarsus slightly compressed laterally, metatarsomere 1 about twice as long as metatarsomere 2; claws small, simply arcuate.

Abdomen. With five ventrites, all ventrites flat, without any longitudinal carina; posterior margin of ventrite 5 without apical notch nor the median group of stout setae.

Male genitalia. Aedeagus (Figs 15–16) with rather long and well developed symmetrical phallobase; parameres wide throughout; median lobe wide basally, with a pair of short basal projections, more or less gradually narrowing apicad, gonopore distinct, subapical. Sternite 9 wide basally, bearing rather narrow tongue-shaped median projection, lateral struts arcuate, slightly shorter than median portion.

Key to species

- Microsculpture on the clypeus consisting of transverse ridges restricted to a narrow area on anterior and lateral margins (Fig. 31); pronotal disc without apparent microsculpture. Preepisternal plate narrow, arrow-shaped, weakly produced laterad (Fig. 33). Lateral margin of the elytron very narrowly explanate only in posterior half (Fig. 1). Basal portion of the median lobe with a deep emargination medially; parameres with apical portion pronouncing into slightly prolonged apex (Fig. 15). ... *L. luederwaldti* Orchymont, 1937
- Microsculpture on the clypeus mesh-like, present on the whole clypeus; lateral portions of the pronotum bearing distinct reticulate microsculpture. Preepisternal plate broad, spade-shaped, widely produced sidewards (Fig. 34). Lateral margin of the elytron distinct-ly explanate along its length (Fig. 9). Basal portion of the median lobe at most with a shallow and rather indistinct emargination medially; parameres with apical portion not much pronouncing and rather wide (Fig. 16). L. saundersi Orchymont, 1937

Species treatments

Lachnodacnum luederwaldti Orchymont, 1937

(Figs 1–8, 11, 13–15, 19–33, 35, 37–75)

Lachnodacnum lüderwaldti Orchymont, 1937: 139.

Type locality. Brazil, São Paulo, São Sebastião, Ilha de Alcatrazes.

Type material examined. PARATYPE: 1 unsexed specimen (BMNH): "Para- / type // Ilhadas Alcatra- / jes (São Paulo) / X.1920 (H. Lüderwaldt) // Brit. Mus. / 1937-180 // Para- / type // A. d'Orchymont det. / Lachnodacnum lüderwaldti m."

Non-type adult specimens examined (206). BRAZIL: BAHIA STATE: 3 pinned spec. (BMNH): "BRAZIL/ Itabuna / Bahia / J. A. Wunder // ex: epiphytic bromeliads". ESPÍRITO SANTO STATE: 8 pinned spec. (MZSP): "Linhares / Espirito Santo / Brasil 1-8.II.1995 / H. Briski col". RIO DE JANEIRO STATE: 26 pinned spec. (MZSP): "Angra dos / Reis RJ / 28.XII.1951"; 1 pinned spec. (MZSP): "São João da Barra / RJ - Brasil / 16.VIII.1963 - W. Baker- / Mann col. - Em Bromélia"; 9 pinned spec. (MZSP): "Sernambetiba / Rio de Janeiro - GB / 13.VII. 1963, Vanzolini / e Reichardt col. / Em Bromélia". SANTA CATARINA STATE: 1 spec. in alcohol (DZRJ): "Brasil: SC, Blumenau / Parque Spitzkoft, / vegetação junto a represa (B05) / 19.I.2011 / Braga R. B. // Lachnodacnum / luederwaldti / Orchymont, 1937 / Clarkson, B. det."; 9 spec. in alcohol (MZSP 010.257); "Florianópolis, Joaquina, Restinga, Vriesea friburgensis (LANUFSC 88), 27.v.2003, A. Zillikens & J. Steiner col."; 2 spec. in alcohol (MZSP 010.262): (one reared from pupa), same locality, but "10.iii.2009, F.F. Albertoni & J. Linemburg col."; 2 spec. in alcohol (MZSP 010.256): "Florianópolis, Restinga, Vriesea friburgensis // 11.x.2010, F. F. Albertoni col."; 1 3 in alcohol (MZSP 010.260): same locality and collector, but "04.xii.2009"; 2 spec. in alcohol (MZSP 010.258); "Lagoa Pequena, 17.iii.2009, criação, F. F. Albertoni"; 14 pinned spec. (MZSP): "Campeche – Joaquina, 27.v.2003, A. Zillikens leg". São PAULO STATE: 94 adults in alcohol (DZRJ): all with locality data "Brasil: SP, Ubatuba, Parque Estadual da Serra do Mar, Núcleo Picinguaba" and identification label "Lachnodacnum / luederwaldti / Orchymont, 1937 / Clarkson, B. det." and following additional label data: Lote 1504: "03.VII.1999 / bromélia (Neuregelia, Aechmea and Bilbergia)" [2 spec.]; Lote 1505: "27.XI.1999/ Água de Bromélia / Nicollini, L." [2 spec.]; Lotes 2708, 2710, 2933, 2934, 2936, 2937, 2938, 2940: "30.VI.2006 / Bromélia / Ferreira-Jr, N. & Braga, R. B." [29 spec.]; Lote 2712: "06-07.XI.2006 / Bromélia / Braga, R.B.; Ferreira-Jr, N.; / Clarkson, B." [3 spec.]; Lote 2767: "29.X.2004 / em Bromélia / Ferreira-Jr, N. & Braga, R. B." [25 spec.]; Lote 2780: "25.X.2004 / Bromélia na trilha do Tronco / Ferreira-Jr, N. & Braga, R. B." [19 spec.]; Lote 2797: "27.XI.1999 / Água de Bromélia / Nicollini, L." [1 spec.]; Lote 2801: "25.X.2007 / Bromélia, próx. ao camping Caracol / Ferreira-Jr, N." [10 spec.]; Lote 2946: "29.X.2004 / Em Bromélia / Ferreira-Jr, N. & / Braga, R.B. col." [3 spec.]; 10 pinned spec. (SEMC): "Brasil: SP, Ubatuba / Parque Estadual da / Serra do Mar / Núcleo Picinguaba / 30.VI.2006 / em Bromélia / Ferreira-Jr, N. & Braga, R. B. col."; 2 pinned spec. (MZSP): "Coll.



Figs 33–36. Mesoventral elevation of *Lachnodacnum* Orchymont, 1937, SEM micrographs. In ventral (33–34) and lateral (35–36) views. 33, 35 – *L. luederwaldti* Orchymont, 1937; 34, 36 – *L. saundersi* Orchymont, 1937 (arrow indicates the anepisternal suture).

Knisch / No. 20227 // São Paulo / Alcatrazes / x / Coelostoma / lüederwaldti m. / A. Knisch det. 1921 / nov. spec. // Lachnodacnum / lüderwaldti / Orch., 1937 / H. Reichards det. 1962 / 2.532"; 5 pinned spec. (MZSP): "São Paulo / I. Alcatra-/ zes. / Coelostoma / lüederwaldti Km. / Knisch det. 21 // Lachnodacnum / lüderwaldti / Orch., 1937 / H. Reichards det. 1962 / 2.533"; 3 pinned spec. (MZSP): "Brasil, SP, Ubatuba / Parque Estadual / da Serra do Mar, / Núcleo Picingua / 30.06.2006 // Em Bromélia / Ferreira-Jr, N. & / Braga, R.B. col. // Lachnodacnum / luederwaldti / Orchymont, 1937 / Clarkson, B. det."; 10 pinned spec. (NMPC): "Brasil: SP, Ubatuba / Parque Estadual da / Serra do Mar / Núcleo Picinguaba / 30.VI.2006 / Bromélia / Ferreira-Jr, N. & Braga, R. B. // Lachnodacnum / luederwaldti / Orchymont, 1937 / Clarkson, B. det."; 4 spec. (NMPC, alcohol collection): "Brasil: São Paulo / Ubatuba, P. E. Serra / do Mar, 22.VI.2013, núcleo Picinguaba / Bromelia / Clarkson B. coll. // Lachnodacnum / luederwaldti / Orchymont, 1937 / Clarkson, B. det."

Immature stages examined (37): BRAZIL: SANTA CATARINA STATE: Florianópolis city: 5 egg cases in alcohol (MZSP 010.258): "Restinga, *Vriesea friburgensis* // 17.iii.2009, F. F. Albertoni col"; 2 larvae (one 1st instar - hatched and fixed on 23.x.2010 and one 2sd instar - fixed on 03.xi.2010) in alcohol (MZSP 010.259): same locality, additional label data:

"reared from egg collected on 11.ix.2010 in association with adults, hatched on 23.x.2010, F. F. Albertoni col"; 1 larva of 1st instar [reared from eggs collected in association with adults, dried and coated by gold for SEM] (MZSP): same locality, additional label data: "11.x.2010, fixed 16.x.2010, F. F. Albertoni col."; 1 larva of 3rd instar (MZSP): same locality, additional label data: "11.x.2010, fixed 16.x.2010, F. F. Albertoni col."; 1 larva of 3rd instar (MZSP): same locality, additional label data: "11.x.2010, pixed on 30.ix.2009"; 2 pupae in alcohol [reared from larvae] (MZSP): same locality, additional label data: "11.x.2010, pupation on 14.x.2010 and 20.x.2010, F. F. Albertoni col."; 1 larva of 3rd instar, dried and coated by gold for SEM] (MZSP): same locality, additional label data: "11.x.2010, pupation on 14.x.2010 and 20.x.2010, F. F. Albertoni col."; 3 larvae in alcohol [reared from eggs] (MZSP): additional label data: "11.x.2010, F. F. Albertoni col."; 3 larvae in alcohol [reared from eggs] (MZSP): additional label data: "Restinga, Lagoa Pequena, *Vriesea friburgensis*, 04.xii.2009, fixed on 22.xii.2009, F. F. Albertoni col.". **SÃO PAULO STATE:** 6 egg cases, 6 larvae of 1st instar, 2 larvae of 2rd instar [reared from eggs], 3 larvae of 3rd instar [reared from eggs] all in alcohol (DZRJ) (Lotes 5700, 5701, 5702, 5703, 5704, 5705, 5707): "BRASIL: São Paulo / Ubatuba, P. E. Serra / do Mar, N. Picinguaba / 15.viii.2011 / Clarkson, B. col." with identification label: *"Lachnodachnum/ luederwaldti/*Clarkson, B. det." and additional label data: "criação"; 1 larva of 2rd instar, 1 larva of 3rd instar, all in alcohol (NMPC): "BRASIL: São Paulo / Ubatuba, P. E. Serra / do Mar, N. Picinguaba / 15.viii.2011 / Clarkson, B. col."

Redescription of adult. Body length 6.8–7.5 mm, body width 4.1–4.5 mm. Entirely black in dorsal and ventral views; maxillary and labial palps dark brown, maxillary palpomere 4 reddish in distal third; antennae pale brown. Coxae, femora and tibiae black, tarsi brown.

Head. Clypeus and frons finely punctate, the punctures about a third the width of one ommatidium, interstices of the clypeal disc without microsculpture, anterior and lateral margins with a narrow area bearing fine microsculpture consisting of transverse ridges (Fig. 31). Frons with a distinct transverse microsculpture posteriorly, lacking microsculpture in anterior portion. Labrum about $0.4 \times$ as wide as maximum width of head. Maxillary palpomere 1 minute, palpomeres 2 and 4 subequal in length, slightly longer than palpomere 3; palpomere 2 slightly widened distally; palpomere 3 narrower than distal portion of palpomere 2, slightly curved inwards and widened distally; palpomere 4 narrowest. Antennal scapus rather long and thick, about as long as pedicel and antennomeres 3-6 combined.

Prothorax. Pronotal interstices lacking microsculpture on whole surface, including lateral portions.

Mesothorax. Preepisternal plate narrow, arrow-shaped (Fig. 33), weakly produced sidewards, bare; median longitudinal portion broad, bearing sparse long setae in ventral view, widely attaching metaventral process. Lateral margin of elytron with bead throughout, very narrowly explanate on posterior half (Fig. 1). Outer bare portion of epipleuron (= "pseude-pipleuron") about $0.3 \times$ as wide as inner pubescent portion (= "epipleuron") in basal third, about $0.7 \times$ as wide as inner pubescent portion in distal two-thirds.

Male genitalia. Aedeagus 1.0-1.1 mm long (Fig. 15). Phallobase ca. $0.7 \times$ as long as paramere, with only distinctly defined basal manubrium. Paramere wide throughout, slightly sinuate on lateral margin, apical portion pronouncing into slightly prolonged apex. Median lobe slightly shorter than parameres, narrowing apicad, indistinctly constricted in apical third; basal portion with a deep emargination medially; gonopore distinct, subapical.

Description of egg case. Egg case rounded to elliptical in shape, about 2.5–3.5 mm wide, 3.0–3.5 mm long (Fig 19). Flat, made of two thin layers of silk, first layer attached to the leaf, second layer covering the egg, mast absent; egg case attached to the surface of leaf bases in the central part of bromeliad rosette, usually at water-saturated (but not necessarily submerged) places near the micro-pool, sometimes attached to the detritus accumulated in the rosette. Each egg case with one egg. Individual eggs white and elongate, about 1.5–1.8 mm long.D

Description of larva. General morphology. *Third instar.* Body slender, almost parallelsided (Figs 4–5); living specimens usually covered with slime-like matter. Membranous part greyish to brownish white. Sclerotized parts dark to light brown.

Head capsule subquadrate (Figs 7–8), strongly compressed dorsoventrally (Fig. 37); maximum width 1.02-1.07 mm (n = 4). Cervical sclerites present, suboval. Frontal lines more strongly marked in posterior half, lyriform, fused at base of head capsule, coronal line very short. Surface of head capsule smooth. Each anterolateral part of head with six stemmata, four anterior larger and largely fused, two posterior small, separated from remaining ones; stemmata not protuberant. Nasale slightly asymmetrical, distinctly projecting anteriad mesally, tridentate; middle tooth the biggest, lateral teeth smaller, asymmetrically inserted on each side, the right one projecting further than the left one. Epistomal lobes nearly symmetrical, indistinctly angulate at apex, projecting almost as far as nasale.

Antenna (Figs 65–66) three-segmented, rather thin and long, but much shorter than mandible. Antennomere 1 ca. twice as long as antennomere 2, antennomere 2 twice as long as antennomere 3, ca. as long as antennal sensorium SE1.

Mandibles (Fig. 71) symmetrical; tridentate, with long and slender distal tooth and two retinacular teeth; distal retinacular tooth slightly larger than basal one; basal retinacular tooth



Figs 37–39. Third instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937, SEM micrographs. 37 – head in lateral view; 38 – abdominal segment 8 in dorsal view; 39 – abdominal proleg.

smallest and slightly curved backwards. Inner face of retinacular and distal teeth without denticles; inner basal portion of mandible with strong cuticular spines directed backwards.

Maxilla (Figs 67–68) elongate, longer than mandible; cardo small, subtriangular; stipes ca. 2.5× longer than palpomeres 1–4 combined; distal part of stipes with a large sharp sclerotized spine on inner face; laterodorsal portion of stipes with numerous trichoid cuticular projections. Maxillary palps rather short and stout, palpomeres 1–4 subequal in length, palpomere 1 ca. twice as wide as palpomere 2, incompletely sclerotized dorsally. Inner appendage longer than wide, shorter than palpomere 2, partly sclerotized.

Labium (Figs 69–70) well developed, ligula present. Submentum fused to head capsule, subpentagonal, distinctly wider than mentum. Mentum slightly wider than long, wider than prementum, with slightly arcuate lateral margins, dorsal surface with large cuticular teeth. Prementum subquadrate. Ligula weakly sclerotized, shorter than labial palpi. Labial palpi two-segmented, ca. as long as prementum.

Thorax (Figs 7–8). Prothorax slightly wider than head capsule. Proscutum formed by one large plate subdivided by a sagittal line, its anterior portion membranous, lacking series of marginal setae; surface with sparse seta, surroundings of some setal articulations less pigmented. Prosternum with large multisetose sclerite subdivided mesally by sagittal line in posterior part. Mesonotum ca. $0.75 \times$ as long as pronotum, with large subrectangular plate subdivided by sagittal line, bearing few stout setae with less pigmented articulations. Metanotum ca. $0.75 \times$ as long as mesonotum, with strongly sclerotized anterior trapezoid portion, posterior portion less sclerotized with exception of a pair of small strongly sclerotized patches. Meso- and metasternum not sclerotized. Legs short, 5-segmented, all three pairs equal in size; prothoracic legs separated by less than length of the leg, meso- and metathoracic legs separated by almost 2× the leg length; trochanter in anterior view with series of 9 moderately long spine-like setae.

Abdomen (Figs 4–5) 10-segmented, membranous, covered with very densely arranged microtrichia. Segments 1–7 similar in shape and size, each subdivided into longer anterior and shorter posterior fold, with few long setae laterally. Anterior lobe of segment 1 anteriorly with a pair of transverse subquadrate sclerites, segment 2–7 without sclerotized plates. Anterior fold of segments 2–7 with a pair of prolegs bearing numerous setae and fine apically curved spines (Fig. 39).

Spiracular atrium (Figs 13–14, 38). Abdominal segment 8 with a pair of dorsal sclerotized plates; inner part of spiracular atrium with a part of subtrapezoid sclerites (ventral plates of segment 8) between spiracles; posterior part of atrium (segment 9) with a pair of large mesal and a pair of smaller sublateral sclerites, procerci setose, situated laterad of the lateral pair of sclerites. Urogomphus large, strongly sclerotized, situated posteriorly of the median pair of sclerites; posterior margin with one large sclerite on median lobe, and a pair of smaller sclerites on lateral lobes. Acrocerci present, cone-like.

Second instar. Similar to third instar, slightly less sclerotized, with sclerotized parts brown to light brown; maximum width of head capsule 0.75-0.77 mm (n=2). Frontal lines lyriform, well developed throughout head length, reaching lateral margin of antennal sockets. *Antenna* relatively shorter and thicker. *Mandibles* relatively slightly shorter and wider basally than in third instar. *Labium* with mentum slightly narrower than in third instar, prementum ca. half as long as mentum. *Spiracular atrium*: Dorsal plate subdivided medially, similar to that of third instar.

First instar (Figs 6, 40–62). Similar to third instar larva, but less sclerotized, sclerotized parts yellowish brown; maximum width of head capsule 0.50-0.55 mm (n = 8). Thorax and abdomen ca. as wide as head. Body pubescence proportionally longer and darker. Frontal lines (Fig. 52) lyriform, well developed throughout head length, reaching lateral margin of antennal sockets. *Antenna* (Figs 49, 54–55) relatively shorter and thicker than in third and



Figs 40–45. First instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937, SEM micrographs. 40 – whole larva in lateral view; 41 – thorax in lateral view; 42 – abdominal segments 7–10 (including abdominal tergite 8 and spiracular atrium) in dorsolateral view; 43 – head in dorsal view; 44 – labium and maxilla in ventral view; 45 – detail of the base of mandible, with basal inner cuticular spines.



Figs 46–50. First instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937, SEM micrographs. 46 – antennomeres 2–3 in dorsal view; 47 – mesothoracic leg; 48 – labial palps; 49 – maxillary palpus; 50 – inner appendage of maxilla.

second instars. *Mandibles* (Figs 43, 45, 60) relatively shorter and wider basally than in third instar; cuticular spines directed backwards on inner basal face more evident. *Maxilla* (Figs 44, 49–50, 56–57): spine on anteromesal margin of stipes relatively shorter and stouter than in third instar. *Labium* (Figs 44, 48, 58–59) with mentum distinctly longer than wide; prementum ca. half as long as mentum; ligula relatively longer than in third instar, ca. as long as prementum. *Thorax* (Fig. 41): legs of equal size and very similar shape as in third instar; median and posterior legs separated by less than the leg length; anterior legs slightly closer; trochanter with the same chaetotaxy as in third instar. *Spiracular atrium* (Fig. 42): Abdominal segment 8 with a single sclerotized dorsal plate.

Chaetotaxy of head. *First instar, primary chaetotaxy. Frontale* (Figs 52–53) altogether with 38 primary sensilla. Central part with three pairs of sensilla (FR1–3) divergent posteriad; FR1 moderately long seta close to the frontal line; FR2 pore-like, situated anteriorly of FR1; FR3 short seta anteromesally of FR2. Pore-like sensillum FR4 and setae FR5–6 and FR9 situated in line posteromesally of antennal socket; FR5 and FR9 moderately long seta; FR6 long seta. Moderately long seta FR7 situated on inner face of antennal socket; long seta FR10 situated between FR7 and FR9. Basal portion of each epistomal lobe with three sensilla (FR11–13); FR12 a short seta situated anteromesally of FR10; FR11 and FR13 pore-like, situated more or less in a row between FR12 and the emargination between nasale and epistomal lobe. FR14 absent. Anterior margin of each epistomal lobe with two short stout sensilla directed mesally

(gFR2). Nasale with a pair of long setae (FR8) basally, and a pair of pore-like sensilla (FR15) anteromesally of FR8; anterior margin of nasale with six stout sensilla (gFR1) situated slightly ventrally (i.e. below anterior margin of head): four setae on both sides of median tooth of nasale, one seta in emargination between nasale and each epistomal lobe.



Figs 51–53. Head capsule of the first instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937. 51 – ventral view; 52 – dorsal view; 53 – detail of anterior margin of head capsule, dorsal view.

Parietale (Figs 51–52). Dorsal surface with a longitudinal series of five sensilla (PA1–5) posteromesally; PA1-2 and PA4-5 very short setae; PA3 pore-like, situated slightly more laterally, PA6 pore-like, situated posteromesally, ca. at midlength between coronal line and the group of PA1-5. PA7+12+13 forming a sublateral group ca. at midlength of head, consisting of two long and one moderately long seta. PA8 long seta situated behind antennal socket ca. at level of FR2, closer to frontal line than PA7. PA10 pore-like, situated lateral of PA8. Very long seta PA9 situated on outer face of antennal socket. Lateral portion of parietale with one pore-like sensillum dorsally (PA19) and three long setae (PA20-22) ventrolaterally on anterior margin, one short seta (PA11) on the level of PA8, one long seta and one pore-like sensillum (PA14 and PA15, respectively) slightly anteriad of the group of PA7+12+13. Ventral surface with tree pore-like sensilla (PA23-25) situated close to the ventral mandibular articulation, PA23 most laterally, PA25 most mesally. Anterior third with a longitudinal group of three sensilla (PA26-28) situated close to each other: anterior one (PA26) long seta, median one (PA27) pore-like, posterior one (PA28) long seta. A group comprising of a pore-like sensillum (PA17) and a long seta (PA16) situated lateral of the group of PA26-28 and ventrad of the lateral pores (PA15+PA11/14). Posterior half of ventral surface with one por-like sensillum (PA29) at midwidth of parietale, one long seta (PA18) and one pore-like sensillum (PA30) sublaterally.

Antenna (Figs 54–55). Antennomere 1 with five pore-like sensilla (AN1–5); AN1 dorsally in posterior fifth, AN2 in anterior third; AN3 on outer face of intersegmental membrane, AN4–5 on inner face of intersegmental membrane. Antennomere 2 with one dorsal pore-like sensillum (AN6) situated on distal part of sclerite; setae AN7–8 and AN10–11 and sensorium SE1 on intersegmental membrane between antennomere 2 and 3, AN9 absent. AN7–8 and SE1 on lateral face, AN7–8 minute setae, SE1 long and thin, slightly longer than antennomere 3; AN10 long seta, AN11 short seta, both on inner face close to each other. Antennomere 3 without sensilla on sclerite, with apical sensilla (gAN) in apical membranous area.

Mandible (Fig. 60) with 6 primary sensilla. MN1 moderately long seta situated laterally ca. on mandibular midlength. Pore-like sensilla MN2–4 situated anteriorly of MN1, forming a triangle; MN3 close to base of apical retinacular tooth, MN2 ca. at midlength between MN1 and MN3. MN5 minute pore-like sensillum situated subapically on outer face, MN6 minute pore-like sensillum situated on inner face at midlength of the apical mandibular tooth.

Maxilla (Figs 56–57). Cardo with one long ventral seta (MX1). Stipes with a row of ca. 25–30 short stout setae along the inner face; setae separated by larger distance distally, becoming closer to each other basally, the basalmost seta slightly more distant from the others (likely homologous to MX7). Ventral surface of stipes with two pore-like sensilla, one situated ca. at midlength (MX2), the other in distal third (MX3). Sensilla MX4–6 forming a group laterally on distal margin of the sclerite; MX4 pore-like, MX5–6 long setae. Dorsal surface of palpomere 1 with one moderately long seta (MX16). Three sensilla (MX12–14) situated lateroventrally in distal half of palpomere 1; MX12 pore-like, MX13–14 moderately long setae. Pore-like sensilla MX15 and MX17 situated on membrane below inner appendage, MX17 dorsally, MX15 ventrally. Inner appendage with few setae (gAPP) of which two are long setae and one short and stout seta. Palpomere 2 with one minute basal seta (MX27) and one distal pore-like sensillum (MX18) on outer face, and with one pore-like sensillum (MX19) on inner face on membrane between palpomeres 2 and 3. Palpomere 3 with four sensilla;



Figs 54–62. First instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937. 54–55 – antenna (54 – dorsal view, 55 – ventral view); 56–57 – maxilla (56 – ventral view, 57 – dorsal view); 58–59 – labium (58 – ventral view, 59 – dorsal view); 60 – right mandible, dorsal view; 61 – prosternum; 62 – mesothoracic leg, anterior view.



Figs 63–64. Head capsule of the third instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937. 63 – ventral view, 64 – dorsal view.

pore-like MX20 and moderately long seta MX23 on outer face close to distal margin of sclerite, pore-like MX22 on ventral surface ca. at midlength, and moderately long seta MX21 distally on inner surface of sclerite. Palpomere 4 with moderately long seta (MX24) basally, and a digitiform sensillum (MX25) and a pore-like sensillum (MX26) distally on lateral face. Apical membranous area of palpomere 4 with several minute setae (gMX).

Labium (Figs 51, 58–59). Submentum with two pairs of setae (LA1–2), LA1 long, situated in lateral corner of submentum, LA2 short, on anterior margin laterally of articulation of mentum. Ventral surface of mentum with two pairs of sensilla, LA3 long seta at ca. midlength of sclerite, LA4 pore-like at anterior margin. Ventral surface of prementum with three pairs of sensilla; short setae LA5 close to proximal margin, long setae LA6 in anterior third of sclerite slightly mesally of LA5, pore-like LA7 at anterior margin of sclerite. Dorsal surface of prementum with a sub-basal pair of pore-like sensilla (LA8). Membranous base of ligula



Figs 65–71. Mouthparts of the third instar larva of *Lachnodacnum luederwaldti* Orchymont, 1937. 65–66 – antenna (65 – dorsal view; 66 – ventral view); 67–68 – maxilla (67 – ventral view, 68 – dorsal view); 69–70 – labium (69 – ventral view, 70 – dorsal view); 71 – right mandible, dorsal view.

with two pairs of dorsal (LA9–10) and one pair of ventral (LA11) sensilla; LA9 pore-like, situated on small cone-like projections, LA10 long seta situated distally of LA9, LA11 pore-like, situated at same level as LA10. Apical portion of ligula with a pair of cone-like sensilla (LA12) dorsally. Labial palpomere 1 with one pore-like sensillum (LA13) basally on ventral surface and one pore-like sensillum dorsally on intersegmental membrane between palpomere 1 and 2. Palpomere 2 with one distal pore-like sensillum (LA15) and a group of sensilla in the apical membranous area (gLA).

Second instar. More similar to the third instar than to the first, but not studied in detail. Lateral face of mentum with series of secondary long setae, lateral face of stipes with numerous long secondary setae, dorsolateral face of stipes with long but still not articulated cuticular projection (compare to third instar).

Third instar. Frontale (Fig. 64) with two pairs of secondary setae, each laterally of FR2 very close to remnants of frontal lines. *Parietale* (Figs 63–64) with two short secondary setae anteriorly of PA6 close to remnants of frontal line, one secondary pore between PA9 and PA19, one secondary short seta posteromesally of PA9, one secondary short seta anteriorly of PA8. Lateral portion with 2–3 short secondary setae dorsally of PA16. *Antenna* (Figs 65–66) without secondary sensilla. *Mandible* (Fig. 71) with one secondary seta and two pores on basal lateral face, and with numerous secondary micropores in apical portion. *Maxilla* (Figs 67–68): stipes with two secondary moderately long setae scattered between this group and MX2; lateral face of stipes with numerous very long secondary setae, dorsolateral face with densely arranged secondary short but stout setae which seem to be homologous to cuticular projections observed in this area in first instar. Palpomere 1 with secondary short seta mesally of MX14. Digitiform sensillum (MX25) of palpomere 4 relatively much shorter than in first instar. *Labium* (Figs 69–70): Mentum with a pair of moderately long setae ventrally between both LA4, and with a series of six extremely long setae in anterior half of lateral face.



Figs 72–74. Pupa of *Lachnodacnum luederwaldti* Orchymont, 1937. 72 – dorsal view; 73 – ventral view; 74 – detail of pronotal stylus. Abbreviations: Ms – stylus of pronotal margin; Ds – stylus of pronotal disc; Ab – abdominal segment.

Description of pupa (Figs 72–74). Exarate and adectic. Length: 5.8–6.3 mm. Maximum width: 3.1-3.6 mm (n = 2). Color white (slightly vellow after fixation). *Head*. Not visible on dorsal view; with two pairs of supraorbital styli; mandibles and maxillae apparent under labrum; eves of the same color as remaining parts of head during majority of pupal stage, brown in pharate imago; clypeolabral suture weakly marked. *Thorax*. Prothorax strongly convex dorsally; with 12 styli on each side, all visible in dorsal view; one longitudinal row of five styli near posterior margin and one row of five styli near anterior margin (marginal styli – Ms), one stylus medially near midline and one between Ms2 and Ms3 (closest from the later one) near anterior margin (discal styli – Ds); mesonotum with one stylus on each side of an elevated triangular scutellar shield; metanotum subtrapezoidal, posterior margin slightly projecting posteriad mesally, with one pair of styli more distant from each other than on mesonotum, *Legs*. Pro- and mesothoracic legs folded over wingpads, lacking apical spur; metathoracic legs covered by wingpads, metatibia bearing few tubercles and with a short apical spur. Abdomen with nine visible segments in dorsal view; segment 8 as long as segment 1, but almost $3 \times$ narrower, strongly convex dorsally; sternites 3-6 with one long stylus on each lateral margin; tergites with two conspicuous patterns of styli: a long stylus on each lateral margin of each segment, and short styli (ca. 0.5× shorter than lateral styli) on medial portion of each tergite. Tergite 1 with one pair of medial styli, tergites 2-7 with two pairs of medial styli on each side. Lateral styli on tergites situated near to those on sternites; tergite 8 with one pair of styli near apex. Segment 9 strongly bilobed.

Biology. See below.

Distribution (Fig. 75). The distribution corresponds with the range of the Atlantic rain forest which originally extended along the Brazilian coast. The species occurs from the state of Santa Catarina in the southern region of Brazil to the state of Bahia in the northeast of Brazil; it is also recorded from the states of São Paulo (in which type locality is situated), Rio de Janeiro and Espírito Santo States in southeastern Brazil.

Lachnodacnum saundersi Orchymont, 1937

(Figs 9-10, 16, 34, 36, 75)

Lachnodacnum saundersi Orchymont, 1937: 138.

Type locality. Brazil, Pernambuco.

Type material examined. HOLOTYPE: unsexed specimen (BMNH): "Type [rounded label with red margin] // TYPE // from terrestrial brom-/eliad/BRAZIL:/Pernambuco/14.ix.1923//L.G. Saunders./B. M. 1936-646 // Pernambuco/14.ix.23 / terrest. brom // A. d'Orchymont det. / Lachnodacnum / saundersi m.". PARATYPES: 1 male (specimen with missing prothorax and head, BMNH): "Para-/ type [rounded label with yellow border] // Para-/ type", further labels same as in holotype; 1 spec. (teneral specimen, BMNH): "Para-/ type [rounded label with yellow border] // Para-/ type // terrestrial bromeliad / BRAZIL: / Pernambuco / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / B. M. 1936-646 // P'buco, Brazil / 14.ix.1923 / L.G. Saunders / terrest bromelias // A. d'Orchymont det. / Lachnodacnum / saundersi m."

Non-type material examined (1). BRAZIL: PERNAMBUCO STATE: 1 spec. (IRSNB): "Dois irmãos, 28.iv.1935, Bromelicola, O. Schubart".

Redescription. Body length 6.1–6.7 mm (holotype 6.7 mm), body width 4.1–4.5 mm (holotype 4.5 mm). Entirely black in dorsal and ventral views; maxillary and labial palps dark brown; antennae pale brown. Legs dark brown.

Head. Clypeus and frons finely punctuate, the punctures are about a third the width of one ommatidium, interstices of whole clypeus with reticulate microsculpture consisting of fine scattered ridges. Labrum about $0.5 \times$ as wide as maximum width of head. Maxillary palpomere 1 minute, palpomeres 2 longer than palpomere 4, palpomere 3 shorter than 4; palpomere 2 slightly widened distally; palpomere 3 narrower than distal portion of palpomere 2, slightly curved inwards and widened distally; palpomere 4 narrowest. Antennal scape about as long as pedicel and antennomeres 2-6 combined.

Prothorax. Lateral portions of pronotum bearing distinct reticulate microsculpture, median portion of pronotum with indistinct microsculpture only.

Mesothorax. Preepisternal plate very produced laterally, spade-shaped, bare, anterior portion conspicuously more elevate than the median longitudinal posterior portion; median longitudinal portion broad, bearing sparse long setae in ventral view, widely attaching metaventral process. Lateral margin of elytron distinctly explanate along its length (Fig. 9). Outer bare portion of epipleuron (= 'pseudepipleuron') about $0.3 \times$ as wide as inner pubescent portion (= 'epipleuron') in basal third, about $0.7 \times$ as wide as inner pubescent portion in distal two-thirds.

Male genitalia. Aedeagus 1.05 mm long (Fig. 16). Phallobase ca. $0.5 \times$ as long as parameres, symmetrical, with only indistinctly defined basal manubrium. Paramere wide throughout, slightly situate on lateral margin, apical portion not much pronouncing and rather wide. Median lobe slightly shorter than parameres, narrowing apicad, slightly constricted in apical third; basal portion at most with a shallow and rather indistinct emargination medially; gonopore distinct, subapical.

Biology. The type specimens were collected from a terrestrial bromeliad.

Distribution. Only known from two closely situated localities in northern Brazil (Pernambuco state).

Biology of Lachnodacnum luederwaldti

Almost all known specimens of this species were collected between the leaf bases of epiphytic and terrestrial bromeliads (Fig. 18): we have recorded the species from the genera *Aechmea* Ruiz & Pav., *Billbergia* Thunb., *Neoregelia* L. B. Smith and *Vriesea* Lindl. A single adult was collected in the vegetation at the margin of a dam in Ecological Park Spitzkoft near Blumenau, Santa Catharina state in southern Brazil.

In the field, most egg cases were found attached to the basal portion of leaves within the bromeliad rosette (Fig. 19), usually on wet portions near the micro-pool or directly on the moist detritus. In captivity, adults laid eggs directly on the container wall near the water level or partially submerged. After hatching, the larva moves inside of the egg case, sometimes in a circular movement, before it cuts a hole in the silk layer of the egg case using its mandibles and leaving the egg case.

The larvae of all instars were observed submerged and sandwiched between the leaves. When they were not sandwiched, they were rapidly seeking for the place to be sandwiched. In the laboratory, when bromeliad leaves were not made available and the larva was not able to keep sandwiched after leaving the egg case, some larvae were observed to use the egg case



Fig. 75. Distribution of Lachnodacnum luederwaldti Orchymont, 1937, L. saundersi Orchymont, 1937 and Phaenostoma urichi (Scott, 1913).



Figs 76–81. *Phaenostoma urichi* (Scott, 1912). 76–77 – general habitus (76 – lateral view, 77 – dorsal view); 78 – dorsal view of the head; 79 – whole beetle in ventral view; 80 – head in ventral view; 81 – mesoventrite and mesofemur.

as a shelter for a while. They opened the case in two places and stayed with the head in one aperture and with the spiracular atrium in the other. Eventually they went partly out of the shelter to hunt small crustacenas (copepods) that were near the shelter. It was not observed whether the larva that completely left the shelter returned. The larvae also fed on *Enchytraeus* sp. (Annelida: Enchytraeidae) placed in the container, and were observed to feed on chironomid larvae in the field.

The pupae were found among the leaf bases, placed in a pupal chamber built by the third instar larva on the internal face of the more external leaves using the humid detritus available in the bromeliads rosette (Figs 20–22).

The adults are completely aquatic, living submerged in the film of water between the leaves of the bromeliads. In captivity, the adults also stayed submerged (Fig. 23). Usually they are not very active, but they forage among the leaves, probably feeding on the decaying material (detritus and decaying parts of bromeliad leaves) in the water. The unique specimen not directly collected inside a bromeliad was found at night on bush vegetation, which may indicate a nocturnal activity for dispersal.

Taxonomic changes outside of Lachnodacnum

Phaenostoma Orchymont, 1937

Phaenostoma Orchymont 1937: 133. Type species: Cyclonotum posticatum Sharp, 1887, by original designation.
= Psilodacnum Orchymont 1937: 134, syn. nov. Type species: Cyclonotum urichi Scott, 1912, by original designation.

Comments on Psilodacnum. The detailed examination of Lachnodacnum urichi, which is the type and sole species of the genus *Psilodacnum* described by ORCHYMONT (1937) and later synonymized with Lachnodacnum by HANSEN (1991), revealed that the species is not congeneric with the two species treated above. Psilodacnum differs from Lachno*dacnum* e.g. by completely obliterated anapleural sutures of the mesoventrite, aedeagus with largely reduced phallobase and femora without ventral hydrophobic pubescence. In all these characters, it agrees with the remaining coelostomatine genera occurring in the Neotropics. Moreover, Psilodacnum agrees well with Phaenostoma in all characters considered at the moment as diagnostic at the generic level: antennal club is loosely segmented, elytra lack punctural series but bear the sutural stria, prosternum is flat mesally, meso- and metaventrite form a composite structure, mesocoxal cavities are rather widely separated, all femora lack the ventral hydrophobic pubescence, the first abdominal ventrite lacks the median carina, and the fifth abdominal ventrite lacks the apical emargination. The only difference between *Psilodacnum* and *Phaenostoma* is the shape of the clypeus, the relative size of the eyes, and the detailed morphology of the aedeagus, plus very likely also the preferred habitat. All these differences are too weak to justify the separate position of *Psilodacnum*, and it is hence synonymized here with *Phaenostoma*, and its type species is transferred to Phaenostoma as well. Phaenostoma urichi comb. nov. is redescribed in detail below, to illustrate its differences from *Lachnodacnum* and to justify the changes at the genus level proposed here.

Phaenostoma urichi (Scott, 1912) comb. nov.

(Figs 12, 75-86)

Cyclonotum urichi Scott, 1912: 435. Coelostoma Urichi: KNISCH (1924: 113). Psilodacnum urichi: ORCHYMONT (1937: 134). Lachnodacnum urichi: HANSEN (1991: 207).

Type locality. Trinidad and Tobago, Trinidad, El Tucuche.

Type material examined. HOLOTYPE: unsexed specimen (BMNH): "Trinidad [handwritten directly on the label with the beetle] // Type [rounded label with red margin] // 1912 – 435 [handwritten] // Bromeliaceae / Tucuche Mt. 3100 ft. / Trinidad / 20. March 12-26. 1912 / H. Scott // Cyclonotum / urichi H. Scott / TYPE".

Additional material examined (28 spec.): TRINIDAD AND TOBAGO: 1 spec. (MCZ): Trinidad, Cedros [= Cedros Forest Reserve, ca. 10°7/N 61°46′W], 4.v.1929, lgt. Darlington; 1 $\stackrel{\circ}{\bigcirc}$, 4 spec. (BMNH, IRSN, MCZ): Mt. Tucuché [10°44.33′N 61°24.64′W], without date, lgt. R. Thaxter; 14 spec. (MCZ, NMPC): same locality, iv.1929, lgt. Darlington; 3 spec. (MCZ): same locality, in bromeliads, iv.1929, lgt. Darlington; 3 spec. (BMNH, IRSN): same locality, 14 May 1912, lgt. F. W. Urich; 2 spec. (MCZ): same locality, 16.xii.1934, lgt. N. A. Weber.

Redescription. Body length 4.1–4.6 mm, body width 2.7–2.9 mm. Body widely oval, weakly convex in lateral view; pronotal and elytral outline continuous in dorsal and lateral views. Entirely black in dorsal and ventral views; antennae, maxillary and labial palps pale brown. Coxae, femora and tibiae brown, tarsi pale brown.

Head. Clypeus (Figs 78, 80) wide anteriorly, only slightly narrowing before eyes, with anteromedian margin truncate. Frontoclypeal suture conspicuous, Clypeus and frons finely punctuate, the punctures are about a third the width of one ommatidium, interstices with microsculpture: reticulate on anterior margin and with fine transverse longitudinal ridges medially on clypeus, reticulate on posterior margin of head; lateral portions of frons between anterior margin of eye and frontoclypeal suture lacking punctuation, only with sparse micropunctures. Eyes small, not protruding laterad, oval in dorsal view, surrounded by micropunctures, separated by $7 \times$ the width of one eye, distinctly emarginate anteriorly in lateral view. Labrum small, membranous, totally concealed under clypeus, ca. $0.6 \times$ as wide as maximum width of head. Mentum 1.4× as wide as long; surface bearing dense long yellow setae; lateral margins nearly parallel-sided, each bearing row of setae; anterior margin deeply bisinuate. Maxillary palps with four palpomeres, short and rather stout; palpomere 1 minute, palpomeres 2 and 4 subequal in length, slightly longer than palpomere 3; palpomere 2 very wide, somewhat bulbous; palpomere 3 slightly curved inwards and widened distally; palpomere 4 narrowest. Labial palps with three palpomeres: palpomere 2 bearing dense brush of long setae on its outer face anteromedially. Labial palpomere 3 about $0.8 \times$ as long as palpomere 2, much narrower. Submentum pubescent. Gula slightly constricted between tentorial pits. Antenna (Fig. 85) with nine antennomeres; scape about as long as pedicel and antennomeres 3-6, its basal portion bent dorsally; pedicel cylindrical; cupula large and short, bare, concealing basal portion of antennomere 7; antennal club loosely segmented, depressed dorsoventrally, densely pubescent with few longer and thicker setae on sides and on distal margins of antennomeres.

Prothorax. Pronotum weakly convex, with bead on anterior and lateral margins including antero- and posterolateral corners; anterior and posterior corners weakly angulate; posterior margin slightly arcuate. Prosternum (Fig. 82) not carinate medially, weakly convex. Procoxal cavities large, opened posteriorly, anterolateral aperture of procoxal cavity opened. Hypomeron with very large pubescent inner portion, marginal glabrous portion rather narrow (Fig. 82).

Mesothorax. Mesoventrite completely fused with an episternum 2, an episternal suture absent (Figs 79, 81); epimeron 2 well delimited, divided from an episternum 2 by a suture, pubescent; anterior collar of mesothorax broad, well demarcated. Mesoventrite highly elevated medially into preepisternal plate; preepisternal plate longitudinal and linear, somewhat tectiform with the sides sloping laterally, bare; bearing sparse long setae in ventral view, narrowly attaching metaventral process, not forming a common keel with it; surface of preepisternal plate nearly straight, as laying slightly lower than the surface of metaventrite; anteromedian pit-like groove present, partly overlapped by anterior portion of preepisternal plate. Grooves for reception of



Figs 82–86. *Phaenostoma urichi* (Scott, 1912), SEM micrographs. 82 – prothorax in ventral view (prosternum and hypomeron); 83–84 – mesoventral elevation (83 – lateral view; 84 – ventral view); 85 – antenna; 86 – protarsus.

procoxae weakly defined (Figs 79, 81). Elytron highly convex; lateral margin beaded along its length, very narrowly explanate on posterior half; elytral series of punctures absent; elytral surface smooth, homogenously punctated, punctation as dense as on pronotum, denser than on head; punctures slightly larger than the pronotal ones. Sutural stria very weak, rather indistinct, developed only on distal portion of elytron, not reaching elytral apex. Epipleuron wide and strongly inclined throughout, very wide anteriorly, strongly narrowing posteriorly; outer bare portion (= "pseudepipleuron") about $0.3 \times$ as wide as inner pubescent portion (= "epipleuron") in basal third, about $0.6 \times$ as wide as inner pubescent portion in distal two-thirds. Mesocoxal cavities transverse, narrowly divided medially by meso-metaventral keel.

Metathorax. Metaventrite with pubescent surface, slightly elevated into a longitudinal bare plate medially; median plate projecting anteriorly into a rhomboid metaventral process situated above level of mesoventral plate in lateral view (Figs 79, 83); meso-metaventral plate constricted at junction. Posterior half of metaventral keel with weak longitudinal groove. Median bare portion of metaventrite with scattered punctures in anterior part and somewhat on posterior margin. Metepimeron rather large with long posterior projection. Hind wing (Fig. 12) with R-M loop distally the maximum width of the wing; RA₁₊₄ reduced, not attached to RA basally, forming an opened radial cell; radial cell large, subrectangular, pigmented on anterior two-thirds; r3 absent; r4 developed, but is not attached to R-M loop, and not connecting RA, to R-M loop; apical field with RA, well defined, short, not reaching the margin of the wing apically; RA, fused with RP,, together forming a pigmented area almost reaching wing margin apically; base of RP1 far of R-M loop; RP2 very weak, forming a triangular pigmented area, almost reaching R-M loop basally and is almost invisible distally; RP₃₊₄ very weakly defined, narrow and long, beginning from R-M loop, near to the base of medial spur, curved posteriad and reaching wing margin apically; medial field with medial spur reduced; MP₃₊₄ developed, nearly connected with MP_{1+2} , not attached to MP_3 and MP_4 +CuA₁; MP_3 and MP_4 +CuA₁ well defined, connected basally, and attached with CuA₁, reaching wing margin posteriorly; CuA₁ developed, without connection with MP₃₊₄, but connected with MP₃ and MP₄+CuA₁; CuA₂ present and well defined, reaching the posterior edge of the wing apically; Cu in this genus is longer than observed in Lachnodacnum; CuA₃₋₄ absent and hence wedge cell missing; AA₃ and AA₄ defined and long, nearly reaching posterior margin of the wing; anal field with venation reduced, composed of a long AP_{3+4} and with AP_{1+2} absent.

Legs. Procoxa globular, pubescent; profemur with deep tibial groove delimited by high ventral and low dorsal ridges, ventral surface pubescent except for small bare distal area; protibia cylindrical, bearing series of stout spines and irregularly arranged small spines, distal portion bearing "crown" of smaller stout spines and two large spurs. Mesotrochanter slightly sinuate on posterior margin; ventral surface of mesofemur bare, only with few scattered long setae on anterior and posterior margins, its surface reticulated; tibial groove deep, developed throughout, delimited by high ventral and low dorsal ridges; mesotibia flattened, sparsely covered by short and stout spines, bearing longitudinal series of larger spines and a subapical transverse series of larger spines; distal apex with series of short spines and two long spurs on inner margin. Metatrochanter slightly sinuate on posterior margin, pubescent on basal portion; metafemur large and wide, ventral surface bare except of sparsely arranged setae on extreme anteroproximal portion, surface reticulated with scattered setiferous punctures; tibial groove well developed, deep, delimited by high ventral and low dorsal ridges. Metatibia flattened,

bearing scattered short spines and two series of larger spines on outer margin; distal half with transverse series of moderately long spines and two long spurs on inner margin. Tarsi much shorter than tibiae, each tarsomere bearing a dense brush of long setae ventrally (Fig. 86), with longer setae sideward and with single to few long setae dorsally. Metatarsus slightly compressed laterally, metatarsomere 1 slightly longer and ca. twice wider than metatarsomere 2; claws small, simply arcuate.

Abdomen. With five ventrites, all ventrites flat, without any longitudinal carina; posterior margin of ventrite 5 without apical notch nor the median group of stout setae.

Male genitalia (Fig. 17). Aedeagus 0.65 mm long. Phallobase symmetrical, extremely short, with very long and distinctly detached manubrium. Parameres rather narrow basally, slightly bent mesally, gradually narrowing towards apex. Median lobe wide basally, bearing two long and wide basal projections, slightly widening towards basal 0.4, then abruptly strongly narrowing into an extremely narrow apical portion; apex rounded, gonopore distinct, situated in apical third. Sternite 9 moderately wide basally, bearing rather wide tongue-shaped median projection, lateral struts arcuate, slightly shorter than median portion.

Differential diagnosis. *Phaenostoma urichi* may be distinguished from all other described species of the genus by the following characters: body larger than 4.0 mm (smaller than 4.0 mm in remaining species), eyes very small, separated by 7× the width of one eye in dorsal view (Fig. 78) (eyes larger, separated by 4–5× the width of one eye in dorsal view in remaining species), clypeus very wide, only slightly narrowing anteriad, straight on anterior margin (Fig. 78) (clypeus strongly narrowing anteriad, arcuate on anterior margin in remaining species) and median lobe of the aedeagus very narrow apically, gonopore situated in apical third (Fig. 17) (median lobe wide apically, gonopore subapical in other species). See GUSTAFSON & SHORT (2010) for details about the remaining species.

Biology. The type specimens were collected between the leaf bases of the epiphytic *Tillandsia* sp. (Bromeliaceae) in the tropical montane forest (SCOTT 1912). Part of the non-type specimens from Mt. Tucuché also bear a label indicating they were collected in bromeliads.

Distribution. The species is known from two rather distant localities in Trinidad, and is likely distributed throughout the island in suitable habitats.

Updated key to the Neotropical genera of the Coelostomatini

The genus *Badioglobus* Short, 2004 from Central America, originally considered as belonging to the Coelostomatini, was recently excluded from the tribe by SHORT & FIKAČEK (2013). See the identification key in the latter paper to distinguish *Badioglobus* from the Coelostomatini. The genus *Galapagodacnum* Orchymont, 1937 is treated on two places in the key, as its punctural series on the elytra (couplet 1) may be easily overlooked.

_	First abdominal ventrite without median carina
3	Body rather compressed in lateral view, elongate oval and parallel-sided in dorsal view.
	Antennal club compact. Mentum of males without dense yellowish pubescence
	Galapagodacnum Orchymont, 1937
_	Body highly convex, widely oval. Antennal club loosely segmented. Mentum of males
	covered with short, dense yellow setae Cyclotypus Sharp, 1882
4	Mesofemur with dense hydrofuge pubescence in basal three fourths (Fig. 29). Anapleural
	suture of mesoventrite very distinct (Fig. 27) Lachnodacnum Orchymont, 1937
_	Mesofemur glabrous, at most with very sparsely arranged setae. Mesoventrite largely
	fused to anepisterna, anapleural sutures indistinct or totally absent 5
5	Each elytron with distinct sutural stria in posterior half
_	Elytra without distinct sutural striae
6	Antennal club compact. Prosternum carinate mesally. Body compressed dorsoventrally.
	Galapagodacnum Orchymont, 1937
_	Antennal club loosely segmented. Prosternum without median carina. Body more or less
	highly convex Phaenostoma Orchymont, 1937
8	Median portions of meso- and metaventrite fused in a common keel more or less widely
	separating mesocoxal cavities (e.g., see DeLer-Hernández et al. 2013: Figs 9-11)
—	Meso- and metaventrite well separated from each other, not forming a common ventral
	keel. Mesocoxal cavities very narrowly separated from each other (see Archangelsky
	1992: Fig. 2) Hydroglobus Knisch, 1921

Discussion

Current state of the systematics of the Coelostomatini. The current understanding of the taxonomy of the Coelostomatini is very limited. Most genera and subgenera are defined by relatively few characters of uncertain significance (see e.g. HANSEN 1991). The internal phylogeny of the tribe has never been examined and thus the phylogenetic importance of many of the characters used to diagnose genera have not been tested. As a result, the concepts of many coelostomatine genera largely follow those introduced by ORCHYMONT (1937). Orchymont's concept was based on three widely defined and more or less speciose genera (Coelostoma Brullé, 1835 in the Old World, Phaenonotum Sharp, 1882 in the New World, and the world-wide Dactylosternum Wollaston, 1854), from which numerous small narrowly-defined genera were separated, usually defined by a single or few unique characters sometimes together with the occurrence in geographically isolated regions (e.g. Galapagodacnum Orchymont, 1937 endemic to Galapagos Islands, and Bourdonnaisia Scott, 1913 endemic to the Seychelles). More recent authors followed this tradition, establishing the monotypic genera Kruia Spangler & Perkins, 1981, Toma Hansen, 1989, Elocomosta Hansen, 1989, Rhachiostethus Hansen, 1989 and Hemikruia Hebauer & Hansen, 2002. As a result, the tribe Coelostomatini in the current understanding (i.e. after excluding the genera Adolopus Sharp, 1884, Cyloma Sharp, 1872 and Badioglobus Short, 2004; SHORT & FIKÁČEK 2013, FIKÁČEK et al. 2013) contains 17 genera and ca. 220 described species

(SHORT & FIKAČEK 2011). Fourteen of these genera are very narrowly defined and often monotypic, containing only 22 species in total. The remaining ca. 200 species are placed in the three widely defined genera (*Coelostoma*: ca. 110 species, *Dactylosternum*: 77 species, *Phaenonotum*: 19 species).

Taxonomic status of *Lachnodacnum*. It is very difficult to evaluate the taxonomic status of *Lachnodacnum* following current generic concepts within the Coelostomatini as described above. Nevertheless, our study demonstrates that *L. luederwaldti* and *L. saundersi* (i.e. members of *Lachnodacnum* in its original sense by ORCHYMONT (1937)) are very similar to each other, and that they largely differ from *L. urichi*, as indicated originally by ORCHYMONT (1937). As a result, *Lachnodacnum sensu* HANSEN (1991) does not seem to form a monophyletic group. To address this problem, we are here excluding *L. urichi* from *Lachnodacnum* and proposing the placement of the species into the genus *Phaenostoma*.

After excluding *L. urichi, Lachnodacnum* forms a small but likely monophyletic lineage characterized by several shared characters: (1) mesofemora with ventral hydrofuge pubescence (Fig. 29; within Coelostomatini present only in the subgenus *Lachnocoelostoma* Mouchamps, 1958 of *Coelostoma*, absent in all remaining genera/subgenera); (2) anapleural sutures on mesothorax well developed (Figs 27, 34; within Coelostomatini only present in part of *Coelostoma* and few aberrant *Dactylosternum*, largely or totally obliterated in all other Coelostomatini including *Lachnodacnum urichi*); and (3) phallobase well developed, long, without reduced anterior portion (Figs 15–16; in Coelostomatini also found in some *Dactylosternum*, but distinctly shortened in all other taxa, extremely so in many *Coelostoma*). All three mentioned character states are moreover shared with *Badioglobus* (an early branching taxon of the Sphaeridiinae) and the Rygmodinae (sister-group of the Sphaeridiinae), and are therefore very likely plesiomorphies within the Coelostomatini. This underlines the need to include *Lachnodacnum* in future phylogenetic analyses and justifies our attempt to redefine the genus to represent an unambiguous monophylum.

The identity of *Psilodacnum*. HANSEN (1991) followed ORCHYMONT (1937) in considering Lachnodacnum and Psilodacnum as closely related based on relatively small eyes and enlarged clypeus. The fact that both genera are specialized in bromeliads very likely also played some role. We have demonstrated that Lachnodacnum differs from Psilodacnum in many characters of supposed phylogenetic significance (morphology of mesothorax and genitalia, presence/absence of the femoral hydrophobic pubescence). At the same time, Psilodacnum agrees with *Phaenostoma* in all important characters, which is the reason for which we synonymized it with the latter genus. The shape of the clypeus and eyes varies considerably also within the broadly defined genus Dactylosternum and was demonstrated to be affected by the biology in some sphaeridiine taxa (FIKÁČEK et al. 2013, FIKÁČEK et al., in prep.). The preference for bromeliads clearly developed several times independently within the Sphaeridiinae (except Lachnodacnum and Psilodacnum, it is known for few Phaenonotum and two species of the omicrine genus *Omicrus*: ORCHYMONT 1937; HANSEN & RICHARDSON 1998; ALBERTONI & FIKAČEK, in press). Based on the detailed comparison of Lachnodacnum and Psilodacnum performed here, we suppose that both genera represent two independent shifts to bromeliads, and that the similarities highlighted by ORCHYMONT (1937) and HANSEN (1991) are convergencies gained due to the similar life style.

Immature stages of Lachnodacnum luederwaldti. Very little is known about the immature stages of the Coelostomatini. So far, larvae of four genera and seven species have been described: Coelostoma orbiculare (Fabricius, 1775) (HRBÁČEK 1943), Hydroglobus puncticollis (Bruch, 1915) (Archangelsky & Fernandez 1994), Phaenonotum exstriatum (Say, 1835) (Archangelsky & Durand 1992, Archangelsky 1997) and four species of Dactylosternum (one unidentified to species) (ARCHANGELSKY 1994, 1997; COSTA et al. 1988; DE MARZO 2000). The larva of L. luederwaldti seems to be most similar to Phaenonotum exstriatum, based on the nasale with three teeth (without teeth in other genera), epistomal lobes symmetrical and with 2-3 stout setae only (without setae in Dactvlosternum cacti (LeConte, 1855), otherwise shared with all other taxa), mandible with two retinacular teeth (with reduced retinacular teeth in Dactvlosternum abdominale (Fabricius, 1792) and D. cacti, two teeth shared with other taxa), labium with ligula (with reduced ligula in *Dactylosternum cacti*, present in all other taxa, unknown in D. abdominale) and the tergite on 8th abdominal segment divided in two halves in the third instar (shared with *Coelostoma* and *Phaenonotum* only). On the other hand, it differs from all remaining described coelostomatine larvae by the nasale asymmetrically tridentate, extremely depressed head capsule (possibly the adaptation to the life sandwiched between bromeliad leaves), and mandibles with inner basal face bearing small cuticular spines directed backwards. The head chaetotaxy may be compared in detail only with that of Coelostoma orbiculare (M. Fikáček, unpublished), with which Lachnodacnum shares the closely aggregated parietal setae PA7+12+13 (unique within Hydrophilidae, and hence a possible candidate for the autapomorphy of the Coelostomatini).

Two additional characters deserve the detail attention in the further studies of the larval Sphaeridiinae: the setation/chaetotaxy of the dorsolateral portion of the stipes, and the morphology of the abdominal tergite 8. Dorsolateral portion of stipes of Lachnodacnum bears short stout cuticular projections in the first instar (Fig. 57), these projections became longer in the second instar and in the third instar articulated setae (part of them long, part of them short and stout) are present in this area (Fig. 68). The setae of the third instar seem homologous with the cuticular spines of earlier instars. The transformation between instars was not studied in detail in other taxa, but numerous setae are also present in the dorsolateral portion of the stipes in the third instars of Phaenonotum exstriatum, Hvdroglobus puncticollis and Dactylosternum subrotundum (Fabricius, 1792). The transformation of cuticular projections of first and second instars into setae of the third instar may hence represent another candidate for the tribal apomorphy of the Coelostomatini. The abdominal tergite 8 is entire in the first instar of Lachnodacnum (Fig. 42), but becomes partly subdivided in the second instar and totally subdivided in the third instar (Fig. 38). It is not known whether the same is the case in other coelostomatine genera, but the presence of the subdivided tergite 8 in the third instar in Phaenonotum exstriatum and *Coelostoma orbiculare* may indicate so. In contrast, entire tergite 8 is present in the third instars of Dactylosternum and Hydroglobus. Further studies are needed to reveal whether the betweeninstar transformation series of tergite 8 is the same in all three genera.

Pupae of few sphaeridiinae taxa were described so far and only two of them belong to the Coelostomatini (*Dactylosternum cacti* described by ARCHANGELSKY (1994), *Phaenonotum extriatum* described by ARCHANGELSKY & DURAND (1992) and ARCHANGELSKY (1997)). The pupa of *Lachnodacnum luederwaldti* agrees with both these taxa in meso- and metanotum each bearing a pair of styli; it is similar to *D. cacti* by the number of styli on the pronotum,

and to *P. exstriatum* by the shape and distribution of the abdominal styli. On the other hand, the pupa of *L. luederwaldti* differs from pupae of *D. cacti* and *P. exstriatum* by having 24 pronotal styli, of which four are on the pronotal disc, two mesally near midline and two near anterior margin (*D. cacti* has 24 styli on pronotum, of which four are on the pronotal disc but are arranged in a transverse row near midline; *P. exstriatum* has a intraspecifically variable number of 20–26 styli on pronotum, 2–6 on the pronotal disc forming a transverse row near midline). *Lachnodacnum luederwaldti* has the strongly elevated scutellar shield (not elevated in *D. cacti* and *P. exstriatum*), pro- and mesotibia without apical spur but metatibia with short apical spur (all tibiae with apical spur in *D. cacti*, weakly bilobed in *P. exstriatum*).

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