An Acad Bras Cienc (2020) 92(3): e20190967 DOI 10.1590/0001-3765202020190967
Anais da Academia Brasileira de Ciências | *Annals of the Brazilian Academy of Sciences*
Printed ISSN 0001-3765 I Online ISSN 1678-2690
www.scielo.br/aabc | www.fb.com/aabcjournal

BIOLOGICAL SCIENCES

Description of the immature stages of *Stenocrates agricola* Dechambre & Hardy (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini) with redescription of the adult and discussion of its tribal position

MARIO G. IBARRA-POLESEL, JHON C. NEITA-MORENO & BRETT C. RATCLIFFE

Abstract: The enigmatic genus Stenocrates Burmeister has 52 species that are widely distributed from Mexico to Argentina, but mainly in South America. In the present study, the larva of the third instar and pupa of *Stenocrates agricola* Dechambre & Hardy, 2004 are described and illustrated based on specimens from Argentina, this being the first description of immatures for the genus. The adult is also redescribed, significantly expanding the number of characters and providing information on the natural history of this species. In addition, 28 species of Cyclocephalini and 20 species of Pentodontini are morphologically compared, emphasizing the most useful larval characters used among these beetles. *Stenocrates agricola* shows frequent and common characters of Pentodontini species but scarce (and even absent) characters typical of Cyclocephalini species, including some considered diagnostic for this tribe. Accordingly we consider that the tribal position of *Stenocrates* remains controversial and more study is needed to clarify the tribal status of *Stenocrates*. We believe that larval morphology provides important information in systematics studies that can clarify tribal relationships within the Dynastinae.

Key words: larva, morphology, pupa, scarab beetle, taxonomy.

INTRODUCTION

The larvae of pleurostict Scarabaeidae are commonly known as "white grubs", and some species are considered important crop pests, mainly due to the rhizophagous habit of their larvae (Ratcliffe & Cave 2006, Ritcher 1966, Rodrigues et al. 2018). In spite of this, taxonomic knowledge of the immature stages is scarce worldwide. In the Americas, the subfamily Dynastinae is divided into the following tribes: Cyclocephalini, Pentodontini, Oryctini, Phileurini, Agaocephalini, and Dynastini (Ratcliffe & Cave 2006). In the New World, Cyclocephalini comprises ca. 500 species (Ratcliffe & Cave 2015), but only 28 species (≈5.6%) have had larvae formally described (see Table I). Likewise, Pentodontini is comprised of 151 species in the New World (Morón 2017), but the larvae of only 20 species have been described (≈13.2%). Despite this, research interest in immature stages has increased in recent times. According to Moore et al. (2018), 80% of the descriptions of larvae and pupae of Cyclocephalini were published after 1990.

In several scarabaeoid studies, larval characters were used either alone or in combination with adult characters to establish natural groups and phylogenies (Micó et al. 2008). Since the larval morphology can reveal

Table I. **Described third instars of Cyclocephalini and Pentodontini species. *1 - cited as *Cyclocephala abrupta* Casey, 1863 (junior synonym) by Ritcher (1966); *2 - cited as *C. immaculate* (Olivier, 1789) (junior synonym) by Ritcher (1966); *3 - cited as *Bothynus gibbosus* (De Geer, 1774) (new combination) by Ritcher (1966); *4 - cited as *Ligyrus gianucai* Dechambre & Lumaret (1985) (junior synonym) by Neita & Ratcliffe (2017); *5 - cited as *Cheiroplatys pyriformis* (LeConte, 1847) (junior synonym) by Ritcher (1966).**

Cyclocephalini species	References	Pupa
Ancognatha manca (LeConte, 1866)	Ritcher (1966)	No
Ancognatha scarabaeoides Erichson, 1847	Vallejo & Morón (2008)	Yes
Ancognatha sellata Arrow, 1911	Ramirez-Salinas (2004)	Yes
Ancognatha ustulata Burmeister, 1847	Neita-Moreno & Morón (2008)	Yes
Aspidolea singularis Bates, 1888	Neita-Moreno et al. (2007)	Yes
Cyclocephala barrerai Martínez, 1969	Morón et al. (2014)	No
Cyclocephala borealis Arrow, 1911	Ritcher (1966)	No
Cyclocephala celata Dechambre, 1980	Souza et al. (2014b)	Yes
Cyclocephala comata Bates, 1888	Garcia et al. (2009)	No
Cyclocephala distincta Burmeister, 1847	Souza et al. (2014a)	Yes
Cyclocephala fasciolata Bates, 1888	Morón et al. (2014)	No
Cyclocephala fulgurata Burmeister, 1847	Bran et al. (2006)	Yes
Cyclocephala gregaria Heyne & Taschenberg, 1908	Bran et al. (2006)	Yes
Cyclocephala jalapensis Casey, 1915	Morón et al. (2014)	No
Cyclocephala longula LeConte, 1863 *1	Ritcher (1966)	No
Cyclocephala lunulata Burmeister, 1847	Morón et al. (2014), Bran et al. (2006), Stechauner & Pardo-Locarno (2010)	Yes
Cyclocephala lurida Bland, 1863 *2	Ritcher (1966)	No
Cyclocephala melanocephala (Fabricius, 1775)	Rodriguez et al. (2018)	Yes
Cyclocephala paraguayensis Arrow, 1903	Albuquerque et al. (2014)	Yes
Cyclocephala parallela (Casey, 1915)	Gordon & Anderson (1981)	No
Cyclocephala pasadenae (Casey, 1915)	Ritcher (1966)	No
Cyclocephala signaticollis Burmeister, 1847	Morelli (1991)	Yes
Cyclocephala sinaloae Howden & Endrödi, 1966	Morón et al. (2014)	No
Cyclocephala tucumana Bréthes, 1904	Fuhrmann et al. (2019)	Yes
Dyscinetus dubius (Olivier, 1789)	Neita-Moreno & Yepes (2011)	Yes
Dyscinetus morator (Fabricius 1789)	Ritcher (1966)	No
Dyscinetus rugifrons (Burmeister, 1847)	Vincini et al. (2000)	Yes
Stenocrates agricola Dechambre & Hardy, 2004	present publication	Yes

Pentodontini species	References	Pupa
Aphonus castaneus (Melsheimer, 1845)	Ritcher (1966)	No
Aphonus densicauda Casey 1915	Ritcher (1966)	No
Aphonus tridentatus (Say, 1823)	Ritcher (1966)	No
Bothynus medon (Germar, 1824)	Pereira et al. (2013)	No

Table I. Continuation

Pentodontini species	References	Pupa
Coscinocephalus cribrifrons (Schaeffer, 1906)	Morón & Deloya (1991)	Yes
Coscinocephalus tepehuanus Prell, 1936	Morón & Ratcliffe (1996)	Yes
Euetheola humilis rugiceps (LeConte, 1856)	Ritcher (1966)	No
Ligyrus (*Ligyrodes*) *relictus* (Say, 1825)	Ritcher (1966)	No
Ligyrus (*Ligyrodes*) *sallei* Bates, 1888	Ramírez-Salinas et al. (2004)	Yes
Ligyrus (*Ligyrus*) *gibbosus* (DeGeer, 1774) *3	Ritcher (1966)	No
Ligyrus (*Ligyrus*) *nasutus* (Burmeister, 1847)	Ramírez-Salinas et al. (2010)	Yes
Ligyrus (Ligyrus) rubripes (Boheman, 1858) *4	Dechambre & Lumaret (1985)	No
Neoryctes galapagoensis (Waterhouse, 1845)	Lumaret (1991)	No
Orizabus isodonoides Fairmaire, 1878	Morón (1976)	No
Orizabus pyriformis (LeConte, 1847) *5	Ritcher (1966)	No
Orizabus brevicollis Prell, 1914	Morón & Deloya (1991)	No
Oxygrylius ruginasus (LeConte, 1856)	Ritcher (1966)	No
Tomarus subtropicus (Blatchley 1922)	Gordon & Anderson (1981)	No
Philoscaptus bonariensis (Burmeister, 1847)	Morelli (1997)	Yes
Saccharoscaptus laminifer (Dechambre, 1979)	Morón (2017)	No

diagnostic characters that are informative at different taxonomic levels, some provide more reliable information than adult morphology alone on phylogenetic relationships of taxa because of the constancy of character states (Micó et al. 2008, Ritcher 1966, Sípek et al. 2009, Verdú et al. 2004).

With regard to the current classification at the tribal level of Dynastinae, some authors believe there are problems due to doubts about the characters distinguishing each of the tribes (Albertoni et al. 2014, Clark 2011, López-García et al. 2015, Morón & Ratcliffe 1996, Ratcliffe & Cave 2006, 2017). Some tribes that are sometimes separated by a unique, variable (or transition) character that is unreliable for grouping taxa at the tribal level (Ratcliffe & Cave 2015, 2017). Some specialists question whether the Cylcocephalini and Pentodontini are monophyletic clades (Albertoni et al. 2014, Clark 2011, López-García et al. 2015, Paucar-Cabrera & Moore 2018, Ratcliffe & Cave 2017). There are a few studies that, based on larval characters, have transferred from one tribe to another some taxonomically problematic genera, e.g., *Platyphileurus* Ohaus was transferred from Phileurini to Oryctini by Albertoni et al. (2014); *Scatimus* Erichson and *Heliocopris* Hope from Coprina to Dichotomiina by Edmonds & Halffter (1978); and *Coscinocephalus* Prell was transferred from Cylcocephalini to Pentodontini by Morón & Ratcliffe (1996). Others were transferred based on adult characters [*Parapucaya* Prell and *Pucaya* Ohaus were transferred from Pentodontini to Cylcocephalini by Paucar-Cabrera & Moore (2018) and *Acrobolbia* Ohaus from Rutelinae to Cyclocephalini by Jameson et al. (2002)].

The genus *Stenocrates* Burmeister (Dynastinae: Cyclocephalini) comprises 52 species distributed from Mexico to Argentina, with most occurring in South America (except Chile), and one species is known from the West

Indies (Jamaica) (Moore et al. 2018, Ratcliffe & Figueroa 2018). This is possibly the most difficult Dynastinae in the Americas with which to work (Ratcliffe & Cave 2015). Most of the species are externally similar and difficult or almost impossible to distinguish one from the other based on external characteristics, and great confidence is placed oin the form of the parameres to distinguish species (Ratcliffe & Figueroa 2018). Most females not associated with males cannot usually be identified with reliability, even by being taken in the same collecting event, since some species are sympatric. Ratcliffe (2015) provided the most recent comprehensive checklist for *Stenocrates*.

Because of the high number of cryptic species in *Stenocrates*, new species continue to be discovered and described (Ratcliffe & Cave 2015). Endrödi (1966, 1985) provided the latest synopsis of the genus, but 26 new species have been described since that time, including ten new species described in recent studies (Dechambre 2006, Dechambre & Hardy 2004, Ratcliffe 2015, Ratcliffe & Figueroa 2018). These species remain unincorporated in any of the currently available keys (a difficult task when emphasis must be placed on the parameres), and so an updated key to species is needed (Ratcliffe 2015). Nothing is known about the natural history of *Stenocrates* species. Adults can be collected at lights at night (Ratcliffe & Cave 2006). Until now, the immature stages were not described for the genus.

Stenocrates agricola Dechambre & Hardy (2004) occurs in Argentina and Paraguay. However, its description was remarkably brief and contained a small number of characters lacking detail; only the posterior view of the parameres was illustrated. In the paper, no information was provided about the habitat where the specimens were found.

Taking into account the unknown immature stages for *Stenocrates*, the brief description of the adult of *S. agricola*, the lack of information about its life history, and the importance of larval characters to establish hypotheses of phylogenetic relationships, the objectives of our study are: (1) describe and illustrate in detail the larva and pupa of *S. agricola*; (2) redescribe the adult, notably enlarging both the number of characters and the detail thereof in line with what has been used in recent taxonomic studies; (3) provide information about its natural history; (4) perform a comparative study of the characters present in all species of Cyclocephalini and Pentodontini formally described so far, emphasizing the larval characters most used in the systematics of these beetles. Unlike scarab beetles with large horns and marked sexual dimorphism (Dynastini, Agaocephalini, and Oryctini), or those with the mentum strongly expanded and body usually flattened (Phileurini), the Cyclocephalini and Pentodontini are characterized by only slight sexual dimorphism, and many characters are shared or transitional between both groups (both larval and adult).

MATERIALS AND METHODS

Specimens examined

The description of the immature stages is based on four third instars, one prepupa, seven larval exuviae, and five pupae. Twelve third instars were found in the soil under tree trunks inside a forest. Locality data: "ARGENTINA: Chaco, Bermejo, General Vedia, 26°56'2.60"S, 58°38'50.53"O, 64msn, 10.XII.2014, bosque, colecta directa, M. Ibarra Polesel col." The larvae were transported to the laboratory where they were individually kept in 1-L plastic containers with a 5 cm deep soil layer and small logs in order to recreate the same environmental conditions where they were found. The specimens were maintained in the laboratory at room temperature (25 ± 3 °C), 60–80% humidity, and a natural photoperiod (13 hr light, 11 hr dark). Seven larvae were reared, five reached the pupal stage (two females and three males), and two the adult stage (males).

The description of the adult stage is based on six females and 14 males. Locality data: “ARGENTINA: Chaco, 1° de Mayo, Reserva Educativa Colonia Benítez, 27°19’5.14”S, 58°57’0.98”O, 54msn, 13.XII.2010, bosque, trampa de luz, col. M. Ibarra Polesel. Chaco, San Fernando, Estancia San Francisco, 27°30’39.80”S, 59°4’49.30”O, 56msn, 17.X.2013, bosque, trampa de luz, col. M. Ibarra Polesel. Chaco, Bermejo, Estancia San Carlos, 26°58’40.6”S, 58° 39’03.0”O, 63msn, 7.XII.2015, selva galería, trampa de luz, col. M. Ibarra Polesel”. All specimens are placed in the collection of the Cátedra de Biología de los Artrópodos, Departamento de Biología, Universidad Nacional del Nordeste, Corrientes, Argentina

Specimens preparation, illustration and terminology

Larvae used for morphological studies were killed by immersion in boiling water for 20 seconds and preserved in 70% alcohol for description. The photographs were taken using a Canon EOS T3i digital camera mounted on a Leica EZ4 stereomicroscope, and an Olympus CH-2 light microscope (for the spiracular holes). The software Combine ZP, Photoshop CC, and Illustrator CC were used for image processing. The specimens preserved in alcohol were weighed using a precision balance, UWE NJW 150. Characters and terms used in the larval and pupal descriptions were adopted from Morón & Ratcliffe (1996), Ritcher (1966) and Sawada (1991).

Considerations

Due to the particular morphological characteristics found in the larva of *S. agricola*, a comparative analysis was carried out among the 27 species of Cyclocephalini and the 20 known species of Pentodontini. The characters examined and compared are those commonly used in taxonomic keys to species of larval Cyclocephalini and Pentodontini, as well as those considered diagnostic at the tribal and generic levels (Moore et al. 2018, Morón 2017, Morón & Ratcliffe 1996, Neita-Moreno & Morón 2008, Neita-Moreno & Yepes 2011, Pardo-Locarno et al. 2009, Pereira et al. 2013, Ritcher 1966). Because some works are inconsistent in the description and illustration of certain morphological characters, we illustrate characters that are of greatest descriptive value.

Diloboderus abderus Sturm is not included in this study because, based on larval characters, it was transferred to the tribe Agaocephalini (see Morón 2017). *Cyclocephala testacea* Burmeister, described by Morelli & Alzugaray (1994) is also not considered because it has characters more in common with the subfamily Melolonthinae. We also do not include species that have no formal description, such as *Cyclocephala modesta* Burmeister and *Cyclocephala putrida* Burmeister that were included only in a key to *Cyclocephala* larvae from Uruguay (Morelli & Alzugaray 1994).

RESULTS

Description of third instar of *Stenocrates agricola*

Dorsal body length 65.9–68.2 mm, width 8.7–9.2 mm, weight 1.7–1.9 g (preserved specimens).

Head. *Cranium* (Fig. 1a): Width of head capsule 4.7–5.7 mm. Color dark brown to black. Surface strongly punctate, with moderately

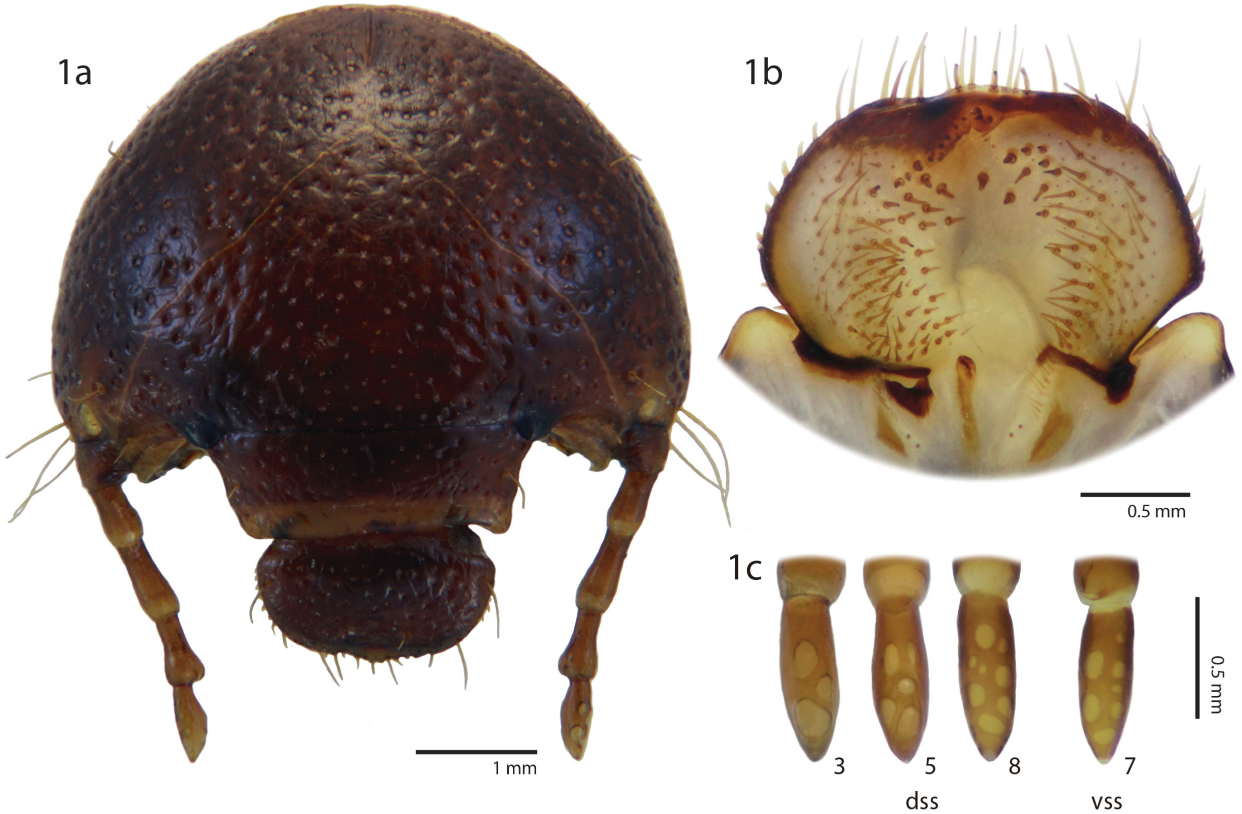

Figure 1. ***Stenocrates agricola*, third instar. Head and antenna (a–c). (a) Cranium in frontal view. (b) Epipharynx. (c) Terminal segment of antenna with three, five, and eight dorsal sensory spots (dss) and with seven ventral sensory spots (vss).**

scattered pits. Epicranial, frontal, and clypeo-frontal suture distinct. *Frons* (Fig. 1a): Exterior, posterior, and anterior frontal setae absent. Each anterior angle with 1–2 setae. Pits slightly smaller than those of the dorsal cranial surface. Remaining cranial surface with 1 posterior epicranial seta on each side, 1 anterior epicranial setae near each stematta, and 3 exterior epicranial setae each side. Non-pigmented stematta present. *Clypeus* (Fig. 1a): Trapezoidal. Surface of postclypeus well sclerotized, with only 2 exterior clypeal setae. Punctures smaller than those of frons. Surface of preclypeus dark brown, lacking punctures. *Labrum* (Fig. 1a): Slightly asymmetrical, with pits similar to those of postclypeus, with 2 exterior labral setae, 2 anterior labral setae, and 2 paramedian labral setae. *Epipharynx* (Fig. 1b): Transversely suboval in shape, slightly asymmetrical, left lateral margin angulate. Haptomeral process entire, obliquely crenulated, not notched, sensilla present. Right chaetoparia with 81 setae, left chaetoparia with 53 setae, and with about 90 sensilla interspersed among setae of in both right and left chaetoparia. Acroparia with 12–14 straight, long, thick setae; corypha with 9 long setae; right and left acanthoparia with 8–12 short, curved, spine-like setae. Pedium 1.4 times longer than wide, without setae. Dexiotorma narrow, elongate; laeotorma shorter than dexiotorma; pternotorma rounded. Dexiophoba and laeophoba absent; mesophoba well-developed between haptolachus and inner side of laeotorma, formed by 16–20 small, slender

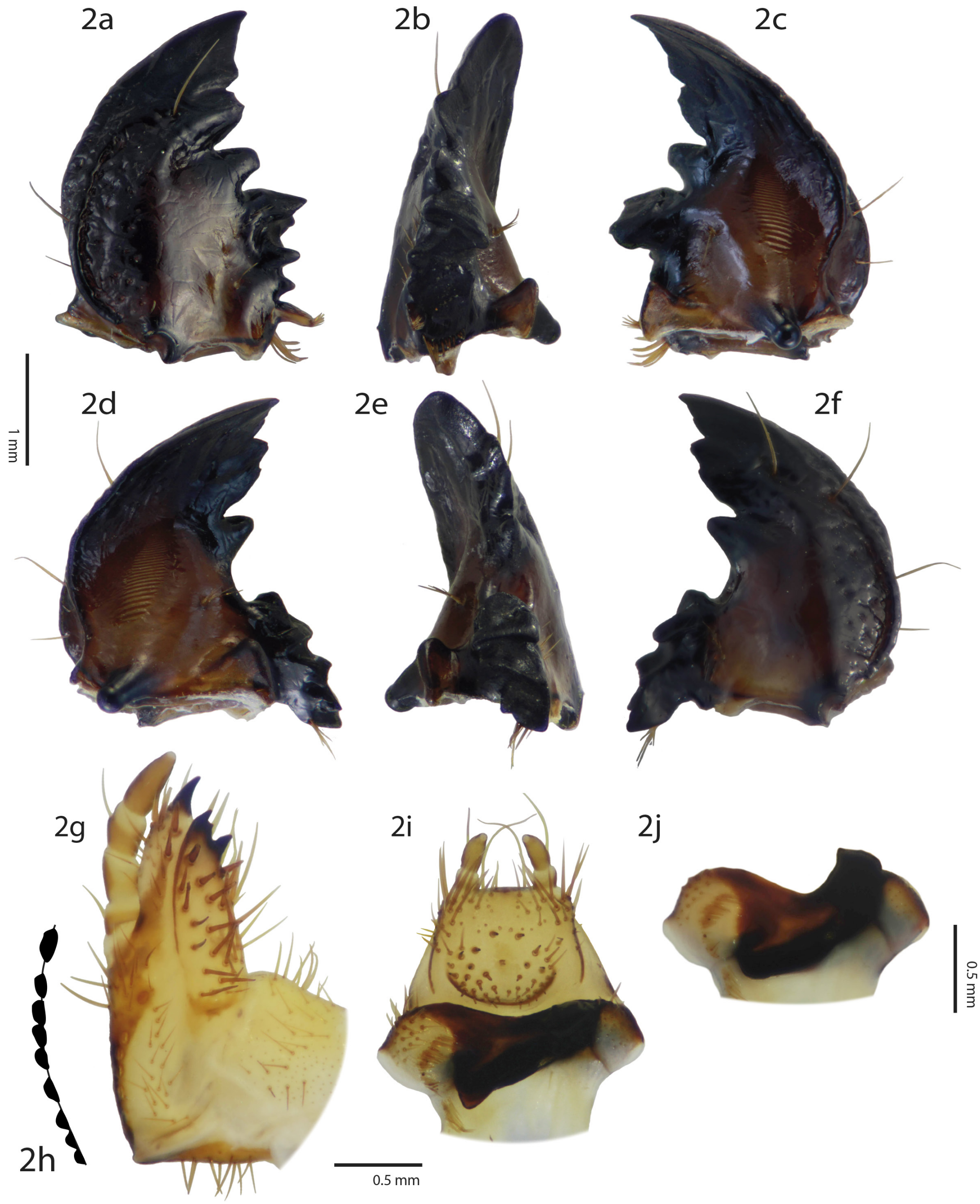

Figure 2. ***Stenocrates agricola*, mouthparts of third instar. (a–j). (a) Left mandible in dorsal view, (b) lateral view, and (c) ventral view. (d) Right mandible in ventral view, (e) lateral view, and (f) dorsal view. (g) Left maxilla in dorsal view and (h) detail of stridulatory teeth. (i) Dorsal view of labium and (j) detail of hypopharyngeal sclerome.**

setae. Sclerotized plate of right nesium well-developed, acute at apex, with 8 setae on the base. Sense cone on left nesium represented by longitudinal, sclerotized, rounded plate. Crepis slightly defined, with 4 lateral sensilla. *Antenna* (Fig. 1c): Four antennomeres; antennomeres 1–3 and 2–4 subequal in length, antennomere 3 with a process distally; terminal antennomere about

0.75–0.85 times longer than antennomeres 3–1 respectively, and 1.05 times length of antennomere 2. Dorsal surface of terminal antennomere with 3–8 dorsal sensory spots (mostly with 3 or 4), ventral surface with 3–6 sensory spots and a sensory spot at apex.

Mouthparts. *Left mandible* (Figs. 2a–c): Scissorial region with 4 teeth, teeth S1 and S2 forming a broad apical plate, separated from S3 by a shallow scissorial notch. Tooth S3 rounded, separated from S4 by acute and deep postincisor notch. S4 cylindrical and blunt apex. Scrobis with 2 long, stout setae and 2–4 slender, short setae. Basolateral area broadly concave. Acia well developed, acute, with 5–7 basolateral setae. Dorsal surface with 1 long, stout seta at level of apex of tooth S3; dorsomolar area with row of 6–9 slender setae. Preartis evident, concave. Ventral surface with elongated stridulatory area formed by approximately 28 subparallel ridges, ridges widely separated at the base and narrowing gradually towards the apex. Molar area with 3 lobes, first molar lobe (M1) large, not subdivided and below 2 acute lobes and with a tuft of 5 ventral molar setae at the center. Brustia with 10–14 robust, long bristles. Postartis large, rounded. Ventral process triangular, well developed. *Right mandible* (Figs. 2d–f): Scissorial region with 4 teeth, basal tooth separated from S1–S3; S1 and S2 separated from S3 by scissorial notch, S4 entire, well developed, conical. Dorsal surface with 2 stout, long setae at level of S2 and S3. Scrobis with 2 long, stout setae and 2–4 slender, short setae. Basolateral area broadly concave. Dorsomolar area with row of 6–9 slender setae. Preartis evident, concave. Ventral surface with elongated stridulatory area formed by 26 subparallel ridges. Molar area with a tuft of 6 ventral molar setae. Molar crown with 3 large lobes. Calyx well developed, dorsally ending in slightly acute denticle. Ventral process triangular. Brustia with 6–9 stout setae. Postartis large, rounded. *Maxilla* (Fig. 2g): Galea and lacinia fused, forming a mala. Galea dorsally with 3 strong, spine-like setae and 1 well developed uncus at the apex, approximately 0.6 times length of last segment of maxillary palpus. Lacinia with 2 unci, apical uncus with 2 teeth fused at their bases; dorsal area with approximately 20 spine-like setae. Maxillary palpus with 4 palpomeres; palpomeres 3, 2, and 1 are 0.6, 0.7, and 0.4 times length of palpomere 4 respectively. Stridulatory area formed by 6–9 blunt, truncated teeth and a truncated anterior process (Fig. 2h). *Labium* (Figs. 2i, j): Hypopharyngeal sclerome asymmetric, medially concave; right side with well-developed, truncate process forming a right angle on inner side; left side with well-developed basal process. Glossa with 25–30 long setae and 30–35 short, spine-like setae; apical area with approximately 15 sensillae. Left lateral lobe with 16–20 slender, moderately long setae; right lateral lobe with 5–12 slender setae. Left margin with row of 22–28 setae grouped in a compact line, directed toward center of sclerome and a row of approximately 12 setae near base of sclerome.

Thorax. Pronotum weakly sclerotized, with 20 slender, long setae (Fig. 3a, Table II). Prothoracic spiracle 0.6 mm long, 0.38 mm wide (Fig. 3b); respiratory plate yellowish brown, "C" shaped, spiracular bulla rounded, barely elevated; distance between 2 lobes of respiratory plate much smaller than dorsoventral diameter of bulla. Plate with 25–30 microscopic pores across diameter at middle, holes with regular edges, not in definite rows (Fig. 4). Mesonotum and metanotum with variable number of setae (Table I). *Legs*: Tarsal claws falcate, with 1 basoexternal seta and 1 internal, preapical seta (Fig. 3c). All tarsal claws of similar size (0.46–0.53 mm). Legs gradually increase in length from first to third pair (Fig. 3d). Coxa, trochanter, femur, and tibia of all legs with many long, stout setae.

Table II. Chaetotaxy on thoracic and abdominal segments of third instar *Stenocrates agricola*. Long (L) and short setae (S) are mentioned for prescutum (PRSC), scutum (SCU), scutellum (SCL), spiracular area (SPA), pleural lobe (PLL), pedal area (PEA) and eusternum (EUS).

Segment/Terguite	PRSC		SCU		SCL		SPA	PLL	PEA	EUS
	L	S	L	S	L	S	L	L	L	L
Pronotum			20							
Mesonotum	2		8					3		
Metanotum	2		8					2		
Abdominal segment I		4	8	8	2	14	1	1		2
Abdominal segment II		11	8	30	2	28	1	3	1	2
Abdominal segment III		30	8	28	4	26	1	3	1	2
Abdominal segment IV		28	8	26	2	24	1	3	1	2
Abdominal segment V		26	8	32	2	24	1	3	1	2
Abdominal segment VI		32	8	18	2	8	1	3	1	2
Abdominal segment VII			4				1	3	1	2
Abdominal segment VIII			4				1	3	1	2
Abdominal segment IX+X			4					3		

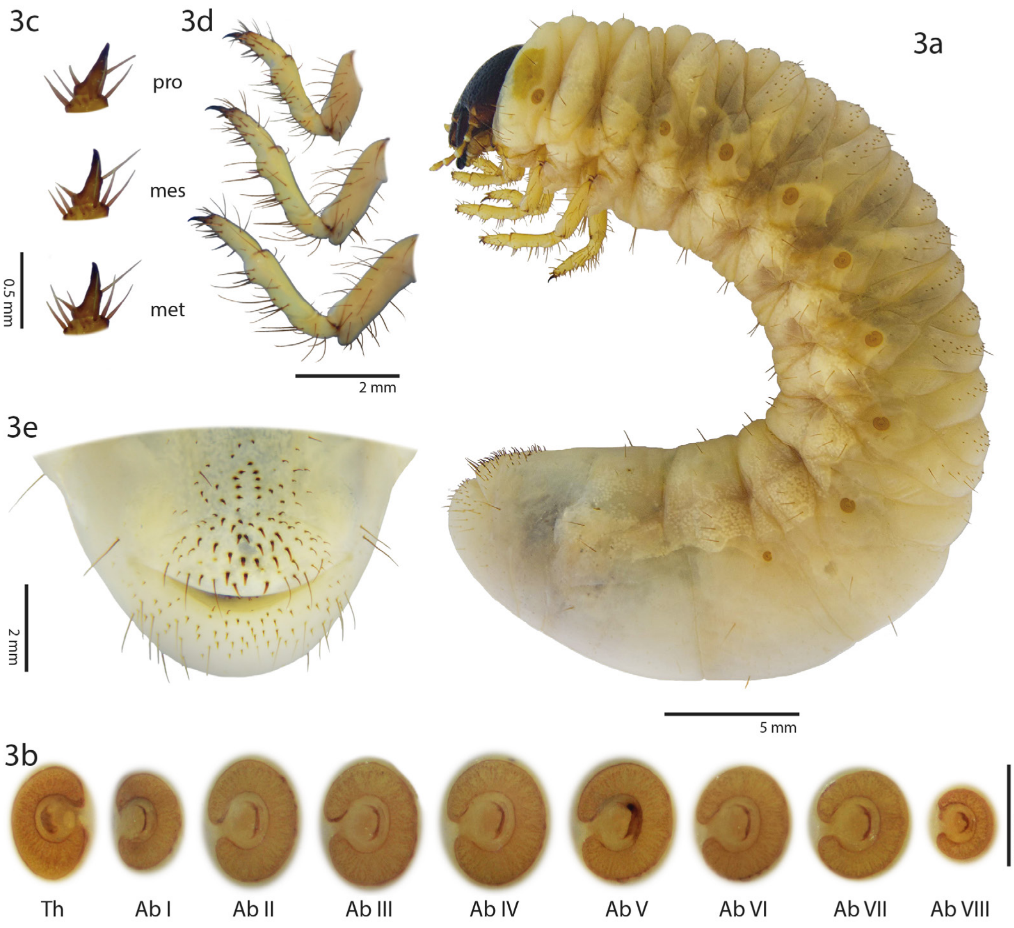

Figure 3. *Stenocrates agricola*, third instar. (a) Habitus of larva in lateral view. (b) Thoracic spiracle (Th) and sequence of abdominal spiracles from first (Ab I) to last (Ab VIII). (c) Claws in dorsal view from prothoracic (pro), mesothoracic (mes), and metathoracic (met) legs. (d) Lateral view of prothoracic (pro), mesothoracic (mes), and metathoracic (met) legs. (e) Detail of the last abdominal segments in dorsal view.

Figure 4. ***Stenocrates agricola*, thoracic spiracle and detail of the spiracular holes.**

Abdomen. Abdominal spiracle I 0.51 mm long and 0.33 mm wide (Fig. 3b), smaller than spiracles II–VII. Spiracles of segments II and V of subequal size (0.65 mm long and 0.45 mm wide), spiracles VI, VII, and VIII progressively reduced in size (Fig. 3b), the last is the smallest (0.35 mm long and 0.31 mm wide). Abdominal segments with a relatively constant number of setae (Fig. 3a; Table II); segments VII–X without short setae. *Raster* (Fig. 3e): Surface with palidia, sometimes not well defined, that generally forms an oval septula; each palidium formed by row of 5–8 short, thick, spine-like pali directed caudally. Campus without setae; tegillum with 18–22 hamate setae. Barbula with 2–4 long setae. Ventral anal lip with 15–20 stout, flattened setae, curved at the center; laterally with 20–24 short, slender setae; anal margin with 4–6 long, cylindrical setae. Dorsal anal lip with 36–50 short, flattened setae and 20–30 long, cylindrical setae. Anal slit transverse.

Description of pupa of *Stenocrates agricola*

Female

Length 17.9–18.9 mm; greatest width 8.8–9.2 mm; weight 0.49–0.51g (preserved specimens). Form adecticous, exarate, body oval, slightly elongate, stout. Color yellowish brown (Figs. 5a–c).

Head. Surface glabrous, mouthparts directed ventrally; antenna, labrum, mandibles, maxillae, and palps discernible; antennal thecae expanded, stout, with rounded apices. Compound eyes sunken, partially covered by anterior edges of pronotum.

Thorax. Surface glabrous. Pronotal disk slightly convex, wider than long, wider posteriorly, basal margin and center of base clearly rounded. A narrow, median, longitudinal sulcus extends from apex to base. Pronotum, mesonotum, and metanotum discernible. Thoracic spiracle prominent, with sclerotized peritreme, in cavity formed between anterior and medial legs, hypomeron, and elytral thecae. Metasternum wider than long. Elytral and posterior wing thecae appressed, curved ventrally around body; elytral thecae extending to middle of abdominal segment III; posterior wing thecae extending to end of abdominal segment IV. *Legs*. Protibia with 3 distinct teeth on external edge. Mesotibiae and metatibiae with inner and outer spines well developed at apices. Mesotibiae and metatibiae each with 2 tubercle-like, apical spurs. Metafemora and metatibiae covered by elytra and wings. Tarsomeres and pretarsus slightly indicated.

Abdomen. Tergites III–X well defined, convex, segments III and IV the widest; pair of

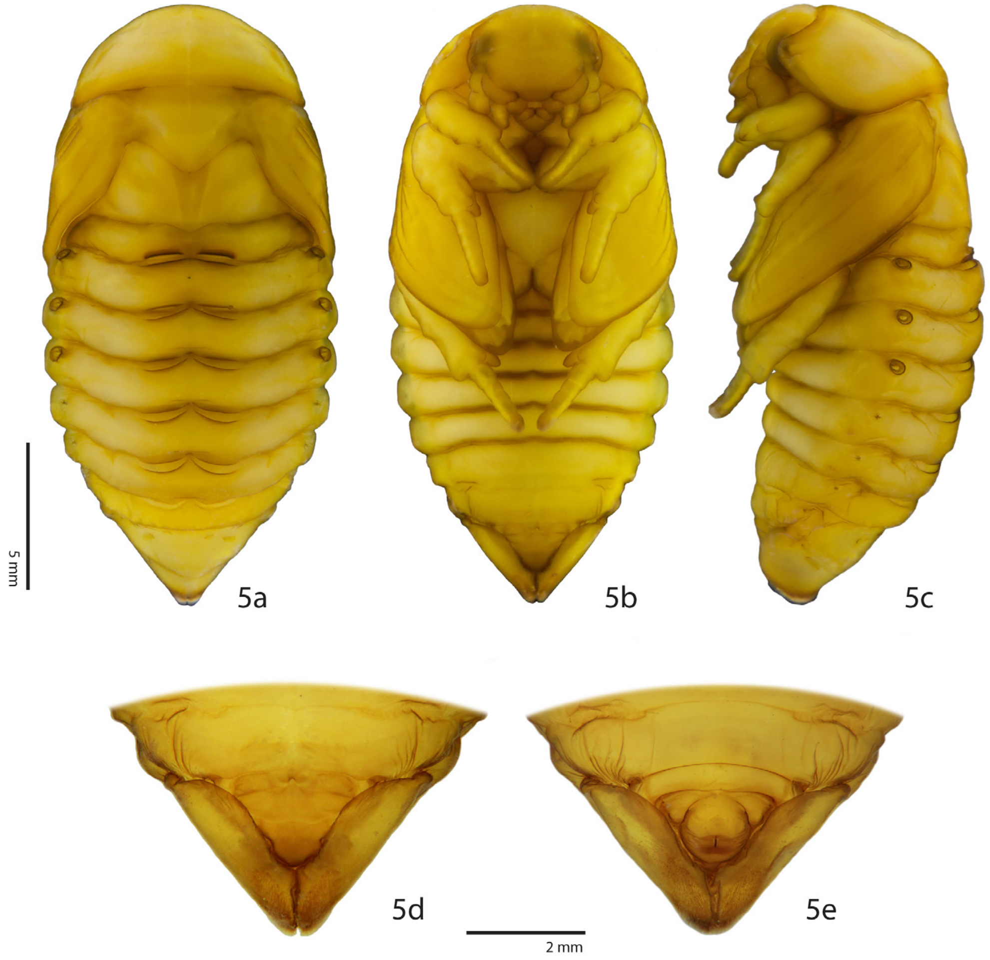

Figure 5. ***Stenocrates agricola*, female and male pupa. Female: (a) dorsal view. (b) Ventral view. (c) Lateral view. (d) Ventral view of apex with genital ampulla. Male: (e) ventral view of apex with genital ampulla.**

dioneiform organs present between segments I–II, II–III, III–IV, IV–V, V–VI, and VI–VII, the last pair scarcely sclerotized. Spiracle I elongate, with fine peritreme, covered by wing thecae; spiracles II–IV ovate, prominent, each with strongly sclerotized peritreme; spiracles V–VIII closed. Pleural lobes rounded. Sternites II–VI distinct; sutures between segments VII and X not complete, partially fused. Sternites XII and XIII longest. Terminal tergite without urogomphi, fleshy lobes with an apical, velvety, white-gold vestiture extending ventroapically. Surface of last sternite smooth; genital ampulla and genital pore distinct (Fig. 5d).

Male pupa: Length 16.1–17.8 mm; greatest width 7.8–8.7 mm; weight 0.36–0.47 g (preserved specimens). Same as female, but sternite IX anteriorly convex. Genital ampulla subtriangular, basal area a rounded structure with the circular area glabrous at base, glabrous area with longitudinal, dark line at apex (Fig. 5e).

Redescription of adult of *Stenocrates agricola*

Male

Length 14.3–17.8 mm; width 7.6–8.6 mm. Body elongated, subparallel, slightly enlarged backwards. Color shiny black (Figs. 6a–d).

Head. Clypeus trapezoidal, apex with truncated upper border and lower edge slightly emarginate and slightly thickened, lateral

Figure 6. *Stenocrates agricola*, habitus of male adult: (a) ventral view. (b) Dorsal view. (c) Lateral view. (d) Perspective view. (e) Female, detail of abdominal sternum.

margins straight and slightly arched towards ocular canthus; surface on anterior half and basal margins strongly rugopunctate, middle area smooth with small punctures (Fig. 7a). Frontoclypeal furrow well defined, preceded by thin carina interrupted at middle by 2 weakly oblique sections. Ocular canthus thick, rounded, not protruding. Frons with surface moderately punctate, only basal margin densely punctate. Interocular width equals 4.0 transverse eye diameters. Antenna with 10 antennomeres, club subequal in length to antennomeres 2–7. *Mandibles:* external border and apex rounded (Fig. 7b). Mandibular molar area of right mandible with surface slightly convex, with 8 transverse keels and rows of circular micropunctures in valleys of the keels, distal portion with a round depression (Fig. 7c). Mandibular molar area of left mandible with surface slightly concave, with 3 transverse keels, distal portion with a round depression. *Maxilla:* Moderately robust; galea on inner surface with 6 long teeth, 1 apical and 1 shorter preapical teeth, 1 central tooth and 3 basal teeth aligned transversely (Fig. 7d); paraglossa developed, apex slightly concave at center. *Labium:* Slightly longer than wide, paraglossa well developed, apex slightly concave at center and margin setose; disk of mentum with scattered, long setae (Fig. 7e). *Labrum:* Wider than long, anterior border slightly sinuate (Fig. 7f).

Thorax. *Pronotum:* Wider than long (1: 0.65); anterior angles acute, posterior angles rounded; surface shiny, with sparse, small punctures on disc and a field of large, dense punctures in small area of anterior angle and larger area

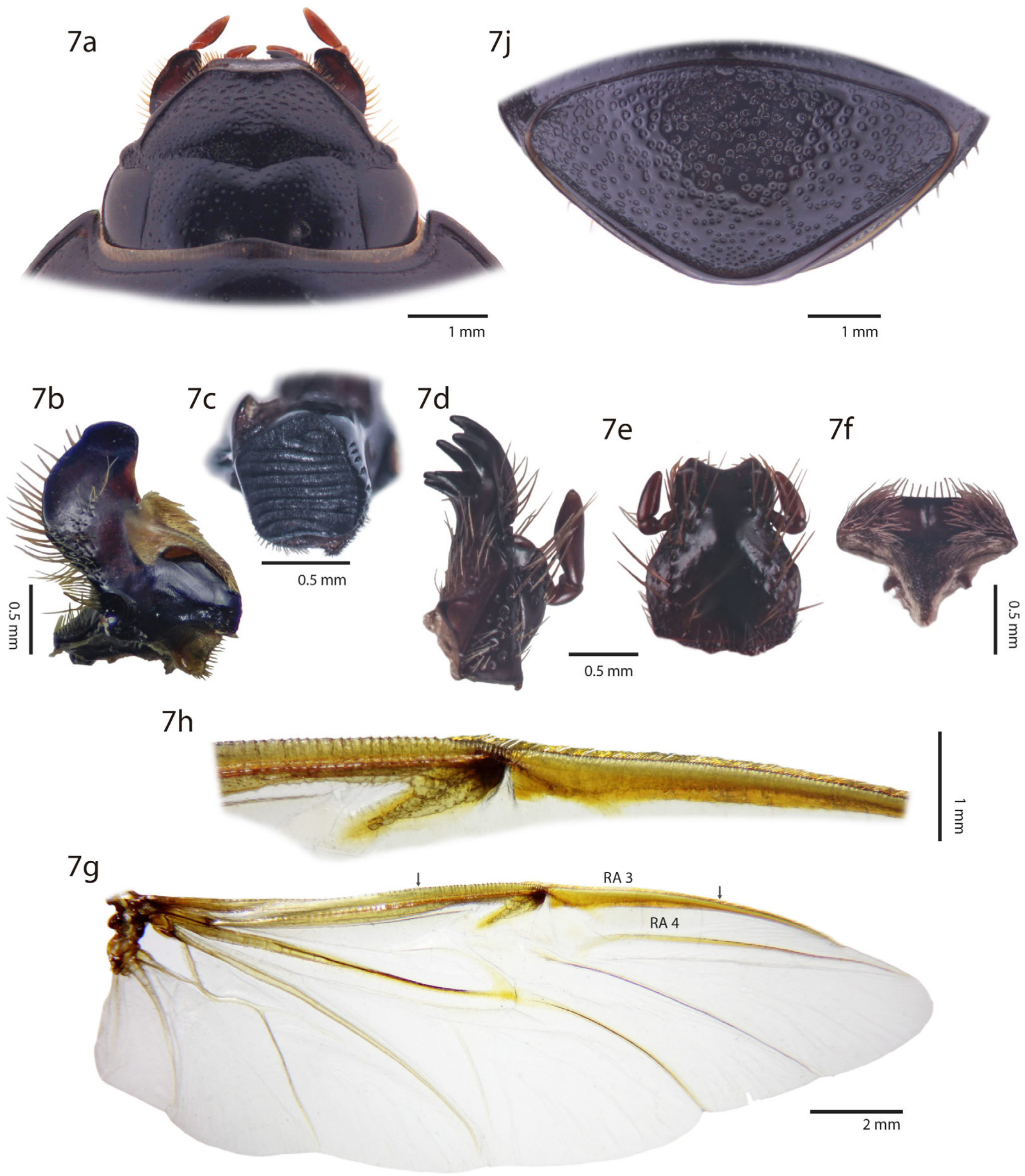

Figure 7. *Stenocrates agricola*, morphological characters (a) head, dorsal view. (b) Left mandible, dorsal view, and (c) detail of molar area. (d) Left maxilla, ventral view. (e) Mentum, ventral view. (f) Labrum. (g) Hind wing and (h) detail of veins RA and RA 3 showing presence of setae befor and after the apical hinge.

of posterior angle (Figs. 6b–d). Lateral margins with thick marginal bead, anterior margins with bead briefly interrupted at middle, base without marginal bead. Scutellum finely and more densely punctuate on basal area, becoming smooth on apical area. *Elytra:* Longer than wide (1: 0.87); surface shiny, with strong, horseshoe-shaped punctures, punctate sutural stria, 2 pairs of distinct discal striae, and 2 pairs of indistinct striae behind humerus; each stria comprised of large, deep, closely adjacent punctures (Figs. 6b–d). First broad interval with simple or double, irregular row of similar punctures, second interval with simple row of punctures only on apical third. *Hind wings:* Radius vein with single row of pegs, area near apical hinge with row of long, erect setae (Figs. 7g, h), anterior edge distal to apical hinge with erect setae and lacking membranous border. Veins RA 4 and RA 3 separated at their bases.

Abdomen. *Pygidium:* Subtriangular, wider than long (1: 0.5); surface shiny, glabrous, strongly and densely punctate, punctures large, strongly ocellate. In lateral view, surface regularly convex (Fig.7j). *Legs:* Protibia tridentate, basal tooth slightly removed from other teeth, spur straight. Protarsus simple, not enlarged. Mesotibia and metatibia dorsoventrally flattened, with 2 external, transverse carinae, each with row of spine-like setae; mesotibial carinae crenulated. Metatibia with apex truncate and a few, short, thick setae (usually 7). Metatarsus shorter than metatibia. Mesocoxae and metacoxae adjacent, not widely separated. *Venter:* Prosternal process columnar, moderate in length, not extending beyond level of procoxae; in lateral view apex slightly transversely acuminate, with slender, long, reddish setae; shape suboval in ventral view. Mesosternum slightly concave, surface glabrous, nearly smooth at middle and strongly punctate on sides, punctures horseshoe-shaped. *Genitalia:* Aedeagus with short phallobase, 1.4 times as long as parameres. Parameres symmetric, about 0.65 times wider than long, with angular lateral lobes, apex narrow and curved outwards (Figs. 8a–c). Spiculum gastrale Y-shaped; basal sclerite straight; lateral sclerites longer than basal; associated plates short (Fig. 8d). The internal sac armature consists of 4 well defined sclerites (Figs. 8e–i).

Female: Length 16.7–18.1 mm; width 8.3–8.6 mm. Similar to male, but pygidium of female 1.14 times longer and less convex than in male. Last sternite of female twice as long as in male (Fig. 6e). Gonopods IX monomeric (Fig. 8j), reduced to coxosubcoxite (a fusion of subcoxite IX and coxite IX). Subcoxal part broad, convex, weakly sclerotized, with 7–9 long setae on inner margin. Coxal part smaller, subtriangular, well sclerotized, slightly concave, with posterior edge bearing a brush of elongated, dense setae.

Life History Notes

Stenocrates agricola probably completes its life cycle in one year. Larvae were found in the soil under tree trunks at the beginning of December. In the laboratory, the first pupae were observed in late December and were retained in the larval exuvium, and the adults emerged in mid-January. Some of the larvae were already parasitized by Tachinidae (Diptera).

In northeastern Argentina , adults were captured at light traps from October to February. *Stenocrates agricola* seems to be an exclusive species of wooded environments. It is frequently captured in gallery forest and rarely in quebrachal forest; it has never been captured in pastures, where light traps are more efficient, and only one specimen was collected in a palm grove of *Copernicia alba* Morong (Arecaceae) (Ibarra-Polesel M.G., unpublished data).

During a three-year study conducted by Ibarra-Polesel & Damborsky (2018) at a small protected forest in Argentina, *S. agricola* was one of the most abundant species in 2010, although it was not collected in 2011, and in low abundance in 2012. The authors attributed the population fluctuation over the years to climatic variations, especially to the amount and duration of rainy periods. The highest annual rainfall values were recorded in 2010, which coinciding with the largest catch of this species. In the framework of a study conducted by Ibarra-Polesel et al. (2015), for dung beetles (Scarabaeidae: Scarabaeinae) in the aforementioned protected area, *S. agricola* specimens were caught in baited pitfall traps with 85% of the individuals captured in traps baited with carrion, and the remaining 15 % in traps baited with fecal matter.

Comparison with other larvae of Cyclocephalini and Pentodontini

Out of the 13 larval characters analyzed throughout the 48 species considered from both

Table III. **Main characters used in the systematics of larvae of species of New World Cyclocephalini and Pentodontini. Cranium: color; presence or absence anterior frontal seta (AFS); posterior front seta (PFS); number of dorsal sensory spots (DSS) in antenna. Mouthparts: shape of haptomeral process (HP); presence of post-scissorial tooth on left mandible (PT-S4); shape of maxillary stridulatory teeth (SMST); number of maxillary stridulatory teeth (NMST). Thorax: number of holes in respiratory plate (Holes). Abdomen: size of abdominal spiracles I–VIII (SAS I–VIII); presence or absence of palidia.**

Tribe/Species	**Cranium**			**Mouthparts**				**Thorax**	**Abdomen**	
	AFS	**PFS**	**DSS**	**HP**	**PT-S4**	**SMST**	**NMST**	**Holes**	**SAS I–VIII**	**Palidia**
Cyclocephalini										
Ancognatha manca	No	No	2	entire	Yes	truncate	9–10	20–35	similar	No
Ancognatha scarabaeoides	No	No?	2	notched	Yes	truncate	11	–	I,II>III–V>VI–VIII	No
Ancognatha sellata	No	No	2	notched	Yes	truncate	7–9	–	similar	No
Ancognatha ustulata	No	No	2	notched	Yes	truncate	9	≈27	I–VI<VII,VIII	No
Aspidolea singularis	Yes	Yes	2	notched	No	truncate	7	21	I–VI<VII,VIII	No
Cyclocephala barrerai	Yes	Yes	2–3	notched	No	truncate	8–10	–	I–VI<VII,VIII	No
Cyclocephala borealis	Yes	Yes	2	notched	No	truncate	7–9	12–22	I–VI<VII,VIII	No
Cyclocephala celata	Yes	Yes	2	notched	No	–	4	–	–	No
Cyclocephala comata	No	No	–	–	–	–	–	–	–	No
Cyclocephala distincta	Yes	Yes	2	notched	Yes	truncate	6–9	–	I–VI<VII,VIII	No
Cyclocephala fasciolata	No	Yes	2	notched*	Yes	truncate	8	–	II–VI>I,VII,VIII	No
Cyclocephala fulgurata	Yes	Yes	2	notched	No	truncate	9–10	–	I–VI<VII,VIII	No
Cyclocephala gregaria	Yes	No	2	notched	No	truncate	8–9	–	I–VI<VII,VIII	No
Cyclocephala jalapensis	No	Yes	2	notched*	Yes	truncate	5–6	–	I–VI<VII,VIII	No
Cyclocephala longula	Yes	Yes	2	notched	No	truncate	≈10	15–19	I–VI<VII,VIII	No
Cyclocephala lunulata	Yes	Yes	2	notched	No	truncate	7–8	–	I–VI<VII,VIII	No

Table III. Continuation

Tribe/Species	Cranium			Mouthparts				Thorax	Abdomen	
	AFS	PFS	DSS	HP	PT-S4	SMST	NMST	Holes	SAS I–VIII	Palidia
Cyclocephala lurida	Yes	Yes	2	notched	No	truncate	7–9	14–22	I–VI<VII,VIII	No
Cyclocephala melanocephala	Yes	Yes	2	notched	No	truncate	13	11–16	I–VI<VII,VIII	Yes<
Cyclocephala paraguayensis	Yes	Yes	2	notched	No	–	10	–	I–VI<VII,VIII	Yes<
Cyclocephala parallela	–	–	2	notched	–	–	–	–	–	No
Cyclocephala pasadenae	Yes	Yes	–	notched	No	–	–	9–16	I–VI<VII,VIII	No
Cyclocephala signaticollis	Yes	Yes	2	notched	No	truncate?	9	–	–	No
Cyclocephala sinaloae	Yes	Yes	2	notched	Yes	truncate	7	–	I–VI<VII,VIII	No
Cyclocephala tucumana	Yes	Yes	2	notched	No	truncate	9–10	14–17	I–VI<VII,VIII	Yes
Dyscinetus dubius	No	Yes	2	entire	Yes	truncate	7	≈27	I–VI<VII,VIII	No
Dyscinetus morator	No	Yes	2	entire	Yes	truncate	≈10	23–34	similar	No
Dyscinetus rugifrons	No	Yes	2	entire?	Yes	truncate	7–11	≤38	II–VII>I,VIII	No
Stenocrates agricola	No	No	3–8	entire	Yes	truncate	6–9	25–30	II–V>I,VI–VIII	Yes
Pentodontini										
Aphonus castaneus	Yes	Yes	1	entire	No	sharp–pointed	9?	12–17	I–IV>V–VIII	No
Aphonus densicauda	Yes	Yes	1	entire	No	sharp–pointed	9–11	12–20	I–IV>V–VIII	No
Aphonus tridentatus	Yes	Yes	1	entire	No	sharp–pointed	10–12	≤20	I–V>VI–VIII	No
Bothynus medon	No	Yes	12	entire	Yes	truncate?	10–11	≈35	I–VII>VIII	No
Coscinocephalus cribrifrons	Yes	Yes	2	entire	Yes	truncate	8–9	–	similar	No
Coscinocephalus tepehuanus	Yes	Yes	2	entire	Yes	truncate	8–9	38–43	similar	No
Euetheola humilis rugiceps	Yes	No	2	entire	Yes	truncate	≈9	16–32	II–V>I,VI–VIII	Yes

Table III. Continuation

Tribe/Species	**Cranium**			**Mouthparts**				**Thorax**	**Abdomen**	
	AFS	**PFS**	**DSS**	**HP**	**PT-S4**	**SMST**	**NMST**	**Holes**	**SAS I–VIII**	**Palidia**
Ligyrus (*Ligyrodes*) *relictus*	No	No	2–4	entire	Yes	truncate	7–10	≤40	similar	Yes
Ligyrus (*Ligyrodes*) *sallei*	No	No	2–3	entire*	Yes	truncate	6–9	–	similar	Yes
Ligyrus (*Ligyrus*) *gibbosus*	Yes	No	2	entire	Yes	truncate	≈8	20–36	II–VII>I,VIII	No
Ligyrus (*Ligyrus*) *nasutus*	No	No	2	entire?	Yes	–	8–10	–	similar	Yes
Ligyrus (*Ligyrus*) *rubripes*	No	No	2	entire	No	truncate	8	–	–	No
Neoryctes galapagoensis	No	No	5–6	entire	Yes	truncate	8–12	37–41	–	No
Orizabus isodonoides	No	Yes	1	entire?	No	sharp–pointed	9	–	I–IV>V–VIII	No?
Orizabus pyriformis	Yes	Yes	1	entire	No	sharp–pointed	8–10	13–25	I–IV>V–VIII	No
Orizabus brevicollis	–	–	2	entire	No	sharp–pointed	–	–	I–IV>V–VIII	No
Oxygrylius ruginasus	No	No	2	entire	Yes	truncate	8–10	14–16	similar	No
Tomarus subtropicus	No	–	4–7	entire*	Yes?	truncate?	–	–	–	No
Philoscaptus bonariensis	Yes	No	4–5	entire	No	–	7	–	–	No
Saccharoscaptus laminifer	No	Yes	6–8	entire	No	truncate	7	25–30	I–IV>V–VIII	No

(–) lack of data in description; (?) data from illustrations or unclear description; (*) change made by us according to data from illustrations. Palidia: septula barely distinct (Yes<).

tribes, *S. agricola* has four characters considered relevant for its diagnosis (Table III). These are mentioned below in order of importance: (1) terminal antennal segment with 3–8 dorsal sensory spots; (2) abdominal spiracles VI, VII and VIII progressively reduced in size; (3) raster with a shortened palidia; (4) haptomeral process entire.

The number of dorsal sensory spot, abdominal spiracle size, and, to a lesser extent, the shape of the haptomeral process were relatively stable at the tribal level. Some characters were relatively consistent at the generic level, mainly the shape of the stridulatory teeth and the presence/absence of the 4th tooth of the left mandible; the presence of anterior and posterior frontal setae showed a lower consistency. The range in the number of thoracic spiracular holes is described for only 25 of the 48 species in both tribes. Regarding the number of maxillary stridulatory teeth, most species have 7–10 teeth, so the utility of this character is also weak. Three characters were

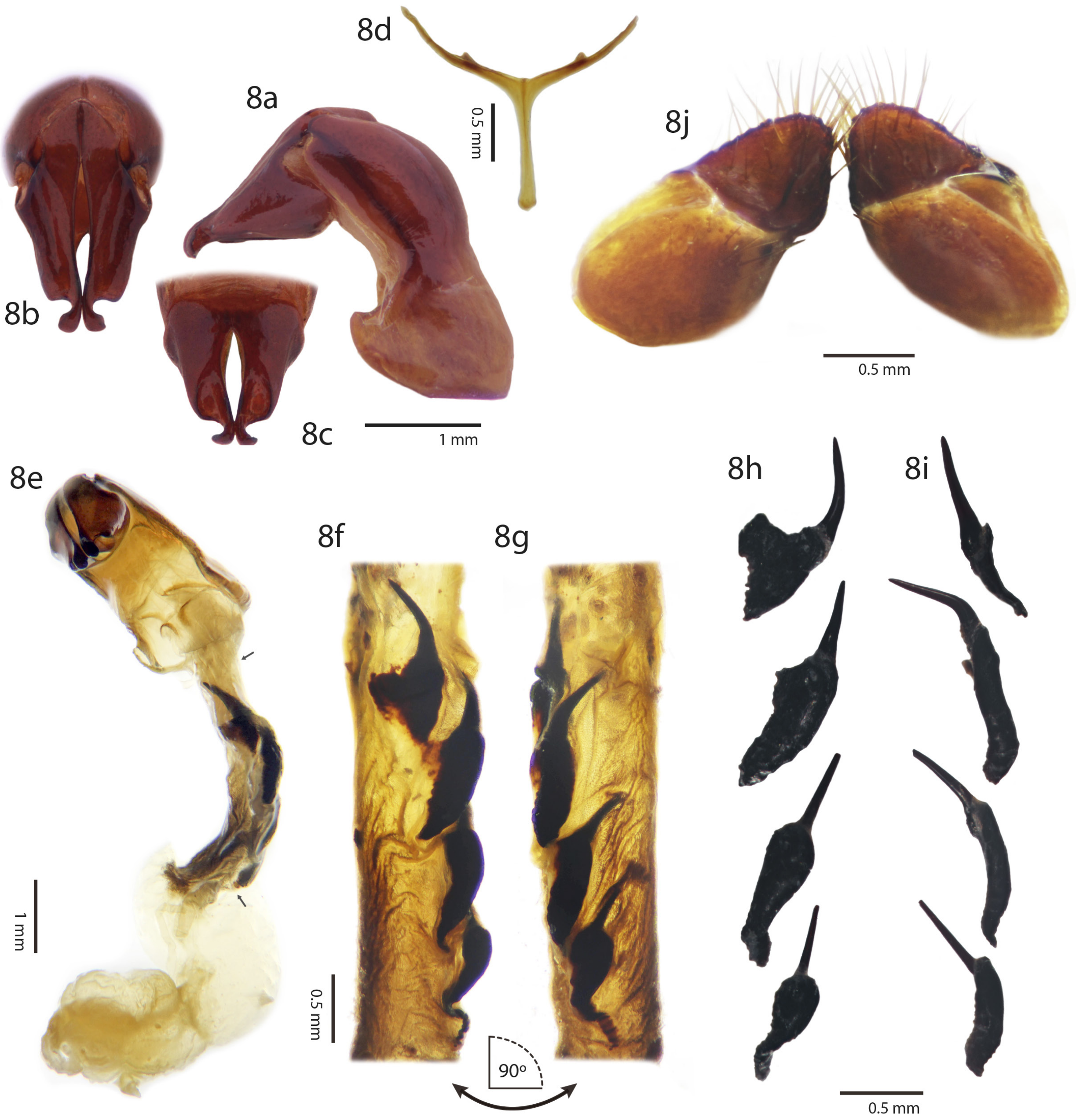

Figure 8. *Stenocrates agricola*, morphological characters: (a) aedeagus, lateral view. (b) Parameres, caudal view. (c) Parameres, anterior view. (d) Spiculum gastrale. (e) Parameres and internal sac. (f, g) Disposition of sclerites of internal sac. (h) Detail of sclerites of internal sac in dorsal view and (i) lateral view. (j) Gonopods IX of female in ventral view.

common to almost all species of Cyclocephalini and Pentodontini (with very few exceptions), and they were not included in Table I. These characters were: tarsal claw with two setae (one basoexternal seta and one internal, preapical seta), presence of stematta, and absence of plegmatia.

DISCUSSION

Comparison with larvae of Cyclocephalini and Pentodontini species

Characters of the cranium

One of the most striking characters found in *S. agricola* was the number of dorsal sensory spots of the last antennomere, with 3–8 spots (3 or 4 in most specimens), whereas in all the Cyclocephalini species so far described, they are found with a constant number of 2 (with the exception of *Cyclocephala barrerai* Martínez that also has a third spot). Since Ritcher (1966) first mentioned the number of sensory spots as a diagnostic feature of *Cyclocephala* species, it has proven to be one of the most constant characters in the species of the four known cyclocephaline genera (Moore et al. 2018, Morón et al. 2014, Neita-Moreno & Yepes 2011, Neita-Moreno et al. 2007, Rodrigues et al. 2018). On the other hand, the range of variation in the number of sensory spots in the Pentodontini is relatively constant among congeneric species but varies more between genera, e.g., one in *Aphonus* species (Ritcher 1966) to 12 in *Bothynus* species (Pereira et al. 2013). It is possible that this higher variation between genera of Pentodontini is due to the larger sample size, since 11 genera were described whereas only 4 were described for Cyclocephalini. Another relatively consistent character at the generic level is the presence (or absence) of frontal setae (anterior and posterior), mainly in Cyclocephalini, where it is also used for the identification of genera (Neita-Moreno et al. 2007) and species (Albuquerque et al. 2014, Neita-Moreno & Yepes 2011, Rodrigues et al. 2018).

Characters of the mouthparts

According to Ritcher (1966), the haptomeral process of the epipharynx has a raised, bilobed or entire ridge in the subfamily Dynastinae. It is notched (or with two teeth) in 22 species of the 28 described of Cyclocephalini, which includes the representatives of three genera: *Ancognatha*, *Aspidolea*, and *Cyclocephala* (with the exception of *Ancognatha manca* LeConte), while three species of *Dyscinetus* and *S. agricola* have an entire haptomeral process. According to Moore et al. (2018), this character may prove useful for diagnosing larvae of *Cyclocephala*-like genera if they are described in the future (e.g., *Arriguttia* Martínez, *Augoderia* Burmeister, former *Mimeoma* Casey species, and some additional *Cyclocephala* species). In the Pentodontini however, all the species have an entire haptomeral process with the exception of *Tomarus subtropicus* (Blatchley) and *Ligyrus sallei* Bates that have a bidentate haptomeral process. As a cautionary note, there is a discrepancy between the description and the illustration of the aforementioned species. For *T. subtropicus*, Gordon & Anderson (1981) state ". . . epipharynx with haptomeral process bearing 2 distinct marginal notches", but the illustration shows that it is clearly entire (see their Fig. 43). Similarly, *L. sallei* is described as ". . . haptomerum prominente y ligeramente bidentado", while the illustration shows that it is complete, oblique, and with a central notch (which could make it appear bidentate) [see Fig. 27 in Ramírez-Salinas et al. (2004)]. Therefore, based on the illustrations in both works, we can conclude that all the Pentodontini species described so far have an entire haptomeral process.

The presence (or absence) on the left mandible of the postscissorial tooth (or fourth tooth) is a relatively constant character at the generic level and therefore of systematic utility. In Cyclocephalini, *Aspidolea* species and most *Cyclocephala* species do not have a postscissorial tooth as do the pentodontine genera *Aphonus*, *Orizabus*, *Philoscaptus*, and *Saccharoscaptus*. This is why this character is commonly used in larval identification keys of both Cyclocephalini (Neita-Moreno et al. 2007, Ritcher 1966, Souza et al. 2014a) and Pentodontini (Morón 2017, Morón & Ratcliffe 1996, Pereira et al. 2013).

In all Cyclocephalini species described, the shape of the maxillary stridulatory teeth is truncated as well as in the majority of the Pentodontini, the exception being the genera *Aphonus* and *Orizabus* that have anterior projection points. Ritcher (1966), in relation to this character and the presence of a single dorsal sensory spot on the antenna, stated that both genera belong in a distinct tribe and perhaps in the same genus, and that the larvae of both of these genera show Rutelinae affinities. On the other hand, the number of maxillary stridulatory teeth is a character that in most species of both tribes have 7–10 teeth. The degree of differentiation is limited, and so the number of stridulatory teeth may depend on the number of specimens used in descriptions. This might explain why the number of maxillary stridulatory teeth is not a taxonomically reliable character in the determination of Pentodontini species (Morón 2017, Pereira et al. 2013), whereas in Cyclocephalini it has only been used for the determination of *Cyclocephala* species (Albuquerque et al. 2014, Rodrigues et al. 2018, Souza et al. 2014a).

Characters of the thorax

The number of holes on the respiratory plate has a relatively constant range between species of the same genus (e.g., 9–22 holes in *Cyclocephala* species and 23–38 in *Dyscinetus* species); however, its usefulness is limited because only 13 of the 28 species of Cyclocephalini and 12 out of the 20 species of Pentodontini have been described.

Characters of the abdomen

The size of the abdominal spiracles is another prominent character, although it has not been taken into account as a possible diagnostic character of Cyclocephalini. The majority of species of Cyclocephalini are characterized by spiracles VII and VIII larger than the preceding ones, a characteristic present in all *Cyclocephala* species and *Aspidolea singularis* Bates, (with the exception of *Cyclocephala fasciolata* Bates and some species of *Dyscinetus* and *Ancognatha*). Conversely, the size of the abdominal spiracles in *S. agricola* showed the same pattern as that described in pentodontine species of the genera *Euetheola*, *Aphonus*, *Orizabus*, and *Saccharoscaptus*, in which the last spiracles (V–VIII) are progressively smaller with VIII being the smallest.

The presence of a raster with palidium in the subfamily Dynastinae has been reported in four genera belonging to three tribes: *Cyclocephala* in Cyclocephalini; *Euetheola* and *Ligyrus* in Pentodontini, and *Heterogomphus* in Oryctini. Within *Cyclocephala*, there are five species with a raster and palidium: *C. modesta*, *C. testacea*, *C. paraguayensis* Arrow, *C. melanocephala* (Fabricius), and *C. tucumana* Bréthes (Fuhrmann et al. 2019, Rodrigues et al. 2018), and, as previously mentioned, the first two were not considered in this study. The larva of *C. modesta* was never formally described, whereas the larval characters described for *C. testacea* (Morelli & Alzugaray 1994) do not have several elemental characteristics typical for larvae in the subfamily Dynastinae (mandibles with a ventral stridulatory area, haptomeral process entire or notched, maxillary stridulatory area with anterior process) but do have common characteristics in the larvae of the subfamily Melolonthinae (epipharynx with plegmatia and laeophoba, haptomerum formed by numerous heli, and palidia divergent in the posterior half at the edge of the ventral anal labium). It leads us to ponder if the larval characters of *C. testacea* are inconsistent with those for Dynastinae.

In the description of *C. melanocepala*, Rodrigues et al. (2018) mentioned the presence of palidia based on the 3–4 short, bifurcate setae of each palidium (see Fig. 43) as well as similar characteristics for *C. paraguayensis*. The palidia of both species differ markedly from that of the larvae of other dynastine species (as well as some species of Rutelinae and Cetoniinae), where the pali are arranged in an adjoining row with their distal ends generally oriented towards a clearly defined septula.

This difference did not go unnoticed by Rodrigues et al. (2018), who mentioned in their *Cyclocephala* species identification key "Palidia present, sometimes pali irregularly distributed and septula barely distinct, but pali even easily differentiated from tegillar setae" [see their couplet 7(2)]. Therefore, the concept and types of palidia should be re-defined in upcoming studies. In addition, we consider that the presence of bifurcate setae is a relevant feature, which should be considered in future studies on this genus.

With respect to *Heterogomphus* species, the presence of this character has been cited only for *H. ochoai* Martínez (Ochoa 1974). We believe there was an error by Ochoa in interpreting this character since he stateed the septula is part of the ventral anal lip, and that the "palus" setae are on the edge of the dorsal anal lip (see Ochoa's Fig. 14). Accordingly, the presence of palidia in *Heterogomphus* is erroneous, and the presence of palidia within Dynastinae (so far as is known) is restricted to larvae of *Euetheola*, *Ligyrus*, *Cyclocephala*, and *Stenocrates*.

The palidia in *S. agricola* shows great similarity with that of *Euetheola humilis rugiceps* (LeConte) [see Fig. 370 in Ritcher (1966)], since both are of the monostichous type. Each palidium is comprised of a single row of 5–10 pali that do not extend to the lower anal lip. In contrast, the palidum in *Ligyrus* species is polystichous and formed by 2–5 irregular rows of 15–25 short pali, extending to the lower anal lip (Ramírez-Salinas et al. 2004, 2010, Ritcher 1966). Out of the five species described for the genus, *Ligyrus gibbosus* (DeGeer) and *Ligyrus rubripes* (Boheman) lacks palidia.

The characters that were common to most species of both tribes were: presence of stematta, absence of plegmatia, and tarsal claws with 2 setae with the first two considered as diagnostic characters of the subfamily Dynastinae by Ritcher (1966). Among the exceptions are *Ancognatha scarabaeoides* Erichson and *Dyscinetus rugifrons* (Burmeister) which are the only species of Cyclocephalini that do not have stematta, as well as *Neoryctes galapagoensis* (Waterhouse) and *Saccharoscaptus laminifer* (Dechambre) in the Pentodontini. The presence of plegmatia is a character that has been reported only in Cyclocephalini for the species *C. testacea* and *Aspidolea singularis* Bates. The presence of plegmatia in *C. testacea* does not correspond to Dynastinae, while in *A. singularis* the plegmatia is remarkably narrow and reduced, which contrasts markedly with species of Melolonthinae and some Rutelinae where it is well defined and clearly visible. Finally, in relation to tarsal claws, only *Cyclocephala celata* Dechambre has been reported with more than two setae, which, in addition to the single basoexternal seta and single internal, preapical seta, also has an internal basal seta (Souza et al. 2014b), a character that unfortunately is not illustrated in the description of this species. Other Oryctini such as *Heterogomphus chevrolatii* Burmeister and all species of *Strategus* Kirby have tarsal claws with four setae.

Remarks on adult morphology

In our redescription of the adult of *S. agricola*, we enlarged both the number of characters as well as their details. We also provide details of armature of the internal sac since these sclerites are the most visible structures. A recent study on *Tomarus* Erichson (Neita-Moreno & Ratcliffe 2017) shows notable differences in the internal sac structures of the eight species studied. When comparing the internal sac of *S. agricola* with that of other species of the genus [*S. cultor* Burmeister, *S. holomelanus* (Germar) and *S. rufipenis* (Fabricius)], notable differences were observed, especially in the shape, size, and number of sclerites corresponding to the copulatory armor. Only one small sclerite was found in *S. holomelanus* and six sclerites in *S. rufipenis* (forming two groups of three sclerites, one group located apically separated by a short distance from the other at the base), whereas in *S. cultor* there were four sclerites of different shapes and sizes than those of *S. agricola* and accompanied by tiny spinules on the basal area. These sclerites are probably highly relevant structures in future taxonomic studies of both *Stenocrates* species and other Dynastinae.

Stenocrates: Discussion on its tribal position

As mentioned previously, many of the diagnostic characters in larvae of Cyclocephalini species were not found in *S. agricola*, such as (a) two dorsal sensory spots on the last antennomere, present in all other cyclocephalines; (b) abdominal spiracles XII and XIII larger than the preceding ones; and (c) haptomeral process notched or with two teeth, both present in most species. Conversely, there are shared characters with some species of Pentodontini such as (a) the pattern and size of the abdominal spiracles and (b) the presence of palidia.

These character states suggest two possible explanations about the tribal position of *Stenocrates*:

- There are many more larval descriptions for Pentodontini genera, which is almost three times greater than those for Cyclocephalini, which may explain why variation in the known characters of Cyclocephalini may be smaller. *Stenocrates* would be the fifth genus of larval descriptions known to the tribe and would considerably expand the breadth of morphological characters known for Cyclocephalini larvae.
- The other possible explanation supports the idea that *Stenocrates* should be included in the Pentodontini and not in its current position in the Cyclocephalini. A phylogenetic analysis based on adult morphology conducted by Clark (2011) indicated that *Stenocrates* is not be a member of Cyclocephalini and is more closely related to *E. humilis* within Pentodontini. Many morphological characters described for the larva of *S. agricola* coincids with that of *E. humilis*, especially the presence of monostichous palidia, a character that so far is present only in these two species within the Dynastinae.

The absence of a robust data set for larval characters of New World Dynastinae inhibits establishment of relationship hypotheses. It is evident that more studies are needed to clarify the taxonomic position of *Stenocrate*s. As we mentioned previously, some studies have transferred some genera to different tribes based on the morphology of both adults and larvae. However, they are genera with few species, unlike *Stenocrates* that currently has 52 species, thus leading to ambivalence. Finally, this present study is a call to specialists to provide more detailed illustrations and more detailed descriptions with a greater number of characters, both of the immature stages and of the adults, in order to obtain useful data that allows for more comprehensive and complete taxonomic revisions.

CONCLUSIONS

Some characters considered diagnostic in larvae of Cyclocephalini are absent in the larval stages of *S. agricola*, but there are characters in common with Pentodontini. species, so two possible explanations are raised in relation to this result. On the other hand, most of the characters compared in this study were consistent at the generic level but inconsistent at the tribal level. A character that should be taken into account in future studies is the size of the abdominal spiracles VII and VIII, that are larger than the rest and are common to most Cyclocephalini species. We believe that larval morphology provides important information in systematics studies that can clarify tribal relationships within the Dynastinae.

Acknowledgments

We are grateful to Miryam Damborsky for her constructive suggestions for the manuscript. We thank two anonymous reviewers for their constructive comments that improved the manuscript. The first author obtained a scholarship from the Consejo Nacional de Investigaciones Científicas y Técnicas and Universidad Nacional del Nordeste (CONICET-UNNE), Argentina. This study was funded by the Agencia Nacional de Promoción Científica y Técnica and Universidad Nacional del Nordeste, Argentina (PICTO-UNNE 11-0244) and Secretaría General de Ciencia y Técnica, UNNE, Argentina (N° F005/2011).

REFERENCES

ALBERTONI FF, KRELL FT, STEINER J & ZILLIKENS A. 2014. Life history and description of larva and pupa of *Platyphileurus felscheanus* Ohaus, 1910, a scarabaeid feeding on bromeliad tissues in Brazil, to be excluded from Phileurini (Coleoptera, Scarabaeidae, Dynastinae). Zookeys 389: 49-76.

ALBUQUERQUE LSC, SOUZA TB, MAIA ACD & IANNUZZI L. 2014. New biological and immature morphological records of the masked chafer, *Cyclocephala paraguayensis*. J Insect Sci 14:1-11.

BRAN AM, LONDOÑO ME & PARDO LC. 2006. Morfología de estados inmaduros de tres especies de *Cyclocephala* (Coleoptera: Melolonthidae) con una clave para larvas de tercer estado en Colombia. Rev Corpoica - Cienc y Tecnol Agropecu 7: 58-66.

CLARK DR. 2011. Phylogenetic analysis of the scarab beetle tribe Cyclocephalini (Coleoptera: Scarabaeidae: Dynastinae) based on adult morphological characters. M.Sc. Thesis. Department of Biological Sciences, Wichita State University, Wichita, Kansas, United States of America, 68 p. Available from: https://pdfs.semanticscholar.org/3bc0/91dcc1bf679072581d6bec7476d6eaac2a42.pdf?_ga=2.229619676.195803821.1573231747-577251994.1573231747. (Unpublished).

DECHAMBRE RP. 2006. Deux nouvelles espèces de *Stenocrates* Burmeister, 1847 (Coleoptera, Dynastidae). Coléoptères 12: 19-21.

DECHAMBRE RP & HARDY M. 2004. Quatre nouvelles espèces de *Stenocrates* Burmeister, 1847 (Coleoptera, Dynastidae). Coléoptères 10: 209-214.

EDMONDS WD & HALFFTER G. 1978. Taxonomic review of immature dung beetles of the subfamily Scarabaeinae (Coleoptera: Scarabaeidae). Syst Entomol 3: 307-331.

ENDRÖDI S. 1985. The Dynastinae of the World. Dordrecht, Netherlands: Dr. W. Junk Publisher, 800 p.

ENDRÖDI S. 1966. Monographie der Dynastinae (Col. Lam.) I. Teil. Entomol. Abhandlungen Museum Tierkunde, Dresden 33: 1-457.

FUHRMANN J, RIBEIRO-DIAS BM & RODRIGUES SR. 2019. Population dynamics and description of larva and pupa of *Cyclocephala tucumana* Bréthes, 1904 in West-Central Brazil, and remarks on immatures of other *Cyclocephala* species (Coleoptera: Scarabaeidae: Dynastinae). Rev Brasil Entomol: https://doi.org/10.1016/j.rbe.2019.08.003

GARCÍA GL, ORTEGA-ARENAS L, HERNÁNDEZ HG, GARCÍA A, NÁPOLES JR & CORTÉS RR. 2009. Descripción de las larvas de tercer instar de Melolonthidae (Coleoptera) asociadas al cultivo de *Agave tequilana* var. *azul* y su fluctuación poblacional en Jalisco, México. Neotrop Entomol 38: 769-780.

GORDON RD & ANDERSON DM. 1981. The species of Scarabaeidae (Coleoptera) associated with sugarcane in south Florida. Florida Entomol 64: 119-138.

IBARRA-POLESEL MG & DAMBORSKY MP. 2018. Changes in the structure of Melolonthidae (Coleoptera: Scarabaeoidea) assemblages along a temporal gradient in a natural reserve in Chaco, Argentina. Austral Entomol 57: 377-386.

IBARRA-POLESEL MG, DAMBORSKY MP & PORCEL E. 2015. Escarabajos copronecrófagos (Scarabaeidae: Scarabaeinae) de la Reserva Natural Educativa Colonia Benítez, Chaco, Argentina. Rev Mex Biodivers 78: 459-482.

JAMESON ML, RATCLIFFE BC & MALY V. 2002. Review of the genus *Acrobolbia* Ohaus with remarks on its classification and key to the world genera of Cyclocephalini (Coleoptera: Scarabaeidae: Dynastinae). Fol Heyrovskyana 10: 1-15.

LÓPEZ-GARCÍA MM, GASCA-ÁLVAREZ HJ, CAVE RD & AMAT-GARCÍA G. 2015. An annotated checklist of the New World pentodontine scarab beetles (Coleoptera: Scarabaeidae: Dynastinae: Pentodontini). Zootaxa 4170: 491-509.

LUMARET JP. 1991. Le genre *Neoryctes* Arrow, 1808: description de la larve et position taxonomique du genre (Coleoptera: Scarabaeoidea: Dynastidae: Pentodontini). Elytron 5: 337-341.

MICÓ E, MORÓN MÁ, ŠÍPEK P & GALANTE E. 2008. Larval morphology enhances phylogenetic reconstruction in Cetoniidae (Coleoptera: Scarabaeoidea) and allows the interpretation of the evolution of larval feeding habits. Syst Entomol 33: 128-144.

MOORE MR, CAVE RD AND BRANHAM MA. 2018. Synopsis of the cyclocephaline scarab beetles. Zookeys 745: 1-99.

MORELLI E. 1997. Descripción de los estados inmaduros y notas sobre la biología de *Diloboderus abderus* (Sturm, 1826) y *Philoscaptus bonariensis* (Burmeister, 1847) (Coleoptera, Melolonthidae, Dynastinae). Acta Zoológica Mex nueva Ser 71: 57-70.

MORELLI E. 1991. Descripción de la larva y de la pupa de *Cyclocephala signaticollis* Burmeister, 1847 (Coleoptera: Scarabaeidae: Dynastinae) y observaciones sobre su biología. Elytron 5: 189-195.

MORELLI E & ALZUGARAY R. 1994. Descripción de la larva de *Cyclocephala testacea* Burmeister, 1847 y clave para la determinación de larvas de cuatro especies del género *Cyclocephala* en el Uruguay (Coleoptera, Dynastinae). Rev Bras Biol 54: 77-84.

MORÓN MA. 1976. Descripción de las larvas de tres especies mexicanas de melolontinos (Coleoptera, Melolonthidae, Dynastinae y Rutelinae). An Inst Biol Univ Nac Auton Méxicana Ser Zool 47: 119-134.

MORÓN MA. 2017. Description of the third instar larva of *Saccharoscaptus laminifer* (Dechambre) (Coleoptera: Melolonthidae: Dynastinae). Rev Bras Entomol 61: 354-358.

MORÓN MA & DELOYA C. 1991. Los coleopteros lamelicornios de la Reserva de la Biosfera "La Michilia", Durango, México. Folia Entomológica Mex 81: 209-283.

MORÓN MA, LUGO-GARCÍA GA & ARAGÓN-GARCÍA A. 2014. Description of the third instar larvae of five species of *Cyclocephala* (Coleoptera , Melolonthidae, Dynastinae) from Mexico. Rev Bras Entomol 58: 219-228.

MORÓN MA & RATCLIFFE B. 1996. New Tribal Placement of the genus *Coscinocephalus* Prell , 1936 , with description of the larva , pupa and adult of a new species from Mexico (Coleoptera : Scarabaeoidea ; Dynastinae). J New York Entomol Soc 104: 48-61.

NEITA-MORENO JC & MORÓN MA. 2008. Estados inmaduros de *Ancognatha ustulata* (Coleoptera: Melolonthidae: Dynastinae: Cyclocephalini). Rev Mex Biodivers 79: 355-361.

NEITA-MORENO JC & RATCLIFFE BC. 2017. The genus *Tomarus* Erichson (Coleoptera: Scarabaeidae: Dynastinae: Pentodontini) in Argentina, Chile, and Uruguay. Insecta Mundi 0547: 1-36.

NEITA-MORENO JC & YEPES F. 2011. Description of the larva and pupa of *Dyscinetus dubius* (Coleoptera: Melolonthidae: Dynastinae: Cyclocephalini). Rev Colomb Entomol 37: 152-156.

NEITA-MORENO JC, RATCLIFFE BC & CALBERTO G. 2007. Immature Stages of *Aspidolea singularis* (Coleoptera: Scarabaeidae: Cyclocephalini). Rev Colomb Entomol 33: 178-182.

OCHOA O. 1974. Ciclo biológico, morfología y comportamiento de *Heterogomphus ochoai* Martínez, 1966 (Coleop.: Scarabaeidae, Dynastinae). Soc Entomol Peru 17: 3-9.

PARDO-LOCARNO LC, STECHAUNER-ROHRINGER RM & MORÓN MA. 2009. Descripción de larva y pupa, ciclo de vida y distribución del escarabajo rinoceronte *Podischnus agenor* Olivier (Coleoptera: Melolonthidae) en Colombia, con una clave para larvas de tercer estadio de Dynastinae neotropicales. Kempffiana 5: 20-42.

PAUCAR-CABRERA A & MOORE MA. 2018. New tribal placement and review of *Parapucaya* Prell and *Pucaya*

Ohaus (Coleoptera, Scarabaeidae, Dynastinae). ZooKeys 805: 127-158.

PEREIRA AF, RODRIGUES SR & IDE S. 2013. Biology and description of the third instar of *Bothynus medon* (Germar, 1824) (Coleoptera: Scarabaeidae: Dynastinae). Coleopt Bull 67: 328-334.

RAMÍREZ-SALINAS C, MORÓN MÁ & CASTRO-RAMÍREZ AE. 2004. Descripción de los estados inmaduros de tres especies de *Anomala*, *Ancognatha* y *Ligyrus* (Coleoptera: Melolonthidae: Rutelinae y Dynastinae) con observaciones de su biología. Acta Zoológica Mex 20: 67-82.

RAMÍREZ-SALINAS C, PACHECO-FLORES C, CASTRO-RAMÍREZ AE & MORÓN MA. 2010. Descripción de los estados inmaduros de *Ligyrus nasutus* (Burmeister, 1847) (Coleoptera: Melolonthidae: Dynastinae) con información sobre su biología. Acta Zoológica Mex 26: 617-625.

RATCLIFFE BC. 2015. A revised catalog of the species of *Stenocrates* Burmeister (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini), with descriptions of three new species from Peru and Brazil and *Stenocrates inpai* Ratcliffe, 1978 placed in junior synonymy with *Stenocrates popei* Endrödi, 1971. Coleopt Bull 69: 773-779.

RATCLIFFE BC & CAVE RD. 2006. The dynastine scarab beetles of Honduras, Nicaragua, and El Salvador (Coleoptera: Scarabaeidae: Dynastinae). Bull Univ Nebraska State Museum 21: 1-424.

RATCLIFFE BC & CAVE RD. 2015. The Dynastine scarab beetles of the West Indies: (Coleoptera: Scarabaeidae: Dynastinae). Bull Univ Nebraska State Museum 28: 1-346.

RATCLIFFE BC & CAVE RD. 2017. The dynastine scarab beetles of the United States and Canada (Coleoptera: Scarabaeidae: Dynastinae). Bull Univ Nebraska State Museum 30: 1-298.

RATCLIFFE BC & FIGUEROA L. 2018. Description of a New Species of *Stenocrates* Burmeister (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini) from Peru. Coleopt Bull 72: 797-800.

RITCHER PO. 1966. White Grubs and Their Allies: a Study of North American Scarabaeoid Larvae. Corvallis, Oregon, USA: Oregon State Univ. Press, 219 p.

RODRIGUES SR, BARBOSA CAF, FUHRMANN J & AMARO RA. 2018. Mating behavior and description of immature stages of *Cyclocephala melanocephala* (Fabricius, 1775) (Coleoptera: Scarabaeidae: Dynastinae), identification key and remarks on known immatures of Cyclocephalini species. Rev Bras Entomol 62: 205-219.

SAWADA H. 1991. Morphological and phylogenetical study on the larvae of pleurostict lamellicornia in Japan. Tokyo, Japan: Tokyo University of Agriculture Press, 290 p.

SÍPEK P, GILL BD & GREBENNIKOV VV. 2009. Afromontane *Coelocorynus* (Coleoptera: Scarabaeidae: Cetoniinae): Larval descriptions, biological notes and phylogenetic placement. Eur J Entomol 106: 95-106.

SOUZA TB, MAIA ACD, ALBUQUERQUE CMR & IANNUZZI L. 2014a. Description of *Cyclocephala distincta* Burmeister (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini) immatures and identification key for third instars of some *Cyclocephala* species. Zootaxa 3872: 180-186.

SOUZA TB, MAIA ACD, SCHLINDWEIN C, ALBUQUERQUE LSC & IANNUZZI L. 2014b. The life of *Cyclocephala celata* Dechambre, 1980 (Coleoptera: Scarabaeidae: Dynastinae) in captivity with descriptions of the immature stages. J Nat Hist 48: 275-283.

STECHAUNER-ROHRINGER R & PARDO-LOCARNO LC. 2010. Redescripción de inmaduros, ciclo de vida, distribución e importancia agrícola de *Cyclocephala lunulata* Burmeister (Coleóptera: Melolonthidae: Dynastinae) en Colombia. Boletín Científico do Mus História Nat 14: 203-220.

VALLEJO F & MORÓN MA. 2008. Description of the immature stages and redescription of the adults of *Ancognatha scarabaeoides* Erichson (Coleoptera: Scarabaeidae: Dynastinae), a member of the soil white grub assemblage in Colombia. Coleopt Bull 62: 154-164.

VERDÚ JR, GALANTE E, LUMARET JP & CABRERO-SAÑUDO FJ. 2004. Phylogenetic analysis of Geotrupidae (Coleoptera: Scarabaeoidea) based on larvae. Syst Entomol 29: 509-523.

VINCINI AM, LÓPEZ AN, MANETTI PL, ALVAREZ-CASTILLO H & MABEL C. 2000. Description of the immature stages of *Dyscinetus rugifrons* (Burmeister, 1847) (Coleoptera: Scarabaeidae: Dynastinae). Elytron 14: 91-98.

How to cite

IBARRA-POLESEL MG, NEITA-MORENO JC & RATCLIFFE BC. 2020. Description of the immature stages of *Stenocrates agricola* Dechambre & Hardy (Coleoptera: Scarabaeidae: Dynastinae: Cyclocephalini) with redescription of the adult and discussion of its tribal position. An Acad Bras Cienc 92: e20190967. DOI 10.1590/0001-3765202020190967.

Manuscript received on August 20, 2019;
accepted for publication on December 2, 2019

MARIO G. IBARRA-POLESEL[1]
https://orcid.org/0000-0002-3211-4438

JHON C. NEITA-MORENO[2]
https://orcid.org/0000-0003-2998-2063

BRETT C. RATCLIFFE[3]
https://orcid.org/0000-0002-0589-8791

[1]Universidad Nacional del Nordeste, Facultad de Ciencias Exactas y Naturales y Agrimensura, Avda. Libertad 5470, 3400, Corrientes, Argentina

[2]Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colecciones Biológicas-Entomología, Claustro de San Agustín, Carrera 8, No. 15-08, Villa de Leyva Boyacá, Colombia

[3]University of Nebraska, Systematics Research Collections, W436 Nebraska Hall, 68588-0514, Lincoln, NE, U.S.A.

Correspondence to: **Mario G. Ibarra-Polesel**
E-mail: mario.ibarrapolesel@gmail.com

Author contributions

Mario Ibarra-Polesel: Collection and preparation of specimens; photography and edition of plates; analysis and interpretation of information; writing of the manuscript. Jhon Neita-Moreno: Contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content. Brett Ratcliffe: Contribution to data analysis and interpretation; contribution to manuscript preparation; contribution to critical revision, adding intellectual content. Revision and correction of the writing in English.