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Authors: Pardo-Locarno, Luis Carlos, Montoya-Lerma, James, Bellotti,

Anthony C., and Van Schoonhoven, Aart

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STRUCTURE AND COMPOSITION OF THE WHITE GRUB COMPLEX (COLEOPTERA: SCARABAEIDAE*) IN AGROECOLOGICAL SYSTEMS OF NORTHERN CAUCA, COLOMBIA

Luis Carlos Pardo-Locarno¹, James Montoya-Lerma², Anthony C. Bellotti³ and Aart Van Schoonhoven³ ¹Vegetales Orgánicos C.T.A.

²Departmento de Biología, Universidad del Valle, Apartado Aéreo 25360, Cali, Colombia

³Parque Científico Agronatura, CIAT, Centro Internacional de Agricultura Tropical Apartado Aéreo, 6713 Cali, Colombia

ABSTRACT

The larvae of some species of Scarabaeidae, known locally as "chisas" (whitegrubs), are important pests in agricultural areas of the Cauca, Colombia. They form a complex consisting of many species belonging to several genera that affect the roots of commercial crops. The objective of the present study was to identify the members of the complex present in two localities (Caldono and Buenos Aires) and collect basic information on their biology, economic importance, and larval morphology. The first of two types of sampling involved sampling adults in light traps installed weekly throughout one year. The second method involved larval collections in plots of cassava, pasture, coffee, and woodland. Each locality was visited once per month and 10 samples per plot were collected on each occasion, with each sample from a quadrants 1 m2 by 15 cm deep, during 1999-2000. Light traps collected 12,512 adults belonging to 45 species and 21 genera of Scarabaeidae within the subfamilies Dynastinae, Melolonthinae, and Rutelinae. Members of the subfamily Dynastinae predominated with 48% of the species (mostly Cyclocephala), followed in decreasing order by Melolonthinae (35%) and Rutelinae (15%, principally Anomala). Melolonthinae comprised 60% of the specimens (Plectris spp. 59.5% and Phyllophaga spp. 35.9%). A total of 10,261 larvae of 32 species was collected, including 12 species each of Melolonthinae (Phyllophaga, Plectris, Astaena, Macrodactylus, Ceraspis, Barybas, and Isonychus), Rutelinae (Anomala, Callistethus, Stigoderma, and Leucothyreus) and Dynastinae (principally Cyclocephala). At least a third of the species sampled as larvae are rhizophagous pests. Taken together, adult and larval sampling methods permitted a more precise definition of the whitegrub complex in Caldono and Buenos Aires.

Key Words: beetles, scarabs, rhizophagous pests, crop pests

RESUMEN

Las llamadas "chisas" son larvas de algunas especies de Scarabaeidae, consideradas plagas rizófagas, que actuan en complejos integrados por varias especies y géneros de difícl separación taxonómica. La presente investigación tuvo como objetivos dilucidar el complejo chisa en Caldono y Buenos Aires, dos localidades del Departamento del Cauca. Además se obtuvo información básica sobre su biología e importancia económica. Los adultos fueron colectados semanalmente con trampas de luz. Las larvas se obtuvieron a partir de parcelas de yuca, pastizal, café y bosque. Cada parcela se visitó una vez por mes, entre 1999 y 2000. Se realizaron 10 muestras por parcela en cada ocasión, cada muestra consistió en cuadrantes de 1 m² por 15 cm de profundidad. Las trampas de luz reunieron 12.512 adultos correspondientes a 45 especies y 21 géneros de Scarabaeidae, la mayor diversidad correspondió a la subfamilia Dynastinae (48%, mayoría Cyclocephala) seguida por Melolonthinae (35%) y Rutelinae (15%, principalmente Anomala). La mayor abundancia se observó en Melolonthinae (60%), con Plectris spp., representando el 59.48% y Phyllophaga spp. el 35.89%). Se colectó un total de 10.261 larvas distribuidas así: 12 especies de Melolonthinae (Phyllophaga, Plectris, Astaena, Macrodactylus, Ceraspis, Barybas e Isonychus), 12 de Rutelinae (Anomala, Callistethus, Stigoderma y Leucothyreus) y 5 Dynastinae (principalmente Cyclocephala). Se concluye que al menos la tercera parte de las especies muestreadas a nivel de larvas presentan hábitos rizófagos, además la conjugación de muestreo de larvas y adultos facilitó el reconocimiento del complejo chisa local lo cual se recomienda implementar en otras regiones agrícolas con similares problemas fitosanitarios.

Translation provided by the authors.

^{*}Only the subfamilies Dynastinae, Rutelinae and Melolonthinae.

Immature stages of some species of rhizophagous beetles of the family Scarabaeidae (Coleoptera: Scarabaeoidea) are among the most important economic pests in Colombia (Pardo-Locarno 1994; Londoño 1999). These insects feed on roots of various crops in different agro-ecological zones (Pardo-Locarno 1994; Pardo-Locarno et al. 2003a). They comprise a species complex. Larvae are very similar and only distinguishable based on size and, less precisely, body form and color of the head. Several genera and species cannot be distinguished, even based on these criteria. Taxonomic characters are present on the mouthparts and raster, but these must be associated with reared specimens.

Preliminary analyses are available on some of the white grubs of major economic importance in Colombia, with details of species compositions, localities, and crops affected (Pardo-Locarno 1994, 2000a; Restrepo & López Avila 2000). Composition of the complexes and their respective economic impact vary according to regions and species involved (Pardo-Locarno 2000a; Pardo-Locarno et al. 2003a). The affected agro-ecosystems represent most of the physiographic areas of the country, including very humid tropical forest (e.g., Puerto Leguízamo) (Department of Putumayo) and possibly the Chocó region (Pardo-Locarno 2000a; Pardo-Locarno et al. 2003a).

The complex of rhizophagous beetles constitutes an important problem in cassava, sisal, pineapple, vegetables, flowers, and pasture in the municipalities of Santander de Quilichao, Buenos Aires, Toribío, and Caldono, all in the Department of Cauca (Pardo-Locarno et al. 2003c, d; Victoria & Pardo-Locarno 2000a).

Studies carried out in one municipality of the region (Santander de Quilichao) have identified about 30 species of white grubs with different degrees of economic importance to cassava cultivation and varying patterns of adult seasonal abundance (Pardo-Locarno et al. 1993). The same authors identified the larvae responsible for economic damage with notes on their natural enemies (Pardo-Locarno et al. 1999a, b). Further, feeding preferences were established with living larvae, randomly collected in cassava, pasture, and other crops and individually reared under laboratory conditions (Victoria & Pardo 2000a, b). Nevertheless, there are still many gaps in the association of adults and immatures of Scarabaeidae present in the area. In this paper we define and compare the regional complex of white grubs present in four agroecosystems of the municipalities of Caldono and Buenos Aires, Cauca, Colombia.

MATERIAL AND METHODS

Characteristics of the Study Area

Sampling was carried out in Pescador and Cascajeros, localities within the municipalities of Caldono and Buenos Aires respectively in the De-

partment of Cauca (Fig. 1). Pescador was selected because of previous research (Pardo-Locarno et al. 1999a, b; Pardo-Locarno 2000a; Victoria & Pardo 2000a, b). Cascajeros was chosen as it represents a different ecology. This permitted data on the spatial heterogeneity in the region (Wiens 1989; Levin 1992; Hulbert 1984).

Annual rainfall in northern Cauca fluctuates between 2000-2300 mm and shows a bimodal pattern (April-May and October-November) (IGAC, 1988). The area is predominantly agricultural. Caldono is the leading producer of sisal in the department although as in Buenos Aires, coffee and cassava production has increased in recent years. In Buenos Aires the production of fruits (oranges, lemons, guavas, etc.) predominates, followed in importance by cash crops such as beans and tomatoes.

Field Phase

Four plots were chosen to study composition, diversity, and abundance of the white grub complex in cassava, pasture, coffee, and woodland. Sampling was carried out in 1999-2000 by two methods: collection of larvae in quadrants of 1 m² by 15 cm deep and capture of adults in light traps (Pardo-Locarno 2000a; Pardo-Locarno et al. 2003c, d). Information was also collected on the crops, feeding habits of the beetles and bioecological details. Live larvae were separated according to characters of the head, mouthparts (especially the epipharynx), and abdomen (raster, anal opening).

Adult sampling was carried out weekly with light traps (Pardo-Locarno, et al. 1993). On each occasion the specimens were stored in plastic 1-gallon containers, transported to the laboratory, identified, and counted by species.

Laboratory Phase

Approximately 2,500 larvae were collected in different crops and allowed to complete their life cycle under glasshouse conditions and identified as adults. All the specimens were reared individually in plastic cups containing sterilized soil, rich in organic matter and supplemented with roots or pieces of carrot. Field caught larvae were kept as individuals in disposable cups containing vapor sterilized soil brought from the field. Larvae were fed with fresh chopped carrot. Cups were inspected once per week to control moisture and change food ration. Each larva was randomly labelled according to phenototypic characters observed on head, feet, raster, and anal orifice. As soon as the adults were obtained, the identification was verified. For each "morpho" several voucher specimens were prepared (i.e., larvae were "cooked" in boiling water (until they float), fixed with formalin (10%) and preserved. In very few cases (i.e., larvae with rare or odd characters) larvae were kept alive, and their phenotypic characteristics were drawn. For this,



Fig. 1. Map of the study area in northern Cauca, Colombia

the larva was cooled for a few minutes with ice, and cooling was repeated as many times as necessary (Pardo-Locarno 2002).

Several papers and taxonomic keys were consulted for larval identification, including Ritcher (1966); Boving (1942); Morón (1993); Vallejo et al. (1996); Morón & Pardo-Locarno (1994); and King (1984). Identification of adults was based on the genitalia with the aid of diagnostic keys from Endrödi (1985); Saylor (1942, 1945); Frey (1962, 1964, 1973, 1975); Morón (1986); King (1996); Ohaus (1934); Woodruff and Beck (1989); and Machatschke (1957, 1965). The collection of one of the authors (LCP), which included representatives of many white grub species from Cauca, was examined (Pardo-Locarno 1999a, b). We also consulted the taxonomic specialists R.P. Dechambre (Musee de Histoire Naturelle de Paris) and M. A. Morón (Instituto de Ecología de México).

RESULTS

Capture of Adults

Altogether 12,512 adults were collected in the light traps, with 7,562 from Caldono and 4,953

from Buenos Aires. This included 21 genera and 45 species of Scarabaeidae belonging to the subfamilies Dynastinae, Melolonthinae, and Rutelinae (Table 1).

The greatest species diversity was presented by the subfamily Dynastinae with 48% of the species, followed in decreasing order by Melolonthinae (35%) and Rutelinae (15%). Among the Dynastinae the diversity of the tribe Cyclocephalini was noteworthy with 15 species identified, most belonging to the genus *Cyclocephala*.

Members of the subfamily Melolonthinae were most abundant and comprised 60% of the total specimens collected. Of these, *Plectris*, with two species, comprised 59.5%, followed by *Phyllophaga*, with five species. Among the Dynastinae, the Cyclocephalini predominated, particularly *C. fulgurata* Burmeister, which was especially numerous in Caldono. Among the Oryctini, the predominant species was *Strategus aloeus* L., whose larvae are saprophagous and adults are not recorded as pests of crops. This species was followed in predominance by *Podichnus agenor* Oliv. whose larvae are saprophagus and adults damage sugar cane stems in the region.

TABLE 1. CAPTURE OF ADULTS IN LIGHT TRAPS IN CALDONO AND BUENOS AIRES.

Species	Caldono	Buenos Aires	Specimens 133	
Aspidolea singularis Bates	113	20		
Aspidolea fuliginea Burm	18	1	19	
Cyclocephala sp. 1	30		30	
Cyclocephala amblyopsis Bates	162			
Cyclocephala amazona Linn.	2	2 119		
Cyclocephala melanocephala Fabr	4		4	
Cyclocephala fulgurata Burm	1607	15	1622	
Cyclocephala sp. 2	2	751	753	
Cyclocephala tutilina Burm	10	21	31	
Cyclocephala stictica Burm	1	1	2	
Cyclocephala lunulata Burm	420	115	535	
Cyclocephala weidneri Endrödi		25	25	
Stenocrates bicarinatus Robinson	8	14	22	
Ancognatha vulgaris Arrow	1	_	1	
Dyscinetus dubius Olivier	32	4	36	
Coelosis biloba Linn.	14	6	20	
Strategus aloeus Linn.	82	3	85	
Podischnus agenor Olivier	39	1	40	
Golofa porteri Hope	1		1	
Ligyrus gyas Er.	1		1	
Ligyrus bituberculatus Beauvois	10	4	14	
Phileurus didymus Linn	3	1	4	
Plectris fassli Moser.	733	3019	3752	
Plectris pavida Burm	152	607	759	
Phyllophaga menetriesi Blanch.	2413	9	2422	
Phyllophaga obsoleta Blanch	213	29	242	
Phyllophaga sericata (Blanchard)	25		25	
Phyllophaga thoracica (Burmeister)	2		2	
Phyllophaga schneblei Frey	29	1	30	
Phyllophaga sp. 3	1	-	1	
Astaena valida Burmeister	43	5	48	
Astaena sp2.	9	· ·	9	
Macrodactylus subvittatus Burm	23		23	
Macrodactylus sp. 1	1		1	
Macrodactylus sp. 2	11		11	
Isonychus sp. 1	-11	107	107	
Isonychus sp. 1	2	107	2	
Barybas sp. 2	127	22	149	
Pelidnota prasina Burmeister	22	1	23	
Anomala cincta Say	22 26	4	30	
Anomata cincia Say Anomala inconstans Burm	1029	9	1038	
Anomala inconsians Burm Anomala undulata Melsh.	1028	9	1038	
	121	9 6	9 127	
Anomala sp. 2	141	O	141	
Callisthetus sp.	10	വ	— 41	
Leucothyreus sp.	19	22	41	
Abundance/locality	7562	4953	12512	

Members of the Rutelinae were least abundant, with *Anomala inconstans* Burm., an agriculturally important species, the most numerous. The adults of *Phyllophaga* spp., *Plectris pavida* Burm., *P. fassli* Moser, and other Melolonthinae of economic importance were attracted to light traps mainly in October and November, although some adults were also collected during the rainy season (March-April) and to a lesser degree in May.

Capture of Larvae

A total of 10,265 larvae, representing 32 species of Scarabaeidae, was collected in samples from the four plots (pasture, cassava, coffee, and woodland) in Caldono and Buenos Aires (Table 2). Of the total, 52% corresponded to genera of Melolonthinae, 25% to Dynastinae and 23% to Rutelinae (Table 2).

TABLE 2. SPECIES OF LARVAE OF SCARABAEIDAE COLLECTED AND THEIR RESPECTIVE ABUNDANCES IN THE FOUR PLOTS IN CALDONO AND BUENOS AIRES, CAUCA.

Genus/species	Buenos Aires			Caldono					
	Pasture	Cassava	Coffee	Woodland	Pasture	Cassava	Coffee	Woodland	Total
Phyllophaga sp.	134	25	42	17	23	64	19	4	328
Ph. Menetriesi	1	3	1	20	29	60	22	36	172
Phyllophaga sp. 2		2	1	6		1	9	0	19
Plectris pavida	63	3	13	18	57	34	11	9	208
Pl. fácil	467	27	5	13	338	739	16	5	1610
Cyclocephala stictica Burm						1	3		4
C. amblyopsis				1					1
Cyclocephala sp.	52	51	27	8	19	15	14	1	187
C. lunulata	15			1	1	9			26
C. amazona						2			2
Rutelinae #26	28	101	55	20	22	14	20	9	269
Callistethus cupricollis	8	5	2	2	1	150		1	169
Anomala incostants	13	16	2	1		43	3	1	79
An. Cincta	25	75	110	3	61	20	10		304
$An.\ undulata$		3	11	7		35			56
$An.\ caucana$	1								1
Anomala sp. 2		36	1	9		89	10	1	146
Anomala sp.	71			1	52	126	18	348	616
Astaena sp.	11	1	118	151	45	221	33	12	592
Macrodactylus subvittatus	23	602	6	450	181	222	45	163	1692
Ceraspis innotata	48		19	8	1344	286	47	4	1756
Barybas sp.	24				71	36	92	278	501
Dynastinae #9	1				1				2
Leucothyreus sp.	8	28	8	4	8		8	3	67
Scarabaeidae #27	1				23				24
Scarabaeidae #28					1				1
Scarabaeidae #19								652	652
Rutelinae #30	4				1	12			17
Rutelinae #21				1	104	114	23	444	686
Rutelinae #29					3			16	19
Isonychus sp.							1		1
Melolonthinae #4	12			43	3				58
Total	1010	978	421	784	2388	2293	404	1987	10265

Plectris fassli was the most abundant species, reaching densities of up to 12 larvae per quadrant in pasture and up to six in cassava. Phyllophaga menetriesi Bl. was collected in all the agricultural plots and sporadically in woodland (3-4 larvae/m²). Densities of 6-8 pupae/m² were observed in July-August in cassava, which suffered 33% root yield loss according to growers. A marked seasonality was recorded, with large numbers of first and second instars in November-December and final instars in February-July. These pupated in August-September and their emergence occurred in October-November with the rainfall at the end of the year (data not shown).

The appearance of adults of *Plectris* spp. was October and November, with abundance greater than that of *Phyllophaga* (Table 1). More than 90% of the population was observed pupating in the subsoil at 35-40 cm, with their larvae having

dug into the ground 2-3 months before emergence. This made these species difficult to find in sample quadrants, which only reached down to 15 cm.

Plectris fassli was eight times more abundant than Pl. pavida and was found in all plots, predominating in pasture and cassava (Table 2), where it reached densities of up to 40 and 34 larvae per quadrant, respectively. The larvae of Pl. pavida, active and slender, were abundant in pastures where they reached densities of up to 21 larvae per quadrant.

Ceraspis innotata Blancard was collected in pastures, cassava, coffee, and rarely in forests. In cassava it reached an abundance of up to 45 larvae per quadrant, but in pastures it presented the greatest abundance (up to 86 larvae/m²), with most in the third instar. Their adults, little attracted by light traps, were captured during the day on the ground and on pasture foliage. They

were most abundant in May, almost one month after the initiation of the rains.

Larvae of the rhizophagous species *Astaena valida* Burm. were collected relatively frequently in all plots. This species demonstrated a predilection for coffee plantations and forest, where it was collected frequently and at densities of up to 36 larvae per quadrant. It reached densities of up to 34 examples per quadrant in cassava and on pasture. The genus included other species, one of them identified tentatively as *Astaena colombiana* Blanchard.

Macrodactylus subvittatus Burmeister, whose adults are considered to be a pest of maize, presented abundant rhizophagous larvae, both in pasture and cassava (with 22 and 38 larvae per quadrant, respectively) but particularly in forest (up to 42 larvae).

Among the larvae of Anomalini, the genera *Callistethus* and *Anomala* predominated, the latter distributed in the upper 5 cm of the soil. One species, provisionally identified as *Anomala* sp 2, was most numerous (32 larvae per quadrant in cassaya).

DISCUSSION

The results show that the species compositions of Scarabaeidae in Caldono and Buenos Aires are similar, and compare to those reported for terraced agroecosystems (Pardo-Locarno et al. 2003a, b). The species complex presented marked differences to those in hot, lowland areas with pronounced dry periods (Caribe Seco, Llanos Orientales of Colombia, etc.), which are dominated by species of Pentodontini, such as Euetheola (ICA NNE 1972-1994; Pardo-Locarno 1994, 2000a; Pardo-Locarno et al. 2003a). It also differs from agricultural zones on slopes at 1000 masl with higher humidity regimens (San José del Palmar-Chocó and other mountainous regions), where species of Cyclocephala and Anomalini predominate (Pardo-Locarno 2000b) and hot and moderately humid cultivated land at lower elevations (Villavicencio and foothills of the Llanos Orientales), where species of the Cyclocephalini (Cyclocephala, Stenocrates, Dyscinetus and others) are abundant (Pardo-Locarno 2000a; Pardo Locarno et al. 2003a).

In general the species composition of adults resembled that previously observed for the region (Pardo-Locarno et al. 1993; Pardo-Locarno 2000a; Pardo Locarno et al., 2003a). Nevertheless the capture of Scarabaeidae larvae reaches values that significantly exceed previous data obtained in the area with 14 edaphic species recorded: C. fulgurata Burm., C. amazonica L., C. stictica Burm., C. lunulata Burm., Phyllophaga menetriesi Blanchard, Ph. obsolete Blanchard, Ph. sp. (near elenans Saylor), Plectris sp. 2, Pl. fassli Moser, Anomala inconstans Say, An. undulata

Melsh., An. cincta Say, Anomala sp. 2 and Leucothyreus sp. (Pardo-Locarno et al. 1999a). Cassava crops in Caldono sampled intensively during the first semester of 1999, revealed the presence of 14 Scarabaeidae species of the genera Plectris (2 species) Cyclocephala (4-5), Phyllophaga (5) and Anomala (5-6). Based on study of these larvae, specimens previously thought to be Ph. elenans were identified as Pl. pavida.

Not surprisingly, given the geographical proximity of the two areas, the white grub complex of Caldono and Buenos Aires is similar in species composition to that recorded for Santander de Quilichao (Pardo-Locarno et al. 1993) and complements that observed previously in Caldono and Buenos Aires (Pardo-Locarno et al. 2003b). Despite the greater distance, the white grub complex at Caldono and Buenos Aires presents great similarity to that recorded for the mountainous regions of Ibagué and Cajamarca, Tolima (Pardo-Locarno et al. 2003a; Vásquez & Sánchez 1996). Cyclocephala amazonica L., C. lunulata Burm., Pl. pavida Burm., and Ph. menetriesi Bl. were abundant in samples from this latter region.

With respect to the rhizophagous habit sensu stricto, Phyllophaga species are considered of great economic importance (Vallejo et al. 1997). This genus was represented in three of the agroecosystems, i.e., pasture, cassava, and coffee. This study provides additional evidence to corroborate the results of previous studies (Pardo-Locarno et al. 1999a; Pardo-Locarno 2000a, 2000b) regarding the presence and relative importance of the genera *Plectris*, *Astaena*, *Leucothyreus*, and *Mac*rodactylus. Many of these genera are little known as root-eating pests. In some instances, they reached higher population levels than *Phylloph*aga species and their inclusion in the white grub complex of northern Cauca is suggested. It is possible that larva of the former were previously confused with Phyllophaga, given their similarities in morphology, feeding habits, reflex reactions at the moment of capture and that all of them appear as larvae during the rains of October-November.

The fact that *Plectris* spp. (especially *P. fassli*) predominated in pasture and cassava possibly implicates them in the economic damage of the root systems of these crops. An undetermined species of this genus was incriminated as a root pest in Río Negro, Department of Antioquia (Londoño 1999). It is important to determine the actual economic importance of *Plectris* species, for which Colombian records are scant.

Colombian references to *Astaena* are almost absent in the literature. But many species have adults that are easily confused with other sericines, and some members of the genus (particularly *A. valida*) occurred in all plots, with abundant populations in cassava, pasture and secondary forest.

Macrodactylus subvittatus Burm., is a rhizophagous species which is abundant in pastures, cassava plantations, and forest ecosystems. This species is considered to be a maize pest although Bueno et al. (1998) in their study of its life cycle, state that its larvae "feed on the roots of grasses and stubble and apparently do not cause economic damage".

Other species of *Macrodactylus* collected in northern Cauca include *M. flavolineatus* and *M. pulcripes*, both apparently forest-living and attracted by *Salvia palaefolia* H.B.K (*sensu* Pérez Arbelaez 1990) undergrowth or flowering plants in general.

The findings of the present study support the views of Pardo-Locarno (2000a) regarding the relative importance of larvae of the genus *Ceraspis* in agricultural systems of the foothills and high mountain regions. Other Colombian agroecosystem still need to be sampled (ICA-NNE 1972-1994; Posada 1989; Pardo-Locarno 1994; Restrepo & Lopez Avila 2000). The larvae of *C. innotata* are unknown to the scientific community and have not been reported as pests of agricultural importance (Pardo-Locarno et al. 1999a; Pardo Locarno 2000a; Victoria & Pardo-Locarno 2000b). However, during the present study they were collected on all the crops, especially in pasture.

Based on the results of this study, the white grub complex of Caldono and Buenos Aires, which currently comprises 32 confirmed species, could be increased to more than 40 species. Additional species have been collected in light traps but some lack corroboration in the larval form. In the latter category are species of Stenocrates (ICA 1972-1994; Pardo-Locarno 2000a) such as S. clipeatus Endrodi and S. bicarinatus Robinson; two members of Aspidolea, A. fuliginea Burm., and A. singularis Bates, Dyscinetus dubius Oliv, a species that was moderately abundant in Buenos Aires in light traps (Pardo-Locarno 2000a) and Ligyrus bituberculatus and L. gyas, species whose larvae remain unidentified. The latter are economically important in Central America and the southern US (King 1984; Shannon & Carballo 1986; Gordon & Anderson 1981) but rarely collected in light traps. Since adults of the genus *Isonychus* and the subtribe Anomalini were collected in light traps or on the foliage of the evaluated plots, it is plausible to expect their presence as larvae, as well.

Three large taxonomic groups of the white grubs predominated. The first of these is the subfamily Melolonthinae with species of greatest economic impact, whose larvae are unable to complete their life cycles without the presence of living roots or plant tissue. Members of the tribe Macrodactylini *Plectris*, *Macrodactylus*, *Ceraspis*, *Isonychus*, and the genera *Phyllophaga* (especially *Ph. menetriesi* Blanchard), have the largest rhizophagous larva. Next in importance are the Rutelinae of the tribe Anomalini, which includes

Anomala and Callistethus, two genera with notable species diversity. Finally, the Dynastinae of the tribe Cyclocephalini (especially Cyclocephala) are important, but their economic importance is unknown. Larvae of species such as C. amazonica, C. lunulata, C. stictica, and C. fulgurata, Aspidolea fuliginea, and A singularis were found to be facultative saprophagous and able to develop in the absence of roots or live plant tissue. The possible saprophagous habit was also observed by Deloya (1998) in larvae of C. lunulata Burmeister in maize fields in Morelos, Mexico.

The white grub complex observed in the crops hypothetically is part of a group of edaphicolous species pre-adapted to both an ecological and cultural oversimplification due to selected crops and agronomic practices that dominate in the region. This has permitted selection of a group of predominantly rhizophagous and saprophagous species, whose populations are favored by the possible exclusion of their natural enemies and by soil degradation.

Sampling of both adults and larvae revealed a great overlap of subpopulations associated with the two rainy seasons. Larvae occurred in a disparity of developmental stages from first to third instars. Given the frequent capture of adults throughout the year, this may suggest they have a short reproductive period. This has been observed in other species such as *C. amazonica* and *Ph. me*netriesi. A similar but less marked situation was observed in An. cincta viridicollis. Current agricultural practices and prevailing environmental conditions may have intensified the seasonality of rhizophagous and saprophagous species of Scarabaeidae. They show relatively brief reproductive periods, associated with rainy seasons when adults are abundant and oviposition cycles begin.

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