Diversity and distribution of the scarab beetle tribe Phanaeini in the northern states of the Brazilian Northeast (Coleoptera: Scarabaeidae: Scarabaeinae)

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Abstract. The fauna of Phanaeini of the northeast of Brazil was investigated through fieldwork in the States of Ceará, Maranhão and Piauí, and through study of preserved material from other states. Seven species of Phanaeini are newly recorded from these three states. Of these, two species are also new records for the northeast region: Phanaeus melibaeus Blanchard and an unidentified Dendropaemon Perty species. A total of 13 new state records are given for eight of the 15 species of Phanaeini recorded from the northeast to date, including three new state genus records. A key is provided for identification of all species. Detailed distributional information is presented together with habitat and bait preferences and other ecological data for each species. The diversity and distribution of the tribe in the northeast is discussed in the context of regional biotopes and wider geographic ranges. The fauna is shown to be more diverse than previously believed, containing both endemic and widespread elements occurring in species assemblages that differ according to habitat type and elevation, leading to substantial complementarity of diversity amongst the main biogeographic provinces and biotopes of the region.

Resumo. A fauna de Phanaeini do Nordeste brasileiro é sumarizada, como resultado de novas coletas nos estados do Ceará, Maranhão e Piauí, e pelo estudo de material preservado de outros estados. Sete espécies de Phanaeini são reportadas pela primeira vez para esses estados. Destas, duas espécies são também novos registros para a Região Nordeste: Phanaeus melibaeus Blanchard e uma espécie não identificada de Dendropaemon Perty. Um total de treze novos registros de estatais é apresentado para oito das quinze espécies de Phanaeini reportadas do Nordeste até agora, incluindo três novos registros estatais de géneros. Uma chave é dada para permitir a identificação de todas as espécies. Apresenta-se informação detalhada de distribuição, hábitat e preferências por isca e outros dados ecológicos para cada espécie. A diversidade e a distribuição do tribo no Nordeste são discutidas no contexto de biotopos regionais e áreas geográficas maiores. A fauna é considerada mais diversa do que previamente esperado, contendo tanto elementos endêmicos como de ampla distribuição, ocorrendo em assembléias de espécies que variam de acordo com tipos de hábitat e altitude, levando a grande complementariedade da diversidade entre as principais províncias biogeográficas e biotopos da região.

Key words / Palavras chaves. Dung beetles, Coprophanaeus, Diabroctis, Phanaeus, Dendropaemon, nordeste, Neotropical, Ceará, Piauí, Maranhão, new records, faunistics, biodiversity, ecology.

Introduction

The scarab beetle tribe Phanaeini is exclusive to the New World and is composed of approximately 160 species, described within 12 genera (Arnaud 2002a; Olsoufieff 1924). The tribe has been shown to be monophyletic and is characterized by a suite of synapomorphies (Philips et al. 2004). In general, the tribe contains typical fossorial species which may be either coprophagous, necrophagous or both (Edmonds
However, several genera exhibit atypical ecologies, most notably apparent myrmecophily in *Dendropaemon Perty* and *Tetramereia Klages* (Vaz-de-Mello et al. 1998; Vaz-de-Mello and Génier, 2009) and mycetophagy in some species of *Phanaeus Macleay* (Edmonds 1994). There are no detailed biological data at all for the rare monobasic genera *Homalotarsus Janssens* and *Megatharsis Waterhouse* (Gillett et al. 2009). Amongst the distinctive superficial characters present in most, but not all members of the tribe are bright, often metallic, dorsal coloration and well developed sexual dimorphism.

Members of the tribe inhabit diverse biotopes ranging from super-humid lowland tropical rainforest and montane forests to open grassland and dry scrub across a range of altitudinal gradients. Many species are stenotopic, being limited to a narrow range of habitats or elevation, although several more widespread taxa are less specialized, occupying broader habitat and ecological niches (Edmonds 1994, 2000, Edmonds and Zídek 2004).

Philips et al. (2004) concluded that the tribe Phanaeini originated in South America following the separation of this continent from Africa in the late Mesozoic. Members of the tribe were subsequently able to colonize Central and North America after the Panamanian land bridge connection in the late Pliocene. Based on a dispersal-vicariance computational reconstruction and on molecular phylogenetic data, Price (2009) hypothesized that the ancestors of the diverse genus *Phanaeus* (with about 50 extant species) evolved in the Andes from where some species subsequently dispersed into Amazonia. At a later date, colonization and further diversification took place in southern Brazil and also into the Guianan shield. At least two species in the genus have also reached northeast Brazil.

The scarab fauna of northeast Brazil, including that of the tribe Phanaeini, has received less attention in comparison to that of other parts of the country. Inadequate investigation during the 19th and 20th centuries is probably the best explanation for the small number of scarabaeine species previously recorded in the literature from many northeastern Brazilian states (Vaz-de-Mello 2000). This paucity in published records is not limited to the Scarabaeinae; few published records for other subfamilies (Dynastinae, Cetoniinae, Rutelinae etc.) and for many other groups of arthropods exist for the area. However, it should be pointed out that in recent years, much more attention has been directed toward the region (Hernández 2003, 2005, 2007; Endres et al. 2005, 2007; Silva et al. 2007; Lopes et al. 2006; Costa et al. 2009; Filgueiras et al. 2009; Sampaio et al. 2009).

Because Scarabaeinae have proven to be a reliable group for studying wider biodiversity patterns and have consequently been adopted as a cost-effective bioindicator taxon (Halffter and Favila 1993; Spector 2006; Gardner et al. 2008), the Phanaeini, being a common component of most Neotropical dung beetle communities, is clearly an important group for biogeographic and ecological study. Phanaeines are also undoubtedly an important functional component in many ecosystems (Nichols et al. 2008).
Figure 2-6. Habitats. 2) An opening in the caatinga habitat in the vicinity of Tabatinga, Maranguape, 126 m (CE), where Coprophanaeus pertyi occurs sympatrically with C. cyanescens and Diabrotic mimas. April 2008. 3) Habitats at Maranguape, São Benedito, Sanctuario da Nossa Senhora de Penha, (CE). In the foreground open caatinga area where Coprophanaeus pertyi, C. cyanescens and Diabrotic mimas occur. In the background, on the hills, Atlantic forest where C. cyanescens, C. dardanus and D. mimas occur. March 2008. 4) A typical area of ‘chapada’ at Fazenda Rodiador in the Santa Quiteria de Maranhão municipality (MA). May 2008. This cerrado biotope is the habitat of Coprophanaeus acrisius. 5) Open grassland/palm forest within the cerrado habitat at Fazenda Rodiador in the vicinity of Santa Quiteria de Maranhão (MA). May 2008. This is the habitat for Phanaeus melibaeus. 6) Atlantic forest habitat at Uirapuru, Serra de Baturité, 620 m (CE), where Coprophanaeus cyanescens occurs sympatrically with C. dardanus. April 2008. Photograph 2-3, 6 by C.P.D.T. Gillett and 4-5 by M.P.T. Gillett.
Biotopes of the northeast of Brazil

The political division of the northeast of Brazil (Região Nordeste, NE) encompasses the following Brazilian states: Maranhão (MA), Piauí (PI), Ceará (CE), Paraíba (PB), Rio Grande do Norte (RN), Pernambuco (PE), Alagoas (AL), Sergipe (SE) and Bahia (BA). This vast area, covering approximately one and a half million km², contains a wealth of natural biotopes, although semi-arid habitats predominate, covering approximately half of the total area (Araújo et al. 2005). Morrone (2006) reviewed the classification of Latin American biogeographical areas based on panbiogeographic and cladistic analyses of their entomological fauna. According to the resulting scheme, NE Brazil is located mostly in Morrone’s ‘Chacoan’ subregion, consisting of the ‘Caatinga’ and ‘Cerrado’ provinces. The Caatinga province covers most of the area, with the Cerrado province extending significantly only into PI and MA in the study area. A second region, the ‘Parana’ subregion, comprises both the ‘Brazilian Atlantic Forest’ province, which is located along a narrow band on the coast of several states in NE Brazil and the ‘Paranaian Forest’ province, which occurs further inland and is mostly restricted to BA in the NE. Additionally, a considerable portion of MA is characteristic of the Pará province, belonging to the Amazonian subregion. A map of the NE Brazilian states and approximate coverage of biogeographic provinces is shown in Figure 1.

The caatinga (Figure 2 and 3), as already mentioned, is the most important and distinctive habitat of the NE, covering about 22% of the region (Barbosa et al. 2005), making it the largest dry forest biotope in the whole Neotropical region (WWF 2009a). In contrast to the deciduous thorn-scrub thicket of the caatinga, the cerrado (Figure 4) is an open to closed savannah grassland, but is incredibly variable and usually contains mesophytic forests, gallery forests and palm forests (Figure 5) locally. Cerrado is the world’s most biodiverse savannah region (WWF 2009b), but is mostly found outside of the NE. In the NE, cerrado is often associated with ‘chapadas’ (flat-topped hills and plateaus) and is often found as enclaves, particularly in the northern states of the NE. Other important habitats of the NE include mata Atlântica (Atlantic forest) (Figure 3 and 6). It covers the moist elevated areas near the coast, particularly in the southernmost states, although it stretches in a narrow band along the coast northwards into CE and beyond in discontinuous remnants wherever the elevation and climate permits. These patches of forest clinging to the hillsides are sometimes called ‘brejos’ and have been classified as ‘caatinga enclave moist forests’ by WWF (2009c) in recognition of their diversity. Many other marginal habitat types (e.g. coastal areas) also occur in the region, but their description is beyond the scope of this paper.

Like many other tropical areas, the habitats of the NE are threatened by the activity of man. In caatinga areas, the most important widespread degradation results from the increase in livestock ranching, which affects biodiversity directly through removal/conversion of the local vegetation into pastureland. Deforestation resulting from exploitation of the landscape for charcoal and timber is also an important factor (Barbosa et al. 2005). Cerrado areas in the NE, long considered as infertile, have in recent years disappeared at an alarming rate as innovative soil treatment has allowed exploitation that has resulted in tropical soybean monoculture (Neves et al. 1996). The Atlantic coastal forests of Brazil are well known to have been reduced to less than 10% of their original extent. However, the caatinga enclave moist forests of the NE have suffered even worse rates of deforestation with currently only 4% remaining intact (WWF 2009c).

All of the fieldwork undertaken in this study was broadly conducted in caatinga, cerrado and Atlantic forest biomes.

Scope of this study

Of the approximately 75 currently recognized species of Phanaeini recorded from Brazil (three Gromphas Brullé spp., Homalotarsus impressus Janssens, Tetrameretia convexa (Harold), Megatharsis buckleyi Waterhouse, about 20 Dendropaemon spp., two Diabroctis Gistel spp., about 23 Coprophanaeus Olsoufieff spp., 10 Phanaeus spp., 11 Oxysternon Castelnau spp. and four Sulcophanaeus Olsoufieff spp.), only 12 species have previously been recorded from the NE region (Table 1). Six of these species have hitherto only been recorded from BA, in the south of the region, which contains the highest phanaeine species richness in the NE. The present study focuses on the results of extensive fieldwork undertaken in 2008 in the States of CE, MA and PI (i.e. the three northernmost states of the NE region). Records from other years and other NE Brazilian states are covered in less detail. These three states are amongst those having
received the least attention from the point of view of Scarabaeinae faunistics and biodiversity in the whole of Brazil. Only eight species of Scarabaeinae are recorded from CE, two species from PI (Vaz-de-Mello 2000; Arnaud 2002) and 23 species recently recorded from MA (Sampaio et al. 2009). Only three phanaeines have hitherto been recorded from these same three states: Coprophanaeus (s.str.) acrisius (Macleay), C. (Metallophanaeus) pertyi (Olsoufieff) and C. (M.) vazdemeloi Arnaud (Sampaio et al. 2009; Arnaud 2002a). The last species is endemic to the region.

Although from a taxonomic standpoint the tribe Phanaeini is comparatively well known, with recent revisions of several genera (Edmonds 1994, 2000; Edmonds and Zídek 2004) and an iconographic summary available (Arnaud 2002a), information on the distribution, habitat requirements and ecology of the majority of species from the northeast of Brazil is either minimal or completely lacking. The present report presents new distributional and ecological data for all the species of Phanaeini recorded from the States of CE, MA and PI. This data allowed for a preliminary analysis of the diversity and community structure in each biogeographic province and a comparison with other Neotropical areas.

Materials and Methods

Field observations of Phanaeini were made at several localities in the NE Brazilian States of CE, PI and MA (see Figure 1 and species accounts) during the period February-June 2008. Sampling sites were chosen to represent the most important habitats in the region. Caatinga and cerrado habitats at one locality in PI, Canto do Buriti not shown in Figure 1, were extensively studied, but provided no records of Phanaeini.

The beetles were collected in pitfall traps baited with either human dung or with pieces of chicken carcass that had been left to decay for at least 24 hours prior to use. Traps were not standardized because the priority was not to allow for detailed and reproducible statistical analyses, but rather it was to find and study as many specimens from as many localities as possible using the limited time and transport available. Dung traps consisted of large plastic cups buried into the soil, with the bait wrapped in gauze and suspended above the cup from a stick obliquely inserted into the soil adjacent to the cup. A small quantity of water with a drop of washing-up detergent inside each cup served to ensnare the beetles and prevent their escape through flight. The carrion traps generally consisted of small 500 ml plastic drinks bottles into which were pushed a small quantity of the rotting chicken flesh directly through the mouth of the bottles. Traps were either lightly buried in the ground so that the mouth of each bottle remained flush with the soil, or were most often placed along small inclines in the ground or amongst vegetation. Standard carrion-baited pitfall traps were also used (notably in MA) and comprised large plastic cups buried into the soil with the bait suspended from a protective wire mesh held down over the traps with wooden or metal stakes and weighted down with large stones and logs. These traps were often unproductive as they were subject to interference by wild animals and free-ranging domestic pigs. Traps were placed wherever suitable habitat was available and, equally importantly, where they were least likely to be raided by animals. In each locality, traps were placed either singly or in small groups of between 2-10 traps at random distances from each other, but usually separated by less than 50 m. Traps were normally checked daily and were usually only left for one or two days before being removed and redeployed to further localities. Flight interception traps and mercury vapor lamp-fitted light traps were also deployed at most sites, but caught no phanaeines except for a single Dendropaemon sp. at Riozinho, southern PI. For all specimens, locality and temporal data are presented in full, and where possible, coordinates are given for the general collecting area. The captured beetles were identified using the available literature (Arnaud 2002a, Olsoufieff 1924, Edmonds 1994) and from a number of voucher specimens previously identified by W.D. Edmonds (Marfa, Texas) and by the fourth author. Some specimens of Coprophanaeus from the NE were sent to Edmonds for inclusion in his taxonomic review of the genus and for confirmation of their identities. The numbers of specimens of each species was recorded, as was the sex of each specimen. The male: female sex ratios are given for each species only for the trap data obtained in 2008. The relative abundances of the species recorded in CE and MA were also calculated based on this data. Other significant biological and distributional information, including bait and habitat preferences are presented and new regional and state records are highlighted. Notes on diel activity are based on limited data. The coloration of each specimen was also noted and this is briefly discussed, especially in comparison with conspecific specimens from other parts of Brazil and South America.
In addition to the sampling effort of 2008, some of the same sites were re-sampled in December 2009 and January 2010. Additional specimens collected in April-June 2005 and a further small number of specimens acquired during the period 1975-2000 were also considered in the study. Relevant specimens were also studied from the Fernando Vaz-de-Mello collection (FVMC) now housed at the Universidade Federal de Mato Grosso in Cuiabá, Brazil, the collections of the Natural History Museum, London (BMNH) and the Michael P.T. Gillett collection, Birmingham, UK (MGCB). Whilst this paper concentrates on the diversity of Phanaeini in the states of CE, PI and MA, some additional data from the remaining NE Brazilian states is presented for completeness.

It should be noted that the period March - June 2008, during which most of the fieldwork took place, represented the bulk of the ‘wet season’ in much of the NE of Brazil. In 2008, the rains were particularly abundant, with the whole area appearing lush and verdant, while flooding was widespread, particularly in PI, often to the point of making travel and effective pit-fall trapping difficult.

Material Examined

The following eight species of Phanaeini were recorded from the NE, including two species that are new records for the regional fauna. Note: m = male specimen(s); f = female specimen(s)

*Coprophanaeus* (*Coprophanaeus*) *cyanescens* (Olsoufieff, 1924)

Figure 7

**Collection data. Ceará:** Maranguape, São Benedito, Sanctuário da Nossa Senhora de Penha, 38°40'53"W; 03°52'18"S, 160 m Atlantic forest, carrion traps, 26. iii. 2008: 2m + 1f; idem, 09. iv. 2008: 1m + 1f; Maranguape, Tabatinga, 38°43'48"W; 04°00'42"S, 126 m Caatinga, carrion traps, 31. iii. 2008: 1m + 1f; idem, open area dung traps, 26. iii. 2008: 1 f; Same as before except, carrion traps, 31. iii. 2008: 1f; Serra de Baturité, Uirapuru, 38°54'22"W; 04°17'27"S, 620 m Atlantic forest, carrion traps, 06. iii. 2008: 2m + 5f; idem, carrion traps near house, 27. iii. 2008: 1f; idem, forest carrion traps, 09-10. v. 2008: 7m + 4f; idem, dung traps, 07. iii. 2008: 1 f; Same as before except, carrion traps, 29. iii. 2008: 3m + 1f; Same as before except, 07. iii. 2008: 3m + 1f; Same as before except, forest dung traps, 29. iii. 2008: 1 f; Same as before except, carrion traps, 28. iii. 2008: 2m + 1f; Same as before except, forest carrion traps, 27. iii. 2008: 5m + 1f; Piraponga, 38°41'59"W; 03°53'26"S, 200 m Atlantic forest, carrion traps, 14. ii. 2008: 4m + 5f; idem, 03. iii. 2008: 2m + 2f; Maranguape, São Benedito, Sanc. Nossa Senhora de Penha, 38°40'48"W; 03°52'29"S, 96 m open scrubland / caatinga, carrion traps, 26. iii. 2008: 2m+1f. **NEW STATE RECORDS.**

**Maranhão:** Santa Quitéria de Maranhão, Fazenda Rodiador, 42°40'46"W; 03°24'50"S, 47 m Restinga, under forest cover, dung traps, 12. v. 2008: 1m + 1f; idem, forest carrion traps, 23. ii. 2008: 1m + 2f; idem, forest carrion traps, 22. ii. 2008: 1m + 2f; idem, 18. v. 2008: 1m + 2f; idem, 24. ii. 2008: 1m + 1f; idem, 17. v. 2008: 2m + 6f. idem, palm forest, sandy soil, 07. i. 2010: 1m. Pedrinhas, São Luís, 24. vii. 1984, I.P. Garcia (FVMC). **NEW STATE RECORDS.**

**Pernambuco:** Recife, Dois Irmãos, Universidade Federal Rural de Pernambuco, No dates: 1m + 1f; Caruaru, Brejo Novo, 23. iv. 2004, D. Cabral-de-Melo (FVMC); idem, 27. iii. 2004, F. Silva (FVMC); Várzea, 11. ix. 1995 (FVMC).

**Piauí:** Baixa Grande do Ribeiro, Riozinho, approx. 45°25' W; 8° 50' S, gallery forest in cerrado, v. 2005: remains of a male specimen (pronotum). **NEW STATE RECORD.**

**Results.** 2008 data: 84 specimens; 41 males, 43 females. Male: Female sex ratio 0.95. Bait preference (2008 data): Carrion (79), Dung (4). Temporal distribution (all data): January (1) February (9), March (44), April (1), May (32), September, November (1)

**Distribution.** Widespread in cerrado and similar open habitats through most of Brazil (not in the Amazon basin). Also present in Paraguay (Arnaud 2002a), Bolivia (D. Mann pers. comm.), Argentina (specimens in MGCB) and in areas of Atlantic forest in Brazil. Costa et al. (2009) first correctly recorded the species from the NE when they collected it in the Atlantic forest and open areas in PE.
Remarks. *Coprophanaeus cyanescens* is the most abundant and widespread species of Phanaeini found in the area. It is most common in Atlantic forest enclaves but can also occur less abundantly in open caatinga and cerrado areas at all elevations sampled. It is preferentially necrophagous but can be attracted in small numbers to dung baited traps both in forest and open habitats. The species is sympatric with *C. dardanus* (Macleay) and *Diabroctis mimas* (Linnaeus) in Atlantic forest, with *C. pertyi* and *D. mimas* in caatinga, and with *C. acrisius* and *Phanaeus melibaeus* Blanchard in cerrado habitat.

All previous records for *C. jasius* (Olivier) from NE Brazil (Pessôa 1934, Hernández 2003; Silva et al. 2007, Lopes et al. 2006 and Filgueiras et al. 2009) should actually be attributed to *C. cyanescens*. The two species are closely related, but the authentic *C. jasius* is a widely distributed insect in Amazonian forest habitats and is replaced by *C. cyanescens* in the Atlantic forest, cerrado and caatinga habitats of Brazil (W.D. Edmonds pers. comm.). In the NE, *C. cyanescens* appears to always have the anterior and lateral margins of the pronotum, femora and pygidium of a predominantly bright green, sometimes blue-green color. No completely blue individuals (as illustrated in Arnaud 2002a) have been seen by the authors from the area. There may be a geographic correlation in coloration, as several blue specimens are known to us from SW Brazil and Paraguay, and some from Atlantic forest patches in SE Brazil (where green specimens appear to be confined to open habitats) (F.Z. Vaz-de-Mello personal observation).
Coprophanaeus (Coprophanaeus) acrisius (Macleay, 1819)

Figure 8


Maranhão: Santa Quitéria de Maranhão, Fazenda Rodiador, 42°40'46"W; 03°24'50"S, 47 m palm forest, carrion traps, 23. ii. 2008: 1 m; idem, 120 m chapada, carrion traps, 18. v. 2008: 1m + 1f; idem, carrion traps, 24. ii. 2008: 1 m; idem, 17. v. 2008: 1f; idem, open cerrado area, sandy soil, carrion traps 06-07. i. 2010: 5m + 2f; idem, dung traps: 2f; idem, palm forest, carrion traps 06-07. i. 2010: 2m + 2f.

Pernambuco: Recife, campus of Universidade Federal de Pernambuco, no date: 1m+1f.

NEW STATE RECORD.


Distribution. This species has been recorded from Brazil (Pará), Bolivia (Santa Cruz) and Argentina by Arnaud (2002). The species was first recorded from MA by Sampaio et al. (2009). It is associated with cerrado habitats in Brazil, occurring in both forested and open areas.

Remarks. Coprophanaeus acrisius was preferentially attracted to carrion traps but can be observed in smaller numbers attracted to dung traps (records from MA, January 2010) in cerrado-type habitat (locally called ‘chapada’), which corresponds to slightly elevated regions of open dry woodland with grass. It was also present in an area of dry forest thickets within palm forest. It appears to be an uncommon and patchily distributed species that is sympatric with the more abundant C. cyanescens. Sampaio et al. (2009) recorded a single individual of this species from an area of coastal cerrado habitat in MA. In MA, it has been recorded only on sandy soils. The specimens from MA match the holotype, and other specimens housed in the BMNH, closely in color. The dorsal surface of the elytra and the pronotum (except for the lateral basal areas) are bright greenish, with copper-green colored elytral intervals.

Coprophanaeus (Coprophanaeus) dardanus (Macleay, 1819)

Figure 9

Collection data. Ceará: Baturité, Uirapuru, 38°54'22"W; 04°17'27"S, 620 m Atlantic forest, dung traps, 06. iii. 2008: 2m; idem, carrion traps near house, 27. iii. 2008: 1m; idem, carrion traps, 06. iii. 2008: 3m + 1f; idem, 09-10. v. 2008: 1m + 1f; idem, dung traps, 28. iii. 2008: 1m; idem, dung traps, 29. iii. 2008: 3m + 2f; idem, carrion traps, 07. iii. 2008: 3m + 4f; idem, dung trap near house, 28. iii. 2008: 1f; idem, forest dung trap, 29. iii. 2008: 1f; idem, 29. iii. 2008: 1m + 2f; idem, carrion traps, 28. iii. 2008: 4m + 5f; idem, 27. iii. 2008: 5m + 2f; Maranguape, Piraponga, 38°41’59”W; 03°53’26”S, 200 m Atlantic forest, carrion traps, June 2005: 2m + 2f.

NEW STATE RECORDS.


Distribution. This species has been recorded from BA (Olsoufieff 1924) and recently from PE (Costa et al. 2009) in the NE. It is also known from several other Brazilian states (Santa Catarina, Rio de Janeiro, São Paulo, Minas Gerais, Espírito Santo, Pará), French Guiana and Venezuela (Feer 2000; Arnaud 2002a; Schiffler et al. 2003; F. Z. Vaz-de-Mello personal observation) and is present in Suriname (C. Gillett personal observations). The new records above are intermediate between the other Brazilian records and the Amazonian records, indicating that the species has a more continuous distribution along the coast of Brazil than was previously apparent.

Remarks. Coprophanaeus dardanus is restricted to Atlantic forest fragments and enclaves in the area studied, only at elevations above 200 m (although it occurs above 500 m in SE Brazil – F. Z. Vaz-de-Mello personal observation). The species is preferentially necrophagous but can also be regularly collected in
dung-baited traps. In June 2005 specimens were collected at Piraponga, Maraguape but not at Uirapuru, Serra de Baturité. Conversely in March 2008, specimens were collected at the latter locality but not in the former, possibly indicating very localized shifts in temporal distribution probably related to elevation and climate. At both localities the species occurs sympatrically with *C. cyanescens*. Specimens from CE match those from other areas (French Guiana, Suriname etc.) in color, having only slight metallic greenish reflections on the pronotum and femora.

**Coprophanaeus (Metallophanaeus) pertyi** (Olsoufieff, 1924)

Figure 10

**Collection data.** Ceará: Maranguape, Tabatinga, 38°43′48″W; 04°00′42″S, 126 m Caatinga, carrion trap, 26. iii. 2008: 6m + 3f; idem, 31. iii. 2008: 2m; Cagado, 38°45′05″W; 04°01′57″S, 114 m Caatinga, carrion trap, 28. iv. 2008: 1m. Maranguape, São Benedito, Santuario da Nossa Senhora de Penha, 38°40′48″W; 03°52′29″S, 96 m Scrubland / caatinga, 26. iii. 2008: 2m + 1f.

Piauí: São Raimundo Nonato, i. 1999, C.A. Matrangolo (several specimens, FVMC). NEW STATE RECORD.

Rio Grande do Norte: Rio Grande do Norte, no further data, 1m + 1f (BMNH).


**Distribution.** It has been recorded from RN, CE, AL (as *Phanaeus alvarengai* Pereira and D’Andretta, 1955), BA (Martínez and Pereira 1967; Arnaud 2002a; Lopes et al. 2006), PE (Pereira and D’Andretta 1955; Silva et al. 2007; Costa 2009), PB (Hernández 2007) and MA (Sampaio et al. 2009) and is an endemic species of the caatinga and transition zones, mainly in NE Brazil, but also occurring in northern Minas Gerais (F.Z. Vaz-de-Mello personal observation).

**Remarks.** *Coprophanaeus pertyi* is restricted to open areas of caatinga and associated scrubland at low elevations below 200 m. It was collected exclusively in carrion baited traps and appears to be very patchily distributed. It is (unusually for a *Coprophanaeus*) probably a diurnal species because on several occasions no specimens were collected in overnight traps checked in the morning, but were present in traps checked in the late afternoon or evening. Hernández (2007) also records it as being diurnal. The species occurs sympatrically with *C. cyanescens* and *D. mimas* in open areas. Sampaio et al. (2009) also recorded the species from coastal cerrado habitat in MA. All specimens studied here have greenish-blue metallic reflections on the pronotum, pygidium and femora (a very similar color to that of *C. cyanescens* in the study area), except for those from Piauí, which are much darker, having the pronotum colored dark blue to almost black.

Two other species in the subgenus *Metallophanaeus* are recorded from the NE. One is the endemic *C. vazdemeloi* Arnaud, known only from a caatinga area of PI (Arnaud 2002; Arnaud 2002a). The second species is *C. punctatus* Olsoufieff, a rare inhabitant of the Atlantic forest which has been recently recorded from PE (Costa et al 2009) and is also known from BA in the NE (Olsoufieff 1924; Arnaud 2002a) and from Minas Gerais (Arnaud 2002) and Espíritu Santo (F.Z. Vaz-de-Mello personal observation) elsewhere.

**Coprophanaeus (Megaphanaeus) ensifer** (Germar, 1821)

**Collection data.** Pernambuco: Recife, Dois Irmãos, Universidade Federal Rural de Pernambuco campus, no date (collected most probably in the 1980’s): 2 f; Pernambuco, no date, (BMNH): 1m.

Alagoas: Maceió, no data: several locally collected specimens seen in July 1994 during a visit to the Federal University of Alagoas. NEW STATE RECORD.

**Distribution.** The species has been recorded from many states of central and southern Brazil and also in the NE in BA (Pessôa and Lane 1941; Arnaud 2002a) and PB (Hernández 2003; Endres et al. 2005,
2007) and recently from PE (Costa et al. 2009). The species also occurs in Argentina (Arnaud 2002a), Bolivia (D. Mann personal communication) and Paraguay (specimens in MGCB).

**Remarks.** This is the largest phanaeine present in the NE. It is a necrophagous species associated with Atlantic forest habitats in PE and PB, although it has also been recorded from cerrado-type areas in PB (Endres et al. 2005). In central and southern Brazilian regions it is predominantly a species of the cerrado. Endres et al. (2005) did not detect significant bait preference for three different carrion baits during an ecological study but did demonstrate that adults are only active during the rainy season (April to September in PB). All specimens studied by us from PE and AL were of uniform dark metallic green dorsal coloration. A second species of *Megaphanaeus* Olsoufieff, *C. (M.) bellicosus* (Olivier) has been recorded to date only from BA in the NE (Arnaud 2002a). This species is characteristic of the Atlantic forest, occurring elsewhere in the States of Santa Catarina, Minas Gerais, São Paulo, Rio de Janeiro and Espíritu Santo (Pessôa 1934, Arnaud 2002a).

**Diabroctis mimas** (Linnaeus, 1767)

*Figure 11*

**Collection data.** Ceará: Maranguape, Tabatinga, 38°43'48"W; 04°00'42"S, 126m Caatinga, open area dung traps, 26. iii. 2008: 1m; Maranguape, Piraponga, 38°41'59"W 03°53'26"S, 200 m Atlantic forest, dung trap, 14. ii. 2008: 1f; Maranguape, São Benedito, Santuário de Nossa Senhora de Penha, 38°40'53"W; 03°52'18"S, 160 m Atlantic forest, forest dung trap, 25. iii. 2008: 7m + 4f; Acarau, coastal ‘restinga’ vegetation, in diurnal flight, no date. **NEW STATE GENUS AND SPECIES RECORDS.**

Maranhão: Santa Quitéria do Maranhão, Fazenda Rodiador, 42°40'46"W; 03°24'50"S, 47m Restiinga, forest dung traps, 22. ii. 2008. 1m; idem, under dung in forest, 24. iii. 2008: 1m. **NEW STATE RECORDS.**

Pernambuco: Recife, Guararapes Airport, in diurnal flight, no date (early 1980’s); Recife, Dois Irmãos, dug up from under animal dung in forest, ix. 1988: 1m + 1f.


**Distribution.** A widespread species through much of the northern half of South America. In Brazil it has been recorded from the states of BA, Pará, Amazonas, Goiás, Mato Grosso and São Paolo (Pessôa 1935). Lopes et al. (2006) also record it from BA and Silva et al. (2007) collected it in the Atlantic forest in PE. It has been cited elsewhere from Guyana, French Guiana, Suriname, Venezuela, Bolivia, Paraguay (Arnaud 2002a) and Uruguay (Olsoufieff 1924). We have also seen specimens from Peru (specimens in MGCB) and from the Brazilian Distrito Federal and states of Minas Gerais, Mato Grosso do Sul and Goiás. (specimens in FVMC).

**Remarks.** *Diabroctis mimas* is most commonly found in Atlantic forest remnants in the study area although it can also occur in open caatinga and cerrado habitats. It appears restricted to elevations below 200 m and has been collected in human dung baited traps. In Atlantic forest areas it is not unusual to find the beetles inside burrows on forest paths. The species is sympatric with *C. cyanescens* in Atlantic forest and with *C. pertyi* and *C. cyanescens* in caatinga. Specimens from the NE match those from other distant areas (e.g. Peru) in color.

**Phanaeus** *(Notiophanaeus)* *melibaeus* Blanchard, 1843

*Figure 12 and 13*

**Collection data.** Maranhão: Santa Quitéria de Maranhão, Fazenda Rodiador, 42°40'46"W; 03°24'50"S, 47m open area with palm trees, overnight dung trap, 18. v. 2008: 1 m; idem, open cerrado area, overnight dung trap 06. 1. 2010: 1f. **NEW STATE GENUS AND SPECIES RECORDS.**

Bahia: 150 km W Barreiras, dung trap, i. 2002, P. Schmidt: 1m (FVMC). **NEW STATE RECORD.**
Table 1. Summary of the distribution by state of the 15 species of Phanaeini recorded from northeastern Brazil. Filled boxes indicate presence (green-filled boxes indicate new state records). For state acronyms see text.

* Sulcophanaeus faunus was recorded from Bahia by Arnaud (2002).
** Recorded as Coprophanaeus jasius by Hernández (2003).
*** Recorded as Coprophanaeus jasius by Silva et al. (2007) and Filgueiras et al. (2009).
**** Recorded as Coprophanaeus jasius by Lopes et al. (2006).
***** Recorded as Coprophanaeus (Metallophanaeus) sp. 1 by Costa et al. (2009); identification confirmed by F.Z. Vaz-de-Mello.

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<tr>
<th>Species</th>
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<td>Phanaeus melibaeus Blanchard</td>
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<td>Coprophanaeus bellicosus (Olivier)</td>
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<td>Coprophanaeus cyanescens (Olsoufieff)</td>
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<td>Dendropaemon bahianus Harold</td>
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<td>Dendropaemon smaragdinus Waterhouse</td>
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Distribution. This very rarely recorded species is known from a few scattered localities on the periphery of the southern Amazon basin in the Brazilian states of Goiás, Mato Grosso, Pará, Rondônia and Minas Gerais (Edmonds 1994; Pessôa 1934) as well as from Bolivia (Olsoufieff 1924; Edmonds 1994; Spector 2002; Vulinec et al 2003). The current records from MA and BA represent an enormous range extension of more than 1000 km to the north and east of the nearest published record, taking its range beyond the Amazon basin. We are also aware of its presence in the Brazilian state of Minas Gerais (700 km south of the BA record).

Remarks. Phanaeus melibaeus appears to be a rare species in the study area. The two specimens collected in MA on separate occasions were attracted to human dung-baited pitfall traps. The species appears to be crepuscular or nocturnal because the two MA specimens were collected in the morning after over-night trapping sessions. A related species in the same species group, P. haroldi Kirsch, is also crepuscular or nocturnal in Ecuador (C. Gillett personal observation). The habitat for the species in MA (Figure 4) can be considered a cerrado biotope and consists of the edge of an open grassland with low bushes, originally covered in palm trees. Edmonds (1994) cites the species as being coprophagous, whilst also indicating that due to its scarcity, it may prove to have an unusual ecology. The male specimen from MA is less brightly colored than the specimen illustrated by Arnaud (2002a), although the female agrees in color; the specimen from BA has very dark blue pronotum and elytra, contrary to those from Minas Gerais and Mato Grosso, which tend to have a bright golden-copper pronotum and emerald green elytra.

The only other species of Phanaeus recorded to date from the NE is P. (Notiophanaeus) splendidulus Fabricius, a typical species of the Brazilian Atlantic forest and known only from Bahia in the NE region (Edmonds 1994; Arnaud 2002a) and elsewhere from southern Brazil and northern Argentina.
**Dendropaemon** sp.

**Collection data. Piauí:** Baixa Grande do Ribeiro, Riozinho, approx. 45°25' W; 8°50' S, cerrado, mercury vapour light trap, v. 2005: 1 specimen. **NEW STATE GENUS RECORD.**

**Remarks.** Few records exist for species of *Dendropaemon*. At least two other species have been recorded from the NE of Brazil; both were described from BA and are listed by Olsoufieff (1924). These are *D. bahianus* Harold and *D. smaragdinus* Waterhouse. There are no recent published records for either species. Unfortunately at this time it is not possible to reliably identify species of *Dendropaemon*. However, the genus is currently under taxonomic revision (F. Génier and P. Arnaud personal communication).

**Sulcophanaeus faunus** (Fabricius, 1775)

**Remarks.** *Sulcophanaeus faunus* has been recorded from BA (Arnaud 2002a) without further details. This species is widespread in the Amazon basin in humid rainforest habitats although it has been recorded as far south as Paraguay along gallery forests. If the species is indeed present in the region, it is likely to be restricted to similar humid habitats.

**Identification key to species of Phanaeini recorded from northeast Brazil**

The following simplified key is presented to aid identification of specimens of Phanaeini from the NE of Brazil. The key has been adapted from those published by Edmonds (1972, 1994, 2000), Edmonds and Zídek (2004), Arnaud (2002a) and the descriptions of species in Olsoufieff (1924) and Arnaud (2002). It includes all species recorded from the NE to date, but should be used with care, inasmuch as additional species and even genera are likely to be present, though hitherto unrecorded, from the region. Readers are urged to study the above-cited works for more detailed information on identification. It should also be stressed that phanaeines display marked variation in color and in allometric development of secondary sexual characters such as thoracic and clypeal carinae and horns, which may also be affected by wear. This variability should be borne in mind when using the key. An asterisk “*” indicates specimens of these species were not examined when compiling the key.

1. Middle and hind tarsi each with fewer than five segments; front tarsi absent in males and females.
   Body flattened. Generally smaller species, (length up to 15 mm in NE Brazil) .........................
   - **Genus Dendropaemon** Perty
     [Three species recorded from the NE including *D. bahianus* Harold and *D. smaragdinus*
     Waterhouse. The genus is currently under review by F. Génier and P. Arnaud.]
   - Middle and hind tarsi each with five segments; front tarsi present or absent in females, always
     absent in males. Body convex. Generally larger species, usually longer than 15 mm .......... 2

2(1). Anterior margin of clypeus sharply emarginate medially, giving rise to a pair of acute, dentiform
projections (Figure 7, 8, 9 and 10). Front tibiae distinctly quadridentate (in unworn specimens).
Front tarsi usually absent in females. **Genus Coprophanaeus** Olsoufieff ........................ 3
   - Anterior margin of clypeus not sharply emarginated medially, at most with a pair of round teeth..
   Front tibiae variable. Front tarsi usually present in females .............................................. 10

3(2). Front tarsi present in females (in NE Brazilian species). Posterior surface of each front tibial
tooth with a brush-like clump of short setae. Hind wing not notched basally. Large or very large
species (usually 30 mm or more). Sexual dimorphism distinct (*C. bellicosus*) or indistinct (*C.
ensifer*). **Subgenus Megaphanaeus** Olsoufieff ......................................................... 4
   - Front tarsi absent in females. Posterior surface of each front tibial tooth with a single oblique row
of setae. Hind wing notched or not at base. Sexual dimorphism usually distinct (in NE Brazilian
species). Smaller species, length up to 30 mm ................................................................. 5
4(3). Carinate lateral margins of elytral striae strongly undulate, interstriae strongly granulate. Sexual dimorphism attenuated, both sexes bearing a posteriorly curved horn on the clypeus and a saddle-like process projecting forward from the posterior portion of the pronotum. Very large metallic green colored species (up to 55 mm) .

Carinate lateral margins of elytral striae straight, interstriae smooth. Sexual dimorphism well expressed: males with a long recurved horn arising from the clypeus, females with a shorter trituberculate carina, the middle tubercle higher than the lateral ones. Thoracic projections differing greatly according to sex. Large dull black colored species (up to 38 mm) .

---

5(3). Hind wings not notched basally. Width of lower portion of eyes relatively smaller. Smaller (up to 24 mm), usually metallic colored species (except C. vazdemeloi) with a short or long horn like process on the clypeus of males. Subgenus Metallophanaeus Olsoufieff

5(5). Hind wings distinctly notched basally. Width of lower portion of eyes relatively larger. Larger (up to 33 mm), usually dark colored species though usually with distinct metallic reflections. Male cephalic process a transverse ridge with apical angles raised (C. dardanus) or a trituberculate carina with the central tubercle higher than the lateral ones (all other species). Subgenus Coprophanaeus (s.str.)

6(5). Elytra dark blue. Major male with a long, recurved horn arising from the clypeus. Pronotum bearing a pair of short upwardly projecting spiniform processes separated by rounded concavity. Female with anterior concavity bordered posteriorly by two blunt processes, and anteriorly by a rounded trituberculate carina. Dark blue-black species recorded from Bahia and Pernambuco.

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6(5). Elytra matt black. Major male with shorter erect horn-like carina arising from clypeus. Pronotum with an anterior declivity bordered posteriorly by carina. Female with anterior concavity bordered posteriorly by a carina or not. Pronotum and head with metallic blue-green reflections or entirely matt black .

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7(6). Pronotum and head with distinct metallic blue-green reflections. Anterior prominence of metasternum not a laterally compressed, elongate process. Anterior declivity of male pronotum bordered posteriorly by a carina with a tab-like process projecting anteriorly (Figure 10). Female with anterior concavity bordered posteriorly by a carina. Length 15-22 mm. Widely distributed in the NE .

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7(7). Entirely matt black species. Anterior prominence of metasternum elongate and projecting forwards, laterally compressed. Anterior declivity of male pronotum bordered posteriorly by a carina lacking tab-like process medially. Female with anterior concavity not bordered posteriorly by a carina. 19.5 - 20.0 mm. Known only from Piauí .

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8(5). Anterior marginal ridge (bead) of pronotum distinctly interrupted behind the eyes. Pronotum of major males with a large quadrade median process (Figure 9). Clypeus of males with a transverse parallel-sided or divergent carina with the lateral angles raised as horn-like tubercles. Color black with faint metallic greenish reflections on the pronotum, femora and pygidium .

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8(5). Anterior marginal ridge (bead) of pronotum complete, not interrupted immediately behind the eyes. Pronotum of major males with an anterior concavity delimited posteriorly by a trituberculate carina (Figure 7 and 8). Clypeus of males with a trituberculate horn-like carina, the median tubercle higher than the lateral ones. Color variable but always with more obvious metallic greenish reflections .

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9(8). Elytral striae distinctly carinate (viewed under magnification). Dorsal coloration dark metallic green, except for shining black areas on pronotum (Figure 8). Elytral interstriae often copper.
Area adjacent to anterior clypeal teeth not deeply incised, giving clypeus a rounded appearance. Slightly larger species (up to 33 mm). Cerrado areas ................................................................. *Coprophanaeus (s.str.) acrisius* (Macleay)

— Elytral striae not carinate. Dorsal coloration darker, mostly black, but with extensive areas of metallic green-blue on the pronotum, head, pygidium and femora. Elytral interstriae never copper (Figure 7). Area adjacent to anterior clypeal teeth deeply incised, giving the clypeus a more angular appearance. Slightly smaller species (up to 31 mm). Widely distributed in many habitats .................................................. *Coprophanaeus (s.str.) cyanescens* (Olsoufieff)

10(2). Dorsal surface of clypeus with two transverse carinae. In major males the posterior cairna is raised at each end into upwardly projecting horn-like structures. Large (length up to 35 mm), partly metallic green species (Figure 11) ...................... *Diabroctis mimas* (Linnaeus)

— Clypeus with only a single transverse carina (females), or with a long, partly recurved horn on the head (major males). Size and coloration variable .............................................................. 11

11(10). Anterior marginal ridge (bead) of pronotum complete, not distinctly interrupted by emarginations located immediately behind eyes. Large (length 30 mm or more) black species lacking metallic coloration ................................................................. *Sulcophanaeus faunus* (Fabricius)

— Anterior marginal ridge (bead) of pronotum distinctly interrupted by emarginations behind eyes. Smaller (up to 20 mm) variably metallic colored species. *Genus Phanaeus* Macleay, *subgenus Notiophanaeus* Edmonds ........................................................................ 12

12(11). Front tibiae tridentate. Longitudinal carina of third (basal) tooth very fine or effaced. Anterior prominence of metasternum acuminate, produced into acute tubercle (when seen in profile). Cephalic horn of major males slightly widened and compressed apically; smaller males have the horn reduced to a weak tubercle or bituberculate carina. Female pronotum with anteromedian concavity bordered by U shaped trituberculate carina. Basal pronotal fossae absent or weakly indicated .................................................. *Phanaeus (Notiophanaeus) splendidulus* (Fabricius)

— Front tibiae strongly quadridenate. Longitudinal carina of third tooth distinct. Anterior prominence of metasternum rounded (when seen in profile). Cephalic horn of major male rounded apically, not widened and compressed, almost vertical (Figure 12 and 13); in smaller males this is reduced to a short conical tubercle. Pronotum of female with anteromedian concavity, lacking U shaped carina but preceded by three strong tubercles, the middle of which is quadrate. Basal pronotal fossae conspicuous .................. *Phanaeus (Notiophanaeus) melibaeus* Blanchard

**Discussion**

In summary, five species of Phanaeini are newly recorded for the States of CE, MA and PI, which were the main states under study. Two of these records are also new species records for the NE region. A total of 13 new state records are presented above for eight of the 15 species of Phanaeini recorded from the NE region. The distribution by state of all species recorded to date from the NE is summarized in Table 1. Habitat preference for the species from CE, MA and PI is summarized in a schematic cross-sectional diagram of the most important habitat types found in the area (Figure 14). Rank abundance charts are presented for Phanaeini collected in CE and MA during February - June 2008 (Figure 15 and 16 respectively). The chart for CE also indicates the proportion of specimens observed in caatinga and Atlantic forest habitats. It was not possible to similarly partition the MA records according to habitat type.

The two species of Phanaeini here newly recorded for the NE from the States of CE, MA and PI (including the unidentified *Dendropaemon* sp.), raises the total number of species recorded from NE Brazil to 15, putting the diversity of this tribe in the region more in line with (though still below) that of other parts of Brazil (e.g. approximately 20 species are present in the well studied southeast, not including *Dendropaemon*). In comparison to the fauna of other seasonally dry ecoregions of the Neotropics, it appears that NE Brazil has a moderate diversity of Phanaeini. For example the tropical dry scrub forest along the Ecuadorian and Peruvian coasts harbor only 3 or 4 species (all endemic), although admittedly
this is a smaller area. The Argentinean, Bolivian and Paraguayan Chaco probably offers a more suitable comparison. In this broad region, approximately 20 species of Phanaeini (not including *Dendropaemon*) have been recorded (Edmonds 1994, 2000; Edmonds and Zídek 2004; Arnaud 2002a). A recent study of the community structure of Scarabaeinae from a site containing a mosaic of habitats in the cerrado of Minas Gerais recorded eight species of Phanaeini to be present in a limited, but heterogenous area (Almeida and Louzada 2009). These comparisons both highlight the considerable diversity of the NE region and also the relative dearth of research on the Scarabaeinae fauna of the area, which still requires more attention from taxonomists and ecologists.

Of the species known from the NE, only three can be considered as restricted to the area (or nearly so). These are three species of *Coprophanaeus*, all in the subgenus *Metallophanaeus* Olsoufieff: *C. pertyi* (also present in transitional areas in northern Minas Gerais), *C. punctatus* Olsoufieff (also present in northern Minas Gerais and in Atlantic forest in Espírito Santo) and *C. vazdemeloi* (known only by the type series from PI).

The subgenus *Metallophanaeus* has diversified in the Chacoan subregion *sensu* Morrone (2006). *Coprophanaeus pertyi* appears to be a diurnal, necrophagous, dry-habitat specialist restricted to the caatinga biome that is so characteristic of the region. It may be regarded as an indicator taxon for that habitat. Of particular interest to the fauna of the NE is *C. vazdemeloi* Arnaud, a species described from a unique pair of specimens collected at São Raimundo Nonato municipality in PI (Arnaud 2002). The remaining species present have broader distributions which extend either further south along the Atlantic forest (*C. dardanus*) or deeper inland along the cerrado belt (*C. acrisius*), or in some cases, both (e.g. *C. ensifer* and *C. cyanescens*). The discovery of *Phanaeus melibaeus*, previously restricted to cerrado areas delimiting the southern Amazon basin, in a cerrado area of MA, raises the possibility that other species chiefly distributed in the periphery of the Amazon basin may await discovery in the NE region. Such species may enter the region via the transition zone between Amazonian and Chacoan subregions located in MA. The only species in the NE that has also been recorded from true Amazon rainforest areas is *C.*

**Figure 14.** Schematic cross-section diagram of the distribution of Phanaeini species by habitat type and elevation in Ceará, Maranhão and Piauí.
dardanus, a well-known insect in French Guiana and Suriname (Feer 2000; C. Gillett personal observation), where it is found in humid lowland tropical forest. The species is restricted, in NE Brazil, to elevated areas along the coast, undoubtedly because it is in these restricted areas of humid Atlantic forest that it has found a suitable alternative to lowland rainforest. It is also present in lower elevation Atlantic forest through southeastern and southern Brazil. Other species currently only known from Atlantic forest areas further to the south, may yet be recorded in similar suitable areas in the NE.

The Phanaeini fauna of NE Brazil comprises an interesting assemblage of species adapted to specific, but varied biotopes often located in great proximity to one another. In general, there is substantial exclusivity of diversity between habitats (Figure 14 and 15). However, the most successful species are those that are less stringent and are able to colonize a variety of habitats and utilize a wider range of food sources. The best example of a phanaeine with broad ecological requirements is C. cyanescens, the most abundant and widespread species in the region. It occurs in caatinga, cerrado and Atlantic forest, at elevations of less than 100 m to more than 600 m, and utilizes both carrion and dung resources. Another habitat generalist, D. mimas, appears to be more abundant in forest biotopes than in the open habitats of the region, which is contrary to its habitat preference in other parts of its range (C. Gillett personal observation).

The collection of a single specimen of Dendropaemon at mercury vapour light in PI indicates that members of this genus can be nocturnally active in the area. Several species of Dendropaemon have been collected in association with attine leaf-cutter ants (Vaz-de-Mello et al. 1998), which are quite common in many parts of NE Brazil. More records of this genus will undoubtedly surface from the region.

Of the species of Phanaeini presently recorded in the NE, some should also be present in the other, less studied states (e.g. in SE, which has no recorded Phanaeini to date). Similarly, other species so far known only from the southern NE states (e.g. the six species currently recorded only from BA in the region) may eventually be found to have wider distributions in the NE.

**Conclusion**

The insect fauna of the Brazilian NE has been relatively poorly studied because the area seems to have been regarded by naturalists as being less interesting than other Brazilian regions due to its semi-arid nature. This study clearly shows that the region hosts a diverse and interesting fauna of Phanaeini composed of both endemic species and species with wider distributions. The observed species diversity is often complementary across a structurally complex and heterogenous mosaic of habitats, with each pos-
sessing its unique assemblage of Phanaeini. Many of these typically Brazilian biotopes are threatened through the proliferation of livestock ranching, deforestation and other agricultural practices. Undoubtedly, the fauna of Phanaeini, together with that of the remaining Scarabaeinae will be shown to be even more diverse with further study, and it is clear that urgent work is necessary to fully document this neglected fauna and to preserve the important unsung biotopes of the ‘nordeste’.

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