12-11-2004

Revision of the Phyllophaga of Hispaniola (Coleoptera: Scarabaeidae: Melolonthinae) — PART 1

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Revision of the *Phyllophaga* of Hispaniola (Coleoptera: Scarabaeidae: Melolonthinae)

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ABSTRACT: With this study, the fauna of Hispaniolan *Phyllophaga* is now composed of 48 species, all of which are endemic (precinctive), including 22 new species described herein (4 attributed to Woodruff and Sanderson: *approxima, bonfils, jimenezi, rex*; 18 to Woodruff: *aceitillar, alcoa, androw, baoruco, carnegie, davidsoni, eladio, haitiensis, jaragua, larimar, marcano, nunezi, ortizi, pedernales, rawlinsi, rustica, santachloe, toni*). Additionally, allotypes are described for 7 species with previously unknown males (*aliada, canoa*) or females (*esquinada, fossoria, imprima, kenscoffi, panicula*), and 6 new country records (Dominican Republic) are provided (*aliada, leptospica, minutissima, panicula, permagna, recorta*). Of the 48, only 1 male remains unknown (*barrosa*), and 9 females are missing (*aceitillar, carnegie, costura, davidsoni, espina, garrota, probaporra, rustica, toni*); 32 are recorded only from the Dominican Republic, and 5 are known only from Haiti. The 727 Figures include 50 habitus illustrations for all species, as well as SEM photos of male and female genitalia, and other salient morphological characters. The discovery of "sister species", on opposite sides of the Enriquillo basin, provides significant data to support the 2 island concept; 15 species are known only from the paleo "south island", and 23 are restricted to the "north island".

RESUMEN: De acuerdo con este estudio, la fauna de *Phyllophaga* en la isla Española, en el mar Caribe, está compuesta por 48 especies, todas endémicas (precinctivas), incluyendo a 22 nuevas especies aquí descritas (4 atribuídas a Woodruff y Sanderson: *approxima, bonfils, jimenezi, rex*; 18 a Woodruff: *aceitillar, alcoa, androw, baoruco, carnegie, davidsoni, eladio, haitiensis, jaragua, larimar, marcano, nunezi, ortizi, pedernales, rawlinsi, rustica, santachloe, toni*). Adicionalmente, se describen los alotipos de 7 especies, de las cuales no se conocían los machos (*aliada, canoa*) o las hembras (*esquinada, fossoria, imprima, kenscoffi, panicula*), y se reportan por primera vez a 6 especies para la República Dominicana (*aliada, leptospica, minutissima, panicula, permagna, recort*a). De las 48 especies, solo un macho no se conoce (*barrosa*) y 9 hembras aún no se describen (*aceitillar, carnegie, costura, davidsoni, espina, garrota, probaporra, rustica, toni*); 32 de estas especies se conocen solo de la República Dominicana y solo se conocen 5 de Haití. Las 727 ilustraciones incluyen a 50 figuras completas de todas las especies, al igual que microfotografías electrónicas (SEM) de las genitalias de machos y hembras. El hallazgo de "especies hermanas" en lados opuestos la cuenca Enriquillo es un indicador significativo que apoya al concepto de dos islas; 15 especies se conocen solo en la "isla sur", y 23 estan restringidas a la "isla norte".

Introduction

This study had its beginning over 50 years ago, shortly after the previous revision by Sanderson (1951). He acquired additional records, and new species, especially during a 3 week trip to Haiti and the Dominican Republic in 1959. Health problems prevented him from finishing the work, and it was relegated to Woodruff for completion. Originally Sanderson had recognized 5 new species, 4 of which are described jointly herein. The fifth species was discovered later to be the unknown male of one described earlier from a unique female. The additional 18 new species described here, are solely attributed to Woodruff.

Over a period of 33 years, Woodruff made 46 trips to the Dominican Republic, and new species were encountered on a regular basis. In each new and remote area, unique and endemic forms were often collected. For that reason, this revision has been long in preparation. We do not believe this is the entire fauna, and we are certain that additional new species remain to be discovered. In the remainder of this treatment, reference to "I" or "me" refers to the senior author and "we" to both authors. The final manuscript was solely prepared by the senior author, and I

take full responsibility for any errors of omission or commission.

Sources of specimens. Although the bulk of the material examined was from the authors' collections, valuable material was generously loaned by the major museums that house Hispaniolan specimens. Although a few were seen from the Museo Nacional de Historia Natural in Santo Domingo, most of their material is on loan to a graduate student, and was unavailable for our studies. No major collections were seen from Haiti. A few private collections and the museum depositories are listed in the text in brackets and their curators are thanked in the acknowledgments section. Abbreviations (codens) follow those in Arnett, et al. (1986):

CMNH: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania.
EGRC: E. G. Riley, Texas A and M University, College Station Texas.
EJMC: E.J. Marcano, Santo Domingo, Dominican Republic (now in FSCA).
FSCA: Florida State Collection of Arthropods, Florida Department of Agriculture, Gainesville, Florida.
INHS: Illinois Natural History Survey, Urbana-Champaign, Illinois.
MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
MHND: Museo Nacional de Historia Natural, Santo Domingo, Dominican Republic.
NHMB: Naturhistorisches Museum, Basel, Switzerland
RHTC: R.H. Turnbow, Ft. Rucker, Alabama.
TAMU: Texas A and M University, College Station, Texas.
UMMZ: University of Michigan Museum of Zoology, Ann Arbor, Michigan.
USNM: United States National Museum, Washington, D.C.(we used USNM here because many of the holotypes carry that abbreviation, with a number. It currently uses the coden NMNH).
ZMHB: Humboldt -Universität Museum für Naturkunde, Berlin, Germany.

Historical Resumé

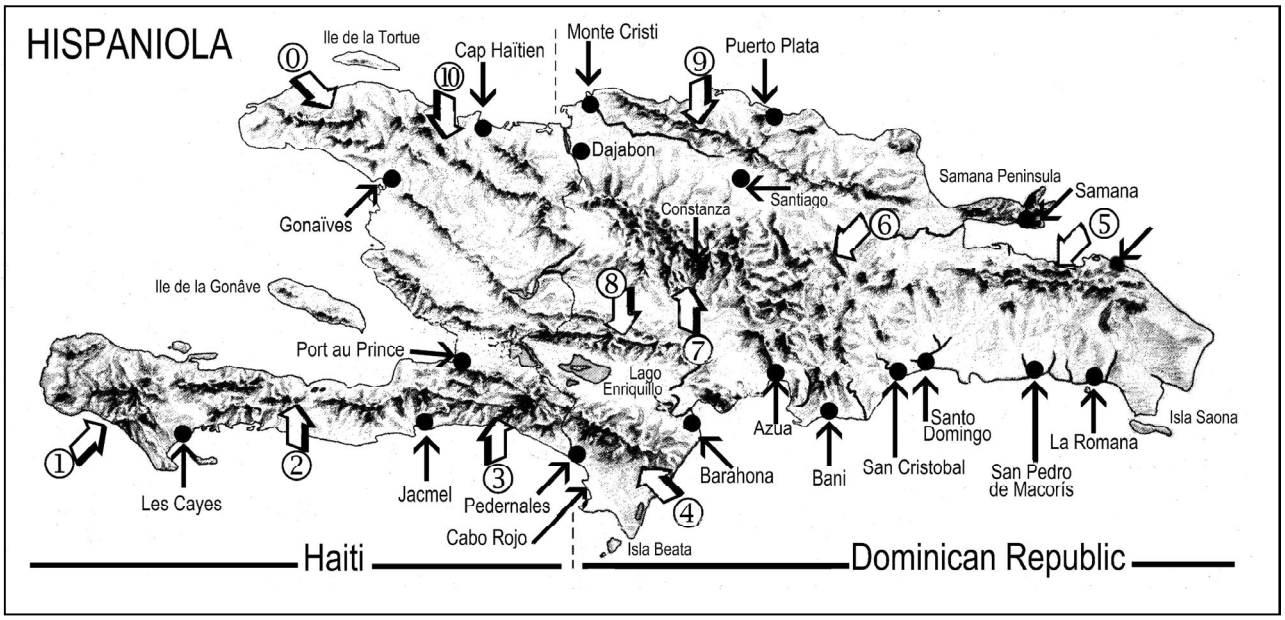
For such a large fauna, there is little literature and few authors dealing with Hispaniolan species. The first 2 species (*neglecta* and *hogardi*) were described by Blanchard (1850). Two more species (*major* and *permagna*) were described by Moser (1918). The Haitian species were treated by Wolcott (1928a,b), who named 5 additional species (*audanti, kenscoffi, latiungula, mali*, and *minutissima*). Saylor (1940, 1946) described 2 more (*pseudocalcaris* and *romana).* The remaining 15 species (*aliada, barrosa, canoa, cartaba, costura, espina, esquinada, fossoria, garrota, imprima, leptospica, mella, panicula, probaporra, recorta*) were described by Sanderson (1951).

Hispaniola: The Island

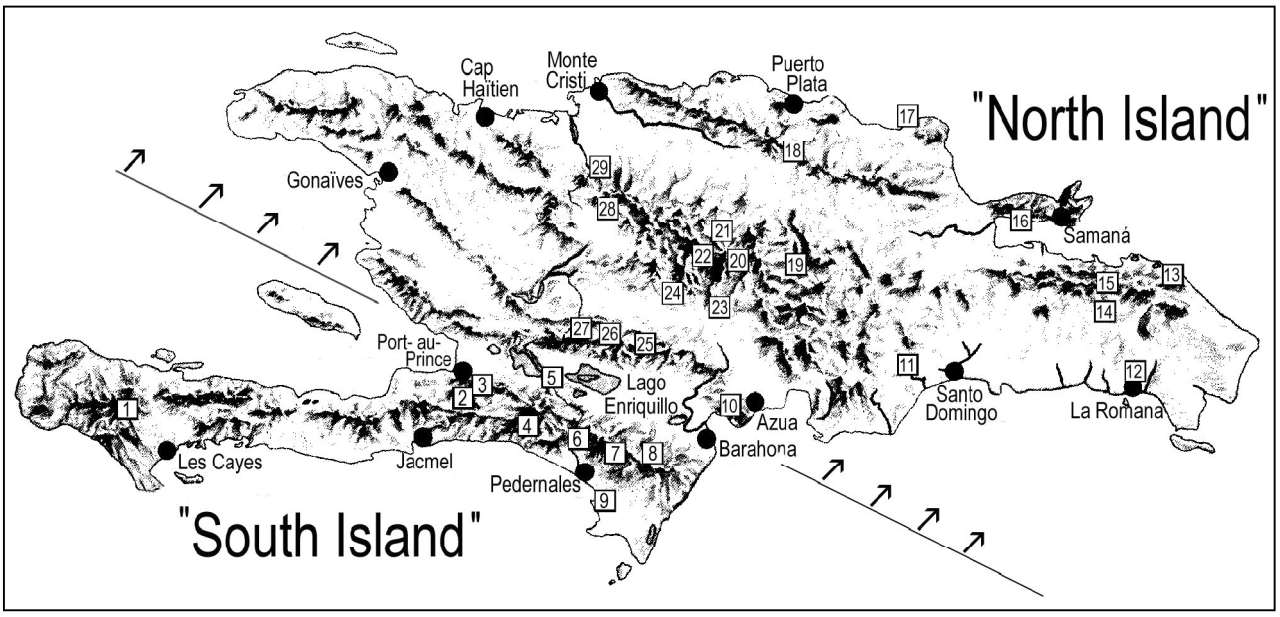
Occupying a central position in the Greater Antilles, Hispaniola is composed of 2 countries: Haiti and the Dominican Republic [DR]. The faunal differences do not coincide with their political boundaries, but are a reflection of the paleogeography (discussed later under Zoogeography). However, the cultural differences between the 2 countries have greatly affected which animals and plants can survive there. In area it is about 77,150 km², with Haiti about one-third and the remainder DR. The island is located between 17°26' and 19°56' N latitude, and 74°26' and 68°30' W longitude. It is 77 km from Cuba (Windward Passage) on the west, 102 km from Puerto Rico (Mona Passage) on the east, and 200 km from Jamaica to the southwest.

It contains several mountain ranges (Map 1) running mostly east-west, with some northwest-southeast directions. The southwestern portion ("south island") is separated from the remainder ("north island") by a depression crossing both countries from above the Barahona peninsula in the DR to Port-au-Prince, Haiti (Map 2). This basin was occupied by the sea during the Pleistocene, and now has a relictual salt lake (Enriquillo) at the lowest point on the island (40 m below sea level!). The "north island" occupies 67,700 km², the "south island" only about 9,450 km². There are 3 high peaks in the north (all higher than any in the eastern U.S.): Pico Duarte (3087 m), La Pelona (3075 m), and Pico del Yaque or La Rucilla (3038 m). The Haitian mountains consist of 3 main ranges: Massif de la Hotte (highest Pic Macaya, 2347m,), Massif de la Selle (highest Pic la Selle, 2574 m), and the Sierra Baoruco, which also extends into the DR. Under a 1989 contract with USAID, this area was investigated and conservation strategies were recommended (Woods and Ottenwalder, 1992; Woods, et al., 1992; Sergile, et al., 1992; Ottenwalder, 1989; Paryski, et al.,1989). Some of our few Haitian *Phyllophaga* were collected by Dr. M.C. Thomas on one of their study trips.

Ecologically it is extremely varied, leading to the title of the most comprehensive book on the DR: "The Dominican Republic, a country between rain forest



Map 1. Mountain ranges (hollow arrows & numbers) and major cities (solid arrows & dots) in Haiti and the Dominican Republic. ⓪=Montagnes du Nord-Ouest; ①,②=Massif de la Hotte; ③=Massif de la Selle; ④=Sierra de Baoruco; ⑤=Cordillera Oriental; ⑥=Sierra de Yamasá; ⑦=Cordillera Central; ⑧=Sierra de Neiba; ⑨=Cordillera Septentrional; ⑩=Massif du Nord. [1 inch = approximately 50 miles]. Map modified from Schwartz (1989).



Map 2. Arrows indicate the line marking the division of the paleo "North and South Islands" at the Enriquillo basin, and direction of plate subduction. Major *Phyllophaga* collecting localities (boxes) are as follows (1-4, Haiti; 5-29, Dominican Republic): 1) Ville Formon, Massif de la Hotte; 2) Furcy and Kenscoff; 3) Petionville; 4) La Visite, Massif de la Selle; 5) Jimaní; 6) Banano and Agua Negra; 7) Las Abejas and Aceitillar; 8) Larimar Mine, Filipinas; 9) Cabo Rojo, Alcoa Headquarters; 10) Sierra Martin Garcia; 11) Medina and San Cristobal; 12) Casa de Campo, La Romana; 13) Nisibon; 14) Loma de Chivo, 7 km N. Pedro Sanchez; 15) El Seibo; 16) Las Garitas, Samaná; 17) Rio San Juan; 18) La Cumbre; 19) Bonao; 20) Constanza and Valle Nuevo; 21) Jarabacoa; 22) La Cienega, Manabao, Pico del Yaqui; 23) Padre de las Casas; 24) San Juan; 25) Vallejuelo; 26) El Cercado; 27) Hondo Valle; 28) Rio Limpio; 29) Dajabon. The area between 7 and 9 is the Mercedes road on which several new species were collected. Map modified from Schwartz (1989).

and desert" (Bolay, 1997). Because Haiti has been largely devastated by clearing for crops, and we have few specimens from there, our remarks on climate pertain mainly to the DR, and are mostly taken from Lora Salcedo, et al. (1983). In temperature it ranges from a mean annual low of 18°C (Constanza) to 28.3°C (LaDescubierta); the high of 40°C (Bonao, Samaná, Sánchez) and low of 0°C (Constanza). It should be noted that our new species *rex* occurs at Constanza and larvae may be pests of strawberries there. Rainfall is extremely varied, from over 300 inches recorded at Miches on the north coast, to none some years (average of 4 inches) at Cabo Rojo in the southwest.

In the DR, Ottenwalder (1989) indicated that 5,250km² was set aside in 9 National Parks and 5 Scientific Reserves, or about 10% of the country. Several of our new *Phyllophaga* have come from 3 of these: Parque Jaragua (900km²), created in 1983; Parque Armando Bermudez (766km²), created in 1956 and encompassing Pico Duarte; and Bahoruco [or Baoruco] (700km²), created in 1983. In Haiti, Paryski, et al. (1989) listed Parc National la Visite (3,000 ha), established in 1983; Parc National Pic Macaya (5,500 ha), established in 1983; and Parc National Historique la Citadelle, Sans Souci, Ramiers (2,200 ha), established in 1968. The establishment of such parks and their continued preservation depend heavily on government's ability and willingness to enforce laws and protect them. The road from Cabo Rojo to Aceitillar, from which many of our specimens came, is a prime example of encroachment by squatters and agricultural development.

Much destruction is the result of charcoal being the primary energy source. Ottenwalder (1989) estimated that 45% of Dominican households (much higher in Haiti) depend on firewood and charcoal for fuel. At that time, deforestation rates were estimated at 100,000 hectares per year, and the needs have increased. His conservative estimate of 277 species of endangered or threated plants gives little encouragement for their future survival. Recent floods and landslides are partially the result of deforestation.

There are 4 sizeable islands off Hispaniola, some of which may harbor unique *Phyllophaga*, especially Gonâve in the bay opposite Port-au-Prince. In the DR, 3 other larger islands have had no specimens collected: Saona, Beata, and Catalina. However, a new species is under study from Navassa, a much smaller island off the western tip of the southern peninsula of Haiti.

Methods and Materials

Most of the methods used for this study are those employed previously (Woodruff and Beck, 1989). The greatest modification has been in the improvement of scanning electron microscope (SEM) equipment, which permitted digital photography of uncoated genitalic specimens (JEOL: JSM-5510LV). With digital images recorded on compact discs, we were able to edit these easily (compared to hand painting backgrounds as before) on a computer, using Paint Shop™ Pro® software. Scale lines accompanied each image, but these were often modified in the finished version. Dirt and extraneous material was electronically eliminated. In the plates dealing with morphological characters, this software enabled labeling various parts on the image.

Most genitalia were removed from alcoholic preserved specimens, dried, and mounted traditionally on card points below the specimen. Some earlier material (especially Sanderson types) had the genitalia preserved in glycerin vials pinned in the same fashion. It was discovered early that specimens could be digitally photographed in the SEM directly from alcohol (with surface briefly dried). This was especially advantageous for female genitalia that are often softer, more flexible, and prone to shrinkage or misplacement when thoroughly dried. Some pinned specimens were placed directly in the SEM, and their parts easily photographed. None of our specimens required critical point drying, although some may have been prepared with this technique by other museums.

Specimen preparation. Because of the external similarity of many species, and the diagnostic nature of the genitalia, we extracted these from 99% of the material studied. We recommend that this routinely should be done, or specimens may be misidentified. The technique is simple, easy to learn, and requires minimal time. Material preserved in 70% isopropyl alcohol has proven to be the most satisfactory, even superior in some cases to fresh specimens. As long as they are not overcrowded, specimens stay perfectly preserved in this fashion for more than 50 years. To extract genitalia from dried specimens, they may be relaxed in a moist chamber for 2-3 days; we found the best way (without damaging specimens or genitalia) was to strip data labels (not to get wet) and place the beetle in a glass, fireproof container (a pyrex lab beaker) with about 2 inches of water and a small amount of household ammonia (10%, preferably lemon scented). This was then heated on a hotplate until it came to a rolling boil and the heat turned off; the

process usually took less than 5 minutes. Immediately the specimen was removed and even the oldest, driest specimens were readily dissected. Because *Phyllophaga* have relatively long legs, which are precarious in dried museum specimens, for relaxed specimens we recommend carefully tucking legs near the body to avoid later breakage. Usually overnight drying in position will suffice for both boiled and alcoholically preserved specimens.

Dissection. Although a certain amount of dexterity is assumed, the actual dissection was normally easy. Difficulties arose only with smaller and softer females, or when parts broke from poor relaxation (both the beetle and the dissector); patience is a virtue. The abdomen often was opened at the pygidial apex with forceps, but large tight fitting male specimens often required small cuts in the lateral membrane to allow space for removal of the large genitalia in some species. Gentle pressure on the sternites, and a bent insect pin or forceps were usually used to pull out the genital capsule (males) or genital plates (females). In obstinate cases, the specimen was re-boiled or relaxed again. Female plates were usually extruded, but not removed (except for photographic purposes), whereas the male genitalia are easier to study when mounted on points below the specimen. Clearing in KOH was not necessary, although occasionally done to elucidate various parts; these were subsequently stored in glycerin.

Once the male genital capsule has been dissected, it must be cleaned of membranes and extraneous tissue. Normally the apical structures are well-sclerotized and such material is easily picked off or flushed with alcohol to assist the process; forceps, insect pins, and fine brushes were the only tools needed. A little experience, coupled with attention to the various parts in our illustrations, should make this an easy process. The aedeagi are often sufficiently visible, but occasionally require gentle teasing or pulling to see all relevant portions. The resultant ease with which they can be identified, makes it a rewarding experience. Dawson (1935) provided additional details on dissection.

Collecting. Every child knows how easy it is to collect May or June "Bugs". And every entomologist knows how abundant they can sometimes be, and how readily they are attracted to lights. Some common pest species in coastal areas of Hispaniola (e.g., *romana, hogardi, mali*) fit this picture. However, many species occurring at higher elevations are very localized, have limited seasons, or are actually rare (several described here are known from 2 or 3 specimens, and some have not been collected for over 50 years). We suspect that some of these are more common than our records show, and the more we learn of their habits and habitats, the greater chance we will have of finding them.

The advent of blacklight traps (Hollingsworth, et al., 1963) revolutionized the surveys for such beetles. Although a few were taken in Malaise traps (some diurnal), probably 95% of all specimens we examined were from UV (blacklight) or Mercury vapor lights (either as traps or attractants). We used mainly 15 watt blacklight [BL] fluorescent tubes, but even an 8 watt blacklight can attract hundreds on a given night. Specimens were usually preserved in 70% isopropyl alcohol (even overproof rum works) in the field, and later dissected, mounted, or conserved in the same fluid (often changed from field samples). It was especially useful for our SEM studies to have access to alcoholically preserved specimens. They were cleaner (or more easily cleaned), could be manipulated with little fear of breakage, and the female plates retained their original shape and position. I highly recommend storing samples of each species in 70% isopropyl alcohol, where even large collections occupy much less museum drawer space than when pinned. Who knows, additional information may be discovered in alcohol preserved specimens that is unusable in those dried. When properly preserved as described, specimens have been adequate for DNA studies.

Habitus illustrations (Fig. 62-111). Most of our habitus photographs were made from digital images produced on an Auto-Montage Pro©, and later edited as were the genitalia photographs. A few, especially large species, were photographed with a digital camera (Nikon Coolpix®). Because most beetles are shiny, a diffuser provided better images (this consisted of either frosted paper or a translucent mixing bowl, surrounding the specimen). In a few cases, where beetles were too large to be entirely photographed in one image on the automontage (e.g., *toni*), 2 separate photos were made and digitally merged. All specimens were photographed as pinned specimens, but the pins were removed digitally in Paint Shop Pro.

Format. To save space, and because the paper deals only with the genus *Phyllophaga*, the species names are used mostly without the genus or its abbreviation (*P.*). Most morphological characters are illustrated with labeled SEM photographs prior to the species descriptions. Keys are presented to the 48 species known, with emphasis on genitalic structures. Species treatments and associated figures are arranged alphabetically. Full technical descriptions

and genitalic illustrations are provided for each of the 22 new species treated. Because of space restrictions, for all previously described species, reference is provided to Sanderson's (1951) treatment; here, only a brief description, new records and notes, and genitalic illustrations are presented. One new species (near *fossoria*) is illustrated for identification purposes, but its description and naming are reserved for a Dominican graduate student.

Because we treat only adults and to conserve space, any statements (other than those in the larval discussion) refer to that stage only. We have given relative size terms (within the genus), and we believe that it is understood and shorter to say "large species" with accompanying measurements, rather than the cumbersome "individuals of this species are large". We have used length (L., the style manual indicates that lower and upper case have both been used for liter, and the confusion with the numeral 1) and width (W.) measurements to nearest half millimeters (to avoid redundancy we use "mm" only after the last numeral). Specimens were measured from tip of head to tip of elytra, but exact measurements are not possible because of variable positioning of parts (head or abdomen distention, etc.). We have listed them thusly: 10-12.5, avoiding the decimal after whole numbers, as a result of the inexact nature of the measurements (to 0.5 mm only). We have used numerical label data as it appeared, without risk of converting all to metric.

Names. Of the 22 new species, names for the 4 jointly described species were chosen by Sanderson; the remaining 18 by Woodruff. Most were chosen to recognize places (e.g., *pedernales*), beetle features (*rustica*), institutions (*alcoa*), or people (*marcano*). In all cases where names were not Latinized (e.g., *eladio*) they are treated as nouns in apposition, for the sake of euphony.

Types. Holotypes (males) and allotypes (females) are designated for all new species described herein; females remain unknown for 10 species, and 1 male is unknown (see Table 1). In 7 cases the opposite sex of a known species is described for the first time, and allotypes are here designated. Because the genitalia are diagnostic in both sexes, it is important to designate both holotypes and allotypes, which are of equal significance. In this study we have associated male specimens for 2 of the 3 species described by Sanderson (1951) from unique females. Although the holotype females were described more than 50 years ago, we believe that describing allotype males now is both useful and relevant for nomenclatural stability. Fernald (1939: 691-692) defined the term "allotype" as originally coined: "A specimen of opposite sex to holotype, chosen later, either by the author or by any subsequent student, not necessarily from the original type series. Muttkowski, 1910." For 7 previously described species, by this definition we establish the allotype males for *aliada* and *canoa* Sanderson (1951), as well as female allotypes for *esquinada, fossoria, imprima*, and *panicula* Sanderson (1951), and *kenscoffi* Wolcott (1928a).

Maps. The major mountain ranges, the Enriquillo basin, and major cities are shown on Map 1; some of the major collecting sites are shown in Map 2. Specific distribution maps were planned for each species, and full data were recorded for each specimen. However, space restrictions prevented including them here. They should form the basis for future detailed zoogeographic studies, when all records can be plotted. Many of the Carnegie specimens had GPS readings on the labels; much more exact localities than are generally recorded with label data.

Specimens examined. In specimen data recorded here, new country records are indicated in boldface. The total number of specimens examined was recorded first, followed by country, province, number of specimens in parentheses, precise locality, date (month in Roman), and other label data, followed by the depository in brackets (used throughout the text). The listing of depositories is provisional at this writing; with cooperation among institutions, attempts will be made to distribute as many species as possible to each lending museum, especially the Museo Nacional de Historia Natural (Santo Domingo).

The individual species treatments are followed by sections on Questionable and Erroneous records, Acknowledgments, and References.

Morphological Characters

The terminology used here is that traditionally used in *Phyllophaga* (Böving, 1942b; Sanderson, 1951; Morón, 1986; Woodruff and Beck, 1989). Because of the external similarities in habitus (Fig. 62-114), greater reliance is placed on the diagnostic features of the male and female genitalia. However, the latter are often so radically different, and homologies have not been established for various parts, that they defy description. For this reason, emphasis has been placed on illustrating these features, rather than detailed descriptions. All new species have been described in more detail, with less detail for previously described species; all include citations to Sanderson's previous descriptions, and references to his and our illustrations. The characters and their character

PLATE 1: *Phyllophaga* Morphological Characters: Head

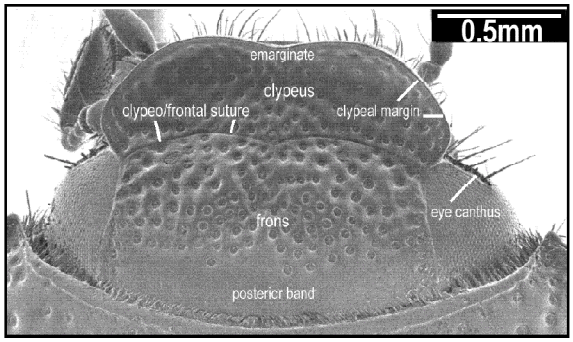


Fig. 1. *panicula* Sanderson. Head (dorsal) with parts labeled. Note clypeus shorter than frons, emarginate, coarsely punctured (non-setigerous), posterior angles converging to frontal suture, which is deeply impressed, emarginate, and coarsely punctate (denser in 2 center spots), posterior band impunctate.

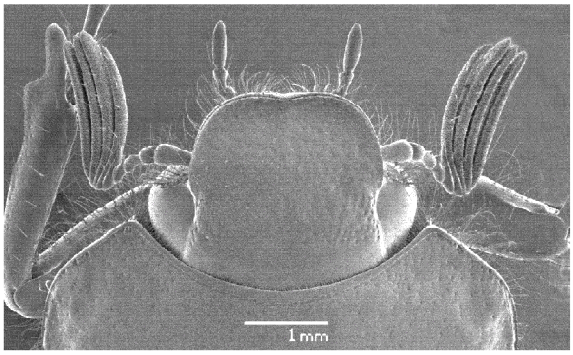


Fig. *3. garrota* Sanderson. Head (dorsal); note 4 lamellae in antennal club. Clypeus rounded on sides, barely emarginate in middle, weakly reflexed; clypeus and frons nearly equal in length, suture weakly impressed, surface evenly and shallowly punctate, non-setigerous.

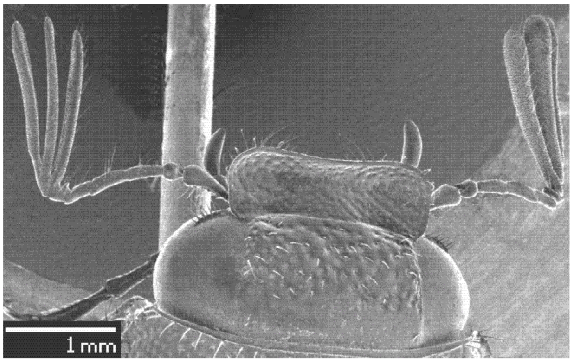


Fig. 5. *fossoria* Sanderson. Dorsal view of head; note 3 lamellae in antennal club. Clypeus nearly quadrate, sides converging abruptly at frontal suture, evenly emarginate in middle, noticeably reflexed; clypeus shorter than frons, suture strongly impressed, nearly straight, surface coarsely punctate, frons with some setigerous punctures.

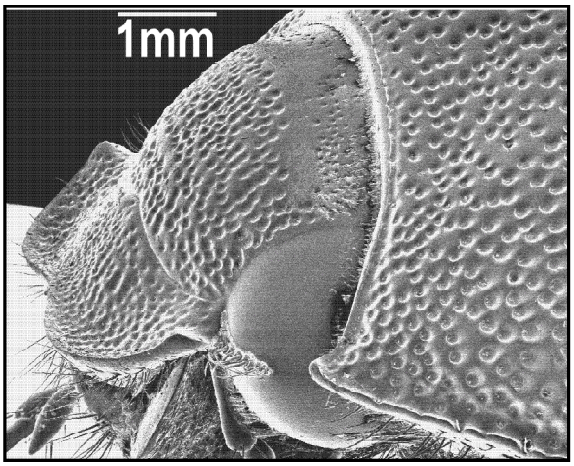


Fig. 2. *marcano* Woodruff. Head (lateral), showing reflexed (upturned) clypeal margin, sharp posterior angles, dense, coarse punctation of clypeus, frons, pronotum, and punctures in posterior band of head.

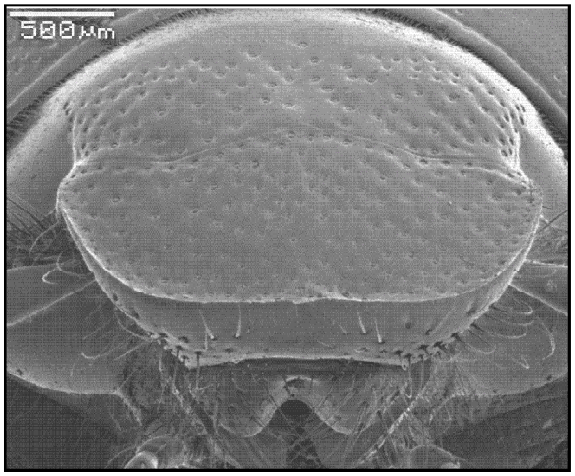


Fig. 4. *garrota* Sanderson. Head (frontal), showing clypeal margin barely reflexed, emargination minimal, punctures shallow and widely separated; clypeo/frontal suture barely impressed, indicated by wavy line.

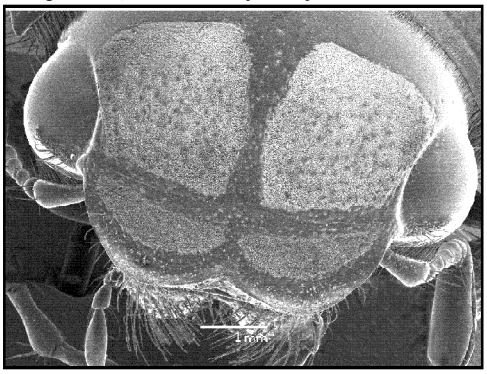


Fig. 6. *rex* Woodruff and Sanderson. Head (dorsal), showing velvety spots, clypeus deeply emarginate, clypeo/frontal suture indicated by dark curved line.

PLATE 2: *Phyllophaga* Morphological Characters: Antennae

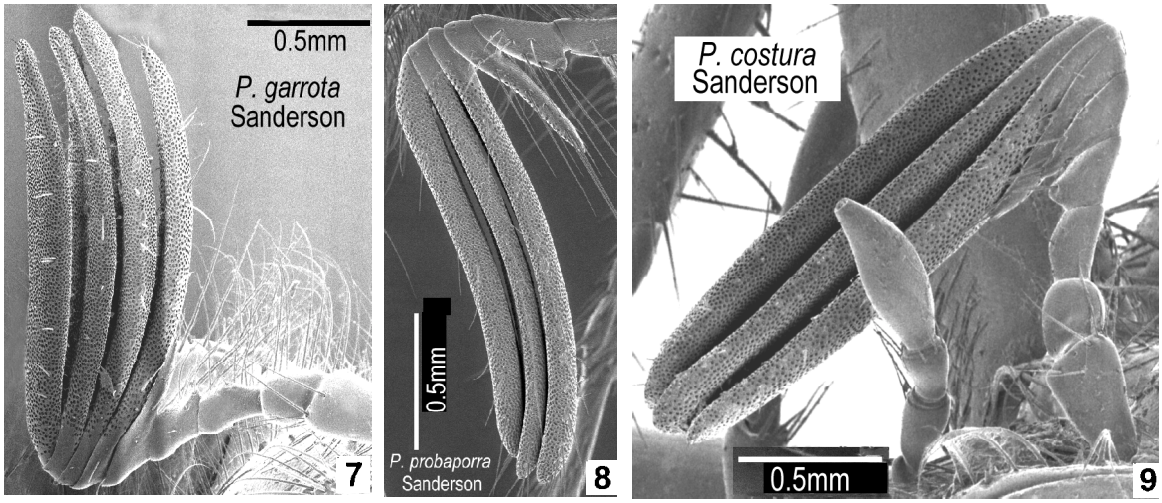


Fig. 7-9. These 3 species have noticeable receptors (indicated by dots) at 20X, and all appear to be diurnal: 7) club with 4 lamellae (unique); 8) partial 4th lamella, about one-third length of others; 9) partial 4th lamella, about one-fourth length of others. Enlargements below:

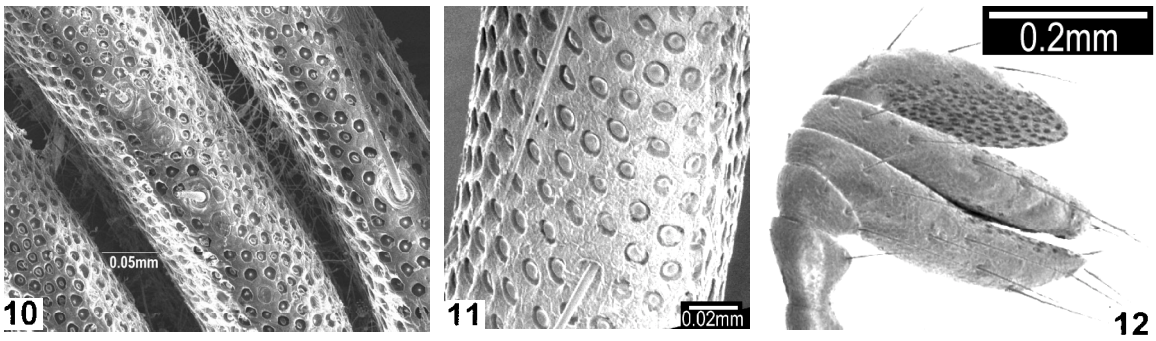


Fig. 10-12. Antennal receptors: 10) *garrota* Sanderson, male; 11) *fossoria* Sanderson, male; 12) *panicula* Sanderson, female (note receptors beneath terminal lamella and margins of lower two).

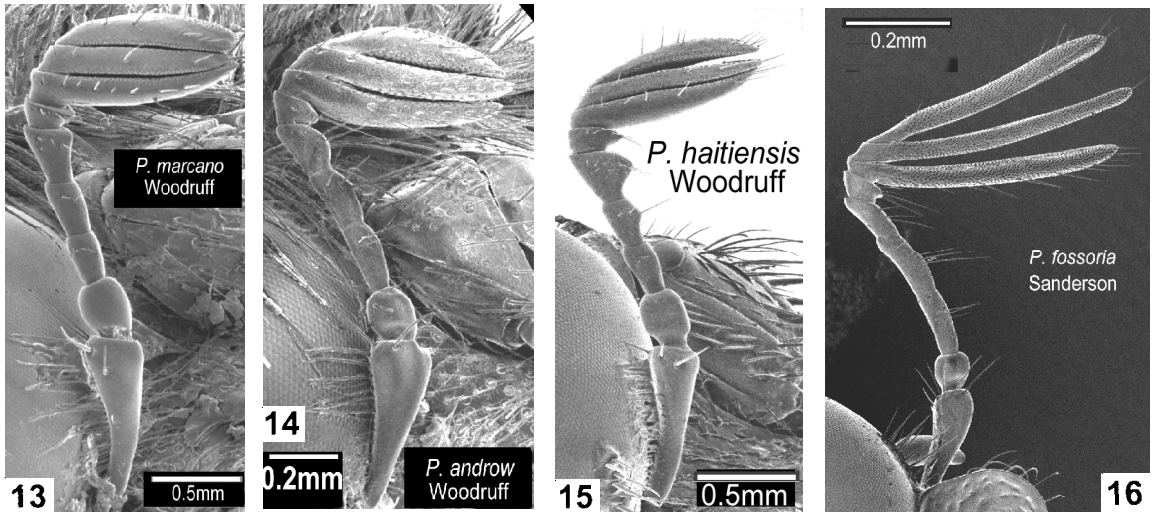


Fig. 13-16. Shapes of antennal segments (antennomeres): 13) male, club ovate, antennomeres 3-5 subequal; 14) female, club ovate, antennomeres 3-4 elongate, cylindrical, division not deeply impressed; 15) male, club ovate, but elongate, antennomeres 3-5 different lengths, fifth with external projection; 16) male, club elongate (longer than 5 preceding antennomeres), lamellae flattened, antennomeres 3-5 cylindrical, weakly divided.

PLATE 3: *Phyllophaga* Morphological Characters: Tibiae

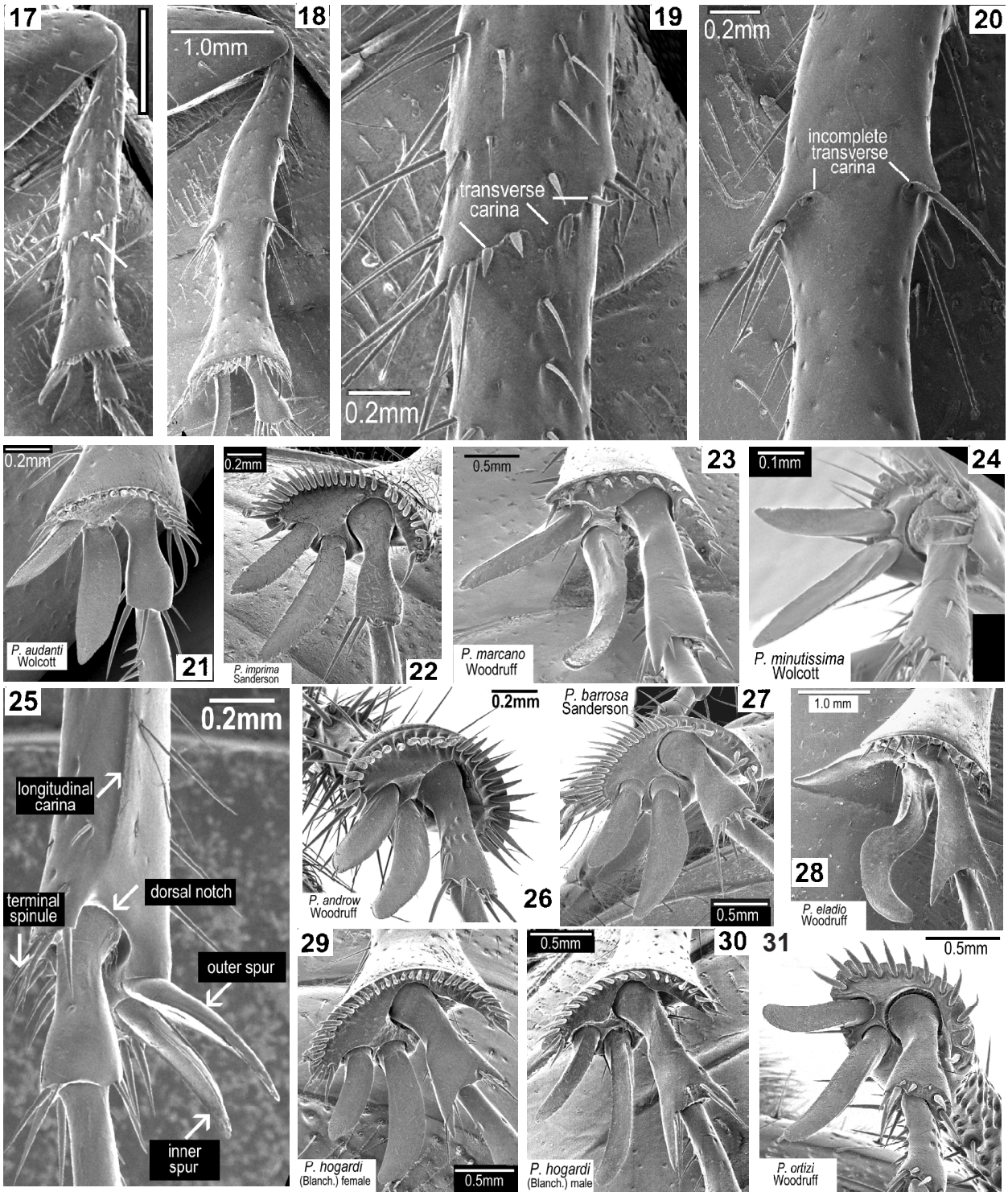


Fig. 17-31. Metatibial character states: 17) *androw* Woodruff, entire, ventral, line =1mm; 18) *rawlinsi* Woodruff, same; 19) *androw*, enlargement of transverse carina; 20) *rawlinsi*, enlargement of incomplete carina; 21-31 tibial apices, number of spines in apical fringe in brackets: 21) *audanti* Wolcott, female [20]; 22) *imprima* Sanderson, female [29]; 23) *marcano* Woodruff, male [13]; 24) *minutissima* Wolcott, male [13]; 25) *imprima* Sanderson, dorsal view with parts labeled; 26) *androw* Woodruff, female [25]; 27) *barrosa* Sanderson, female [28], notice 3 spines missing; 28) *eladio* Woodruff, male, note unique S-shaped long spur [13]; 29-30 *hogardi* (Blanchard), note sexual dimorphism: 29) female [35]; 30) male [19]; 31) *ortizi* Woodruff, female [12].

PLATE 4: *Phyllophaga* Morphological Characters: Tarsi

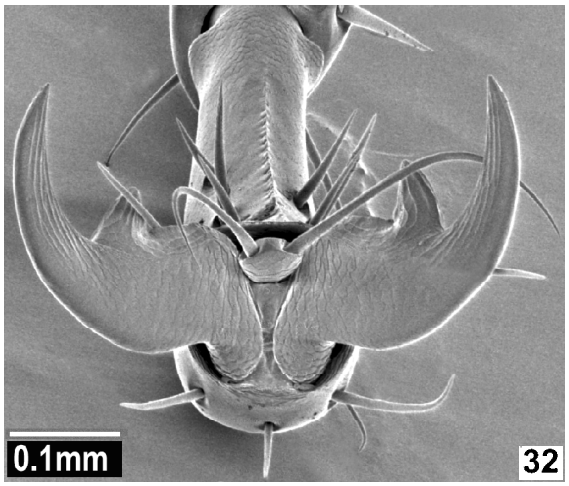


Fig. 32. *audanti* Wolcott (female). Metatarsal claws, with pulvillus between. Note ridges on teeth and scale-like pattern on claw body. Some species have more extensive ridges. Note also the saw tooth carina on venter of fifth tarsal segment and lobes on each side at base.

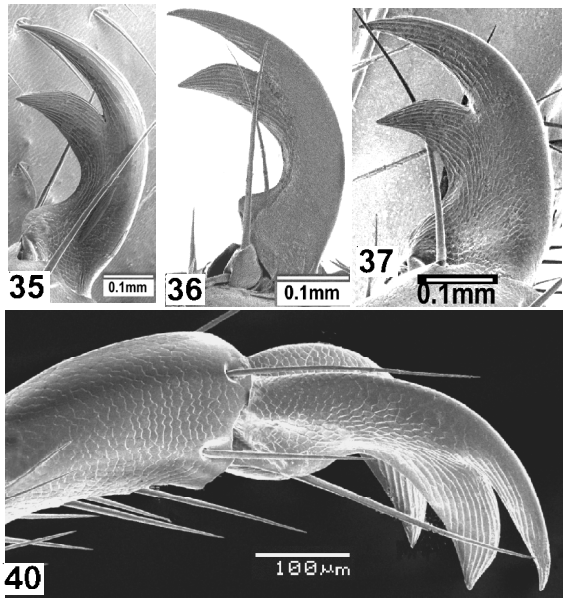


Fig. 35-37,40. Examples of "cleft" tarsal claws (lateral): 35) *fossoria* Sanderson, 36) *aliada* Sanderson, 37) *androw* Woodruff, 40) *nunezi* Woodruff.

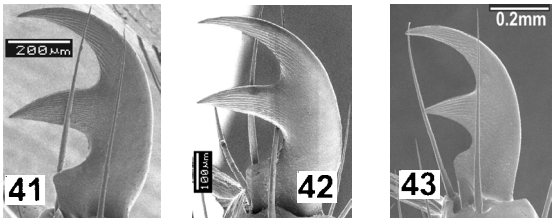


Fig. 41-43. Tarsal claws: examples of middle tooth central, first 2 are nearly length of terminal tooth: 41) *haitiensis* Woodruff, 42) *recorta* Sanderson, 43) *alcoa* Woodruff.

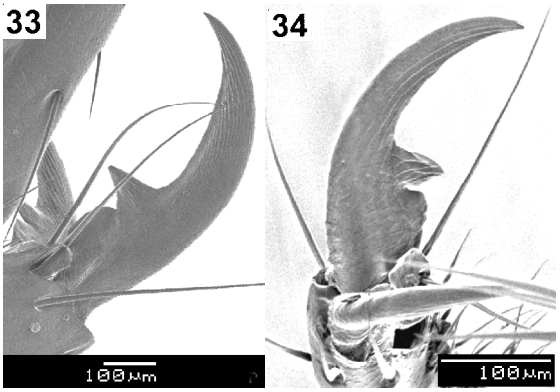


Fig.33-34. Tarsal claws: examples of middle tooth nearer base than tip of long tooth: 33) *probaporra* Sanderson, middle tooth short, triangular, with small notch at base; ridges of terminal tooth not parallel to inner curve; 34) *minutissima* Wolcott, middle tooth heavily ridged, distinct notch behind, base very broad; terminal tooth long, narrow, with ridges curved with curve of tooth.

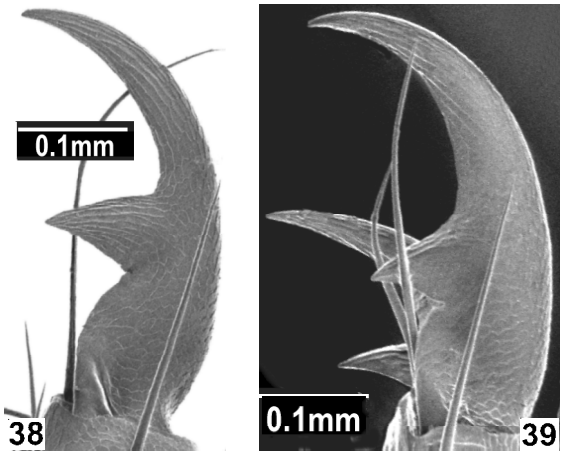


Fig. 38-39. Tarsal claws: examples of middle tooth central, but short, triangular, with the base rounded, and not forming a distinct notch as above: 38) *esquinada* Sanderson, 39) *audanti* Wolcott

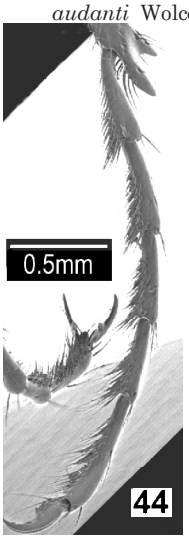


Fig. 44. Anterior tarsus of *minutissima* Wolcott. Note first 4 segments about equal in length, with the fifth more elongate. All segments have brush-like setae on their inner surface. Note tarsal claws are elongate, the middle tooth barely visible. This species is the smallest known from Hispaniola (Fig. 95), but its anterior tarsi are proportionately longer than any other species.

PLATE 5: *Phyllophaga* Male Genital Characters

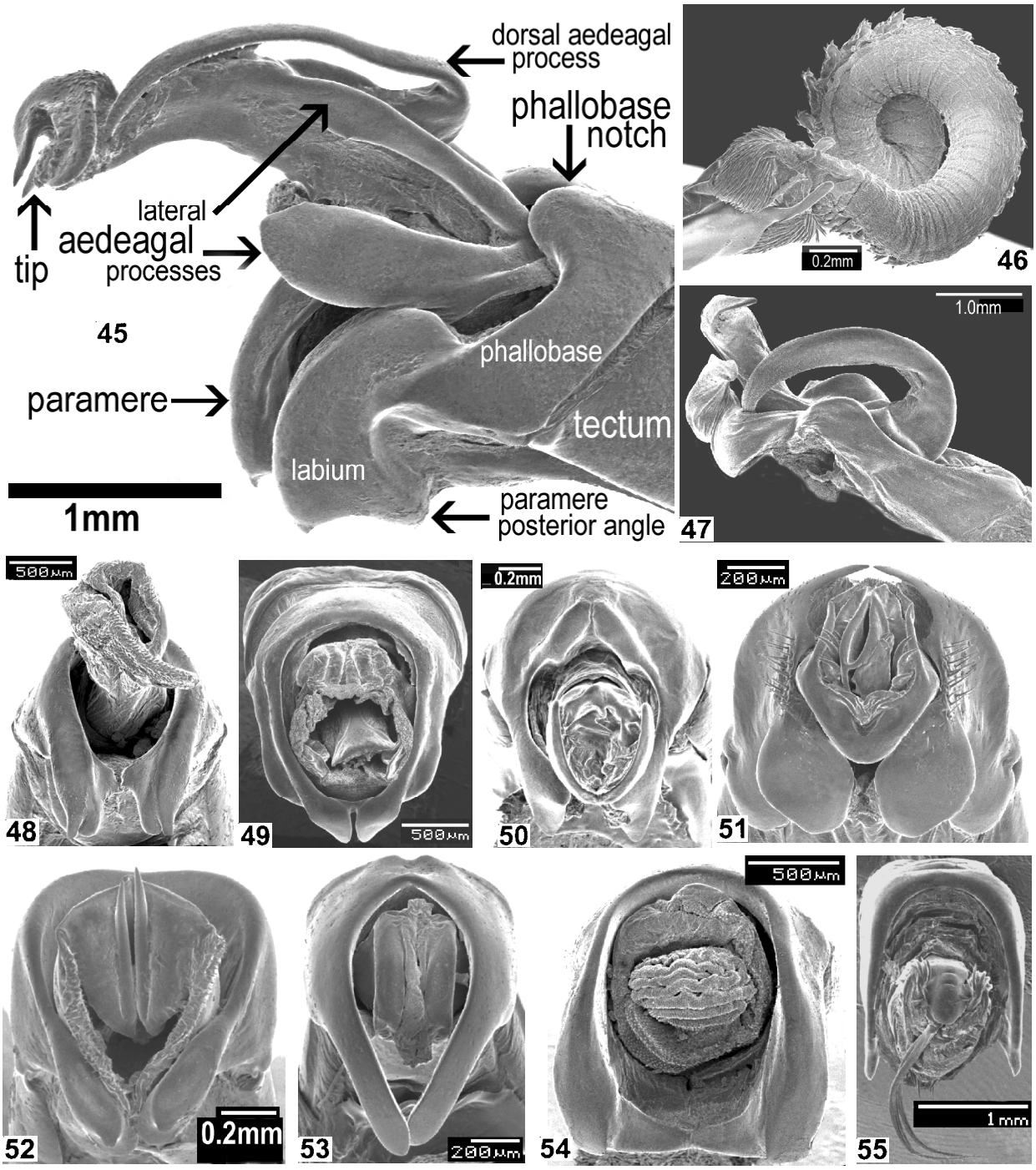


Fig. 45-55. Genitalia*:* 45) lateral, *mali*, with parts labeled; 46-47 bizarre asymmetrical aedeagi: 46) *rawlinsi* Woodruff, left lateral; 47) *bonfils* Woodruff and Sanderson, right lateral; 48-55 caudal views: 48) *baoruco* Woodruff; 49) *aliada* Sanderson; 50) *aceitillar* Woodruff; 51) *fossoria* Sanderson; 52) *imprima* Sanderson; 53) *ortizi* Woodruff*;* 54) *hogardi* (Blanchard); 55) *espina* Sanderson.

PLATE 6: *Phyllophaga* Female Genital Characters

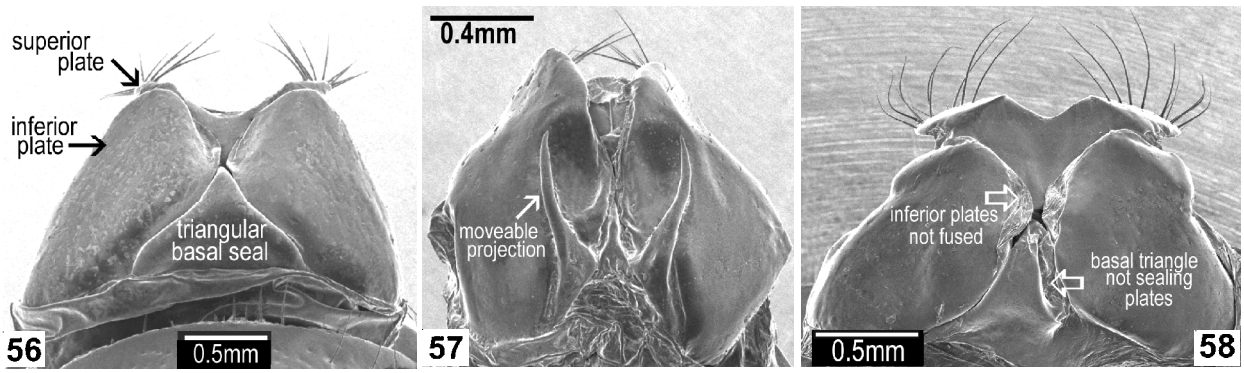


Fig. 56-57. Ventral views with parts labeled: 56) *recorta* Sanderson, few species have this triangular basal seal; 57) *mella* Sanderson, the moveable projections are unique to this species (see species plates for further views); 58) *jaragua* Woodruff, prominent superior plate, basal triangle present but not sealing plates.

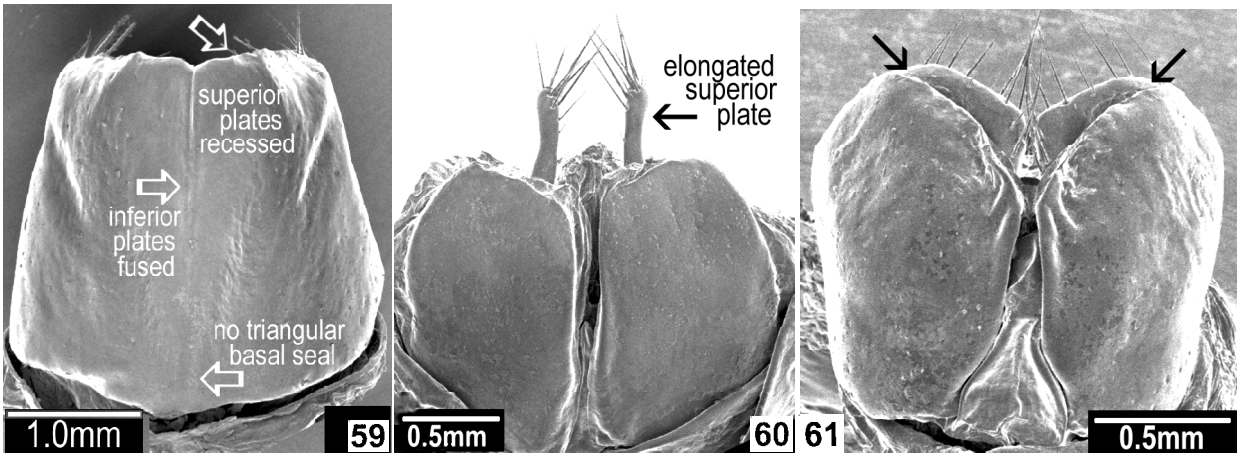


Fig. 59-61. Ventral views with parts labeled: 59) *santachloe* Woodruff, inferior plates completely fused in center; 60) *canoa* Sanderson, inferior plates separated most of their length and superior plates (pubic process?) elongate, separated; 61) *fossoria* Sanderson, inferior and superior plates fused at apex (arrows).

states, which are used for description herein, are explained below (illustrated in Fig. 1-61).

Head (Fig.1-6).The head often contains diagnostic features on the clypeus, especially the shape, punctation, and margin. The clypeus may be strongly (Fig. 2, 6) or weakly (Fig. 3, 5) emarginate (medial area indented) or not; the anterior angles may be rounded (Fig. 1,6) or quadrate (Fig. 5); the sides may converge toward the frontal suture at various angles (Fig. 1-5). The margin may be reflexed or raised (Fig. 2) or barely elevated (Fig. 4).The suture between the clypeus and frons is referred to as the frontal suture (=clypeal/frontal) and may be deeply (Fig. 1,2,5) or shallowly impressed (Fig. 3,4), or raised in one species, *costura* (Fig. 253-254), and its outline may vary. The main features of the frons are the extent of punctation and its length in relation to the clypeus. The posterior band (Fig. 1, 482) is the area behind the frons and is usually impunctate, except for punctures above the eyes and portions often covered by the head in repose. The eye has a canthus (Fig. 1) which varies in length, in convexity (in *imprima* it is depressed, Fig. 379-380), and in the number, size, and color of setae. Mouthparts were not examined in detail, but in the related genus *Diplotaxis*, and some continental *Phyllophaga,* diagnostic characters are present (McCleve, in litt.).

Antennae. Although a part of the head, the antennae are especially noted because of significant character states. A separate plate (Fig. 7-16) is devoted to these. Important features involve number of segments (9 in all species here, but 8-10 elsewhere); the number of lamellae in the club (4 in *garrota*, Fig. 7; 3+ in *costura*, Fig. 8, and *probaporra*, Fig. 9; only

3 in all others, Fig. 13-16); shape of the club, from flattened lamellate (Fig. 7-9, 16) to oval (Fig. 13-15) and sometimes differing between sexes; receptors are present on entire lamellae (Fig. 7-10), on a portion (Fig. 12, 147), or not noticeable at 20X (Fig. 361, 669). The lengths and shapes of the 6 antennomeres (=segments) and their relative lengths to the club are often useful (especially 3-6).

Pronotum (Fig. 62-111). The shape, size, vestiture, punctation, anterior and posterior angles, and margins are all useful characters. Often the punctation and/or vestiture differ between pronotum and elytra. The lateral pronotal margin can be smooth, with few setae or it may have large setae, whose bases give the margin a crenulate appearance. The marginal setae may or may not continue around the posterior margin, which may be obsolete (especially medially) or entire. The lateral margin and anterior margin may be variously reflexed.

Scutellum. Although a small structure, normally V- or U-shaped, it can sometimes be used to separate closely related species (Fig. 474*, marcano* punctate; Fig. 77-78, *eladio* impunctate). It may be shiny, smooth, hirsute, velvety (Fig. 670-671), convex or flat.

Elytra. As can be seen in the habitus illustrations (Fig. 62-114), the elytra vary from hirsute to glabrous, pruinose to shiny, convex to flattened, rugose to smooth, coarsely to finely punctate, spinose sutural apex to smoothly rounded, and with costae obscure or noticeably convex.

Pygidium. Character states include surface shiny, pruinose (in *imprima* and relatives it is both, Fig. 374-375) glabrous, hirsute [partially or totally, with setae long (Fig. 531-532), curved, or short, stubby (Fig. 546)], apically truncate or rounded, but invariably with a marginal fringe of very long, curved setae. The shape is roughly triangular, but varies in width/length proportions. In *kenscoffi* (Fig. 414-415) and lesser so in *jimenezi* and *santachloe*, the apex is upturned medially, forming a lip. The punctation varies from coarse (sometimes coalescing to form longitudinal ridges) to fine, but is sometimes obscured by the pruinosity.

Legs. All legs have important characters, most of which are illustrated in Fig. 17-44. The anterior or protibiae are usually tridentate, but the extent and position of dentition varies, as does the sculpture and vestiture of the dorsal surface. In *garrota* (Fig. 332) the basal (lower) tooth is reduced and in *eladio* (Fig. 267) well developed. The meso- and metatibiae have many important character states (Fig. 17-31). Most Caribbean species (subgenus *Cnemarachis*) have clusters of spines on the inside and outside of the metatibiae (Fig. 18, 20), marking the location where a transverse carina (Fig. 17, 19) rarely is complete (e.g., *androw*). The mesotibiae are usually the same, but a few have the carina complete. A longitudinal carina (often hidden behind the tibiae, Fig. 25) is well developed in a few species, but more commonly incomplete or poorly developed. The metatibial apex has a fringe of spines or spinules that vary from thick and short to long and fine; they are often closely spaced (Fig. 22, 27, 29), but sometimes widely so (especially in males, Fig. 23, *marcano* and Fig. 24, *minutissima*). The number of spinules in this fringe is relatively constant for each species, the males often having one-third or less than females. The apex also contains 2 moveable spurs (some N.A. species have one fixed), which are often sexually dimorphic (Fig. 29-30); females are broader, flatter, and shorter. Most are acuminate (usually sharp-pointed, but occasionally blunter) or sickle-shaped, but some are twisted (*eladio*, Fig. 28) or radically bent or spatulate -shaped (*esquinada*, Fig. 281-282). The one nearest to the tarsus is referred to as inner (usually longer) and the other is the outer spur (Fig. 25). The dorsal apex of the metatibia has a notch, exceptionally large in some smaller species (*imprima,* Fig. 25), which enables the beetle to elevate the tarsi almost vertically (reminiscent of the positioning in nature of some species of the genus *Serica*).

Tarsi have fewer characters of value, except the terminal claws. Some species do have special modifications of the first or second tarsal segments, usually with spinose extensions on the outer side. One of the smaller species (*minutissima*) has exceptionally long protarsi with exceptionally long hairs beneath (Fig. 507-508). Types of claws are shown in Fig. 32-43. Cleft (found in the subgenus *Phytalus* elsewhere) signifies the 2 teeth are near each other, with the angle between acute (Fig. 35-37, 40). Non-cleft claws have the middle tooth in varying positions, most frequently central , but varying in size and direction. The area behind the middle tooth may form a large U-shaped notch (Fig. 41-43), a shallow acute notch (Fig. 33-34), or gradually rounded to the tarsi (Fig. 38, 40). The claws are normally the same on all legs, but some variation occurs.

Abdomen. Although certain abdominal characters are distinctive, they are difficult to describe. The abdominal sternites are fused and immovable, the sutures between sometimes barely indicated. In many North American species there is considerable sexual dimorphism, especially in the modifications of the penultimate (seventh) and ultimate (eighth) sterni-

Table 1. *Phyllophaga* of Hispaniola checklist**.** Asterisks indicate new males and females or new country records.

	Male	Female	D. R.	Haiti	So. Isl.	No. Isl.
aceitillar n. sp., Woodruff	X		X		X	
alcoa n. sp., Woodruff	X	X	X		X	
aliada Sanderson (1951:279-280)	X*	X	X*	X		X
androw n. sp., Woodruff	X	X	X			X
approxima n. sp., Woodruff and Sanderson	X	X	X		X	
audanti Wolcott (1928a:27)	X	X	X	X	X	X
baoruco n. sp., Woodruff	X	X	X		X	
barrosa Sanderson (1951:280)		X		X	X	
bonfils n. sp., Woodruff and Sanderson	X	X		X	X	
canoa Sanderson (1951:279)	X*	X	X			X
carnegie n. sp., Woodruff	X		X			X
cartaba Sanderson (1951:274-275)	X	X	X			X
costura Sanderson (1951:264)	X		X			X
davidsoni n. sp., Woodruff	X		X		X	
eladio n. sp., Woodruff	X	X	X			X
espina Sanderson (1951:264-265)	X		X			X
esquinada Sanderson (1951:268)	X	X*		X	X	
fossoria Sanderson (1951:258-259)	X	X*	X			X
n. sp. near *fossoria* (see text)	X		X			X
garrota Sanderson (1951:262-263)	X		X			X
haitiensis n. sp., Woodruff	X	X		X	X	
hogardi (Blanchard) (1850:137)	X	X	X	X	X	X
imprima Sanderson (1951:276-277)	X	X*	X			X
jaragua n. sp., Woodruff	X	X	X		X	
jimenezi n. sp., Woodruff and Sanderson	X	X	X			X
kenscoffi Wolcott (1928a:24)	X	X*	X	X	X	X
larimar n. sp., Woodruff	X	X	X		X	
latiungula Wolcott (1928a:28)	X	X		X	X	
leptospica Sanderson (1951:262)	X	X	X*	X	X	
mali Wolcott (1928:25)	X	X	X	X	X	X
marcano n. sp., Woodruff	X	X	X			X
mella Sanderson (1951:278-279)	X	X	X			X
minutissima Wolcott (1928a:28, 76)	X	X	X*	X	X	X
neglecta (Blanchard) (1850:137)	X	X	X	X	X	X
nunezi n. sp., Woodruff	X	X	X			X
ortizi n. sp., Woodruff	X	X	X		X	
panicula Sanderson (1951:275-276)	X	X*	X*	X	X	
pedernales n. sp., Woodruff	X	X	X		X	
permagna (Moser) (1918:57)	X	X	X*	X	X	
probaporra Sanderson (1951:263-264)	X		X			X
pseudocalcaris Saylor (1940:309)	X	X	X			X
rawlinsi n. sp., Woodruff	X	X	X			X
recorta Sanderson (1951:268-269)	X	X	X*	X		X
rex n. sp., Woodruff and Sanderson	X	X	X			X
romana (Saylor) (1946:1)	X	X	X			X
rustica n. sp., Woodruff	X		X			X
santachloe n. sp., Woodruff	X	X	X			X
toni n. sp., Woodruff	X		X		X	

* = first males and females or new country records.

tes. We use the terms instead of numbers, because the first 2 abdominal segments are hidden under the metathorax and coxal plates, confusing the count. The Hispaniolan species show little differences in these last 2 sternites; usually males are less convex, with slight depressions, more setae, or a transverse groove on the ultimate may be deeper and more punctate. Often sexes cannot be distinguished without dissection. One character not found in N.A. species is a patch of pruinosity (Fig. 382, 566) on the

penultimate sternite which varies in intensity, but is usually accompanied by a cluster of long hairs; more noticeable in the dorsally pruinose species. Punctation and setation of most species are usually similar and difficult to assess or compare.

Genitalia. The most useful and diagnostic characters, for identification of species within the genus *Phyllophaga*, are the male and female genitalia. Because of this we have devoted more time and effort to illustrating them. Dr. J.B. Smith (1889) discovered their usefulness, but concluded that "No words could accurately describe their peculiar turnings and twistings..... I shall not undertake verbal descriptions of these parts, but prefer to let my figures answer most questions." It was not until the Scanning Electron Microscope (SEM) that these structures could be properly illustrated. Like Smith, I have only tried to briefly describe the salient features under each species treatment. I have attempted to illustrate the terminology of male morphological features (Fig. 45), but finding a typical species was difficult, as a perusal of the other examples (Fig. 48-55, and under each species) easily will show. An important difference from most continental species is the heavy sclerotization and complicated modifications of the aedeagus. It is often extruded naturally, but sometimes requires dissection. With our studies, none required clearing or slide preparation for viewing diagnostic features. Genitalia were once stored in glycerin vials pinned beneath specimens, but we recommend against this procedure. These are difficult to photograph (because of the viscosity of glycerin), and the vials are precarious for shipping and museum curation. In actuality the corks often desiccate, fall out, and leave the vial to roll around.

Female genitalia (Fig. 56-61, and under each species) are much simpler, usually consisting of 4 plates (rarely 5) and a few setae. In most cases, especially the more heavily sclerotized species, they are sufficiently distinct to be easily recognized. Some of the smaller species, with softer parts, are difficult to dissect and compare. Most consist of 2 relatively simple inferior plates, fused or separated, setate or glabrous, with various ridges and depressions. They sometimes terminate near the suture in an "internal process". Only in *mella* (Fig. 57), are they modified with long, moveable projections ("ice tongs"). Several species have a triangular plate which covers (entirely or partially) the median base of the inferior plates (Fig. 56, 58, 61), but others have no vestige of such a feature (Fig. 59). The superior plates usually extend above the inferior ones and terminate at lateral angles with various numbers, sizes, and positions of setae. A few (Fig. 61, 159) have the inferior and superior plates fused at their apices. The shape of the space between the lateral projections and the setae is often diagnostic, as are the apices themselves. Only *canoa* (Fig. 60) has the superior plate elongated to resemble what is called a pubic process elsewhere. None has been found among Hispaniolan species to possess 3 sets of plates, as in some continental species.

Key to adult *Phyllophaga* of Hispaniola

Traditionally, revisions are accompanied by dichotomous keys to species. We have included this key for that reason, but with certain reservations. Because genitalia are the easiest, and often the only reliable character for species identification, we have illustrated all of them. Most users will find it more practical to peruse these illustrations than to use the key. Although they are referenced in the key, they are not described in detail because of limited space and limited descriptors.

The key is artificial, using easily viewed or compared features, without regard to phylogenetic relationships or function. Some character states (e.g., length) may be inexact or the extent of variability is not known (some known from only 2 specimens); these should be used with caution, and questionable specimens should be compared to the illustrations. In the case of *canoa*, the sexual dimorphism and the nearly cleft tarsal claws require it to appear 3 times. In the case of the unique female *barrosa,* it is placed next to the most similar male, with reference to the genitalia.

1. Antennal club composed of 4 complete lamellae (Fig. 7) or 3 and a partial 4th (Fig. 8-9) 2
1'. Antennal club composed of 3 lamellae only (e.g., Fig. 12-16) 4

2(1). Antennal club of 4 full lamellae and partial 5th; genitalia Fig. 323-325, female unknown .... *garrota* Sanderson
2'. Antennal club of 3 full lamellae and partial 4th (Fig. 8-9) 3

3(2'). Clypeal/frontal suture raised (Fig. 253-254); male genitalia Fig. 248-250, female unknown .... *costura* Sanderson
3'. Clypeal/frontal suture impressed; male genitalia Fig. 603-606, female unknown .... *probaporra* Sanderson

4(1'). Tarsal claws cleft (e.g., Fig. 35-37, 40) 5
4'. Tarsal claws not cleft, lower tooth median or basal (e.g., Fig. 38, 39, 41-43) 12

5(4). Parameres of male genitalia with setae externally on sides (e.g., Fig. 523, 154, 288, 311) 6
5'. Parameres of male genitalia without setae externally on sides (most species) 9

6(5). Dorsally hairy, especially pronotum (Fig. 65, 529, 533) 7
6'. Dorsally with only few setae, pronotal disc glabrous 8

7(6). Smaller (L. 8 mm ±), habitus Fig. 97; tarsal claw Fig. 40; genitalia 523-527 (male), 534-537 (female) ..... *nunezi* Woodruff
7'. Larger (L. 12 mm ±), habitus Fig. 65; tarsal claw Fig. 37; genitalia 149-157 (male), 158-160 (female) ..... *androw* Woodruff

8(6'). Setae on male parameres short, stiff (±15); phallobase dorsally divided, gap on each side with sharp pointed projections; genitalia and other features Fig. 288-310 ..... *fossoria* Sanderson
8'. Setae on male parameres long, numerous (± 40); phallobase dorsally curved, evenly rounded, not divided; genitalia and other features Fig. 311-322 ..... n. sp., near *fossoria*

9(5') Smaller (L. 10 mm ±), pruinose, often bicolored; habitus Fig. 103; genitalia 614-627 .... *pseudocalcaris* Saylor
9'. Larger (L. 13-20 mm ±), pruinose or glabrous; genitalia Fig. 136-143, 167-177, 223-234 10

10(9'). Dark colored, male pruinose, female shiny, larger (L. 20 mm ±), habitus Fig. 71-72; genitalia 223-234 ..... *canoa* Sanderson
10'. Light colored, shiny or matte, smaller (L. 13-14 mm ±), habitus Fig. 64, 66; genitalia 136-143, 167-177 11

11(10'). Dorsally shiny, elytra often translucent; genitalia Fig. 167-177 .... *approxima* Woodruff and Sanderson
11'. Dorsally lightly pruinose, matte, elytra opaque; genitalia Fig. 136-143 ..... *aliada* Sanderson

12(4'). Smaller (L. 10 mm or less) 13
12'. Larger (L. 10 mm or larger) 17

13(12). Elytra wrinkled, body narrow, elongate (habitus Fig. 80); metatibial spurs in both sexes spatulate, curved (Fig. 281-282); antennal club longer than 6 preceding antennomeres; genitalia Fig. 275-279, 284-285; Haiti, La Visite .... *esquinada* Sanderson
13'. Elytra not wrinkled (habitus Fig. 67, 74, 90, 95); metatibial spurs not as above; antennal club shorter than 6 preceding antennomeres; genitalia not as above 14

14(13'). Dorsally noticeably pruinose 15
14'. Dorsally glabrous, shiny 16

15(14). Pygidial punctures regular, surface not wrinkled; habitus Fig. 74; genitalia 241-247 .... *cartaba* Sanderson
15'. Pygidial punctures coalescing medially, surface wrinkled; habitus Fig. 90; genitalia Fig. 429-432, 436-439 ..... *latiungula* Sanderson

16(14'). Smaller (L. 6-7 mm), base color light straw, nearly bicolored; front tarsi exceptionally long, with long setae ventrally (Fig. 508); habitus Fig. 95; genitalia Fig. 501-506; rare .... *minutissima* Wolcott
16'. Larger (L. 8-10 mm), uniformly brown; front tarsi not unusually long; habitus Fig. 67; genitalia Fig. 178-181; common ..... *audanti* Wolcott

17(12'). Larger (L. 19-33 mm) 18
17'. Smaller (L. 10-19 mm) 35

18(17). Dorsum shiny, rarely oily (some *hogardi*) or light violet blush marginally (*santachloe*) 19
18'. Dorsum pruinose or iridescent, not shiny 25

19(18). Pygidium with apical margin upturned into a lip (Fig. 414, 415); genitalia 403-413 .... *kenscoffi* Wolcott
19' Pygidial apex not noticeably upturned, although carinately margined; genitalia not as above 20

20(19'). Pronotum with exceptionally long, reddish hairs (habitus Fig. 70); body color uniformly chocolate brown; male aedeagus asymmetrical, genitalia Fig. 210-222; known from 2 specimens (Haiti: Furcy) ..... *bonfils* Woodruff and Sanderson
20'. Pronotum glabrous, except marginal setae; color variable; male aedeagus symmetrical 21

21(20'). Straw colored, pronotum darker (L. 19-21 mm); habitus Fig. 89; genitalia Fig. 416-424 .... *larimar* Woodruff
21'. Color uniformly dark brown to castaneous (L. 19-27 mm); habitus Fig. 71, 84, 87, 110; genitalia not as above 22

22(21'). Elytral suture terminating in large curved spine (Fig. 362); habitus Fig. 84; genitalia 353-357, 364-367; common lowland species .... *hogardi* (Blanchard)
22'. Elytral suture without large terminal spine; habitus Fig. 87, 71, 110; genitalia not as above .. 23

23(22'). Smaller (L. 17-19 mm); females only (males pruinose); head irregularly punctate, lumpy; habitus Fig. 71; some elytral punctures coalescing,

appearing wrinkled; genitalia Fig. 231-234 .... *canoa* Sanderson

23'. Larger (L. 22-27 mm); head smoothly punctured, not lumpy; habitus Fig. 87, 110; genitalia not as above 24

24(23'). Male aedeagus with dorsal crest or hook near apex on median projection, lateral projections terminating at an angle (Fig. 710-715); female genitalia with inferior plates fused medially, no medial basal depression (Fig. 716-717); lowland species from northeast ..... *santachloe* Woodruff

24'. Male aedeagus without dorsal crest on median projection, lateral projections acuminate and sharp pointed (Fig. 393-398); female genitalia with deep medial basal depression on inferior plates (Fig. 399-402); Cordillera Central, higher elevations ... *jimenezi* Woodruff and Sanderson

25(18'). Elytral suture terminating in a spine (barely noticeable in *marcano)* (habitus Fig. 68, 78, 91, 93, 101, 111) 26

25'. Elytral suture not terminating in a noticeable spine (habitus Fig. 69, 72, 83, 92, 107, 109) 31

26(25). Pronotum and elytra noticeably hirsute; genitalia Fig. 718-722 (only males known); Baoruco Mountains (Larimar Mine) ..... *toni* Woodruff

26'. Pronotum glabrous, elytra with or without scattered setae; genitalia not as above 27

27(26') Elytra without noticeable setae (habitus Fig. 78, 91, 93) 29

27'. Elytra with scattered setae (habitus Fig. 68, 101); aedeagus with boot or sock-like spinose tip (Fig. 191-194, 596-602) 28

28(27'). Male parameres elongate with teat-like projection (Fig. 191-194); known only from Dominican Republic (Baoruco Mountains) .... *baoruco* Woodruff

28'. Male parameres more truncate, apical carina not prolonged (Fig. 596-602); known only from Haiti ..... *permagna* (Moser)

29(27). Smaller (L. 19-20 mm); elytral spine obvious; habitus Fig. 91; genitalia Fig. 440-449; South Island distribution ..... *leptospica* Sanderson

29'. Larger (27-33 mm); elytral spine reduced; habitus Fig. 78, 93; genitalia not as above; Cordillera Central 30

30(29'). Scutellum punctate (Fig. 474); male metatibial long spur gently curved (Fig. 475), not S-shaped; genitalia Fig. 476-481, 461-468; West end of Cordillera Central (Rio Limpio) .... *marcano* Woodruff

30'. Scutellum impunctate; male metatibial long spur bent into an S-shape (Fig. 265-266); genitalia Fig. 261-264, 268-269; East/central Cordillera Central (near Manabao) ..... *eladio* Woodruff

31(25'). Head with large light colored "spots" (Fig. 6, 668); dorsal surface velvety (Fig. 670-671, 673-677); genitalia (Fig. 678-689); habitus unique (Fig. 664-677); Constanza area .... *rex* Woodruff and Sanderson

31'. Head uniformly colored, without "spots"; dorsal surface pruinose, but not velvety; (habitus Fig. 69, 72, 83, 92, 109) 32

32(31'). Base color dark grey, not ferrugineous; pruinosity irregular, reflecting light in a pattern; males only (females shiny), genitalia Fig. 223-230; habitus Fig. 72; Cordillera Central .... *canoa* Sanderson

32' Base color entirely ferrugineous; pruinosity regular, sometimes with iridescent sheen; habitus (Fig. 69, 83, 92, 109); genitalia not as above 33

33(32'). Larger (L. 24 mm); habitus Fig. 83; male genitalia (Fig. 333-338) with parameres elongate basally, aedeagus with long, acuminate, dorsally hinged spine, superimposed over a unique bifurcate lower piece; female genitalia dark colored, heavily sclerotized , with a broad basal triangular plate sealing inferior plates; 2 specimens only from Massif de la Hotte, Haiti .. *haitiensis* Woodruff

33'. Smaller (L. 17.5-23 mm); habitus Fig. 69, 92, 109; genitalia not as above 34

34(33'). Male genitalia (Fig. 450-456) with unique bifurcate tip ("nail-puller") on aedeagus; female genitalia Fig. 457-460; size variable (L. 17-22 mm); common, widespread species ..... *mali* Wolcott

34'. Male genitalia (Fig. 700-707) without bifurcate aedeagal tip; larger (L. 23 mm); pygidium rugose (Fig. 709); only 2 males known; Cordillera Central ..... *rustica* Woodruff

34". Unique female (male unknown; Fig. 199-209); pygidium smooth (Fig. 205); smaller (L. 19 mm); known only from Fond de Negre, Haiti .... *barrosa* Sanderson

35(17'). Dorsal surface velvety, reddish brown, elytral costae darker (habitus Fig. 98); pronotal setae distinct (Fig. 560-562); genitalia Fig. 538-543 (male), 554-556 (female); (L. 14 mm); 2 only from Dominican Republic: Baoruco Mountains, Larimar Mine ..... *ortizi* Woodruff

35'. Dorsal surface shiny or pruinose, not velvety; (L. 10.5-19 mm); genitalia not as above 36

36 (35'). Dorsal surface shiny, no vestige of pruinosity 37

36'. Dorsal surface at least partially pruinose 40

37(36). Larger (L. 17.5-19 mm); straw colored or yellowish; habitus Fig. 106; genitalia Fig. 644-652, 655-658 ..... *recorta* Sanderson

37'. Smaller (L. 10-14 mm); brown or somewhat bicolored; genitalia not as above 38

38(37'). Light chestnut brown, exceptionally convex, parallel-sided (habitus Fig. 105); genitalia Fig. 628-641; "North Island" ..... *rawlinsi* Woodruff

38'. Uniformly dark brown, less convex (habitus Fig. 62, 100); genitalia not as above; Baoruco Mountains,"South Island" 39

39(38'). Habitus Fig. 100; male genitalia (Fig. 584-587) with unique ventral plate between parameres recurved hook-like at tip, with 4 large, heavily sclerotized, aedeagal spines above; female genitalia Fig. 595; elytra slightly flattened medially; sea level to about 2500 ft .... *pedernales* Woodruff

39'. Habitus Fig. 62; male genitalia (Fig. 119-123) with aedeagus scoop-shaped, without ventral recurved tip; female unknown; higher elevations ± 3000 ft ..... *aceitillar* Woodruff

40(36'). Elytral suture terminating in a noticeable spine (habitus Fig. 108); body color dark, pruinosity pronounced; (L. 17-19); genitalia Fig. 690-699; common "North Island" species .... *romana* (Saylor)

40'. Elytral suture not terminating in a noticeable spine; mostly smaller (L. 10-19 mm); genitalia not as above 41

41(40'). Smaller (L. 10-12 mm); habitus Fig. 85, 99 42

41'. Larger (L. 13-19 mm); habitus Fig. 63, 73, 76, 79, 86, 94, 96 43

42(41). Pygidium with dark glabrous center, surrounded by extensive pruinose area (Fig. 374-375), pygidial punctures mostly separated, not coalescing into wrinkles; habitus Fig. 85, females only partially pruinose; genitalia Fig. 368-373, 376-377; "North Island" ..... *imprima* Sanderson

42' Pygidium slightly pruinose, the punctures mostly coalesced into wrinkles, especially medially; habitus Fig. 99; both sexes pruinose; genitalia Fig.569-575, 581-583; "South Island" .... *panicula* Sanderson

43(41'). Larger (L. 15-19 mm); genitalia Fig. 513-522; 484-487,491-494; 270-274; 124-134; 384-389; "North and South Island" 45

43'. Smaller (L. ±13 mm); male genitalia Fig. 235-240; 255-260 (females unknown); "South Island" and Sierra de Neiba 44

44(43'). Pruinosity weak, elytra glabrous; male genitalia Fig. 235-240; Sierra de Neiba .... *carnegie* Woodruff

44'. Pruinosity strong, elytra with scattered setae; male genitalia Fig. 255-260; Sierra de Baoruco .... *davidsoni* Woodruff

45(43). Body color ferrugineous to orange-yellow; pruinosity of elytra and pronotum similar; habitus Fig. 96; genitalia Fig. 513-522 .... *neglecta* (Blanchard)

45'. Body darker, not ferrugineous; pruinosity of pronotum and elytra similar or dissimilar; habitus Fig. 63, 79, 86, 94; genitalia not as above 46

46(45'). Pronotum and elytra pruinose, elytra reflecting light resembling spots; elytra glabrous; genitalia Fig. 484-487, 491-494; "North Island" .... *mella* Sanderson

46'. Pronotum shiny or less pruinose than elytra, elytra pruinose; elytra with golden setae or not; Cordillera Central or "South Island" 47

47(46'). Elytra with golden setae, elytra pruinose, including humeral angles; aedeagus of male genitalia (Fig. 270-274) produced into 2 unique, extremely long flexible processes; female unknown; 2 specimens only from Cordillera Central .... *espina* Sanderson

47'. Elytra without setae, humeral angles at least partially shiny as pronotum, remainder caramel brown with light pruinosity; habitus Fig. 63, 86; "South Island" 48

48(47'). Pygidium irregularly punctate, somewhat rugose; pronotum slightly flattened anterior to scutellum; larger (L. ±18 mm); male genitalia asymmetrical (Fig. 124-134); 2 specimens known .... *alcoa* Woodruff

48'. Pygidium evenly, not rugosely punctate; pronotum evenly convex, not flattened; smaller (L.±16 mm); male genitalia symmetrical (Fig. 384-389) .... *jaragua* Woodruff

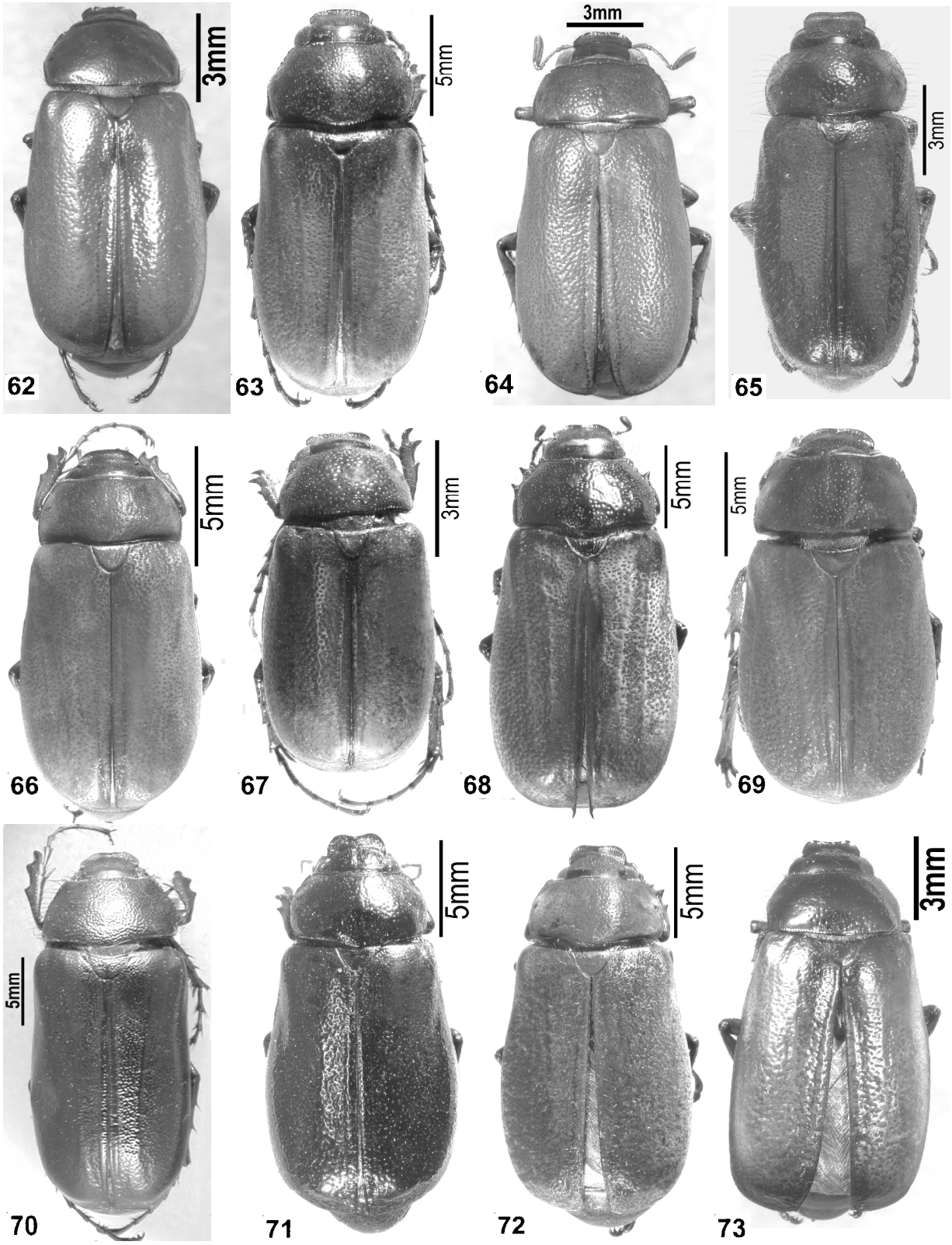


Fig. 62-73. ***Phyllophaga*** **habitus:** 62) *aceitillar* Woodruff; 63) *alcoa* Woodruff; 64) *aliada* Sanderson; 65) *androw* Woodruff; 66) *approxima* Woodruff and Sanderson; 67) *audanti* Wolcott; 68) *baoruco* Woodruff; 69) *barrosa* Sanderson; 70) *bonfils* Woodruff and Sanderson; 71) *canoa* Sanderson, female; 72) *canoa* Sanderson, male; 73) *carnegie* Woodruff.

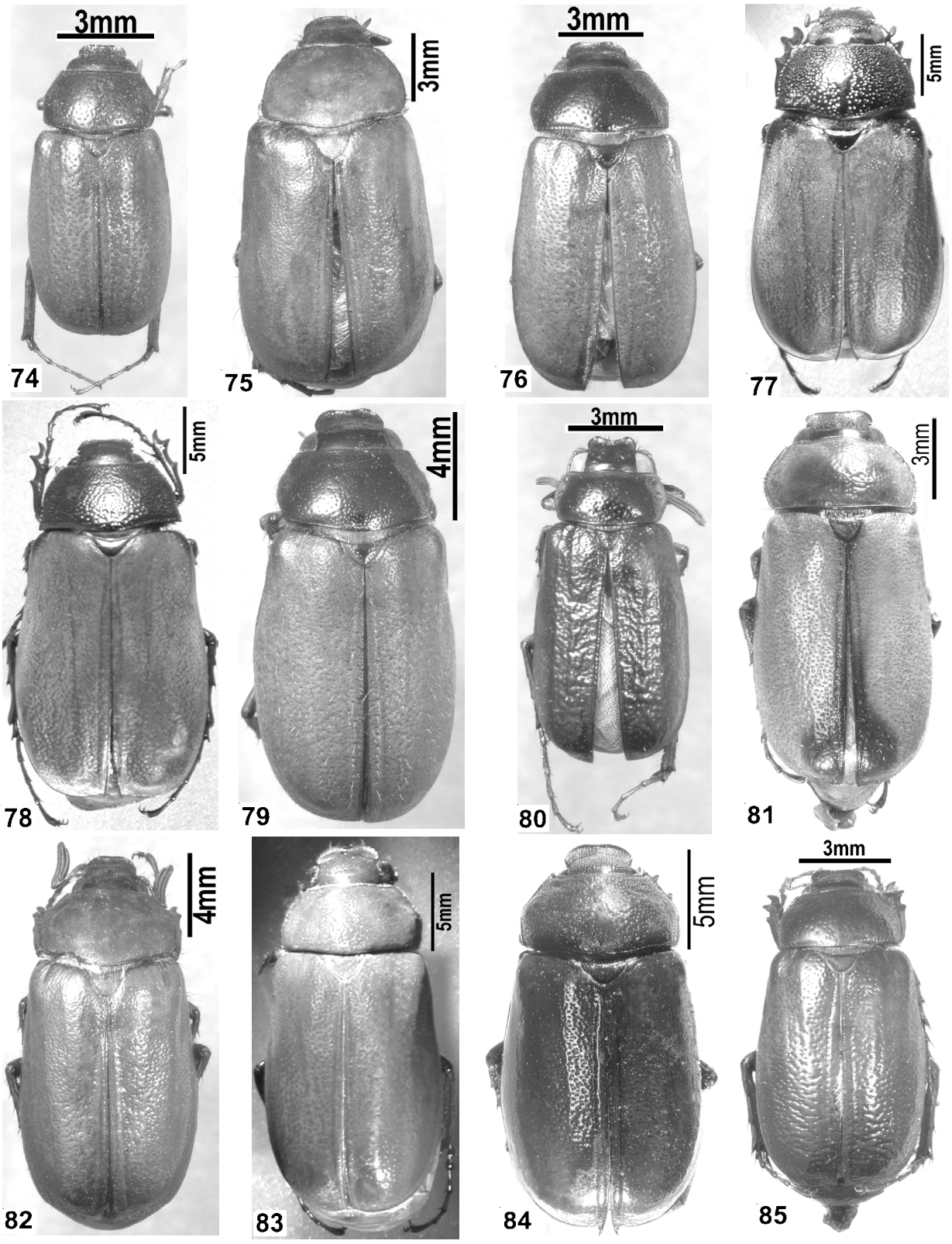


Fig. 74-85. ***Phyllophaga* habitus:** 74) *cartaba* Sanderson; 75) *costura* Sanderson; 76) *davidsoni* Woodruff; 77) *eladio* Woodruff, female; 78) *eladio*, male; 79) *espina* Sanderson; 80) *esquinada* Sanderson; 81) *fossoria* Sanderson; 82) *garrota* Sanderson; 83) *haitiensis* Woodruff; 84) *hogardi* (Blanchard); 85) *imprima* Sanderson.

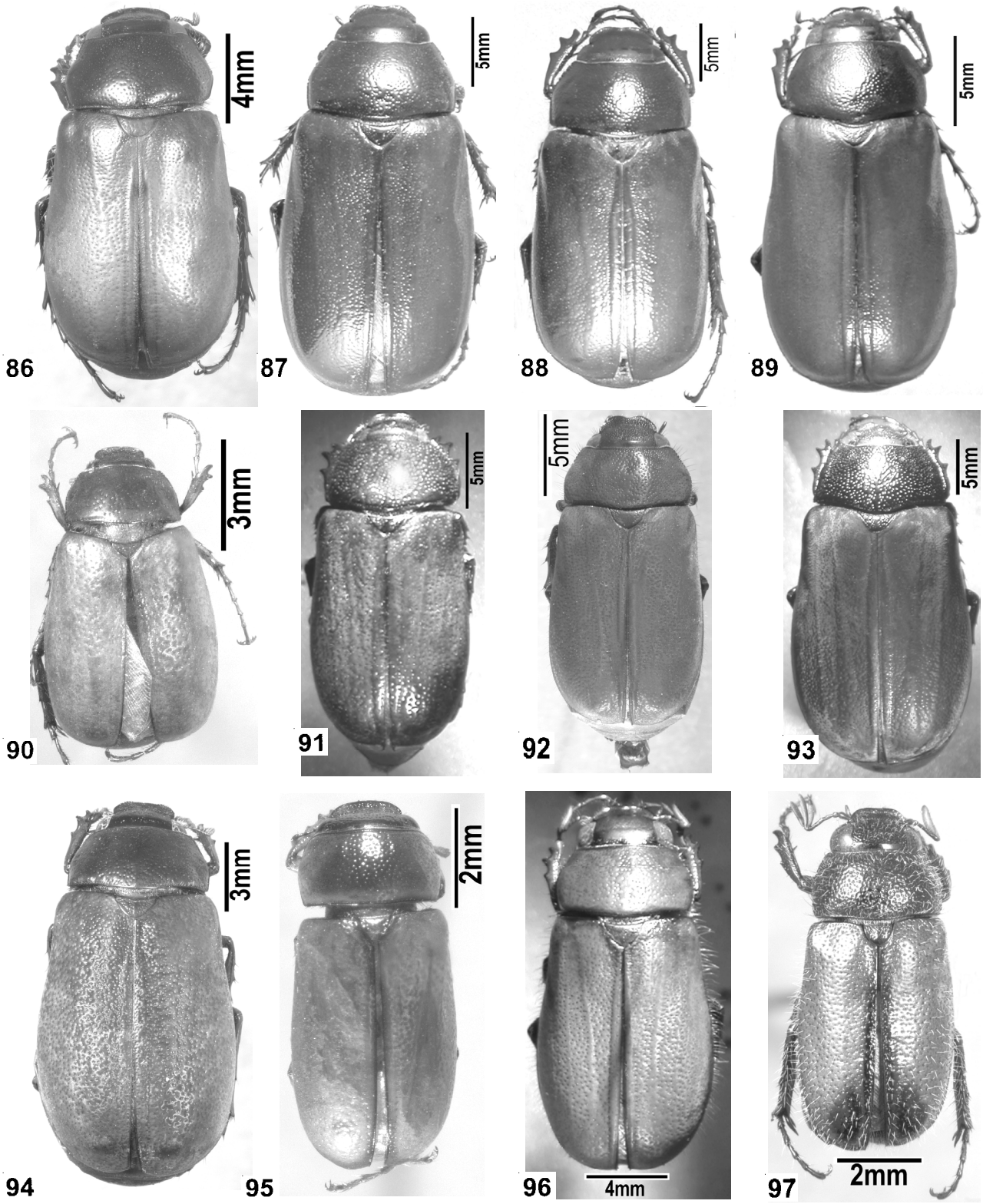


Fig. 86-97. ***Phyllophaga*** **habitus:** 86) *jaragua* Woodruff; 87) *jimenezi* Woodruff and Sanderson; 88) *kenscoffi* Wolcott; 89) *larimar* Woodruff; 90) *latiungula* Wolcott; 91) *leptospica* Sanderson; 92) *mali* Wolcott; 93) *marcano* Woodruff; 94) *mella* Sanderson; 95) *minutissima* Wolcott; 96) *neglecta* (Blanchard); 97) *nunezi* Woodruff.

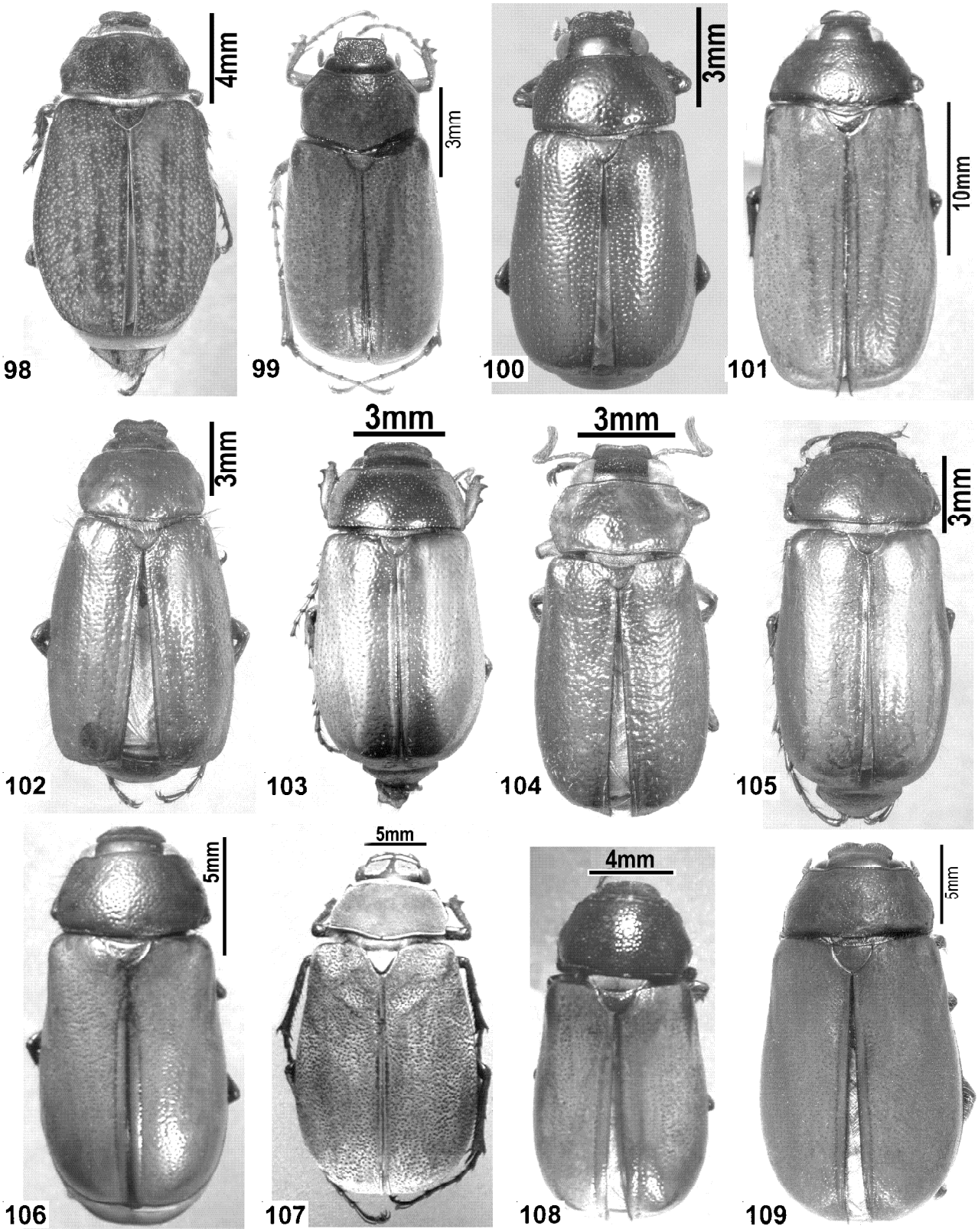


Fig. 98-109. ***Phyllophaga*** **habitus:** 98) *ortizi* Woodruff; 99) *panicula* Sanderson; 100) *pedernales* Woodruff; 101) *permagna* (Moser); 102) *probaporra* Sanderson; 103) *pseudocalcaris* Saylor; 104) *n. sp.* near *fossoria* (see text); 105) *rawlinsi* Woodruff; 106) *recorta* Sanderson; 107) *rex* Woodruff and Sanderson; 108) *romana* Saylor; 109) *rustica* Woodruff.