A Revision of the Genus *Strategus* (Coleoptera: Scarabaeidae)

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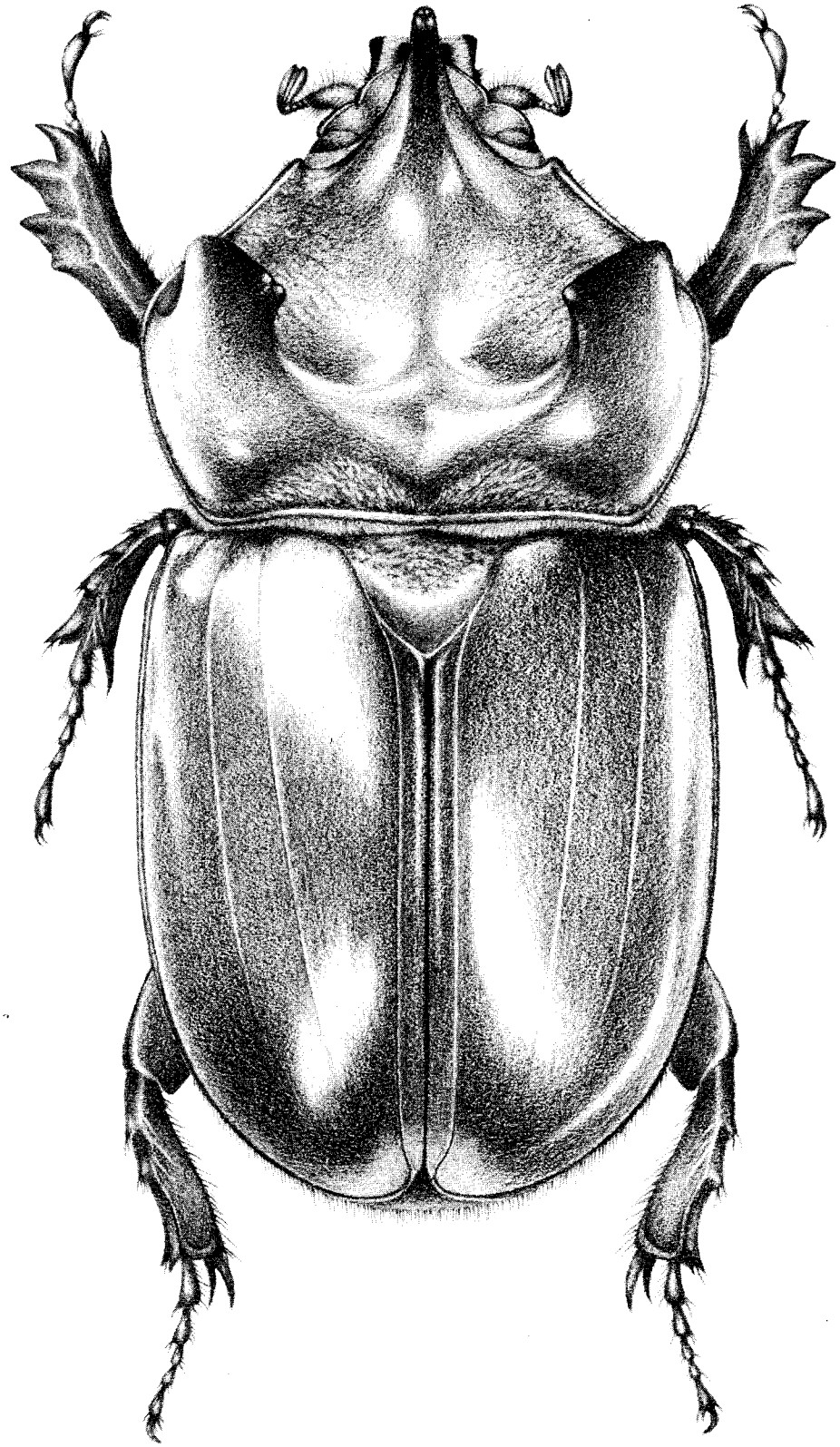

Frontispiece.—*Strategus aloeus* (L.), type of the genus.

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ABSTRACT

A Revision of the Genus *Strategus* (Coleoptera: Scarabaeidae)

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The New World genus *Strategus* Kirby is here defined and revised for the first time. Eight species are described as new: *S. atlanticus, S. caymani, S. craigi, S. hipposiderus, S. howdeni, S. longichomperus, S. symphenax,* and *S. tarquinius*; 12 new junior synonyms are established (including the rejection of six previously valid species); one species is raised from synonymy; and two new replacement names are proposed. *Strategus* now contains one fossil species and 31 valid extant species. A key to the males and females of all the species is provided for the first time. All taxa are described or redescribed and illustrated by habitus figures and drawings of the male genitalia. Biologies are discussed when data are available. Extensive distributional data and locality record dot maps are presented as well as a zoogeographical analysis of the genus. Lastly, a computer-assisted cladistic reconstruction of the presumed phylogeny of the genus is provided.

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Ratcliffe[1]

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INTRODUCTION

The genus *Strategus* was established by William Kirby in 1828 when he listed those species to be included in the new genus; these were *S. aloeus* (L.), *S. antaeus* (Drury), *S. syphax* (Fabr.), and *S. titanus* (Fabr.) (= *S. simson* (L.)). A subsequent definition of what characterized the genus based on all the included species has never been given although Burmeister (1847) made a good attempt and Paulian (1947), LeConte (1861–62), and Saylor (1946) established partial descriptions. The genus as a whole has not been treated in a monograph nor has there ever been a dichotomus key to all of the species. Most of those species descriptions given in the past have been very short and vague. Regional works with keys to the local species (primarily the U. S. species) have been provided by Casey (1915), Chapin (1932a and b), Dillon and Dillon (1961), Horn (1875), Paulian (1947), and Saylor (1946). Checklists for *Strategus* have been given by Arrow (1937a), Blackwelder (1944), Bruch (1911), Dejean (1836), Fleutiaux and Sallé (1889), Gemminger and Harold (1869), Henshaw (1885), Kolbe (1906), Leng and Mutchler (1914, 1917), Leng (1920), and Wolcott (1923, 1936). Synonymies were somewhat stabilized by Arrow (1937a) and the last species described as new was also established by Arrow (1947). Kolbe (1906) has given the most comprehensive treatment of the genus to date, but did not include a key or describe all the species known to him.

In 1915 Casey erected *Anastrategus* as a new genus in the Pentodontini to include those species of former *Strategus* in which the males lacked horns, i. e., *S. adolescens* Kolbe, *S. cessus* LeConte (and those synonyms of Casey and Kolbe), *S. fallaciosus* Kolbe, and *S. splendens* (Beauvois) (and those synonyms of Casey). Arrow (1937a) synonymized the genus with *Strategus* and Endrödi (1959) resurrected *Anastrategus* as a subgenus of *Strategus* and included in it the same species as had Casey.

Casey (1915) also proposed *Strategodes* as a subgenus of *Strategus* to incorporate those species that lack a sutural stria and have long, slender mandibular teeth; these included *S. antaeus* (Drury) (and synonyms of Casey) and *S. mormon* Burmeister. Chapin (1932a) established *Strategopsis* as a subgenus for those species with an unarmed or unidentate galea; this included *S. sarpedon* (Burmeister).

Subgenera are not recognized in this revision as I do not believe there exist valid reasons for doing so. Certainly Casey's *Anastrategus,* based on a variable male sexual character, cannot be justified as Arrow (1937b) has previously pointed out. Casey's *Strategodes* and Chapin's *Strategopsis* are each based on a single derived and ancestral character state, respectively, and do not reflect probable phyletic relationships.

Only moderate and sketchy biological data are actually known for *Strategus* species even though the majority probably have similar life

[1]Systematics Collections, W-436 Nebraska Hall, University of Nebraska State Museum, Lincoln, Nebraska 68588.

cycles. Distributional information for the species has been noticeably fragmentary and erroneous, and, even after the results of this study, could still be considerably refined.

Strategus has been characterized by Endrödi (personal communication) as the most taxonomically difficult genus of Oryctini in the New World next to *Heterogomphus* because of its high level of intraspecific variation. This state of affairs has undoubtedly discouraged any comprehensive systematic treatment in the past. While concurring with Dr. Endrödi's analysis, it is hoped that this study will sufficiently and accurately interpret the genus so that it will no longer be the source of confusion that it has been.

This systematic treatment delineates the genus and provides keys to the males and females of all the species for the first time. It establishes complete synonymies, provides extensive distributional data, describes each species, brings together most, if not all, the published biological information for the species, and presents a zoogeographic analysis of the genus. All species and all distributions are illustrated. Eight species are described as new, 12 new synonymies are established including the rejection of six previously valid species, one species is raised from synonymy, and two new replacement names are proposed. *Strategus* now contains one fossil species and 31 valid extant species.

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METHODS

The results of this study were based on the examination of 5,115 specimens from 29 institutional and five private collections (see Acknowledgments). Most of the major collections in the United States, Canada, and Mexico were visited, and collecting trips were conducted to Kansas, New Mexico, Arizona, British Honduras (Belize), Mexico, Panama, and to the common borders of Colombia, Brazil, and Peru. Collecting techniques consisted of random searching in favorable areas, blacklighting, and frequenting lights at night in selected locales.

Early in the study an attempt was made to obtain *Strategus* larvae from numerous sources so that a key could be provided for many of the immatures as well as for the adults. Even though the larvae of some species are well known due to their past economic significance, little success was had in trying to obtain larvae on loan and, therefore, plans to key and describe the larvae had to be abandoned (at least for the present). The apparent lack of immature specimens in collections was a major disappointment to the author. The reader is referred to Ritcher (1944, 1966) for keys and descriptions to the larvae of *Strategus aloeus* (L.) (= *julianus* Burmeister), *S. antaeus* (Drury), and *S. splendens* (Beauvois).

A conventional artificial key to the males and females of all the species is presented for the first time. Although many morphological characters within the genus are highly labile, an attempt was made to utilize key characters which were consistantly expressed, low in intrinsic variability, and easily observed with reasonable procedures.

The morphological characters used in this study were selected because they were seen to vary on a consistent basis between phena, thus allowing for separation of different taxa based on the character state. Phena were sorted according to the following characters: length and width measurements; sculpturing and hairiness of the front; shape and sculpturing of the

clypeus; shape and size of the mandibular lobes; size of the head tubercles; interocular width; sculpturing of the mesosternum and pronotum; form and size of the horns; sculpturing of the elytra; the shape, hairiness, and sculpturing of the pygidium; and the form of the parameres of the male genitalia. Sorting was not done on a geographical basis except in the rare instances of morphologically inseparable females.

Taxa were initially defined *a priori* within the limits of existing species descriptions. The use of additional characters never before used and the re-evaluation of previously recognized characters in much larger samples sizes and in the types enabled me to redefine or more precisely limit the definition of the various species. New species were recognized when character states were seen to fall significantly outside the range of my more comprehensive redefinitions of existing taxa.

Several characters were disregarded in delineating taxa because they were either constant, too variable, or examples of random character states. These were: shape and sculpturing of the mentum (two exceptions), palps, antennae, and eye canthus; punctation of the mandibles; general punctation of the horns (two exceptions); curvature of the lateral margin of the pronotum; shape and sculpturing of the scutellum; angle of the elytral apices; size of the stridulatory ridges on the propygidium; punctation and hairiness of the abdominal sternites; shape of the female genital plates; form and sculpturing of the apices of the tibiae; length and ratios of tarsal segments; and size and shape of claws.

Complete synonymies are provided for all the species. The historical usage of names within each species is not given in the synonymy section as is frequently customary. I believe such usage may tend to obfuscate actual synonymies; if different usages of names are significant, they are mentioned in the text. It should be noted that Fabricius often knowingly redescribed in later works species that had been previously named. Those redescriptions listed in the synonymies in this paper appeared without references to any prior publications and could technically, therefore, have been taken as new species descriptions although, of course, they were not.

Reasonably complete and comparable descriptions are given for the males and females of each species for the first time, and all observed variation in the character states is recorded. Technical terminology is essentially that of Torre-Bueno (1937). For greater convenience the species descriptions and illustrations are arranged alphabetically.

Biologies or life history notes, when known, are included in the discussion of the appropriate species.

Locality records are presented in the following format: country; state, province, or equivalent; locale. A temporal distribution follows the records for each country. A few specific literature references and personal communications citing distributional data are used sparingly and are appropriately acknowledged, but checklists were not used. Location and correct spellings of geographic place names were verified by consulting American Geographical Society (1943a–c, 1944a–i) and Bartholomew (1957). Distributional dot maps are provided for each species (except *S. adolescens* Kolbe, for which no specific locales are known).

Dorsal and lateral habitus figures of the male of each species are presented by means of photographs; the females are not similarly illustrated because no appreciable differences would be noticed among them. Lateral and caudal views of the male genitalia of each species are illustrated by line drawings made with the use of camera lucida. Specimens were observed with a Leitz stereomicroscope using magnifications of 12.5 and 50.0 ×.

EXPLANATION OF CHARACTERS USED IN KEYS AND DESCRIPTIONS

Measurements: Length measurements were made from the apex of the clypeus to the apex of the elytra and width measurements were made across the humerus.

Clypeus: Several authors (notably Bates, 1886–1890; Burmeister, 1847; Kolbe, 1906) have referred to the clypeus and its apical shape as this is of considerable importance for correct identifications. From their descriptions, it is apparent that these authors were, in most instances, referring to the form of the apex of the clypeal disc and not to the entire clypeus. If

only the apex of the disc is considered, it is possible to have an apical shape considerably different from that of the entire clypeus which also includes the declivous *sides.* The apex of the clypeus, then, is the true apex and not the apex of the clypeal disc alone. Care should also be taken when arriving at a conclusion about the form of the clypeal apex as this area is very subject to having its shape altered because of abrasion resulting from digging by the beetle. Fortunately, a worn clypeus can usually be recognized as such and so not be misinterpreted.

Mentum: At first thought to be a good character, the mentum was subsequently found to be inconsistently variable in regard to shape and sculpturing of the disc and shape of the apex. With rare exception, this character is not used.

Mandibles: The form of the three lobes of each mandible is of taxonomic significance. Whereas the first and third lobes do not usually vary to any great extent, the middle lobe is differentially developed among many species and is often diagnostic. The mandibles are subject to considerable wearing and, as with the clypeal apex, judicious care should be employed when ascertaining the shape of the lobes.

Interocular width: Measured by the number of transverse eye diameters necessary to span the interocular gap, this character is consistently expressed within the limits of the descriptions.

Mesosternum: The anterior, oblique half, or the entire mesosternum is setigerously punctate. The punctures are usually large and ocellate.

Pronotum: For convenience, the descriptions divide the pronotum into disc, sides, and anterior third or half (which includes the fovea). The base of the pronotum of most species has a transverse band of coarse sculpturing just anterior of the basal bead; this sculpturing is referred to as the band of punctures, rugose band, etc. Pronotal sculpturing tends to decrease proportionately as the size and development of the horns increases and vice versa.

Horns: Most of the species possessing horns are divided into "majors" and "minors" for descriptive purposes. Majors are those individuals within a species with well-developed armature which is possibly the result of an optimum nutritional history in the larval stage. Minors are those individuals within a species whose armature has not developed to the recognized potential development of that particular species. There is no clear boundary separating the two forms of development and all gradations between the two extremes occur.

Elytra: In those species with rows of punctures on the disc, the rows are numbered from the sutural stria laterally to the humerus. The rows on the sides of the elytra are numbered from the median (humeral) border of the sides laterally to the elytral margin.

Pygidium: The basal, transverse band of setigerous punctures or rugosity is of little taxonomic value and is not considered in the species descriptions. The setae referred to on the apical margins mean those setae inside the marginal bead of the pygidium and not those just posterior of the marginal bead. The lateral emargination is the oblong, shallow, excavated, or depressed area near the margins on either side of the apex; it is frequently absent or nearly obsolete.

Genitalia: The shape of the parameres of the male genitalia is an important and rather consistant character. Some species have very similar genitalia, and so this character should be used in combination with other characters for an accurate determination. The female genitalia were not used in this study as a preliminary examination of them revealed few differences in the genital plates.

Punctures: Punctures are considered irregular in distribution and simple unless otherwise noted. Ocellate punctures are ringed with a slightly different color tone, and umbilicate punctures are navel-shaped or have a convex bump at the bottom of the puncture. Minute punctures are generally not seen with 12.5 × magnification, but are easily seen with 50 × magnification. Small punctures are easily seen with 12.5 × magnification and can be seen with the naked eye. Large punctures are easily seen without the aid of instruments. A small puncture is termed deep if the bottom of the puncture cannot be easily seen, and is deemed shallow if the bottom can be readily observ

Large punctures are usually shallow, but may be termed deep if they are roughly ¼ mm or more in depth.

Genus *STRATEGUS* Kirby

STRATEGUS Kirby *in* Kirby and Spence 1828: 349 (not Kirby and Spence, *loc. cit.*, as reported by Neave, 1940). [Type species: *Strategus aloeus* (L.) 1758: 345; subsequent designation by Hope (1837: 87), not Casey (1915: 238) nor Paulian (1947: 78).]

subgenus *STRATEGODES* Casey 1915: 245. [Type species: here designated as *Strategus antaeus* (Drury) 1773: 74. Casey did not designate a type for the subgenus nor have subsequent authors.]

subgenus *STRATEGOPSIS* Chapin 1932a: 302. [Type species: *Strategus sarpedon* (Burm.) 1847: 122.]

ANASTRATEGUS Casey 1915: 231. [Type species: *Strategus cessus* LeConte 1866: 382.]

Description.—Scarabaeidae, Dynastinae, Oryctini. *Form:* Oblong-ovate, robust to very robust, sides subparallel, dorsum convex, apical half of elytra broadly rounded; length from apex of clypeus to apex of elytra 19.5–80.0 mm. *Color:* Castaneous, piceous or black, highly polished to dull, not shining; vesiture normally ferruginous. *Head:* Shape subtriangular; 2 conical tubercles delineate front from clypeus, tubercles obsolete to strong, distinctly separated to connected by a transverse carina. Eyes large; interocular width 1.66–4.5 transverse eye diameters. Antennae 10 segmented, club with 3 segments. Clypeus trapezoidal to triangular, sides sinuate, attenuate; apex reflexed, entire to excised; lateral margin of disc usually carinate with sides weakly to sharply declivous, disc variably sculptured. Mentum with disc variably punctate, setigerous, apex entire to emarginate. Mandibles usually large, always exposed, tridentate. *Pronotum:* Widest at about middle, apex about ⅔ as wide as base, margins distinctly beaded, surface variably sculptured, basal margin just inside of bead with or without a transverse, punctate to rugose band of sculpturing. Anterior half usually clearly foveate, fovea shallow to deep. Subapical margin tuberculate in females, tuberculate or with a forward projecting horn in males of many species, horn variable in length and structure; in addition, males of many species possess 2 triangular bosses or horns postero-lateral of anterior horn, horns variable in length and structure. *Mesosternum:* Completely and setigerously punctate or anterior half setigerously punctate. *Elytra:* Scutellum large, triangular, basal ½–⅔ variably punctate to rugose. Sutural stria usually a distinctly impressed line, although nearly obsolete in one species and punctate in another. Disc of elytra variably punctate; punctures minute to large, simple to ocellate to ocellate-umbilicate, shallow to deep; striae, if present, feebly impressed, incomplete; sides as disc, humeral umbone prominent. *Legs:* Anterior tibia usually quadridentate, tarsus almost as long as tibia. Middle and posterior tibiae each with 2 strong, oblique, spinose ridges; apices variably toothed or sharply angulate. *Abdomen:* Propygidium with numerous fine to moderately coarse, transverse stridulatory ridges. Pygidium in lateral view entirely convex to convex basally and variably concave apically, occasionally protuberant at middle; basal margin always very coarsely and setigerously punctate to rugo-punctate in a wide, transverse band; disc and apical margins variably sculptured and frequently setigerous; lateral emarginations on apical margins either side of middle present or not in females. Apex of last visible sternite emarginate to subtruncate in males, entire in females.

Diagnosis.—*Strategus* may be distinguished from other genera in the tribe Oryctini by the following combination of characters: apex of hind tibiae with sharp angulations or teeth, mandibles exposed and tridentate, pronotum usually foveate and at least tuberculate subapically.

Range.—The combined distributions of the known species extends from the northeastern United States, south to Argentina, and includes the Greater and Lesser Antilles.

KEY TO THE SPECIES OF *STRATEGUS*

1. Apex of last visible sternite emarginate to subtrunctate (Males) 2
   Apex of last visible sternite entire (Females) 36

MALES

2(1). Mesosternum completely, setigerously punctate 3
Mesosternum with at least posterior ¼ to ⅓ without setigerous punctures 9

3(2). Disc of elytra with distinct rows of punctures. San Salvador Island, Bahamas .....*atlanticus* n. sp.
Disc of elytra without distinct rows of punctures 4

4(3). 2 to 3 short rows of moderate to large, ocellate and/or umbilicate punctures behind humerus 5
Rows of ocellate and/or umbilicate punctures behind humerous lacking 8

5(4). Apex of anterior horn usually slightly expanded and weakly to moderately excised (Fig. 50). Colombia .....
.....*fascinus* Burm.
Apex of anterior horn entire 6

6(5). Apex of elytra with minute setae (when not worn off). Posterior horns in majors long, slender, forward projecting, and with moderately large punctures apically. Northwest South America to Mexico . *jugurtha* Burm.
Apex of elytra without setae. Posterior horns of majors short, stout, usually suberect, and with small punctures apically 7

7(6). Base of pronotum with rugose band narrow to moderate. Punctures on disc of pronotum small. Anterior horn of majors with moderate sized punctures. Punctures on disc of elytra small. Pygidium usually with a small, medio-apical band of setigerous punctures. Amazon River south to Argentina .....
.....*surinamensis hirtus* Sternb.
Base of pronotum with rugose band obsolete to narrow. Punctures on disc of pronotum very small. Anterior horn of majors with small punctures. Punctures on disc of elytra minute to very small. Pygidium without a medio-apical band of setigerous punctures. Amazon River north to Venezuela .....
..*surinamensis surinamensis* Burm.

8(4). Apex of clypeus acutely pointed. Middle lobe of mandible very long and slender, apex acutely pointed (Fig. 71). Base of pronotum with a very narrow band of punctures. Southcentral United States .....*mormon* Burm.
Apex of clypeus narrowly truncate. Middle lobe of mandible short and broad. Base of pronotum without sculpturing. Grenada (Lesser Antilles) .....*tarquinius* n. sp.

9(2). Mandibles in dorsal view nearly square (Fig. 44). Pronotum never with horns, but with a moderate to strong tubercle on midapex. Disc of mentum usually coarsely punctate; punctures large, dense, often confluent. Southwest United States to northwest Mexico .....*cessus* LeC.
Mandibles in dorsal view not square. Pronotum armed or not. Disc of mentum not coarsely punctate as above 10

10(9). Disc of elytra, at least on lateral third, with definite rows of moderate to large ocellate and/or umbilicate punctures 11
Disc of elytra without definite rows or moderate to large ocellate and/or umbilicate punctures 21

11(10). Sutural stria a row of close set, moderate to large, umbilicate punctures, punctures not forming an impressed line. Guadeloupe .....*syphax* (Fabr.)
Sutural stria an impressed line, punctate or not within; if punctate, punctures small, often confluent, not umbilicate 12

12(11). Apex of clypeus moderately to strongly excised. Length greater than 50 mm. South America .....*centaurus* Kolbe
Apex of clypeus rounded to truncate or weakly emarginate. Length less than 50 mm 13

13(12). Elytra shining. Base of pronotum with a moderate to wide rugose or punctate band. Anterior horn, if present, always with apex entire 14

Elytra dull, not shining. Base of pronotum with a narrow to obsolete rugose band. Anterior horn of all but the smallest specimens always with apex forked, excised, or emarginate 17

14(13). Length less than 30 mm. Pronotum never with horns. Cuba .... *sarpedon* (Burm.)

Length greater than 30 mm. Pronotum armed or not 15

15(14). Pronotum without posterior horns. Mandibular lobes confluent, not distinct. Disc of pygidium setigerously punctate in a broad, irregular band at midline. Haiti ..... *inermis* Arrow

Pronotum with 3 horns except in minors, and then posterior horns reduced to triangular bosses. Mandibular lobes usually distinct. Disc of pygidium not setigerously punctate at midline 16

16(15). Disc of elytra adjacent to sutural stria with moderate to large ocellate-umbilicate punctures (Fig. 93). Cuba ..... *symphenax* n. sp.

Disc of elytra adjacent to sutural stria without moderate to large ocellate-umbilicate punctures. Cuba .... *anachoreta* Burm.

17(13). Paramere of genitalia weakly flared on lateral margin near apex (Figs. 166–167), never with a well-developed angular prominence. Anterior horn in majors distinctly expanded and forked apically (Fig. 95). Puerto Rico, Virgin Islands ..... *talpa* (Fabr.)

Paramere of genitalia with a well-developed angular prominence on lateral margin near apex. Anterior horn in majors expanded or not .. 18

18(17). Interocular width about 1 ⅔ transverse eye diameters, never more than 2 diameters. Posterior horns completely lacking. Fovea of pronotum nearly obsolete. Cayman Islands .... *caymani* n. sp.

Interocular width 2 or more transverse eye diameters. Posterior horns present in majors, minors with at least low bosses. Fovea of pronotum present 19

19(18). Posterior horns long and slender. Apex of anterior horn expanded and moderately to deeply forked (Fig. 79). Jamaica ..... *simson* (L.)

Posterior horns in form of low, pyramidal bosses. Apex of anterior horn not expanded or forked, but with a small triangular notch 20

20(19). Paramere of genitalia with a spiniform process on lateral margin near apex (Figs. 110–111). Hispaniola .... *aenobarbus* (Fabr.)

Paramere of genitalia lacking a spiniform process on lateral margin near apex (Figs. 112–113). Cuba .... *ajax* (Oliv.)

21(10). Sutural stria effaced, although occasionally present near apex. Eastern United States ..... *antaeus* (Drury)

Sutural stria present 22

22(21). Anterior horn with apex expanded and forked, less so in minors where apex still clearly notched and not merely weakly emarginate. Paramere of genitalia with a well-developed, angular prominance on lateral margin near apex. Elytra dull, not shining 23

Anterior horn with apex attenuate and entire to weakly emarginate. Paramere of genitalia lacking any angular prominance on lateral margin near apex. Elytra shining 24

23(22). Interocular width about 1 ⅔ transverse eye diameters, never more than 2 diameters. Posterior horns completely lacking. Cayman Islands .... *caymani* n. sp.

Interocular width 2 or more transverse eye diameters. Posterior horns present in majors, minors with at least low bosses. Jamaica ..... *simson* (L.)

24(22). Elytra behind humerus with 2–3 short, distinct rows of moderate to large ocellate and/or umbilicate punctures 25

Elytra behind humerus without distinct rows of moderate to large ocellate and/or umbilicate punctures 26

25(24). Apex of clypeus truncate to subtruncate, occasionally weakly emarginate. Middle lobe of mandible short to moderate in length. Brazil to Argentina ..... *validus* (Fabr.)
Apex of clypeus deeply excised. Middle lobe of mandible large and long (Figs. 63, 65). Central America ..... *longichomperus* n. sp.

26(24). Apex of clypeus acuminate. Posterior horns absent. Middle and apical lobes of mandible triangular, both prominent, middle large, about twice as large as apical lobe. Mexico ..... *fallaciosus* Kolbe
Apex of clypeus acuminate or not. Posterior horns present or not. Apical lobe of mandible always much smaller than middle lobe, never prominent and triangular 27

27(26). Base of pronotum with rugose band narrow 28
Base of pronotum with rugose band wide 29

28(27). Length less than 35 mm. Posterior horns absent. Elytra with small punctures only. Eastern United States ..... *splendens* (Beauv.)
Length greater than 35 mm. Posterior horns present in majors. Elytra with small and minute punctures mixed. Hispaniola, Puerto Rico, Grand Cayman Island ... *oblongus* (Beauv.)

29(27). Clypeus rounded to subtruncate. Pronotum never with projecting, acuminate posterior horns, with rounded bosses at most 30
Clypeus emarginate to broadly truncate. Pronotum armed with short to long, acuminate posterior horns in majors, rounded bosses in minors 32

30(29). Pronotum with a short anterior horn and rounded posterior bosses. Disc of pronotum sparsely punctate. Tubercles on head separate to feebly joined 31
Pronotum with an anterior tubercle only. Posterior armature completely lacking. Disc of pronotum with moderately dense punctures. Tubercles on head joined by a strong carina. Mexico. ..... *craigi* n. sp.

31(30). Base of pronotum with rugose band narrow. Sutural stria very feebly impressed. Punctures on elytra small. Color black. Mexico. ..... *adolescens* Kolbe
Base of pronotum with rugose band moderate to wide. Sutural stria strongly impressed. Punctures of elytra small to moderate. Color piceous. Mexico ..... *howdeni* n. sp.

32(29). Paramere of genitalia roughly triangular, usually distinctly wider at base and tapering apically (Figs. 114–117). Southern United States to Brazil ..... *aloeus* (L.)
Paramere not as above 33

33(32). Disc of elytra with punctures small and moderate mixed and of moderate density. Interocular width 2 ⅔ transverse eye diameters or more. Argentina, Uruguay .... *argentinus* Kolbe.
Disc of elytra with punctures small and minute mixed and sparse. Interocular width 2 ½ transverse eye diameters or less 34

34(33). Apex of clypeus broadly and shallowly emarginate. Posterior horns short and triangular in majors. Base of pronotum with rugose band wide. Mexico to Colombia ..... *hipposiderus* n. sp.
Apex of clypeus broadly truncate (occasionally very weakly emarginate). Posterior horns long and slender in majors. Base of pronotum with rugose band narrow to moderate 35

35(34). Dorsal surface of anterior horn nearly flat. Posterior horns in majors project at about 45° from plane of disc. Middle lobe of mandible 2–3 times larger than basal lobe. Hispaniola, Puerto Rico, Grand Cayman Island ..... *oblongus* (Beauv.)
Dorsal surface of anterior horn carinate. Posterior horns in majors project at about 70° from plane of disc.

Middle lobe of mandible 4—5 times larger than basal lobe. Argentina, Brazil, Paraguay .... *mandibularis* Kolbe

FEMALES

(Females of *S. atlanticus, S. craigi, S. fascinus, S. inermis* and *S. symphenax* are unknown. *S. atlanticus* is keyed because I believe the 2 characters involved are sufficiently predictive.)

36(1). Mesosternum completely, setigerously punctate 37
Mesosternum with at least posterior ¼ to ⅓ without setigerous punctures 42

37(36). Disc of elytra with rows of punctures. San Salvador Island, Bahamas .... *atlanticus* n. sp.
Disc of elytra without rows of punctures 38

38(37). Elytra behind humerus with 2–3 short rows of moderate to large ocellate and/or umbilicate punctures 39
Elytra behind humerus without rows of moderate to large ocellate and/or umbilicate punctures 41

39(38). Apex of elytra with minute setae (when not worn off). Pygidium nearly impunctate to moderately punctate. Northwest South America to Mexico ..... *jugurtha* Burm.
Apex of elytra without setae. Pygidium usually densely punctate to subrugose 40

40(39). Pygidium setigerously rugopunctate to subrugose, setae usually dense (except in worn specimens). Disc of pronotum with punctures small. Amazon River south to Argentina .... *surinamensis hirtus* Sternb.
Pygidium setigerously punctate to rugopunctate, setae sprase to moderate. Disc of pronotum with punctures very small. Amazon River north to Venezuela .... *surinamensis surinamensis* Burm.

41(38). Apex of clypeus acutely pointed. Middle lobe of mandible very long and slender, apex acutely pointed. Base of pronotum with a very narrow band of punctures. Southcentral United States ..... *mormon* Burm.
Apex of clypeus narrowly truncate. Middle lobe of mandible short and broad. Base of pronotum without sculpturing. Grenada (Lesser Antilles) ..... *tarquinius* n. sp.

42(36). Mandibles in dorsal view nearly square. Disc of mentum usually coarsely punctate, punctures large, dense, often confluent. Southwest United States to northwest Mexico .... *cessus* LeC.
Mandibles in dorsal view not square. Disc of mentum usually not coarsely punctate 43

43(42). Disc of elytra, at least on lateral third, with definite rows of moderate to large ocellate and/or umbilicate punctures 44
Disc of elytra without rows of moderate to large ocellate and/or umbilicate punctures 51

44(43). Sutural stria a row of close set, moderate to large, umbilicate punctures, punctures not forming an impressed line. Guadeloupe .... *syphax* (Fabr.)
Sutural stria an impressed line, punctate or not within; if punctate, punctures small, often confluent, not umbilicate 45

45(44). Length greater than 50 mm. Base of pronotum with rugose band wide. South America .... *centaurus* Kolbe
Length less than 50 mm. Base of pronotum with rugose to rugopunctate band narrow to obsolete 46

46(45). Elytra shining 47
Elytra dull, not shining 48

47(46). Length less than 30 mm. Pygidium punctate. Disc of elytra adjacent to sutural stria with at least some moderate to large ocellate and/or umbilicate punctures. Cuba .... *sarpedon* (Burm.)
Length greater than 30 mm. Pygidium rugose. Disc of elytra adjacent to sutural stria without moderate to large ocellate and/or umbilicate

punctures. Cuba ..... *anachoreta* Burm.

48(46). Interocular width about 1 ⅔ transverse eye diameters, never more than 2 diameters. Cayman Islands ..... *caymani* n. sp.

Interocular width 2 or more transverse eye diameters 49

49(48). Lateral half of disc of elytra with 2 to several distinct rows of moderate to large ocellate and/or umbilicate punctures 50

Lateral half of disc of elytra usually without distinct rows of moderate to large ocellate and/or umbilicate punctures; if present, feeble and confused. Jamaica ..... *simson* (L.)

50(49). Pygidium not strongly protuberant at middle, not overhanging apical margin in lateral view. Puerto Rico, Virgin Islands ..... *talpa* (Fabr.)

Pygidium strongly protuberant at middle, overhanging apical margin in lateral view. Cuba, Hispaniola ..... *aneobarbus* (Fabr.) and *ajax* (Oliv.)

51(43). Sutural stria effaced, although occasionally present near apex. Eastern United States ..... *antaeus* (Drury)

Sutural stria present 52

52(51). Elytra dull, not shining. Pronotum with basal band of rugosity narrow to obsolete 53

Elytra shining. Pronotum with basal band of rugosity variable 54

53(52). Interocular width about 1 ⅔ transverse eye diameters, never more than 2 diameters. Cayman Islands ..... *caymani* n. sp.

Interocular width 2 or more transverse eye diameters. Jamaica ..... *simson* (L.)

54(52). Apex of clypeus distinctly (though occasionally weakly) excised. Elytra behind humerus usually with 2–3 short rows of moderate to large ocellate and/or umbilicate punctures. Central America ..... *longichomperus* n. sp.

Apex of clypeus rounded or truncate. Elytra behind humerus with or without rows of ocellate and/or umbilicate punctures 55

55(54). Elytra behind humerus with 1–4 short to moderate rows of moderate to large ocellate and/or umbilicate punctures 56

Elytra behind humerus without distinct rows of moderate to large ocellate and/or umbilicate punctures 58

56(55). Pronotum with basal band of rugosity narrow. Middle and apical lobes of mandibles subequal. Amazon River south to Argentina ... *validus* (Fabr.)

Pronotum with basal band of rugosity wide. Middle lobe of mandible at least twice as large as apical lobe 57

57(56). Pygidium completely rugose and densely, setigerously punctate. Interocular width greater than 2 ½ transverse eye diameters. Argentina, Brazil, Paraguay ..... *mandibularis* Kolbe

Pygidium moderately rugopunctate to rugose and sparsely setigerous. Interocular width less than 2 ¼ transverse eye diameters. Mexico to Colombia ..... *hipposiderus* n. sp.

58(55). Interocular width greater than 3 ½ transverse eye diamters 59

Interocular width less than 3 transverse eye diameters 60

59(58). Color black. Sutural stria very weakly impressed. Interocular width greater than 4 ¼ transverse eye diameters. Mexico ..... *adolescens* Kolbe

Color castaneous. Sutural stria strongly impressed. Interocular width less than 4 transverse eye diameters. Eastern United States ..... *splendens* (Beauv.)

60(58). Base of pronotum with rugose band very narrow to obsolete. Pronotum usually without a distinct, depressed, rugopunctate to rugose patch just postero-lateral of fovea. Hispaniola, Puerto Rico, Grand Cayman Island ..... *oblongus* (Beauv.)

Base of pronotum with rugose band moderate to wide. Pronotum usually with a distinct, depressed, rugopunctate to rugose patch postero-

lateral of fovea 61

61(60). Middle lobe of mandible subequal to or slightly larger than apical lobe. Argentina, Uruguay .... *argentinus* Kolbe

Middle lobe of mandible 2 or more times larger than apical lobe 62

62(61). Middle lobe of mandible large, acute. Mexico ..... *fallaciosus* Kolbe

Middle lobe of mandible moderate in size, rounded, never acute 63

63(62). Tubercles on head usually distinctly separated. Sides of clypeus in dorsal view weakly sinuate. Apex of clypeus narrowly subtruncate to truncate. Southern United States to Brazil ..... *aloeus* (L.)

Tubercles on head joined by a moderate to strong carina. Sides of clypeus in dorsal view strongly sinuate. Apex of clypeus very narrowly subtruncate. Mexico ..... *howdeni* n. sp.

Strategus adolescens Kolbe
(Figs. 10–11, 108–109)

Strategus adolescens Kolbe, 1906: 15. [Lectotype male (Figs. 10–11), labeled "Mexico hoppe," "TYPE," "27395" and lectoallotype female, labeled "TYPE," "27395," here designated; at ZMHU with my lectotype labels. Also one female paralectotype at ZMHU. Type locality: Mexico.]

Male.—Length 31.5 mm; width across humerus 16.5 mm. Color black, shining. *Head:* Front strongly rugo-punctate. Clypeus with apex narrowly truncate, slightly reflexed; surface rugo-punctate. Tubercles strong, transverse, weakly connected. Mandibles with basal lobe small, prominently rounded; middle lobe triangular, apex rounded; apical lobe similar to middle lobe but smaller. Interocular width 4.5 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow rugose band, band reduced nearly to basal bead at middle. Disc aciculate, sparsely punctate, punctures small, deep. Sides in basal ⅔ as disc except for a few moderate, very shallow punctures grading to rugosity at anterior third. Anterior third rugose. *Horns:* Anterior short, conical, stout, apex minutely emarginate, anterior face with a faint apical sulcus. Posterior horns are low, rounded, pyramidal bosses; in lateral view anterior edge slopes forward and downward and dorsal edge is subhorizontal; in dorsal view horns are subparallel, bases joined across disc in an arc. *Elytra:* Sutural stria very weakly impressed, weakly crenulate. Disc aciculate, sparsely punctate, punctures small, shallow; lateral half of disc with 3 very feebly impressed, incomplete striae, striae minutely rugulose within. Sides weakly wrinkled behind humerus, otherwise as disc. Apex densely punctate, punctures small to moderately large. *Pygidium:* Convex in lateral view. Disc aciculate, very finely subgranulate, sparsely punctate, punctures small to moderately large, shallow. *Genitalia:* Figs. 108–109.

Female.—Length 30.5–32.5 mm; width across humerus 15.0–15.8 mm. As male except in the following respects: *Pronotum:* Sides posterolateral of fovea with a slightly depressed, rounded patch of moderately dense punctures; punctures moderate to large, shallow, and joined to anterior rugosity of pronotum; margin with a band of sparse, moderate to large, shallow punctures. Fovea shallow, longitudinal, oblong-ovate. Tubercle very low, rounded, nearly effaced. *Pygidium:* In lateral view basal half weakly convex, apical half weakly concave. Lateral depressions shallow.

Biology.—Unknown.

Distribution.—Mexico. Considering the fair amount of collecting conducted in Mexico, it might be reasonable to assume a very restricted range (or extinction?) for *S. adolescens;* this might help to account for the lack of additional specimens taken during the past 70 years of collecting.

Locality Records.—3 specimens examined (1 male, 2 females). Specimens deposited at ZMHU.

MEXICO (3).—No other data (types).

Remarks.—The key characters and the male genitalia should separate this species from all others. Variation in characters undoubtedly occurs as it does in all other species in the genus,

but it cannot be described here because of the lack of additional specimens.

Strategus aenobarbus (Fabr.)
(Figs. 1, 12–14, 110–111)

Scarabaeus aenobarbus Fabr., 1775: 10. [Holotype male at Glasgow University, Glasgow, Scotland. Type locality: America, as originally given by Fabricius, but here restricted to Dominican Republic.]

Scarabaeus eurytus Fabr., 1775: 7. [Holotype male at Glasgow University, Glasgow, Scotland. Type locality: America, as originally given by Fabricius, but here restricted to Dominican Republic.]

Scarabaeus aenoburbns Fabr., 1787: 6. [Misprint. Redescription of *S. aenobarbus*.]

Scarabaeus eurytus Fabr., 1787: 5. [Redescription of *S. eurytus*.]

Scarabaeus fossula Beauvois, 1819: 210. [Types unknown to me, possibly lost. Type locality: Santo Domingo, Dominican Republic.] **New synonymy.**

Strategus laterispinus Chapin, 1932b: 454. [Holotype male at AMNH. Also one male and four female paratypes at AMNH; two male and five female paratypes at USNM. Type locality: Manville, Haiti.]

Male.—Length 28.8–36.0 mm; width across humerus 13.5–17.2 mm. Color piceous, dull, not shining. *Head:* Front coarsely rugo-punctate. Clypeus with apex truncate, occasionally very feebly emarginate, slightly reflexed; surface rugo-punctate. Tubercles conical, transverse, very small. Mandibles small, mostly hidden beneath clypeal fringe; basal lobe small, rounded; middle lobe triangular, apex rounded; apical lobe similar to middle lobe but smaller. Interocular width 2.33–2.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow to obsolete rugo-punctate band, frequently replaced by sparse punctures laterally. Disc aciculate, very finely granulate, sparsely punctate; punctures small and minute mixed, shallow. Sides similar to disc, lateral margin frequently with a narrow, punctate to rugo-punctate band (particularly in minors). Anterior third of pronotum as disc in majors varying to increasingly rugo-punctate to feebly rugose in less-developed individuals. *Horns:* Majors (Figs. 12–13) with anterior long, stout, parallel sided; apex triangularly notched; dorsal surface with a weak, longitudinal, median carina, and with a similar carina on each lateral margin. Posterior horns are strongly developed, laterally compressed pyramidal bosses; in lateral view anterior edge vertical, dorsal edge slopes forward and slightly downward; in dorsal view horns subparallel, bases joined across disc in an arc, arc slightly produced at middle. Minors (Fig. 14) with anterior tuberculate; tubercle conical, moderate to large; apex weakly emarginate to truncate. Posterior horns reduced to low, rounded bosses; bases joined across disc in an arc. *Elytra:* Sutural stria impressed, crenulate. Disc finely granulate, sparsely punctate; punctures small and minute mixed, shallow; lateral ⅔ of disc with 5–7 regular to irregular rows of ocellate-umbilicate punctures; punctures small to moderately large, shallow. Sides similar to disc, rows of punctures usually confused. Apex moderately densely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc finely granulate, sparsely punctate in majors, moderately densely punctate in minors; punctures small, shallow. *Genitalia:* Figs. 110–111.

Female.—Length 32.0–38.0 mm; width across humerus 14.5–17.6 mm. As male except in the following respects: *Head:* Mandibles slightly smaller, especially middle lobe. Interocular width 2.66–4.0 transverse eye diameters. *Pronotum:* Sides just postero-lateral of fovea usually with a slightly depressed, rounded patch of simple to cresent-shaped punctures; punctures small to moderately large, shallow. Anterior third rugose. Fovea shallow. Tubercle subconical, very low, transverse. *Pygidium:* Strongly protuberant at middle, overhanging apical margin in lateral view. Disc densely rugo-punctate to rugose. Lateral emargination deep, rugose.

Biology.—Unknown.

Distribution.—Hispaniola, Navassa Island.

Locality Records (Fig. 1).—47 specimens examined (19 males, 28 females). Specimens

were seen from the following collections: AMNH, BMNH, CASC, TAMU, USNM.

DOMINICAN REPUBLIC (36).—DISTRITO NACIONAL (6): Santo Domingo; LA ALTAGRACIA (5): La Romana; LA VEGA (4): Constanza, Jarabacoa; PERAVIA (1): no data; PUERTO PLATA (1): Puerto Plata; SAMANA (6): Sánchez; SAN CRISTÓBAL (8): San Cristóbal; SANTIAGO (2): Los Hidalgos, Santiago; No data (3). January (2), February (1), March (1), May (5), June (6), July (2), August (1), September (2), November (1), December (6).

HAITI (10).—OUEST (7): Kenscoff, Manville, Petionville, Port-au-Prince; No data (3). February (2), September (3), November (2).

NAVASSA ISLAND (1).—No data (1).

Remarks.—Arrow (1937a), as apparent first revisor, established that *S. aenobarbus* should take precedence over *S. eurytus* even though *S. eurytus* had page priority. Staig (1931) provided an accurate description of the types of *S. aenobarbus* and *S. eurytus* but was incorrect in stating that *S. aenobarbus* was a junior synonym of *Strategus titanus* (Fabr.). *S. titanus* is a junior synonym of the Jamaican *S. simson* (L.), and the illustration and description in Staig indicate that the type of *S. aenobarbus* is definitely not *S. simson.*

Unfortunately, it was not possible to examine the type of *S. aenobarbus* and there remains some doubt as to whether the type and the present delineation of *S. aenobarbus* are the same. *S. aenobarbus* and *S. ajax* are identical except for the male genitalia, and it is conceivable (upon examination of the genitalia of the type) that the type of *S. aenobarbus* (here considered from Hispaniola) could be the same as our current concept of *S. ajax* (here considered Cuban). If this proves to be the case, the characterizations of the two species would have to be reversed. The type of *S. ajax* is probably lost (Besuchet, personal communication), and so the structure of the male genitalia of this type remains academic; it will here be considered different from the type of *S. aenobarbus.*

Arrow (1937a) erroneously synonymized *S. fossula* (Beauv.) with *S. simson* necessitating, in effect, that it be Jamaican which it was not. *S. fossula* is here removed from synonymy with *S. simson* and is placed in new synonymy under *S. aenobarbus* because it was described from the Dominican Republic.

The male genitalia will serve to distinguish this species from *S. ajax* which is otherwise morphologically identical. I have not been able to separate the females of the two species except by association with the males and by place of origin.

Strategus ajax (Olivier)

(Figs. 1, 15–17, 112–113)

Scarabaeus ajax Olivier, 1789: 27. [Type probably lost (Besuchet, personal communication). Type locality: unknown, but designated by Chapin (1932a) as Cuba.]

Male.—Length 22.0–43.8 mm; width across humerus 12.0–20.5 mm. Color piceous, dull, not shining. *Head:* Front rugo-punctate. Clypeus with apex truncate, occasionally very feebly emarginate, slightly reflexed; surface rugo-punctate. Tubercles conical, transverse, low. Mandibles with basal lobe small, rounded; middle lobe triangular, apex rounded; apical lobe similar to middle lobe but smaller. Interocular width 2.33–2.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow to obsolete rugo-punctate band; band frequently replaced by sparse punctures laterally. Disc aciculate, very finely granulate, sparsely punctate; punctures small and minute mixed, shallow. Sides similar to disc, lateral margin frequently with a narrow, punctate to rugo-punctate band (particularly in minors). Anterior third of pronotum as disc in majors varying to increasingly rugo-punctate to feebly rugose in less-developed individuals. *Horns:* Majors (Figs. 15–16) with anterior long, stout, parallel sided, apex triangularly notched; dorsal surface with a weak, longitudinal, median carina, and with a similar carina on each lateral margin. Posterior horns are strongly developed, laterally compressed, pyramidal bosses; in lateral view anterior edge vertical, dorsal edge slopes forward and slightly downward; in dorsal view horns subparallel, bases joined across disc in an arc; arc slightly

produced at middle. Minors (Fig. 17) with anterior conical, moderate to large, apex weakly emarginate to truncate. Posterior horns reduced to low, rounded bosses; bases joined across disc in an arc. *Elytra:* Sutural stria impressed, crenulate. Disc finely granulate, sparsely punctate, punctures small and minute mixed, shallow; lateral ⅔ of disc with 5–7 regular to irregular rows of ocellate-umbilicate punctures; punctures small to moderately large, shallow. Sides similar to disc, rows of punctures usually confused. Apex moderately densely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc finely granulate, sparsely punctate in majors, moderately densely punctate in minors; punctures small, shallow. *Genitalia:* Figs. 112–113.

Female.—Length 28.3–40.4 mm; width across humerus 12.1–18.9 mm. As male except in the following respects: *Head:* Mandibles slightly smaller, especially middle lobe. *Pronotum:* Sides just postero-lateral of fovea usually with a slightly depressed, rounded patch of simple to crescent-shaped punctures; punctures small to moderately large, shallow. Anterior third rugose. Fovea shallow. Tubercle subconical, very low, transverse. *Pygidium:* Strongly protuberant at middle, overhanging apical margin in lateral view. Disc densely rugo-punctate to rugose. Lateral emargination deep, rugose.

Biology.—A detailed life history for *S. ajax* has not been established. It is a common species, apparently breeding in certain species of *Agave* (Chapin, 1932a), and has occasionally been associated with *Agave fourcroydes* Lem. (Chapin, 1932b.). *S. ajax* attacks the roots and seed pieces of sugar cane, *Saccharum officinarum* (L.), but is not considered a major pest except in sporadic instances (Valdes, 1951). *Tiphia argentipes* Cresson (Hymenoptera: Tiphiidae) and *Campsomeris trifasciata* (Fabr.) (Hymenoptera: Scoliidae) are two known natural enemies (Valdes, 1951). Label data indicate specimens have been taken at light, from the stomach of a whip-poor-will, and destroying agave.

Distribution.—Cuba.

Locality Records (Fig. 1).—143 specimens examined (58 males, 85 females). Specimens were seen from the following collections: AMNH, BMNH, CASC, CNCI, FMNH, HAHC, MCZC, USNM.

CUBA (140).—CAMAGUEY (22): Baragúa, Jaronú, Nuevitas; HABAÑA (18): Habaña City, La Alianza, Santiago de las Vegas, Vibora; LAS VILLAS (40): Cayamas, Cienfuegos, Coralillo, Santa Clara, Soledad; ORIENTE (33): Baracoa, Guantanamo, Santiago de Cuba; PINAR DEL RIO (18): Guane, Pinar del Rio City, San Vicente; No data (9). April (1), May (24), June (39), July (29), August (5), September (7), October (8), November (5), December (10).

Remarks.—As noted in the remarks for *S. aenobarbus,* the genitalia will serve to separate the males of *S. aenobarbus* from *S. ajax* although the females remain morphologically inseparable. The females of these two species may be separated by association with the males or by place of origin.

It is not felt at this time that a neotype should be designated since the genitalic structure of the type of *S. aenobarbus* has not been ascertained (see remarks for *S. aenobarbus*).

Strategus aloeus (L.)

(Frontispiece, Figs. 5, 8, 18–24, 114–117)

Scarabaeus aloeus L., 1758: 345. [Holotype male at Zoologiska Museet Uppsala Universitet, Uppsala, Sweden (see Landin, 1956). Type locality: originally given as North America.]

Geotrupes semiramis Fabr., 1801: 12. [Holotype male at Universitetets Zoologiske Museum, Copenhagen, Denmark. Type locality: Essequibo, Guyana.] **New synonymy.**

Scarabaeus aesalus Laporte, 1840: 112. [Types unknown to me, possibly lost. Type locality: Cayenne, French Guiana.]

Strategus julianus Burmeister, 1847: 133. [Lectotype male and lectoallotype female designated by Endrödi (1973a); at Martin Luther Universität, Halle, German Democratic Republic. Type locality: Mexico.] **New synonymy.**

Strategus piosomus Kolbe, 1902: 24. [Holotype male at ZUMHU. Type locality: unknown.] **New synonymy.**

Strategus roosevelti Casey, 1915: 241. [Lec-

totype male, labeled "Tex," "Casey bequest 1923," "Type USNM 48633," and "*roosevelti Csy.*," here designated; at USNM (Casey collection) with my lectotype label. Lectoallotype female, labeled as male except for type label which reads "*roosevelti*–2, Paratype USNM 48633," here designated; at USNM with my lectoallotype label. Also one female paralectotype at USNM. Type locality: Texas, United States.] **New synonymy.**

Strategus frontalis Casey, 1915: 243. [Holotype male at USNM. Type locality: San Pedro Sula, Honduras.] **New synonymy.**

Strategus tarsalis Casey, 1915: 243. [Holotype female at USNM. Type locality: Texas, United States.] **New synonymy.**

Strategus gaillardi Casey, 1915: 244. [Holotype female at USNM. Type locality: Culebra, Panama.] **New synonymy.**

Male.—Length 31.0–60.9 mm; width across humerus 13.8–30.0 mm. Color piceous to black, shining. *Head:* Front densely punctate to rugose behind tubercles; punctures large, shallow, usually confluent; medially front varies from impunctate to variably punctate (punctures small to large) to rugose; setigerous above eye in unworn specimens. Clypeus with apex variable; specimens north of Panama usually with apex subtruncate and very feebly to moderately broadly emarginate, rarely with a small triangular notch at base of emargination; specimens south of Panama usually with apex variably emarginate as northern form and with notch at base of emargination small, triangular, and shallow (very rarely absent) to large, deep, and U-shaped; apex moderately to strongly reflexed; surface aciculate, densely punctate (punctures moderate in size) to rugo-punctate to rugose. Tubercles in specimens north of Panama conical, transverse, low to moderate, distinctly separated to distinctly but weakly joined by a low, transverse carina; tubercles in specimens south of Panama as above but usually stronger and distinctly separated. Mandibles with basal lobe small, rounded to prominently rounded; middle lobe subtriangular, large to very large, apex broadly rounded; apical lobe small, rounded to subtriangular. Interocular width 2.0–2.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide to very wide rugose band, band reduced at middle almost to basal bead. Disc aciculate, sparsely punctate; punctures small, deep; occasionally with minute, sparse secondary punctures. Sides aciculate, a little more densely punctate; punctures small to large; lateral margin frequently with a moderately wide rugo-punctate to rugose band. Base of posterior horns usually with a small, slightly depressed, densely punctate to rugose area; occasionally a band of punctures or rugosity extends from base of posterior horns obliquely to posterior angle. Anterior ⅓ to ½ rugose. Fovea deep, divided longitudinally down middle by a broad, low, rounded carina extending posteriorly from base of anterior horn; anterior angles and fovea either side of median ridge feebly to strongly rugo-punctate to rugose, rarely without sculpturing. *Horns:* Majors (Figs. 18–22) with anterior moderate in length, very stout, attenuate, curving forward and upward; apex subtruncate to emarginate; emargination feeble and shallow to distinct and V-shaped; dorsal surface nearly flat to rounded, occasionally weakly subcarinate longitudinally down middle. Posterior horns short to moderately long, very strongly laterally compressed, variably attenuate, apex acutely rounded to broadly and obliquely truncate with 1–3 weak lobes; in lateral view horns project forward and upward at about 25–65° from plane of disc; in dorsal view horns subparallel to curving slightly toward one another; bases joined across disc in an arc; arc slightly produced at middle. Minors (Figs. 23–24) with anterior similar to that of majors except short in length, apex truncate, and dorsal surface rounded, not carinate. Posterior horns reduced to very short, rounded, laterally compressed horns or low, rounded bosses. *Elytra:* Sutural stria strongly impressed, weakly to strongly crenulate. Disc aciculate, sparsely punctate; punctures small (rarely moderate in size), shallow, and weakly ocellate-umbilicate in specimens from south of Panama; 1–3 feebly impressed, incomplete stria on lateral half of disc. Sides aciculate, wrinkled behind humerus, sparsely punctate, punctures small to moderate, shallow. Apex moderately punctate, punctures small, shallow. *Pygidium:* Weakly convex in lateral view. Specimens north of Panama with disc

sparsely punctate; punctures minute, very shallow; some specimens from Yucatan, Mexico, and many from south of Panama also with a few moderate, very shallow, setigerous punctures at apex. *Genitalia:* Figs. 114–117. Specimens north of Panama (Figs. 114–115) usually with parameres subslender, attenuate apically, widest just before middle; specimens south of Panama (Figs. 116–117) occasionally as above but more frequently with parameres very robust, only slightly attenuate apically.

Female.—Length 31.5–55.8 mm; width across humerus 16.0–26.0 mm. As male except in the following respects: *Head:* Front punctate (punctures small to large mixed) to rugo-punctate to rugose. Clypeus with apex narrowly to broadly subtruncate or rounded, feebly to moderately reflexed; surface rugose. Mandibles similar to those of male but smaller, especially middle lobe. *Pronotum:* Sides rugo-punctate to rugose. Anterior half rugose. Fovea moderately deep. Tubercle conical, moderate to large, transverse, apex usually very feebly emarginate (rounded in worn individuals). *Elytra:* Sides occasionally with sparse, feeble, ocellate-umbilicate punctures. *Pygidium:* In lateral view basal half convex, apical half concave. In specimens north of Panama disc usually sparsely to moderately punctate; punctures small to moderate, shallow, punctuation occasionally very reduced; apical margin with a broad rugo-punctate to rugose band; apex with a few setigerous punctures; lateral emargination very shallow. Specimens south of Panama as above, but discal punctures usually moderately large and confluent; apical ⅓ to ½ completely and densely setigerously punctate.

Biology.—Duges (1876, 1886) was the first to describe the larva and pupa of *S. aloeus,* and Ritcher (1944, 1966) has provided the most recent and accurate description of the larva. Eggs are usually deposited in dead or rotten wood where the larvae develop. Larvae have been found under old logs and boards in Louisiana (Schufeldt, 1884), in a rotten ash tree (*Fraxinus* sp.) in Texas (Ritcher, 1966), from the trunk of a live oak tree (*Quercus* sp.) in Mexico (Duges, 1876, 1886), and in sawdust piles at sawmills and beneath the trunks of felled coconut palms (*Cocos nucifera* L.) and *Erythrina glauca* Willd. in Surinam (Van Dinther, 1956). Bodkin (1919) reported small colonies of larvae in decaying stumps in Guyana, and I have found numerous larvae in a rotten log while collecting in Peru. Clusters of larvae are a result of a fortuitous oviposition site and do not indicate a sub-social ethology as is found in many passalids. Van Dinther also observed in Surinam that larvae were never detected near the roots or stem of a living coconut palmw hereas, on the other hand, Costa Lima (1953) noted that in Brazil larvae attack the roots and lower part of the stipe of new palms. Larvae have also been taken from mango roots (*Mangifera indica* L.) (Bodkin, 1919). Under most circumstances larvae probably feed exclusively on decayed wood although they will apparently feed on root material when necessary. Pupation occurs in the food substrate where an oval pupal chamber is formed.

Hurpin and Mariau (1966) conducted laboratory rearing experiments using 219 larvae and 281 adults from Colombia. The larvae were fed on a mixture of poplar wood and dried cow manure while the adults were maintained best on banana and orange. In the laboratory adult males lived up to five months and adult females up to six months. The maximum number of eggs laid by a single female was 42; eggs were deposited over a period of 1–3 months with several eggs laid weekly. Duration (maximum?) of each stage was as follows: egg, three weeks; first instar, two weeks; second instar, three weeks; third instar, seven months; pre-pupa, two weeks; pupa, six weeks; adult, six months. This provided a total life span of 17 months. Other lengths reported for pupation are 31 days (Van Dinther, 1956) and 43 days (Duges, 1886). Adults can usually be found year round where the climate permits.

Adult beetles have been found feeding on roots of date palms (*Phoenix dactyliferas* L.) in Arizona (Cockerell, 1906); wax palms (prob. *Copernicia cerifera* Mart.) in Brazil (Goncalves, 1946); young oil palms (*Elaeis guineensis* Jacq.) in Colombia (Vayssiere, 1965); *Furcraea cabuya* Trel. and the leaves of *Agave picta* Salm-Dyck in Costa Rica (Nevermann, 1933); and coconut palms (*Cocos nucifera* L.) in Guyana (Bodkin, 1919), Surinam (Van Dinther, 1956), Mexico (Kolbe, 1906), and Venezuela and Brazil (Lever,

1969). Label data indicated feeding on oil palms in Colombia and Ecuador, coconut palms in Costa Rica and Venezuela, sugar cane in Colombia, and in rotten wood in Texas, Mexico, and Peru.

In Van Dinther's (1956) study, feeding damage was restricted to young coconut palms up to four years of age. Reasons were not given as to why older palms were not attacked. Adult beetles burrowed down as far as 40 cm near the base of the palm to a position under the stem base. Tunneling then proceeded upward into the heart of the wood where a 3–5 cm wide shaft was formed. Trees so infested wilted and eventually died. Usually one beetle was found per tree, but as many as four of both sexes have been found in a single palm. However, *Strategus aloeus* is rarely of economic significance to palm plantations.

These large beetles apparently have few natural enemies. The larvae have occasionally been eaten by aboriginal indians in Guyana (Bodkin, 1919) and undoubtedly in other tropical regions as well. The larvae are also a common intermediate host for *Macracanthorhynchus hirudinaceus* (Pallas) (Archiacanthocephala: Oligacanthorhynchidae) in Brazil (Costa Lima, 1953) and possibly in Louisiana (Manter, 1928). The larval host dies after several weeks of infection by these parasites. Adults have been observed trapped in large spider webs in Venezuela on two occasions (Beebe, 1944), and all stages in the life cycle are probably susceptible to various fungi and bacteria.

Beebe (1944) has demonstrated in Venezuela that the males will fight with one another, presumably for females, with the advent of the rainy season or by artifically induced "rain." He stated that the rains "unlock the reproductive reactions" of these insects. While reproductive activity is probably initiated by the rains, Beebe's data are insufficient to warrant describing the males as fighting "for" the female, especially when other studies have shown this not to be true (see Arrow, 1951).

Distribution.—*Strategus aloeus* is the most widespread species in the genus, occurring from the southern United States through Central America to central Brazil and Bolivia.

Locality Records (Figs. 5, 8).—2,203 specimens examined (751 males, 1,452 females). Specimens were seen from the following collections: AHCC, AMNH, BCRC, BMNH, CASC, CNCI, DEUN, FMNH, HAHC, INHS, JDG, KSUC, LACM, MCZC, MHNCM, OSUC, OSUO, PMNH, RLWE, SBMN, SEMC, TAMU, UC, UCMC, UMMZ, USNM, USP, UWEM, UZM, ZMHU.

BELIZE (5).—STANN CREEK (5): Placentia February (1), March (4).

BOLIVIA (12).—BENI (10): Guayaramerin, Reyes, Rurrenbaque (Rio Beni), San Joaquin; COCHABOMBA (1): Chapare; No data (1). January (2), April (1), May (5), June (2), November (1), December (1).

BRAZIL (38).—AMAZONAS (7): Manaus, Porto Santana, Porto Velho de San Antonio, Taracuá, Tefé; BAHIA (2): No data; CEARÁ (2): Fortaleza, Villa Hazaré; GOIAS (1): Magalhaes; GUANABARA (1): Serra da Carioca; MATO GROSSO (1): Amazon region; PARÁ (16): Belém, Maves, Obidos, Oriximina, Santarem; PERNAMBUCO (1); Recife; No data (6). January (1), February (2), March (1), April (1), May (1), July (2), August (9), September (1), November (2), December (1).

COLOMBIA (143).—AMAZONAS (11): Leticia; ANTIOQUIA (1): Antoquia; ATLÁNTICO (2): Barranquilla; CHOCÓ (2): Frigana; CUNDINAMARCA (3): Bogotá, Fusa(gasuga?); MAGDALENA (28): Aracataca, Medialuna, Parque Tayrona (21 mi. E. Santa Marta), Rio Frio, Sevilla; META (1): Cano Grande near Villavicencio; NARINO (1): Tumaco; SANTANDER (3): Rio Opon, Velez; VALLE DEL CAUCA (11): Anchicaya Dam (70 mi. E. Buenaventura), Cali, Palmira, Rio Anchicaya between Buenaventura and Cali; No data (80). February (12), March (3), April (7), May (16), June (4), July (3), August (2), October (1), November (1), December (2).

COSTA RICA (93).—ALAJUELA (1): Alajuela; CARTAGO (4): Irazú, Tres Rios Turrialba; GUANACASTE (3): Finca Jimenez (near Taboga), Liberia, Tenorio; HEREDIA (1): no data; LIMON (15): Guápiles, Hamburg Farm (Reventazón), Las Mercedes, Port Limón, Reventazon; PUNTARENAS (23): Bocca de Barranca, Esquinas near Golfito, Monteverde de Puntarenas, Osa Productos Forest, 1.8 mi. W. Rincon; SAN JOSÉ (29): San

José; No data (17). February (9), March (5), April (7), May (18), June (13), July (1), August (11), September (22), October (2), December (1).

ECUADOR (6).—GUAYAS (2): Balzar, Naranjal; PACHINCHA (2): Santo Domingo de los Colorados; No data (2). March (1), August (1), December(2).

EL SALVADOR (21).—LIBERTAD (1): 20 mi. E. La Libertad; SAN SALVADOR (16): Lake Illopango, San Salvador, Santo Tomás; SONSONATE (1): Sonsonate; No data (3). March (1), May (14), June (3), Augst (1).

FRENCH GUIANA (11).—ININI (7): Maroni River, Saül (Gruner, 1971); GUYAN (4): Cayenne, Crique Gregoíre (Fl. Sinnamary) (Gruner, 1971). October and November (9).

GUATAMALA (36).—ALTA VERAPAZ (5): Baleu, Cobán, Finca San Juan, Senahú; CHIMALTENANGO (2): S. P. Yepocapa; CHIQUIMULA (1): Chiquimula; GUATAMALA (1): Guatamala City; IZABAL (2): Puerto Barrios; PETÉN (8): Sabaneta, Tikal; SASATEPÉQUEZ (3): Acatenango, Santa Maria de Jesus; SAN MARCO (6): Ayutla, Puente Talisman; SOLOLA (1): Panajachel; SUCHITEPÉQUEZ (3): Finca Moca, Cuyotenango; ZACAPA (1): Zacapa; No data (3). February (1), March (4), April (3), May (5), June (9), July (4), August (2), November (1).

GUYANA (13).—DEMERARA (3): Georgetown; ESSEQUIBO (4): Essequibo, Katabo (Bartica), Penal Settlement (Bartica District); No data (6). December (1).

HONDURAS (10).—ATLÁNTIDA (1): Tela; CORTÉS (1): Puerto Cortés; FRANCISCO MORAZAN (5): Esc. Ag. Pan. (Zamorana), Teguicigalpa; YORO (3): El Progreso, 12 km. W. Olanchito.

MEXICO (842).—AGUASCALIENTES (6): Aguascalientes; CAMPECHE (3): Campeche, Matamoros; CHIAPAS (75): Arriga, 7.2 mi. SE. Chiapa de Corzo, 3 mi. SE. Comitan, 5 mi. SW. El Bosque, El Rincon, 25 mi. N. Huixtla, Lagos des Colores (Rt. 17), 10 mi. S. Malpaso, Ocosingo, Ocozocoautla, 12 mi. N. Ocozocoautla, 9 mi. N. Ocozocoautla, Palenque, 5 mi. NW. Pijijiapan, Puerto Arista, San Cristóbal, 6 mi. E. San Cristóbal, 8 mi. NE. San Cristóbal, 2 mi. S. Simojovel, Tonola, Tres Picos (Hwy. 200), Tuxtla Gutierrez, Yerba Buena (20 mi. N. Bochil), 25 mi. E. Zanatepec, Jct. Rts. 190 & 195; CHIHUAHUA (16): Buena Vista, Camargo, 20 mi. SW. Camargo, Catarinas, 10 mi. S. Las Delicas, Primavera, San Francisco del Oro, Santa Barbara; COAHUILA (10): Muralla, Parras de la Fuente, Ramos Arizpe; COLIMA (1): Manzanillo; DISTRITO FEDERAL (8): Escandón, Jacubaua, Mexico City, Nuevo Bosque Chapultepec, Tocubaya; DURANGO (19): 7 mi. SW. Cuencamé, Durango, San Juan del Rio, San Pedro de Guanace, Tlahualilo; GUANAJUATO (2): 22 mi. E. Penjamo, San Miguel de Allende; GUERRERO (3): Iguala, Irapuato, Rio Balsas; HIDALGO (5): Guerrero Mill., 22 mi. NE. Jacala, Pachuca; JALISCO (63): Ajijic, Guadalajara; MEXICO (1): Chapingo; MICHOACAN (6): Morelia, Patzcuaro, Playa Azul, Tancitaro, Tuxpan; MORELOS (10): Antiguo, Cuernavaca, Progresso; NAYARIT (14): 20 MI. SE. Ixtlan del Rio, Tepic, 24 mi. SE. Tepic; NUEVO LEON (99): Chipenque Mesa (Monterrey), Hacienda Vista Hermosa (Villa Santiago), Linares, 28 km. W. Linares, 28 km. NW. Linares, Monterrey, 5 mi. S. Monterrey, Rancho Presa, 17 km. N. Sabinas Hidalgo; OAXACA (50): 2.7 mi. NW. El Camaron, 11.6 mi. W. Jalapa del Marques, 22 mi. S. Jesús Carranza, 20 mi. S. Juchatenango, Juquila Mixes, 3 mi. E. La Ventosa, 8 mi. N. La Ventosa, Oaxaca, Ocotlán, Salina Cruz, Tehuantepec, 6 mi. W. Tehuantepec, 12 mi. W. Tehuantepec, Temascal, Tuxtepec; PUEBLA (15): 3 mi. W. Acatepec, Acatlán, Finca San Juan Apulco (near Zacapoa), 13 mi. N. Huauchinongo, Tezuitlan, 3 mi. E. Tezuitlan, 6 mi. W. Tezuitlan, Xicotepec de Juarez, Zacapoaxtla; QUINTANA ROO (2): Felipe Carrillo Puerto; SAN LUIS POTOSI (106): 18 mi. E. Ciudad Maiz, El Naranjo, El Salto, El Salto Falls, Palitla, 2 mi. SE. Pedro Montoya, Saltillo, 30 mi. SW. San Luis Potosi, Tamazunchale, 25 mi. N. Tamanzunchale, Valles, 36 km. W. Valles, 3 mi. W. Xilitla; SINALOA (30): Excuinapa, Los Mochis, Mazatlán, 5 mi. N. Mazatlán, 9 mi. N. Mazatlán, 4 mi. N. San Blas, 27 mi. E. Villa Unión.; SONORA (10): Alamos, 10 mi. NE Ciudad Obregon, Hermosillo, Navajoa, 30 mi. E. Ures on road to Moctezuma; TABASCO (6): Frontera, Ocotlán; TAMAULIPAS (48): Ciudad Mante, Ciudad Victoria, Gomez Farias (Rio Frio), Guemes, Hidalgo, Llera, Tampico; VERACRUZ (103): 1 mi. N. Antón Lizardo, Banderilla, Catemaco, 5 mi. E. Catemaco, Chicontepec,

Córdoba, Coyame (Lake Catemaco), Dos Amates, Jalapa, 5 mi. N. Huatusco, Montepio (8 mi. N. Sontecomapan), Orizaba, Palmo Sola, 4 mi. SW. Panúco, Puente Nacional (34 mi. E. Jalapa), San Andrés Tuxtla, Tierra Blanca; YUCATAN (61): Chichén Itzá, Pisté, Valladolid, Xcan; No data (50). March (2), April (8), May (123), June (253), July (185), August (16), September (34), October (9), December (1).

NICARAGUA (23).—GREAT CORN ISLAND (2); LEÓN (3): Momotombo; MANAGUA (12): Managua City; ZELAYA (1): Blue Fields; No data (5). January (3), June (11).

PANAMA (93).—CANAL ZONE (63): Ancon, Balboa, Barro Colorado Island, Fort Clayton, Gatun, Madden Dam, Margarita; CHIRIQUÍ (15): Boquete, David, El Valle de Nubes, El Volcan Chiriquí, Rovira; COCLÉ (2): Penonomé; COLON (6): Coconut Point; DARIÉN (1): Darién; HERRERA (1): Santa Maria (El Real); LOS SANTOS (2): Sabana; PANAMÁ (2): Panamá City; No data (1). January (15); February (9), March (14), April (6), May (14), June (5), July (2), September (2), November (2), December (7).

PERU (37).—HUÁNUCO (5): Tingo Maria; LORETO (26): Iquitos, Pucallpa, Yarina Cocha (Rio Ucayali); PIURA (2): Quiroz (Rio Paucartambo); No data (5). January (2), February (12), April (3), May (3), June (4), September (4), November (6).

SURINAM (7).—MAROWIJNE (1): Anapaike (Rio Lawa); SURINAME (6): Lelydorp Bauxite Mine, Paramaribo. January (1), November (2), December (1).

TRINIDAD (60).—MAYARO (2): Mayaro Beach; ST. GEORGE (15): Arima Valley, Las Cuevas Bay, Maraval, Morne Bleu, Port-of-Spain, St. Augustine; ST. PATRICK (34): Icacos; No data (9). January (34), February (3), March (3), April (4), May (4), June (4), November (1).

UNITED STATES (617).—ALABAMA (12): *Conecuh (2):* no data; *Macon (5):* Tuskegee; *Mobile (4):* Mobile; *No data (1).* ARIZONA (167): *Cochise (15):* Ash Canyon, Carr Canyon, Portal, Ramsey Canyon, San Bernadino Ranch, Tombstone; *Coconino (2):* Sedona; *Gila (14):* Globe, Winkelman; *Graham (5):* Gila Valley, Safford; *Maricopa (31):* Mesa City, Phoenix, Tempe; *Pima (27):* Baboquivari Mts., Continental, Madera Canyon, Santa Rita Mts., Tucson; *Pinal (1):* Superior; *Santa Cruz (55):* Douglas, Madera Canyon, Nogales, Patagonia, Tubac; *Yavapai (6):* Prescott, Red Rock Camp, Verde Hot Springs; *Insufficient or no data (11).* ARKANSAS (8): *Hempstead (6):* Hope; *Miller (2):* Texarkana. FLORIDA (1): *Escambia (1):* Pensacola. GEORGIA (3): *Chatham (1):* Savannah; *Jeff Davis (1):* Hazelhorst; *No data (1):* LOUISIANA (144): *Acadia (1):* Crowley; *Caddo (5):* Shreveport; *Jefferson (7):* no data; *Lincoln (6):* Ruston; *Madison (2):* Mound, Tallulah; *Natchitoches (1):* Natchitoches; *Orleans (11):* New Orleans; *Ouachita (1):* Monroe; *Rapides (88):* Alexandria; *St. Landry (1):* Opelousas; *St. Martin (1):* Belle River; *St. Mary (1):* Morgan City; *St. Tammany (8):* Covington; *Vermillion (11):* Gueydan. MISSISSIPPI (29): *Adams (3):* Natchez; *Forest (1):* Hattiesburg; *Grenada (4):* Grenada; *Harrison (17):* Biloxi, Gulfport, Long Beach; *Yazoo (3):* no data; *No data (1)* . NEW MEXICO (1): *Dona Ana (1):* Mesilla Pk.; *Grant:* no data (Fall and Cockerell, 1907). TEXAS (249): *Bastrop (1):* Bastrop; *Bexar (6):* San Antonio; *Brazoria (2):* Freeport; *Brazos (9):* Bryan, College Station; *Brewster (16):* Alpine, Boquillas Basin, Chisos Mts. Basin (Big Bend Nat'l. Park), Glenn Spring, 5 mi. N. Glenn Spring, Juniper Canyon (Chisos Mts.), Panther Junction (Big Bend Nat'l. Park), Rio Grand Camp (Big Bend Nat'l. Park); *Brown (1):* Brownwood; *Burleson (4):* Clay, Somerville; *Calhoun (2):* Ft. Lavaca; *Cameron (33):* Brownsville, Harlingen; *Colorado (1):* Columbus; *Culberson (1):* Van Horn; *Dallas (12):* Dallas; *El Paso (2):* El Paso; *Gillespie (1):* no data; *Hardin (1):* Beaumont; *Harris (4):* Houston, Seabrook; *Hidalgo (28):* Donna, Edinburgh, Mission, San Juan; *Jeff Davis (13):* Davis Mts., Ft. Davis, Valentine; *Jefferson (1):* Port Arthur; *Kerr (4):* Kerrville; *Kleburg (2):* Kingsville; *La Salle (3):* Fowlerton; *Mata Gorda (1):* Palacios; *Maverick (3):* Eagle Pass; *McLennon (1):* Waco; *Menard (1):* Menard; *Nacodoches (1):* Nacodoches; *Polk (5):* Livingston; *San Jacinto (3):* Cold Spring; *Travis (10):* Austin; *Uvalde (7):* Sabinal, Uvalde; *Val Verde (50):* Del Rio, Lake Walker, *Victoria (9):* Victoria; *Wharton (3):* El Campo; *Webb (2):* Laredo; *Insufficient or no data (39).* January (2), March (4), April (6), May (164), June (129), July

(137), August (96), September (23), October (4), November (4).

VENEZUELA (103).—ARAGUAY (6): Maracay, Rancho Grande; BOLÍVAR (28): Moitaco, Suapure (Caura River); CARABOBO (7): San Esteban (near Puerto Cabello), Zapateral; DISTRITO FEDERAL (11): Caracas, El Limón, La Guaira; FALCON (6): Boca de Orda, 60 mi. SE. Maracaibo; MIRANDA (1): Rio Chico; MONAGAS (22): Caripito; SUCRE (2): Puerto Hierro; TRUJILLO (1): Valera; YARACUY (1): Urama; ZULIA (4): Kasmera (12.5 mi. SW. Machique), Los Encentados (Rio Onia E. of Zulia); No data (14). February (3), March (7), April (21), May (12), June (5), July (3), August (1), October (15), November (8), December (2).

Remarks.—The males of *S. aloeus* can be separated from all other species by the characteristic shape of the genitalia; they may be easily confused with other species if external features only are used in identification. The key characters will serve adequately to separate the females from all other species.

Strategus aloeus is the most widespread, abundant, and morphologically variable species in the genus. Until this revision, *S. aloeus* and *S. julianus* were considered distinct species, *S. aloeus* occurring primarily in northern South America and *S. julianus* occurring from the southern United States to Panama. All previous authors have overlooked the use of the male genitalia as a taxonomic character (except Saylor, 1946) and have not examined as many specimens as was done here (2,203 examples). Consequently, there was understandable confusion as to the separation of these two supposed species (see Bates, 1886–1890; Burmeister, 1847; Casey, 1915; Endrödi, 1959; Kolbe, 1906). An analysis of all the taxonomic characters used in this study revealed that *S. julianus* was synonymous with *S. aloeus,* and so *S. julianus* and all its junior synonyms fall into new synonymy under *S. aloeus.*

Laporte (1840) described *S. aesalus* as new although he may not have meant to do so as he cites Fabricius (1801) as a previous (name?) author. Fabricius described *Aesalus* as a new genus in the Lucanidae but not as a species of *Scarabaeus*. In addition, the Fabrician reference given by Laporte is apparently confused and is not traceable. Arrow (1937a) was also perplexed by Laporte's *S. aesalus* for the same reasons. The description of *S. aesalus* is only very general, but the sizes indicated by Laporte suggest that this species should fall into synonymy with *S. aloeus* and not with *S. surinamensis surinamensis* which occurs sympatrically at the type locality.

S. semiramis (Fabr.) and *S. piosomus* Kolbe are entered in new synonomy because the types are conspecific with *S. aloeus.*

A clinal mode in character states is to be seen in a north-south direction. Southern specimens are usually progressively larger, darker, with a deeper clypeal excision, stouter genitalia in the males (Figs. 114–117), and with increased pygidial hairiness in the females. The clinal variation is gradual and not stepped, thus eliminating for the present the possibility of subspecies designations. It should be noted that "northern-like" individuals (smaller in size, lighter in color, etc.) occur occasionally in South America, and "southern-like" specimens (larger in size, darker in color, etc.) occur occasionally in Central America and Mexico. The Isthmus of Panama appears to be a convenient and fairly accurate locale by which to separate the northern and southern populations, but it is by no means a barrier, and mixing between the two populations probably occurs freely.

Schaeffer (1915) described a new variety of *S. julianus* from Arizona (var. *arizonicus*) in which the males have the posterior pronotal horns pointed (Fig. 20) instead of broadly truncate; this character state is part of the normal variation within the species and is to be seen in other localities as well, i. e., Mexico, Central and South America. I have seen a number of specimens from NW. Peru which are proportionately somewhat longer in body length than is considered normal and also a series from eastern Yucatan in Mexico which are consistently darker (black) and more highly polished. Individuals from Venezuela and northern Colombia are usually consistently larger than in any other area. It is not known whether these local variants, or perhaps even the entire cline, are a result of ecophenotypy or whether there are some actual differences in gene pools.

Strategus anachoreta Burmeister
(Figs. 2, 25–28, 118–119)

Strategus anachoreta Burmeister, 1847: 134. [Lectotype male and lectoallotype female designated by Endrödi (1973a); these and one male paralectotype at Martin Luther Universität, Halle, German Democratic Republic. Type locality: Cuba.]

Male.—Length 35.0–50.0 mm; width across humerus 18.0–25.0 mm. Color castaneous to piceous, shining. *Head:* Front finely rugose; setigerous above eye in unworn specimens. Clypeus with apex broadly truncate, slightly reflexed; surface finely rugo-punctate. Tubercles conical, low, occasionally transverse and weakly connected. Mandibles with basal lobe small, prominently rounded; middle lobe subtriangular, large, apex rounded; apical lobe similar to middle lobe but smaller. Interocular width 2.5–3.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide, rugose band; band reduced medially almost to basal bead. Disc aciculate, punctate; punctures sparse, small, shallow. Sides similar to disc plus the following: lateral margin with or without a narrow rugo-punctate band, majors rugose to rugo-punctate from base of posterior horns to anterior angle and into fovea; minors completely rugose in anterior half of pronotum. Fovea deep, divided in half by a low, broadly rounded, longitudinal carina extending posteriorly from base of anterior horn. *Horns:* Majors (Figs. 25–26) with anterior moderate to long, stout, attenuate, curving forward and upward; apex narrowly rounded, dorsal surface rounded to nearly flat, occasionally with a faint, longitudinal carina down middle. Posterior horns moderate to long, stout, laterally compressed, attenuate, apex rounded; in lateral view horns project forward and upward at 45–65° from plane of disc; in dorsal view horns parallel, occasionally with apices turned slightly inwards, bases joined across disc in an arc. Minors (Figs. 27–28) with anterior short, stout, erect, attenuate, apex narrowly rounded. Posterior horns reduced to low, rounded bosses; in lateral view dorsal surface subhorizontal to higher at apex, anterior surface vertical to sloping downward and slightly forward; in dorsal view horns subparallel, bases joined across disc in a shallow arc. *Elytra:* Sutural stria impressed, weakly to strongly crenulate. Disc aciculate, sparsely punctate, punctures small and minute mixed, shallow; 5–7 rows of ocellate-umbilicate punctures on lateral half, punctures large, shallow, rows 3 and 6–7 confused. Sides as disc except with 5 similar rows of ocellate-umbilicate punctures, row 3 confused. Apex densely punctate; punctures small to moderately large, shallow. *Pygidium:* Convex in lateral view, apical ¼ frequently concave. Disc very finely granulate, moderately densely punctate, punctures small and minute mixed, occasionally moderate in size, shallow. Apical margin with a wide, rugose band; rugosity usually spreading to disc in minors; occasionally a short, medio-apical row of setigerous punctures in unworn specimens. *Genitalia:* Figs. 118–119.

Female.—Length 32.7–42.8 mm; width across humerus 14.9–24.0 mm. As male except in the following respects: *Head:* Front rugose to rugo-punctate. Clypeus with apex usually not so broadly truncate as male; surface rugose to rugo-punctate. Mandibles similar but smaller, especially middle lobe which is nearly subequal with basal lobe. *Pronotum:* Sides just posterolateral of fovea usually with a slightly depressed, rounded patch of simple to crescent-shaped punctures, punctures small to moderately large, shallow. Anterior half rugose. Fovea shallow. Tubercle conical, transverse, very low. *Pygidium:* In lateral view basal half convex, apical half concave. Disc entirely rugose to rugo-punctate with very short, sparse setae in unworn specimens. Lateral emargination shallow.

Biology.—Little is known about the life history of *S. anachoreta.* Label data indicate that it has been taken at lights and that it injures coconut palms *(Cocos nucifera* L.). Stahl and Scaramuzza (1929) and Valdes (1951) observed that they attack roots and occasionally the seed pieces of sugar cane *(Saccharum officinarum* (L.)) but are not considered major pests. Chapin (1932a) indicated they are an important enemy of coconut palms. *Tiphia argentipes* Cresson (Hymenoptera: Tiphiidae) and *Campsomeris*

trifasciata (Fabr.) (Hymenoptera: Scoliidae) have been listed as natural enemies (Valdes, 1951).

Distribution.—Cuba.

Locality Records (Fig. 2).—147 specimens examined (54 males, 93 females). Specimens were seen from the following collections: AMNH, BMNH, CASC, CNCI, MCZC, USNM.

CUBA (146).—CAMAGUEY (98): Baraguá, Jaronú; HABAÑA (8): Habaña City, La Alianza, Vibora; ISLA DE PINOS (3): Los Indios, Nueva Gerona; LAS VILLAS (16): Bangos de Ciega Montera, Cayamas, Santa Clara, Soledad; ORIENTE (5): Baracoa, Santiago de Cuba, Sierra de Cristal; PINAR DEL RIO (4): Pinar del Rio; No data (12). January (2), May (43), June (36), July (7), August, (4), September (1), October (4).

Remarks.—*S. anachoreta* is easily separated from all other species by the partially punctate mesosternum; the presence of definite rows of moderate to large, ocellate-umbilicate punctures on the lateral half of the elytral disc; the broadly truncate clypeal apex; the shining elytra; and the presence of three simple horns on the pronotum. This species is very closely related to *S. symphenax* which also occurs in Cuba.

Strategus antaeus (Drury)
(Figs. 4, 29–31, 120–121)

Scarabaeus antaeus Drury, 1773: 74. [Types unknown to me. Type locality: originally published as Jamaica but probably Jamaica, New York, United States.]

Scarabaeus maimon Fabr., 1775: 10. [Holotype at BMNH (Banks Collection) (Zimsen, 1964). Type locality: originally given as America but here restricted to eastern United States.]

Scarabaeus maimon Fabr. 1787: 6. [Redescription.]

Strategus divergens Casey, 1915: 246. [Holotype male at USNM. Type locality: Gulf States, United States.]

Strategus atrolucens Casey, 1915: 247. [Lectotype male, labeled "Fla.," "Casey bequest 1923," "Type USNM 48639," and "*atrolucens* Csy.," here designated; at USNM (Casey collection) with my lectotype label. Two male paralectotypes also at USNM. Type locality: Florida, United States.]

Strategus pinorum jcuasey, 1915: 248. [Lectotype male, labeled "Southern Pines, VII–29, N.C., A. H. Manee, 07," "Casey bequest 1923," "Type USNM 48637," and "*pinorum* Csy.," here designated; at USNM (Casey collection) with my lectotype label. Lectoallotype female, labeled "Southern Pines, VII–20, N. C., A. H. Manee, 07," "Casey bequest 1923," "*pinorum* – 3, Paratype USNM 48637," and "*pinorum* Csy.," here designated; at USNM with my lectoallotype label. Also one male and two female paralectotypes at USNM. Type locality: Southern Pines, North Carolina, United States.]

Strategus septentrionis Casey, 1915: 249. [Lectotype male and lectoallotype female here designated: at USNM with my lectotype labels. Also three male paralectotypes at USNM. Type locality: New Jersey, United States.]

Strategus sinuatus Casey, 1915: 250. [Holotype male at USNM. Type locality: Alabama, United States.]

Strategus semistriatus Casey, 1915: 250. [Holotype male at USNM. Type locality: Texas, United States.]

Strategus antaeus houstonensis Knaus, 1925: 182. [Holotype male and allotype female presumably at KSUC (Knaus Collection). Type locality: Houston, Texas, United States.]

Male.—Length 18.2–40.7 mm; width across humerus 11.0–19.5 mm. Color castaneous to piceous, shining. *Head:* Front coarsely rugo-punctate, setigerous above eye in unworn specimens. Clypeus with apex rounded, usually with an acute, subapical tooth in unworn specimens; surface coarsely rugo-punctate. Tubercles conical, small, connected by a low, transverse carina. Mandibles with basal lobe small, prominently rounded; middle lobe long, slender, apex very narrowly rounded; apical lobe small, rounded. Interocular width 2.75–3.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a very narrow to obsolete feebly punctate to rugo-punctate band. Disc very finely granulate, faintly impressed medially, sparsely punctate; punctures small, moderately deep. Sides as disc except

base of posterior horns with an area of simple to crescent-shaped punctures; punctures moderate to large, dense, shallow. Anterior third as disc in majors; minors with anterior angles, fovea, base of posterior horns, and sides of anterior horn rugose; very small individuals with entire anterior third rugose. Fovea deep, divided longitudinally by a low, rounded carina extending posteriorly from base of anterior horn. *Horns:* Majors (Figs 29–30) with anterior very long, slender, attenuate, curving forward and upward (recurving posteriorly at apex in largest specimens); apex acutely rounded, dorsal surface weakly carinate to rounded, usually very feebly and longitudinally sulcate medially. Posterior horns long, slender (but more robust than anterior), laterally compressed, attenuate, apex narrowly rounded; in lateral view horns curve forward and upward at approximately 45–85° from plane of disc; in dorsal view horns subparallel to slightly diverging, apices curving toward one another; lateral surface convex, median surface nearly flat. Minors (Fig. 31) with anterior short, robust, weakly attenuate; apex usually feebly excised, occasionally blunt. Posterior horns essentially as in majors except very short or reduced to low, rounded to pyramidal bosses; in lateral view dorsal surface subhorizontal, anterior surface subvertical to sloping forward and downward; in dorsal view horns subparallel, bases joined across disc in a weak, medially produced arc. *Elytra:* Sutural stria obsolete, occasionally feebly impressed at base and apex. Disc aciculate, sparsely punctate; punctures small, deep; frequently with moderately dense, weakly raised punctures, punctures very small to minute, very shallow, often in rows. *Pygidium:* Nearly flat in lateral view. Disc usually very finely granulate, sparsely punctate in majors, moderately punctate in minors; punctures large, shallow, some with short setae in unworn specimens. Apical margin similarly punctate but a little more densely so. *Genitalia:* Figs. 120–121.

Female.—Length 22.0–35.4 mm; width across humerus 13.1–18.1 mm. As male except in the following respects: *Head:* Front coarsely rugose. Clypeus with apex broadly to subacutely rounded, occasionally narrowly truncate, lacking a subapical tooth, weakly reflexed; surface coarsely rugose. Mandibles similar to those of male but smaller, especially middle lobe; basal lobe more prominently rounded. *Pronotum:* Sides with punctures becoming moderate to large, often crescent-shaped. Anterior ⅓-½ rugose to rugo-punctate, occasionally reduced (especially in Massachusetts and New Jersey populations). Fovea moderately deep. Tubercle conical, transverse, low, weakly emarginate. *Pygidium:* In lateral view basal half convex, apical half feebly concave. Disc moderately to densely setigerously punctate (usually sparsely punctate in Massachusetts and New Jersey populations); punctures large, shallow. Lateral emargination shallow, more densely punctate.

Biology.—Ritcher (1966) provided a detailed description of the third instar larva. Cockerell (1906) mentioned that the larvae may injure peach *(Prunus)* roots in Alabama, and label data indicate specimens have been taken on peach roots and trunk, in piles of chicken feathers, and at lights. Manee (1908) observed in the sandy barrens near Southern Pines, North Carolina, that *S. antaeus* dig burrows with a 6–8 inch vertical shaft that end with a 1–5 inch horizontal chamber; 2–3 diverging chambers are occasionally present. Each chamber is provided with decayed oak *(Quercus)* leaves which serve as larval food. A single egg is placed in each chamber. Larvae raised in the lab were later seen to be cannabalistic, and Manee concluded that this was probably the reason for a single egg per chamber. Manee further noted that young larvae fed on leaf debris and later on decayed oak roots and that preferred nesting sites were usually near a pile of dead oak leaves blown by the wind into a hollow.

Ritcher (1966) observed *S. antaeus* burrows in a burned-over pine woodland near Newton Grove, North Carolina. "Each was beneath a conspicuous sandy pushup. Burrows usually extended obliquely, were from 8-19 inches in depth, and were provisioned with surface litter. One burrow was straight, one was L-shaped, and the rest had a single branch or were forked. Usually a single egg was found toward the end of each burrow, or each branch of burrows . . . ." Manee found eggs in burrows in early August, and Ritcher found eggs in August and Sep-

tember. Ritcher also found first instar larvae in October, second instar larvae in January, and mentioned a third instar taken in the winter or spring. The composite life cycle that can be derived (at least in North Carolina) is that eggs are deposited from early August to early September, larvae overwinter and pupate in the spring, and adults emerge from late May to late August; adult activity in North Carolina is corroborated by label data.

Individuals from Massachusetts and New Jersey (Casey's *S. septentrionis)* are, with rare exceptions, consistently very small and light reddish brown in color, perhaps demonstrating some form of ecophenotypy. In this regard, I suspect that further investigations into the ecology of the sandy pine barrens of these regions might yield valuable information. Harshberger (1916) has shown that the vegetation of the New Jersey pine barrens decomposes very slowly and may be toxic to animals because of alkaloids, tannins, and other phenols. Many of the plants in this region are poisonous, insecticidal, nervine, emitic, purgative, stimulatory, acrid stimulant, sialagogic, diuretic, nephritic, and irritant in nature. Many of these compounds are commonly found in the soil in such areas (Burges, 1965; Burges *et al.,* 1964; Whitehead, 1964), and they may definitely have a negative effect on the soil and litter organisms (Janzen, 1974). Feeny (1968, 1969) and Miles (1969) have demonstrated specific detrimental effects upon insects. *Strategus antaeus* may be similarly negatively influenced under such conditions.

Distribution.—Eastern United States west to Oklahoma and Texas.

Locality Records (Fig. 4)—736 specimens examined (376 males, 360 females). Specimens were seen from the following collections: AMNH, BCRC, CASC, CNCI, DEUN, FMNH, HAHC, INHS, KSUC, LACM, MCZC, OSUC, OSUO, PMNH, SEMC, UC, UMMC, USNM, UWEM.

UNITED STATES (736).—ALABAMA (33): *Dekalb (4):* Ft. Payne, Mentone (Desoto Caves); *Greene (2):* Eutaw; *Jackson (2):* Bryant, Pisgah; *Lee (3):* Auburn; *Macon (3):* Tuskegee; *Madison (1):* Monte Sano; *Mobile (11):* Grand Bay, Mobile; *Montgomery (1):* Montgomery; *Russel (1):* no data; *Tallapoosa (1):* Alexander City. ARKANAS (10): *Garland (1):* Hot Springs; *Pulaski (6):* Camp Robinson, Little Rock; *No data (3).* CONNECTICUT (1): *New Haven (1):* Woodbridge. DELAWARE (1): *Sussex (1):* Dewey. FLORIDA (368): *Alachua (88):* Archer, Gainesville, High Springs; *Bay (2):* Panama Beach City; *Bradford (2):* Starke; *Brevard (15):* Cape Canaveral, Eau Gallie, Melbourne; *Broward (5):* Ft. Lauderdale; *Charlotte (1):* Punta Gorda; *Clay (1):* Keystone Heights; *Collier (1): no data; Dade (73):* Largo, Miami; *De Soto (1):* Avon Park; *Duval (2):* Jacksonville; *Hardee (1):* Wauchula; *Highlands (1):* Archibold Biol. Stat.; *Hillsborough (5):* Little Manatee River, Plant City; *Indian River (1):* Sebastion; *Jackson (1):* no data; *Jefferson (2):* Monticello; *Lake (1):* Leesburg; *Lee (1):* Ft. Myers; *Leon (4):* Talahasee, Tall Timbers Res. Stat.; *Liberty (3):* Rock Bluff; *Madison (2):* Madison; *Marion (11):* McIntosh, Ocala Nat'l. Forest; *Okaloosa (1):* Niceville; *Orange (5):* Oakland, Orlando, Winterpark; *Palm Beach (7):* Lake Worth; *Pinellas (16):* Cabbage Key, Clearwater, Gulfport, St. Petersburgh; *Polk (10):* Lake Alfred, Lakeland; *Putname (20):* Crescent City, San Mateo, Satsuma; *St. Johns (4):* St. Augustine; *Sumpter (4):* Inverness; *Volusia (20):* Brooksville, Daytona Beach, De Leon Springs, Enterprize, Glenwood, Sanford; *No data (57).* GEORGIA (48): *Camden (1):* no data; *Chatham (3):* Savannah; *Cook (1):* Sparks; *Dekalb (27):* Atlanta, Dunwoody, Ft. McPherson; *Fulton (2):* Atlanta; *Habersham (3):* no data; *Hancock (1):* no data; *Richmond (1):* Augusta; *Thomas (3):* Thomasville; *Tift (1):* Tifton; *No data (5).*IOWA (1): *Lee (1):* Keokuk. KANSAS (3): *Chautauqua (1):* Sedan; *Montgomery (1):* no data (1). KENTUCKY (3): *Bell (3):* Cumberland Gap; *Whitley (2):* Pine Knot. MARYLAND (3): *Prince Georges (2):* Beltsville; *No data (1).* MASSACHUSETTS (50): *Barnstable (12):* Cape Cod, Dennis, Harwhich Port, Sagamore, Truro, Wellfleet, West Yarmouth; *Dukes (3):* Martha's Vineyard; *Hampden (4):* Springfield; *Nantucket (17):* Nantucket; *Plymouth (6):* Wareham; *No data (8).* MISSISSIPPI (5): *Forrest (1):* Brooklyn; *Harrison (4):* Gulfport. NEW JERSEY (114): *Atlantic (4):* Da Costa, Hammonton; *Burlington (79):* Brown's Mills, Masonville, Medford Lakes, Mt. Misery, Rancosas Park, Retreat; *Camden (2):* Clementon; *Cape May (9):* Ocean City,

Wildwood: *Gloucester (1):* Wenonah; *Meddlesex (1):* Jamesburg; *Ocean (16):* Lakehurst, Manahawkin, Seaside Park, Whiting; *No data (2).* NEW YORK (8): *Suffolk (3):* Greenport, Riverhead; *No data (5).* NORTH CAROLINA (27): *Halifax (1):* Halifax; *Johnston (1):* Benson; *Moore (22):* Eagle Springs, Eastwood, Pinehurst, Southern Pines: *Robeson (1):* Maxton; *Wake (2):* Raleigh. OKLAHOMA (5): *Caddo (1):* Anadarko; *Kingfisher* (1): Kingfisher; *Logan (1):* Guthrie; *Tulsa (2):* Tulsa. PENNSYLVANIA (3): *Montgomery (3):* Frankford. RHODE ISLAND (14): *Kent (5):* Buttonwoods; Warwick; *Providence (9):* Providence. SOUTH CAROLINA (24): *Aiken (6):* Aiken; *Beaufort (1):* Hilton Head Island; *Charleston (1):* Santee Plantation (South Santee River); *Chesterfield (1):* McBee; *Colleton (1):* Hendersonville; *Fairfield (1):* Woodward; *Florence (1):* Florence; *Horry (1):* Arrowhead Lake (Myrtle Beach); *Jasper (2):* Bluffton; *Richland (3);* Columbia; *No data (6).* TENNESSEE (21): *Grundy (2):* Camp Mt. Lake; *Hamilton (2):* Signal Mountain; *Knox (2):* Knoxville; *Lake (1):* Tiptonville; *Madison (1):* no data; *Morgan (12):* Burrville, Deer Lodge, Sunbright; *No data (1).* TEXAS (14): *Dallas (3):* Dallas; *Leon (3):* no data; *Nueces (2):* Corpus Christi; *No data (6).* VIRGINA (4): *James City (1):* Newport News; *Nelson (1):* no data; *Southampton (1):* Franklin; *No data (1).* February (2), March (4), April (16), May (35), June (143), July (198), August (118), September (44), October (13), November (2), December (4).

Remarks.—The absence of a sutural stria will easily separate *S. antaeus* from all other species in the genus. *Strategus antaeus* is somewhat variable with regard to shape, size, and color. Specimens from the southern part of the range are generally darker and larger than those from the northern part of the range.

Strategus antaeus houstonensis Knaus (1925) is not a valid subspecies as proposed but merely one aspect of the intraspecific variation seen within the species.

Strategus argentinus Kolbe
(Figs. 8, 32–33, 122–123)

Strategus argentinus Kolbe, 1906: 24. [Lectotype male, labeled "Argentinien, Cordoba, J. Frenzel's," here designated; at ZMHU with my lectotype label. Also one male paralectotype at ZMHU. Type locality: Cordoba, Argentina.]

Male.—Length 31.0–42.0 mm; width across humerus 18.0–21.0 mm. Color castaneous to piceous, shining. *Head:* Front rugose to coarsely punctate; punctures large, shallow, confluent. Clypeus with apex truncate, moderately emarginate; surface rugulose to rugose. Tubercles conical, small to moderate in size, slightly transverse, usually distinctly separated. Mandibles with basal lobe small, rounded; middle lobe large, triangular, apex rounded; apical lobe small, triangular. Interocular width 3.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide rugose band; band reduced medially nearly to basal bead. Disc aciculate, punctate; punctures small and minute mixed, moderate in density, deep. Sides similar to disc except punctures larger; lateral margin with a band of moderate to large punctures, punctures moderately dense, simple to crescent-shaped, shallow. Anterior angles and fovea either side of middle as disc to rugose. Fovea deep, with or without a low, feeble, median, longitudinal ridge extending posteriorly from base of anterior horn. *Horns:* Anterior short to moderate, stout, attenuate, curving forward and upward; apex narrowly rounded, occasionally very feebly emarginate; dorsal surface rounded to nearly flat. Posterior horns vary from low, rounded bosses to very short, triangular, stout, laterally compressed horns; in dorsal view horns parallel, bases joined across disc in a shallow arc. *Elytra:* Sutural stria strongly impressed, weakly crenulate. Disc frequently wrinkled, aciculate, punctate; punctures minute, small and moderate mixed, moderately dense, shallow, occasionally in several incomplete rows; lateral half of disc frequently with 3–5 shallow, incomplete striae; striae occasionally produced into broad, shallow furrows; furrows interrupted, apically branched. Sides similar to disc except punctures slightly larger, striae absent, and wrinkling usually pronounced. Apex densely punctate, punctures as on disc. *Pygidium:* Convex in lateral view. Disc aciculate, usually finely roughened to very finely granulate, punctate; punctures small, moderately dense, very shallow; those on apical midline large,

sparse, deep, setigerous in unworn specimens; punctures often greatly reduced. Apical margins densely punctate to rugose. *Genitalia:* Figs. 122–123.

Female.—Length 30.5–35.0 mm; width across humerus 14.7–17.0 mm. As male except in the following respects: *Head:* Clypeal apex nearly rectangular in unworn specimens, moderately reflexed; apex narrowly to broadly rounded or truncate in worn specimens. Tubercles transverse, usually connected by a weak carina. Mandibles similar to those of male but smaller, especially middle lobe. *Pronotum:* Base with rugose band narrow to moderate. Sides with punctures moderately large, dense, grading into rugosity anteriorly at about middle; a slightly depressed, rounded area of dense punctures postero-lateral of fovea. Anterior third rugose. Fovea shallow. Tubercle strong, conical, transverse. *Pygidium:* In lateral view basal half convex, apical half nearly flat. Disc punctate; punctures small and large mixed, moderately dense, shallow; large punctures simple to oblong, setigerous in unworn specimens. Lateral emargination shallow, more strongly punctured.

Biology.—Unknown.

Distribution.—Uruguay and northeast Argentina. Endrödi (1973b) reported 4 specimens from Bolivia, but without seeing the specimens I am doubtful about this record.

Locality Records (Fig. 8).—23 specimens examined (16 males, 7 females). Specimens were seen from the following collections: BMNH, FMNH, MCZC, UC, URU, USNM, USP, ZMHU.

ARGENTINA (16).—CATAMARCA (2): Catamarca; CÓRDOBA (4): Córdoba; SALTA (2): Coronel Moldes, Gran Chaco; SANTIAGO DEL ESTERO (4): Banda, Chalya; No data (4). February (2), November (5), December (1).

URUGUARY (7).—ARTIGAS (2): Capital, Catalán Chico; COLONIA (1): Piedra de los Indios, PAYSANDÚ (1): Rt. 3 (Km. 383); SALTO (2): San Antonio; TACUAREMBÓ (1): Puntas Arroyo Laureles. January (1), December (6).

Remarks.—Although *S. argentinus* is a rather nondescript species, the key characters will distinguish it from all other species. From the specimens examined, it apparently does not possess what could be called a major stage of development with regard to armature. *S. argentinus* is an uncommon species.

Strategus atlanticus, new species
(Figs. 1, 34–35, 124–125)

Type Material.—Holotype male, labeled "Walting (sic) Island, Bahamas, Oct. 10–21. 91, C. B. Cory (?)," deposited at MCZC.

Holotype.—(Figs. 34–35, 124–125).—Male. Length 32.0 mm; width across humerus 15.4 mm. Color dark castaneous, feebly shining. *Head:* Front distinctly concave, basal half finely granulate, apical half densely punctate; punctures large, shallow, some confluent; a trace of setae above eye. Clypeus with apex broadly rounded, feebly reflexed; surface finely granulate, densely punctate; punctures large and minute mixed, shallow. Tubercles conical, transverse, very low, widely separated. Mandibles with basal lobe small, rounded; middle lobe subtriangular, small, apex nearly right angled; apical lobe small, obtusely rounded. Interocular width 2.33 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pronotum:* Base with a few moderate, elongate punctures either side of midline. Disc extremely finely subgranulate, sparsely punctate; punctures small, moderately deep. Sides in basal ⅔ similar except punctures a little larger and a little more dense, especially near lateral margin. Anterior third rugo-punctate. Fovea virtually effaced, only an extremely shallow, barely noticeable depression remains. *Horns:* None; even anterior tubercle absent. *Elytra:* sutural stria strongly impressed, crenulate. Disc finely granulate, punctate; punctures small and large mixed, small punctures sparse (becoming more so laterally), shallow; large punctures ocellate-umbilicate, moderately dense, shallow, and irregular except for a regular row in center of disc and a regular double row on lateral margin of disc. Sides similar except wrinkled behind humerus, small punctures very sparse, large punctures sparse, a double row of moderate punctures in middle. Apex moderately punctate; punctures moderate

in size, shallow. *Pygidium:* Very strongly convex in lateral view, protuberant at middle. Surface finely granulate, sparsely punctate, punctures small, shallow. *Genitalia:* Figs. 124–125.

Female.—Unknown.

Biology.—Unknown.

Distribution.—Watling Island (San Salvador), Bahamas.

Locality Records (Fig. 1).—One specimen examined (holotype). Specimen deposited at MCZC.

BAHAMAS (1).—WATLING ISLAND. October (1).

Remarks.—The completely punctate mesosternum and the presence of distinct rows of punctures on the elytral disc will distinguish this species from all others. It is unique among *Strategus* in that the pronotal fovea and tubercle are virtually obsolete. The other characters and the genitalia in particular place it in this genus. Zoogeographically, it is the most isolated of the species and is probably derived from close relatives in Cuba or Hispaniola such as the ancestors of *S. aenobarbus, S. ajax,* or *S. talpa.*

Etymology.—From the Latin *atlas,* a mythical god who held up the heavens; here named for its occurrence on San Salvador in the Atlantic ocean.

Strategus caymani, new species
(Figs. 1, 36–39, 126–127)

Type material.—Holotype male, labeled "29 v. 1938, Little Cayman, S. Coast of South Town, light trap A," "17. iv-26. viii 1938, Oxf. Un. Cayman Is. Biol. Exped., Coll. by C. B. Lewis, G. H. Thompson," "*Strategus simson* (L.), local form. det. 1950, E. A. Chapin." Allotype female with same data as holotype. Types deposited at BMNH; 18 males and one female paratypes deposited in BCRC, BMNH, HAHC, SEBO ENDRÖDI.

Holotype.—Male. Length 38.1 mm; width across humerus 18.0 mm. Color piceous, feebly shining. *Head:* Front largely hidden by closely appressed anterior pronotal horn; surface finely granulate, feebly rugo-punctate (especially behind tubercles). Clypeus with apex rounded and weakly emarginate, moderately reflexed; surface finely granulate, feebly rugo-punctate. Tubercles conical, nearly effaced. Mandibles with basal lobe submoderate, prominently rounded; middle lobe moderate in size, subtriangular, apex rounded; apical lobe subtriangular, slightly smaller than middle lobe, apex acute. Interocular width 1.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow, rugose band; band reduced medially almost to basal bead. Disc very finely granulate, punctate; punctures moderate and minute mixed; moderate punctures moderately dense, deep (becoming shallower laterally) minute punctures sparse, shallow. Sides in basal half with punctures a little less dense, slightly larger to large, shallow; sides in anterior half and anterior angles sparsely punctate, punctures small, shallow. Fovea extremely shallow, sparsely punctate, punctures small to very small, shallow. *Horns:* Anterior long, robust, dorsoventrally compressed, expanding apically to a very strongly forked apex, each prong of fork acutely rounded and divided by a deep U-shaped emargination; in lateral view horn curves forward and downward closely over head and then bends upward at about middle; dorsal surface flat to slightly concave, each lateral margin longitudinally carinate. Posterior horns completely lacking. *Elytra:* Sutural stria impressed, crenulate. Disc wrinkled, finely granulate, punctate; punctures small and minute mixed; small punctures moderate in density, shallow, and becoming increasingly ocellate-umbilicate laterally and basally; minute punctures dense, very shallow; 3 shallow, incomplete striae on lateral half of disc. Sides similar to disc except without striae, with increased wrinkling behind humerus, and ocellate-umbilicate punctures moderate to large. Apex densely punctate; punctures small to moderate, simple to ocellate-umbilicate, shallow. *Pygidium:* Convex in lateral view. Disc very finely subgranulate, sparsely punctate; punctures small to moderate, very shallow. Apical margins rugulose either side of midline. *Genitalia:* Figs. 126–127.

Allotype.—Female. Length 37.0 mm; width across humerus 17.7 mm. Color slightly lighter than holotype. As holotype except in the following respects: *Head:* Front finely granulate, strongly rugo-punctate to rugose. Clypeus with apex broadly rounded, very weakly emarginate; surface rugose. Mandibles similar to those of holotype but slightly smaller. *Pronotum:* Base with a narrow rugo-punctate band, band reduced nearly to basal bead at midline; basal fourth of midline with an irregular, longitudinal patch of moderate to large, shallow punctures. Sides in basal half moderately densely punctate; punctures moderate to large, shallow; lateral margin in basal half with a narrow rugose band; just postero-lateral of fovea is a slightly depressed, rounded patch of rugosity. Anterior half rugo-punctate to rugose. Fovea nearly obsolete, faintly carinate longitudinally down middle. Tubercle conical, transverse, nearly effaced. *Pygidium:* Strongly convex and protuberant at middle in lateral view. Disc very finely subgranulate, moderately densely punctate, punctures small and minute mixed, very shallow. Lateral emargination shallow, rugulose.

Variation.—Males (18 paratypes): Length 28.7–39.4 mm; width across humerus 13.4–18.0 mm. *Head:* Interocular width 1.66–2.0 transverse eye diameters. *Mesosternum:* Anterior ½–⅔ setigerously punctate. *Pronotum:* As holotype to base either side of middle with large, simple to oblong punctures. Anterior half with punctures moderate in size. *Horns:* Majors (Figs. 36–37) with anterior narrowly to very widely forked at apex, horn subslender to very stout. Minors (Figs. 38–39) with anterior short, expanded very little apically, apex triangularly notched; dorsal surface rounded to weakly carinate longitudinally down middle or down middle and on lateral margins.

Females (1 paratype): Length 33.2 mm; width across humerus 15.3 mm. *Head:* Interocular width 2.0 transverse eye diameters. *Pronotum:* Fovea obsolete.

Biology.—Label data indicate "attacked by a tachinid" and "taken at lights"; otherwise unknown.

Distribution.—Little Cayman Island and Cayman Brac (West Indies).

Locality Records (Fig. 1).—21 specimens examined (19 males, 2 females). Specimens deposited in the following collections: BCRC, BMNH, HAHC, SEBO ENDRÖDI.

CAYMAN ISLANDS (21).—CAYMAN BRAC (6): north coast Stakes Bay, west end of Cotton-tree land; LITTLE CAYMAN (15): south coast of South Town. May (20), June (1).

Remarks.—The partially punctate mesosternum, rounded and weakly emarginate clypeal apex, dull elytra, distinctly forked anterior horn, lack of posterior horns, and an interocular width of less than two transverse eye diameters will serve to separate *S. caymani* from any other species. In 1950 Chapin concluded that the type series in the BMNH was a local form of *S. simson.* Even though the genitalia are almost identical, I believe other characters are sufficiently distinctive to justify new species status. *S. caymani* is very closely related to *S. simson.*

Etymology.—This species is named after the Cayman Islands on which it occurs.

Strategus centaurus Kolbe
(Figs. 9, 40–43, 128–129)

Strategus centaurus Kolbe, 1906: 29. [Types not seen. Holotype and presumably allotype at ZMHU. Type locality: Brazil.]

Male.—Length 50.5–80.0 mm; width across humerus 24.8–37.3 mm. Color piceous to black, shining. *Head:* Front coarsely rugo-punctate to rugose. Clypeus with apex strongly reflexed, very broadly truncate, and with a moderate to very deep, median, triangular excision; surface usually rugose in minors, moderately punctate in majors; punctures large, shallow. Tubercles conical, strong, transverse, distinctly separated to weakly connected in minors by a weak, transverse carina. Mandibles with basal lobe small, prominently rounded; middle lobe very large, triangular, apex rounded; apical lobe small, triangular, apex usually acute. Interocular width 2.0–2.5 transverse eye diameters. *Mesosternum:* Anterior ⅔ setigerously punctate. *Pronotum:* Base with transverse, rugose band wide to very

wide; band reduced medially almost to basal bead. Disc aciculate, sparsely punctate; punctures small, deep. Sides of minors similar to disc except lateral margin rugo-punctate in basal half, grading to rugose in anterior half; a strong rugo-punctate patch present at base of posterior horns or bosses; sides of majors also similar to disc except marginal band reduced to a few sparse, moderately large punctures, and a rugo-punctate patch present at base of posterior horns. Anterior half rugose except in very large males, and then rugose only in anterior angles. *Horns:* Majors (Figs. 40–41) with anterior long, stout, attenuate, curving forward and upward, apex narrowly rounded, dorsal surface rounded. Posterior horns long, stout, not attenuate, laterally compressed, projecting forward and upward at about 50–80° from plane of disc; apex obliquely truncate, occasionally weakly to moderately scalloped and with posterior flaring in well-developed specimens; in dorsal view horns subparallel to curving toward one another. Minors (Figs. 42–43) with anterior as in majors except short. Posterior horns vary from low, subparallel to slightly divergent pyramidal bosses to short, stout horns; horns attenuate, laterally compressed, apex broadly rounded, projecting vertically to subvertically from plane of disc. *Elytra:* Sutural stria strongly impressed, crenulate. Disc aciculate, sparsely punctate; punctures small and minute mixed; median ⅓–½ frequently with sparse, ocellate punctures; punctures small to moderate; in addition lateral ½–⅔ usually with 6 rows of moderate to large, ocellate punctures, rows 1–2 and 4–5 regular and distinct, rows 3 and 6 irregular and confused; rows 2, 4, and 5 frequently in or adjacent to a shallow, incomplete stria; rows of punctures and size of punctures occasionally reduced, especially row 1. Sides with 3–6 confused rows of punctures; punctures ocellate, moderate to large, becoming obsolete posteriorly. Apex sparsely to moderately punctate; punctures small, shallow. *Pygidium:* In lateral view basal half convex, apical half weakly concave. Surface aciculate, varies from weakly rugo-punctate to punctate; punctures small to moderately large, simple to oblong, shallow, sparse, becoming denser near apical margins either side of middle. *Genitalia:* Figs. 128–129.

Female.—Length 52.5–64.9 mm; width across humerus 25.6–31.5 mm. As male except in the following respects: *Head:* Clypeus with apex rounded to broadly truncate, moderately reflexed. Tubercles transverse, usually connected by a weak, transverse carina. Mandibles similar to those of male but smaller, especially middle lobe. Interocular width 2.33–3.0 transverse eye diameters. *Pronotum:* Sides in basal half rugo-punctate to densely punctate; punctures moderate to large, deep, frequently confluent; a slightly depressed, rounded patch of rugosity present just postero-lateral of fovea. Anterior half rugose. Fovea moderately deep. Tubercle conical, strong, transverse. *Pygidium:* Occasionally as in male, more commonly entirely rugose; sparse setae present apically in unworn specimens.

Biology.—Unknown. Costa Lima (1953) reported that they were a pest of palms at Bahia, Brazil.

Distribution.—South America. The single record from Venezuela (USNM) is somewhat doubtful.

Locality Records (Fig. 9).—28 specimens examined (13 males, 15 females). Specimens were seen from the following collections: AMNH, BMNH, CNCI, FMNH, HAHC, MCZC, UC, USNM.

ARGENTINA (2).—MISIONES (2): El Dorado, Puerto Bemberg. November (2)

BRAZIL (32).—BAHIA (7): Bahia, 20 mi. SW. Salvador, no data; ESPIRÍTO SANTO (2): Espiríto Santo; PARÁ (4): Pará, Santarem; PARANÁ (3): Caviuna, Villa Velha; SANTA CATARINA (6): Corupa, Nova Teutonia, no data; SÃO PAULO (1): Piracicaba; No data (9). January (2), April (3), June (1), November (1), December (3).

PARAGUAY (3).—Insufficient data (3). January (2), December (1).

Remarks.—The large mandibles, the definite rows of moderate to large ocellate punctures on the lateral half of the elytral disc, the strongly excised clypeal apex, and a length greater than 50 mm will serve to separate this, the largest of all *Strategus,* from any other species.

Strategus cessatus Wickham
(Figs. 6, 174)

Strategus cessatus Wickham, 1914: 461. [Holotype at MCZC. Type locality: Florissant, Colorado, United States.]

Remarks.—The reader is referred to Wickham for a description of this, the only known fossil *Strategus*. The single elytron was originally described as being Miocene, but subsequent studies have established that the Florissant deposits are actually Oligocene. My examination of the type initially left some doubt as to whether the specimen was indeed a *Strategus,* especially since there was only one elytron to work with. Wickham placed it in *Strategus* because he thought that it corresponded more to this genus than to any other related genera, and in this regard I now agree with Wickham.

Strategus cessatus is closely related to *S. cessus* and probably occupied a habitat comparable to today's *S. cessus*.

Strategus cessus LeConte
(Figs. 6, 44–45, 130–131)

Strategus cessus LeConte, 1866: 382. [Lectotype female, labeled "Ariz.," "*S. cessus* LeC., Coves/3," and "Type/3780," here designated; at MCZC with my lectotype label. Lectoallotype male, labeled "Ariz.," here designated; at ICCM (Ulke Collection) with my lectoallotype label. Type locality: Arizona, United States.]

Strategus beckeri Kolbe, 1906: 14. [Lectotype male, labeled "Mexico, J. Flohr G.," "70808," and "*beckeri* n. sp.," and lectoallotype female, labeled as lectotype but without number, here designated; at ZMHU with my lectotype labels. Also one male paralectotype at ZMHU. Type locality: Sierra Madre, Durango, Mexico. Lectotype illustrated in Kolbe.] **New synonymy.**

Anastrategus cessus cavicauda Casey, 1915: 233. [Lectotype female here designated; at USNM with my lectotype label. Also one female paralectotype at USNM. Type locality: unknown, but Casey suspected New Mexico, United States.]

Anastrategus durangoensis Casey, 1915: 234. [Holotype male at USNM. Type locality: Tepehuanes, Durango, Mexico.]

Anastrategus inflatus Casey, 1915: 234. [Holotype male at USNM. Type locality: Arizona, United States.]

Anastrategus tantalus Casey, 1915: 235. [Lectotype male, labeled "Oslar, Prescott, Ariz.," "Casey bequest 1923," Type USNM 48627," and "*tantalus* Csy.," here designated; at USNM (Casey collection) with my lectotype label. Lectoallotype female, labeled as male except for type label which reads "*tantalus* – 3, Paratype USNM 48627," here designated; at USNM with my lectoallotype label. Also one male paralectotype at USNM. Type locality: Prescott, Arizona, United States.]

Male.—Length 24.5–41.0 mm; width across humerus 11.0–20.0 mm. Color castaneous to black, shining. *Head:* Front rugose to very coarsely punctate; punctures dense, large, deep, often confluent; setigerous above eye in unworn specimens. Clypeus with apex narrowly rounded (rarely feebly emarginate), moderately reflexed. Tubercles strong, conical, transverse, joined by a moderate to strong, transverse carina. Mentum with disc coarsely punctate; punctures large, dense, often confluent. Mandibles nearly square in dorsal view. Interocular width 4.0–4.5 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow, coarsely rugo-punctate band. Disc aciculate, punctate; punctures moderately dense (sparser along midline), moderate to large, shallow to deep; usually a feeble, longitudinal depression along midline. Sides with large, dense, moderately deep punctures, becoming coarsely rugo-punctate to rugose in anterior quarter. Anterior third rugose. Fovea moderately deep. *Horns:* Anterior a moderate to strong tubercle; tubercle conical, very transverse, apex usually distinctly emarginate, truncate in worn specimens. Posterior horns completely lacking. *Elytra:* Sutural stria weakly to moderately impressed, feebly crenulate; anterior fifth occasionally effaced and replaced by moderate-sized, shallow, irregularly shaped punctures. Disc aciculate, punctate; punctures sparse to moderately dense, small to large, shallow; 2–3

punctures frequently joined to form an irregular, transverse furrow; lateral half of disc with 2 double rows of impressed, occasionally interrupted, punctate striae; punctures moderate to large, deep; striae variably effaced, especially the first. Sides as disc except usually with 1 vague, double row of feebly impressed, punctate striae adjacent to disc; punctures moderate in size; striae often reduced to completely absent; area just behind humerus transversely wrinkled or with a weak to strong row of moderate to large, deep punctures. Apex punctate; punctures dense to rugo-punctate. *Pygidium:* In lateral view basal third strongly convex, apical ⅔ nearly flat. Disc very finely granulate, aciculate, punctate; punctures sparse to moderately dense and coarse, small to large, shallow; a few short setae near apex in unworn specimens. *Genitalia:* Figs. 130–131.

Female.—Length 24.8–37.2 mm; width across humerus 10.0–19.0 mm. As male except in the following respects: *Pygidium:* In lateral view basal half convex, apical half concave. Disc aciculate or not, sparsely punctate; punctures shallow, usually small, occasionally several moderately large. Apical margin densely punctate; a few short setae present in unworn specimens; lateral emargination absent.

Biology.—Unknown. Label data indicate that *S. cessus* has been taken at lights and from 1300–2736 meters in altitude.

Distribution.—Southwest United States and northwest Mexico. The single record from California is possibly erroneous or due to conveyance by man.

Locality Records (Fig. 6).—184 specimens examined (66 males, 110 females). Specimens were seen from the following collections: AMNH, BCRC, BMNH, CASC, CNCI, DEUN, FMNH, HAHC, ICCM, KSUC, LACM, MCZC, PMNH, OSUC, OSUO, SEMC, UMMC, USNM, ZMHU.

MEXICO (29).—CHIHUAHUA (16): 5 mi. N. Cerro Campana (Sierro del Nido), 8 mi. W. Matachic, 10 mi. W. Namiquipa, 15 mi. E. Parral, Santa Barbara, Santa Clara Canyon (5 mi. W. Barrita); DURANGO (10): 3 mi. W. Durango, 25 mi. W. Durango, Javilanes, Otinapa, Palos Colorados, San Pedro de Guanacevi, Sierra Madre; JALISCO (1): no data; No data (2). June (1), July (1), August (11).

UNITED STATES (154).—ARIZONA (138): *Apache (2):* Springville; *Cochise (59):* Carr Canyon (15 mi. S. Sierra Vista), Cave Creek Ranch, Cochise Stronghold, Huachuca Mts., Miller Canyon (Huachuca Mts.), Paradise, Parker Canyon Lake, Portal, Southwest Research Station (Portal), Sunnyside; *Gila (7):* base of Pinal Mts., Globe, Payson; *Maricopa (4):* Phoenix: *Navaho (2):* Kayenta, Snowflake; *Pima (5):* Madera Canyon, Santa Rita Mts.; *Santa Cruz (34):* Gardner Canyon, Hidden Springs Valley (9 mi. E. Sanoita), Madera Canyon, Nogales, 15 mi. NW. Nogales, Peña Blanca Lake, Sondida Creek (9 mi. S. Patagonia), Tubac, west slope Patagonia Mts.; *Yavapai (18):* Congress, Prescott; *No data (7).* NEW MEXICO (15): *Bernalillo (1):* Albuquerque; *Catron (2):* Apache Nat'l. Forest, Reserve; *Grant (5):* Ft. Bayard, Silver City; *San Miguel (2):* La Trementina (Fall and Cockerell, 1907), Las Vegas; *No data (5).* April (1), May (2), June (16), July (86), August (41), September (6).

Remarks.—The nearly square mandibles are diagnostic for *S. cessus.* Because the males lack horns, the males and females more closely resemble each other in this species than in any other. In the presence of larger samples it is now apparent that the diagnostic characters given by Kolbe (1906) for *S. beckeri* are merely part of the normal variation found in *S. cessus.* It is interesting to note, however, that virtually all of the specimens from Durango in Mexico are considerably lighter in color than those from the rest of the range.

Strategus craigi, new species
(Figs. 6, 46–47, 132–133)

Type Material.—Holotype male, labeled "Jalapa, Mexico, M. Trujillo," "B.C.A., Col., II (2), *Strategus julianus,*" and "♂"; deposited at BMNH.

Holotype (Figs. 46–47).—Male. Length 37.7 mm; width across humerus 18.6 mm. Color piceous, feebly shining. *Head:* Front grossly rugo-punctate, no supra-ocular setae seen. Clypeus

with apex broadly rounded, subtruncate, moderately reflexed; surface coarsely rugo-punctate. Tubercles conical, transverse, connected by a strong, transverse carina. Mentum with sparse, small to moderate punctures on disc. Mandibles with basal lobe moderate in size, prominently rounded; middle lobe moderate in size, subequal with basal lobe, also rounded; apical lobe small, rounded. Interocular width 4.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide, rugo-punctate to punctate band; punctures large, dense, shallow, reduced almost to basal bead at midline. Disc aciculate, punctate, punctures moderately dense, small, shallow; a Y-shaped band of moderate to large, shallow punctures extending from base and forking at base of fovea, arms extending obliquely forward; a slightly depressed, rounded area of rugosity just postero-lateral of fovea. Remainder of pronotum rugose. Fovea deep. *Horns:* Anterior a low tubercle, tubercle conical, transverse, apex subtruncate. Posterior horns lacking. *Elytra:* Sutural stria strongly impressed, crenulate. Disc aciculate, weakly wrinkled, moderately punctate; punctures small and minute mixed, shallow; 3 feebly impressed, incomplete striae on lateral ⅔. Sides similar except sparsely punctate. Apex densely punctate; punctures small to moderate, shallow. *Pygidium:* In lateral view basal half convex, apical half nearly flat. Disc roughened, moderately punctate; punctures minute, very shallow, becoming denser and larger in area of lateral emargination; a few sparse, large punctures near midline; a few short setae near apex. *Genitalia:* Figs 132–133.

Biology.—Unknown.

Distribution.—Mexico.

Locality Records (Fig. 6).—One male examined (holotype). Deposited at BMNH.

MEXICO (1).—VERACRUZ (1): Jalapa.

Remarks.—This species is very closely related to *S. cessus* but may be distinguished from it by the less punctate mentum, distinctly lobed mandibles, and a distinct, wide, rugo-punctate band at the base of the pronotum.

Etymology.—This species is named in honor of my younger brother.

Strategus fallaciosus Kolbe
(Figs. 6, 48–49, 134–135)

Strategus fallaciosus Kolbe, 1906: 16. [Lectotype male, labeled "Mexico, Motzerongo (sic), Staat Veracruz, R. Becker," "70832," "Type," and "*fallaciosus,*" here designated; at ZMHU with my lectotype label. Also one male paralectotype at ZMHU. Type locality: Motzorongo, Veracruz, Mexico. Lectotype illustrated in Kolbe.]

Male.—Length 43.5–45.0 mm; width across humerus 20.8–22.5 mm. Color dark castaneous, feebly shining. *Head:* Front grossly rugo-punctate, setigerous above eye in unworn specimens. Clypeus with apex rounded in worn specimens, extended as a rounded to squared tooth in unworn specimens, slightly reflexed; surface rugo-punctate to rugulose. Tubercles strong, conical, transverse, connected by a strong, transverse carina. Mandibles with basal lobe small, prominently rounded; middle lobe large, triangular, apex very acute; apical lobe similar to middle lobe but smaller. Interocular width 3.33 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide, rugo-punctate to rugose band; band reduced nearly to basal bead at midline. Disc faintly impressed medially, aciculate, punctate; punctures moderately dense, small to moderate in size, becoming larger at base of fovea, deep. Sides in basal half similar to disc except punctures moderately large and lateral margin with a narrow rugo-punctate to rugose band; sides grade to rugo-punctate and then to rugose in anterior half; a slightly depressed, rounded area of rugosity postero-lateral of fovea. Anterior third rugose. Fovea subquadrate, deep. *Horns:* Anterior a large, erect tubercle; tubercle conical, transverse, apex very feebly emarginate. Posterior horns are very low, rounded bosses; in dorsal view bases joined across disc in a shallow arc; arc strongly produced at middle. *Elytra:* Sutural stria usually moderately impressed and crenulate, occasionally reduced to a row of ir-

regularly shaped, moderate to large, deep punctures. Disc aciculate, punctate; punctures sparse to moderate, small, deep; usually 2–3 very feebly impressed, incomplete striae on lateral half. Sides wrinkled behind humerus, sparsely to moderately punctate; punctures small to moderate, shallow. Apex densely punctate to rugo-punctate. *Pygidium:* Convex in lateral view. Disc finely granulate, very densely punctate; punctures small to moderately large, shallow; usually a few large, shallow punctures on midline; apical margin with small, sparse setae in unworn specimens. *Genitalia:* Figs. 134–135.

Female.—Length 40.0–43.8 mm; width across humerus 18.7–22.0 mm. As male except in the following respects: *Head:* Apex of clypeus as male to extended as an acute tooth. Mandibles with middle lobe slightly smaller than in male. *Pronotum:* Discal punctures usually do not become larger at base of fovea. Fovea rounded. Tubercle conical, low, transverse; apex weakly but distinctly emarginate. *Pygidium:* In lateral view basal half convex, apical half concave. Disc finely and entirely setigerous in unworn specimens. Apical margins densely punctate to rugo-punctate; lateral emargination extremely shallow.

Biology.—Unknown. Label data indicate specimens have been found dead in a sawdust pile and at elevations of 1,335 and 1,435 m.

Distribution.—Mexico.

Locality Records (Fig. 6).—7 specimens examined (3 males, 4 females). Specimens were seen from the following collections: CNCI, SEMC, ZMHU.

MEXICO (7).—JALISCO (2): 3 mi. SW. Mazamitla, 12.4 mi. S. Tecalitlan; SONORA (3): Yecora; VERACRUZ (2): Motzorongo. June (1), August (1), November (3).

Remarks.—The acutely triangular second and third lobes of the mandibles together with the large, elongate, subparallel body shape will usually serve to distinguish this species at a glance. This species is apparently very rare. The female is recognized and described here for the first time.

Strategus fascinus Burmeister
(Figs. 8, 50–52, 136–137)

Strategus fascinus Burmeister, 1847: 131. [Holotype male at Martin Luther Universität, Halle, German Democratic Republic. Type locality: Colombia.]

Male.—Length 33.4–38.4 mm; width across humerus 16.4–18.7 mm. Color castaneous to piceous, shining. *Head:* Front weakly (but distinctly) to strongly rugo-punctate, setigerous above eye. Clyeus with apex weakly to moderately excised, moderately reflexed; surface rugo-punctate to sparsely punctate; punctures small to moderate, shallow. Tubercles strong, conical, slightly transverse, widely separated. Mandibles with basal lobe small, prominently rounded; middle lobe moderately large, triangular, apex rounded; apical lobe small, triangular. Interocular width 2.33–2.66 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate, often weakly so in posterior half. *Pronotum:* Base with a narrow rugose band; band reduced nearly to basal bead at middle. Disc aciculate, punctate; punctures very sparse, small, shallow. Sides as disc except margin in basal half usually rugo-punctate to punctate in a narrow band; punctures small to moderately large; less-developed individuals with a patch of moderate-sized, shallow punctures at base of posterior horns. Anterior half as disc. Fovea deep, median longitudinal ridge from base of anterior horn very low and broadly rounded, not prominent. *Horns:* Majors (Figs. 50–51) with anterior long, slender, sides subparallel (not attenuate), curving forward and upward, apex slightly expanded and weakly to moderately triangularly notched; dorsal surface round to flat, usually a small, longitudinal, median carina on apical half in large specimens. Posterior horns long, slender, attenuate, laterally compressed, extending forward and upward at about 20–40° from plane of disc; apex acutely rounded; occasionally a slight enlargement on ventral edge about half the distance from apex; in dorsal view horns subparallel to slightly diverging to slightly curved toward one another; bases not appreciably joined across disc in an arc except in smaller specimens. Minors (Fig.

52): True minors not seen. Intermediate specimen illustrated similar to majors except horns reduced. Very small individuals presumably with typical reduction in armature and increase in sculpturing. *Elytra:* Sutrual stria impressed, crenulate. Disc aciculate, sparsely punctate; punctures small, deep. Sides similar except with 2 short rows of ocellate-umbilicate punctures behind humerus; punctures moderately large, shallow, rows occasionally reduced. Apex densely punctate; punctures sparse to moderate in density, small, shallow. *Pygidium:* Convex in lateral view. Disc finely subgranulate, virtually impunctate to very sparsely punctate; punctures small, shallow, more distinct on apical margins and midline of disc. Anterior margins occasionally with a narrow band of rugosity either side of middle. *Genitalia:* Figs. 136–137.

Female.—Apparently unknown.

Biology.—Unknown.

Distribution.—Colombia.

Locality Records (Fig. 8).—9 specimens examined (all males.) Specimens were seen from the following collections: AMNH, BMNH, UNC, USNM.

COLOMBIA (9).—CUNDINAMARCA (3): Bogotá (?), Fusa(gasuga ?); SANTANDER (4): La Cimitarra (about 80 km. NW. Velez); No data (2). March (4), May (2), October (1), November (1).

Remarks.—The completely punctate mesosternum, lack of rows of punctures on the elytral disc, presence of 2–3 short rows of moderate to large ocellate punctures behind the humerus, and the slightly expanded and weakly excised apex of the anterior horn will easily separate this species. It is very closely related to *S. jugurtha* but cannot be confused with it because *S. jugurtha* lacks the expanded and excised apex of the anterior horn. *S. fascinus* is not commonly represented in collections and seems to be rarely collected.

Strategus hipposiderus, new species
(Figs. 7, 9, 53–54, 138–139)

Type Material.—Holotype male, labeled "Valley of Rio Deseads, Nicaragua, April, 1931, C. D. Curran"; deposited at USNM. Allotype female, labeled "Hamburg Farm, Reventazon, Limón, Costa Rica, May 3, 1928, F. Nevermann"; deposited at USNM. Also four male and 11 female paratypes deposited in the following collections: AHCC, AMNH, BCRC, BMNH, DEUN, FMNH, HAHC.

Holotype (Figs. 53–54).—Male. Length 52.7 mm; width across humerus 25.5 mm. Color piceous, shining. *Head:* Front rugose, setae above eye absent (probably worn off). Clypeus with apex broadly truncate, shallowly emarginate, moderately reflexed; surface aciculate, moderately punctate; punctures small, very shallow. Tubercles conical, strong, widely separated. Mandibles with basal lobe small, very prominently rounded; middle lobe large, triangular, apex rounded; apical lobe similar to basal lobe. Interocular width 2.5 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide rugose band; band reduced almost to basal bead at middle. Disc aciculate, sparsely punctate; punctures small, shallow. Sides as disc except a small patch of rugosity at base of posterior horns. Anterior angles and fovea either side of longitudinal ridge rugose. Fovea deep. *Horns:* Anterior short, stout, attenuate, curving forward and upward, apex narrowly rounded, dorsal surface flattened. Posterior horns very short, laterally compressed, reduced to large, prominent, subtriangular bosses; in lateral view dorsal surface slopes backward and downward from a rounded apex, anterior surface vertical; in dorsal view horns divergent. *Elytra:* Sutural stria strongly impressed, crenulate. Disc aciculate, sparsely punctate; punctures small and minute mixed, shallow; 3 shallow, incomplete striae on lateral half of disc; 5 large, ocellate punctures in a slight depression just medial of humerus at extreme base. Sides similar except wrinkled, striae absent; 2 very feeble rows of ocellate punctures behind humerus; punctures sparse, moderate in size, shallow, becoming smaller posteriorly, a few weakly umbilicate. Apex sparsely punctate; punctures small, shallow. *Pygidium:* In lateral view basal half convex, apical half nearly flat. Disc finely subgranulate, aciculate, very sparsely punctate; punctures small, shallow, becoming

slightly more numerous near apical margin either side of midline; 1 setigerous puncture in a slight depression near center of disc. Apical margin either side of midline with a very narrow, feeble, rugose band. *Genitalia:* Figs. 138–139.

Allotype.—Female: Length 50.4 mm; width across humerus 24.1 mm. As holotype except in the following respects: *Head:* Clypeus with apex subacutely rounded; surface rugose. Tubercles transverse. Mandibles with basal lobe as in holotype but slightly larger; middle lobe short, triangular, apex rounded; apical lobe similar to basal lobe. Interocular width 2.0 transverse eye diameters. *Pronotum:* Disc sparsely punctate; punctures small and minute mixed, shallow. Sides and anterior half rugose; a slightly depressed, rounded patch of rugosity just postero-lateral of fovea. Fovea deep. Tubercle strong, conical, transverse. *Elytra:* Disc with punctures as holotype to slightly larger and denser; 2 very feebly impressed, incomplete striae on lateral half; several moderately large, ocellate, confluent punctures just medial of humerus at extreme base. *Pygidium:* In lateral view basal half convex, apical half concave. Disc finely subgranulate, not aciculate, densely punctate; punctures moderate to moderately large, round to oblong, shallow. Apical margins either side of midline rugose, sparsely setigerous; lateral emargination shallow.

Variation.—Males (4 paratypes): Length 48.0–54.0 mm; width across humerus 22.2–26.2 mm. *Head:* Clypeus as holotype to weakly rugulose. *Pronotum:* As holotype to sides with lateral margin rugose in a narrow band in basal half; a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior half rugose. *Horns:* Anterior as holotype to very short, conical, erect. Posterior horns as holotype to very low, rounded bosses. *Elytra:* Disc and sides subgranulate, discal striae reduced to 2, rows of punctures behind humerus more distinct to virtually effaced. *Pygidium:* Disc with a shallow, median, longitudinal depression from center to apex; punctures becoming moderately dense medially; 3–4 large setigerous punctures on disc; apical band of rugosity slightly wider. *Genitalia:* Moderate variation in degree of arcuateness in parameres.

Females (11 paratypes): Length 47.7–55.6 mm; width across humerus 22.4–26.4 mm. *Head:* Front rugose to rugo-punctate, setigerous above eye in unworn specimens. Clypeus with apex subacutely rounded to narrowly subtruncate, occasionally weakly emarginate, strongly reflexed. Interocular width 2.0–2.2 transverse eye diameters. *Pronotum:* Disc as allotype to moderately densely punctate; minute punctures fewer, several large punctures at midline. *Elytra:* Disc with minute punctures very sparse, 3 feebly impressed striae on lateral half, 1–3 very short rows of moderately large, ocellate punctures at extreme base just medial of humerus. Sides with 1–3 short rows of punctures; punctures as in allotype. *Pygidium:* Disc rugo-punctate to rugose, rarely sparsely punctate, sparsely setigerous in unworn specimens. Apical margin moderately setigerous.

Biology.—Unknown. Label data indicate specimens have been taken at lights in Costa Rica and in the trunks of the coconut palm (*Cocos nucifera* L.) in Brazil.

Distribution.—Southern Mexico to Panama, Colombia, and Brazil. The single specimen from Brazil and the two records from Colombia establish a very disjunct distribution. I believe the validity of the Brazilian record is suspect.

Locality Records (Figs. 7, 9).—18 specimens examined (6 males, 12 females). Specimens are deposited in the following collections: AHCC, AMNH, BCRC, BMNH, DEUN, FMNH, HAHC, USNM.

BRAZIL (1).—BAHIA (1): Bahia.

COLOMBIA (2).—CAQUETA (1): Caucaya SE. Tres Esquinas on Rio Putumayo; No data (1). May (1), December (1).

COSTA RICA (11).—LIMÓN (10): Guápiles, Hamburg Farm (Reventazón), Las Mercedes, Pandora; No data (1). March (1), May (2), June (2), August (3), September (1), December (1).

MEXICO (1).—OAXACA (1): Juquila Mixes. July (1).

NICARAGUA (1).—RIO SAN JUAN (1): Valley of Rio Deseads (sic). April (1).

PANAMA (2).—CANAL ZONE (2): Madden Dam. July (1), November (1).

Remarks.—The males of *S. hipposiderus* and the larger, darker forms of *S. aloeus* are virtually identical externally, and examination of the genitalia is required to separate them; fortunately, the genitalia of the two species are vastly different and cannot be confused. Difficulties may also arise when separating males of *S. hipposiderus* from the minor forms of *S. mandibularis.* In general, however, *S. mandibularis* minors have only a narrow to moderate basal band of rugosity on the pronotum whereas it is always wide in *S. hipposiderus;* the punctures on the disc of the mentum are usually large in *S. mandibularis* and small to moderate in *S. hipposiderus,* and there are usually some large punctures on the disc of the pygidium in *S. mandibularis* and none in *S. hipposiderus.* In addition, the parameres of *S. hipposiderus* are normally shorter and form a broader arc than do those of *S. mandibularis,* but I have seen a few specimens of each where this distinction does not hold. The key characters will serve to separate the females of *S. hipposiderus, S. mandibularis,* and *S. aloeus.*

Etymology.—From the Greek *hipposideros,* a horseshoe; here named for the horseshoe-shaped form of the male genitalia as seen in caudal view.

Strategus howdeni, new species
(Figs. 6, 55–56, 140–141)

Type Material.—Holotype male, labeled "Mex: N.L.; Monterrey, Chipenque Mesa, 5400', 22.vi. 1969, S. & J. Peck, forest litter, Berl 64"; deposited in HAHC at CNCI. Allotype female with same data as holotype; deposited in HAHC at CNCI. Also one male paratype deposited in BCRC.

Holotype.—Male. Length 37.3 mm; width across humerus 19.0. Color piceous, shining. *Head:* Front rugose, setigerous above eye. Clypeus with apex rounded, strongly reflexed; surface rugose. Tubercles moderately strong, conical, transverse, weakly connected by a low, transverse carina. Mandibles with basal lobe small, prominently rounded; middle lobe moderate in size, subtriangular, apex rounded; apical lobe very small, rounded. Interocular width 2.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate, a few very sparse setae in posterior half. *Pronotum:* Base with a moderately wide rugose band; band reduced nearly to basal bead at midline. Disc aciculate, sparsely punctate; punctures small, deep. Sides in basal half as disc, punctures gradually becoming larger anteriorly; lateral margin with a narrow rugose band; a slightly depressed, rounded patch of rugosity on side of posterior horns. Anterior half of pronotum rugose. *Horns:* Anterior very short, stout, attenuate, slightly transverse, apex subtruncate. Posterior horns are strong, laterally compressed bosses; in lateral view dorsal surface slopes forward and slightly downward, anterior surface subvertical; in dorsal view horns parallel, bases joined across disc in an arc. *Elytra:* Sutural stria impressed, slightly wavy. Disc aciculate, sparsely punctate; punctures small and minute mixed, shallow; small punctures umbilicate on lateral ⅔, simple on median ⅓; 3 very feebly impressed, incomplete striae on lateral half. Sides wrinkled behind humerus, otherwise as disc except striae absent and all small punctures umbilicate. Apex densely punctate; punctures small and moderate mixed, shallow. *Pygidium:* In lateral view basal half convex, apical half nearly flat. Disc finely subgranulate, densely punctate; punctures small to large, shallow, occasionally confluent, setigerous apically either side of middle, setae small and fine. *Genitalia:* Figs. 140–141.

Allotype.—Female: Length 37.7 mm; width across humerus 18.0 mm. As holotype except in the following respects: *Head:* Front with supraocular setae more pronounced. Clypeus with apex narrowly truncate. Tubercles connected by a moderately strong, transverse carina. *Pronotum:* Disc with punctures slightly smaller. Tubercle strong, conical, transverse, apex truncate. *Elytra:* Sutural stria crenulate. Disc with 2 nearly obsolete striae and only a few scattered, umbilicate punctures. *Pygidium:* In lateral view basal half convex, apical half concave. Disc setigerous in a wide, irregular, median band; setae very small, fine.

Variation.—Single male paratype as holotype except in the following respects: Length 38.0 mm; width across humerus 19.3 mm. *Head:* Interocular width 2.75 transverse eye diameters. *Pronotum:* The slightly depressed area on side of posterior horns sparsely punctate instead of rugose, punctures moderate to large, shallow. *Horns:* Posterior horns in lateral view with dorsal edge subhorizontal, anterior edge sloping backward and upward; bosses not as developed as in holotype. *Elytra:* Sutural stria crenulate. Disc with 2 feebly impressed striae and only a few scattered umbilicate punctures. *Pygidium:* Surface aciculate, only moderately punctate.

Biology.—Unknown.

Distribution.—Chipenque Mesa, Monterrey, Mexico.

Locality Records (Fig. 6).—3 specimens examined (2 males, 1 female). Specimens deposited in BCRC and in HAHC at CNCI.

MEXICO (3).—NUEVO LEON (3): Chipenque Mesa (Monterrey). June (2), July (1).

Remarks.—The partially punctate mesosternum, distinctly lobed mandibles, the lack of rows of moderate to large punctures on the elytral disc or behind the humerus, the shining elytra, the simple and short anterior horn, the presence of a wide basal band of rugosity on the pronotum, the rounded clypeal apex, the absence of strongly developed posterior horns, and the small to moderate punctures on the elytra should serve to separate this species from all others. *S. howdeni* seems to exhibit most of the external features of the Mexican population of *S. aloeus* which is sympatric while the males possess genitalia which are very similar to *S. cessus* which is found further to the west. *Strategus howdeni* seems to be very much isolated in an oak-pine island mesa in a sea of desert scrub.

In late June, 1974, I undertook a collecting trip to Chipenque Mesa specifically to look for additional examples of *S. howdeni*. All levels of the mesa were collected using blacklight and sodium vapor street lights. *S. aloeus* were found in abundance (primarily at the lower levels of the mesa), but additional *S. howdeni* were not found. Quite possibly some sort of vertical isolation might occur between *S. aloeus* and *S. howdeni* as the latter were taken only near the summit of the mesa, but as of now I have no further information to substantiate this.

Etymology.—This species is named in honor of a friend and colleague, Henry F. Howden, who collected the paratype example and in whose collection I first found specimens.

Strategus inermis Arrow
(Figs. 2, 57–58, 142–143)

Strategus inermis Arrow, 1947: 223. [Holotype male at BMNH. Type locality: Haiti.]

Male (Holotype).—Length 33.0 mm; width across humerus 15.5 mm. Color piceous, shining. *Head:* Front densely punctate to rugo-punctate, punctures large, shallow, confluent, setigerous above eye. Clypeus with apex broadly truncate, moderately reflexed; surface densely punctate; punctures large, shallow, confluent. Tubercles conical, very feeble, transverse, widely separated. Mandibles with basal lobe feeble, hardly noticeable; middle lobe large, broadly rounded at nearly a right angle; apical lobe small, feeble, appearing as part of middle lobe. Interocular width 2.33 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a moderately wide band of dense punctures; punctures oval to oblong, deep, some confluent. Disc very finely subgranulate, aciculate, sparsely punctate; punctures small and minute mixed, shallow. Sides in basal half as disc, lateral margin with a moderately wide punctate band; punctures moderately dense, large, shallow, some cresent shaped, some confluent; a slightly depressed, irregular rugo-punctate to punctate patch postero-lateral of fovea; punctures cresent shaped, large, shallow. Anterior half rugose. Fovea shallow. *Horns:* Anterior a low, transverse, conical tubercle, apex emarginate. Posterior horns nearly obsolete. *Elytra:* Sutural stria impressed, crenulate. Disc finely subgranulate, aciculate, with 8 feeble rows of punctures; punctures ocellate, small to moderate, shallow, irregularly spaced; rows 3, 6, and 7 incomplete with punctures sparse, very small. Sides with 5

ill-defined, confused rows of punctures; punctures ocellate, small to large, shallow. Apex densely punctate to rugo-punctate. *Pygidium:* Convex in lateral view. Disc finely subgranulate, densely punctate in a broad, irregular, median band; punctures setigerous, shallow, becoming reduced apically. *Genitalia:* Figs. 142–143.

Female.—Unknown.

Biology.—Unknown.

Distribution.—Haiti.

Locality Records (Fig. 2).—One male specimen examined (holotype). Deposited at BMNH.

HAITI (1).—No data (1).

Remarks.—The partially punctate mesosternum, feebly lobed mandibles (as opposed to square in dorsal view), presence of rows of moderate to large punctures on the elytral disc, broadly truncate clypeal apex, shining elytra, absence of posterior horns, and the presence of a setigerously punctate band on the midline of the pygidium will separate *S. inermis* from all other species. The holotype is the only known specimen of this species.

Strategus jugurtha Burmeister
(Figs. 7, 9, 59–62, 144–145)

Strategus jugurtha Burmeister, 1847: 131. [Lectotype male and lectoallotype female (designated by Endrödi, 1973a) at Martin Luther Universität, Halle, German Democratic Republic. Also two male and two female paralectotypes at Halle. Type locality: Colombia.]

Male.—Length 24.5–39.8 mm; width across humerus 12.2–18.5 mm. Color castaneous to piceous, shining. *Head:* Front behind tubercles strongly rugose in majors, less so to feebly rugose in minors; middle of front nearly impunctate; setigerous above eye. Clypeus with apex acutely pointed to acutely rounded, occasionally produced into an acute or rectangular tooth, moderately reflexed; surface aciculate, weakly rugo-punctate to sparsely punctate; punctures small to moderate, shallow. Tubercles conical, moderately strong, usually distinctly separated. Mandibles with basal lobe small, prominently rounded; middle lobe moderately large, triangular, apex rounded; apical lobe very small, triangular. Interocular width 2.0–2.66 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pronotum:* Base with a narrow to obsolete rugo-punctate to rugose band; band reduced to basal bead medially. Disc aciculate, sparsely punctate; punctures very small, deep, rarely with a few large punctures on midline. Sides as disc to punctures slightly larger, lateral margin frequently with a rugo-punctate to rugose band in basal half; minors rugose in anterior half and with a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior half as disc in majors, usually rugose in minors. Fovea deep, median longitudinal ridge from base of anterior horn very low and broadly rounded, not prominent. *Horns:* Majors (Figs. 59–60) with anterior long, slender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface rounded to nearly flat, when flat weakly and longitudinally carinate on lateral margins and occasionally on midline. Posterior horns long, slender (slightly more robust than anterior horn). Attenuate, laterally compressed, apex narrowly rounded, extending forward and upward at about 20–65° from plane of disc, not posteriorly recurved apically; in dorsal view horns subparallel to curved toward one another, bases joined across disc in a weak arc in all but the largest specimens, and then arc very indistinct. Minors (Figs. 61–62) with anterior as in major except very short, dorsal surface rounded. Posterior horns reduced to low pyramidal bosses; in lateral view dorsal surface horizontal to sloping forward and downward, anterior surface subvertical to sloping upward and slightly backward; in dorsal view bosses laterally compressed, bases joined across disc in an arc. *Elytra:* Sutural stria impressed, crenulate. Disc finely subgranulate, aciculate, sparsely punctate, punctures very small to minute, shallow, some occasionally raised; 1–3 feebly impressed striae on lateral half present or not. Sides as disc except striae absent, punctures slightly larger to moderate on lateral margin; 2 (rarely 3) short rows of large punctures behind humerus; punctures usually ocellate, simple to umbilicate, deep. Apex sparsely to moderately punctate, punctures

small to moderate, setigerous. *Pygidium:* Convex in lateral view, apical half often nearly flat. Disc finely subgranulate, aciculate, very sparsely punctate; punctures minute or minute and moderate mixed, shallow. Apical margin either side of middle with punctures slightly larger, or weakly rugulose in a narrow band, not setigerous. *Genitalia:* Figs. 144–145.

Female.—Length 25.0–36.5 mm; width across humerus 12.3–17.3 mm. As male except in the following respects: *Head:* Front entirely rugose. Clypeus with apex acutely rounded, more broadly so in worn specimens; surface weakly to strongly rugose. Tubercles transverse, frequently connected by a feeble, transverse carina. Mandibles similar to those of male except middle lobe slightly smaller, apical lobe frequently a little larger. *Pronotum:* Base usually with a narrow rugose band; band reduced to basal bead at middle. Sides with a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior half rugose. *Pygidium:* In lateral view basal half convex, apical half weakly concave to nearly flat. Disc finely subgranulate, virtually impunctate to moderately punctate; punctures small to moderate, shallow, setigerous in unworn specimens. Lateral emargination very shallow to obsolete, occasionally weakly rugose.

Biology.—Basically unknown. Lamb (1974) reported that *S. jugurtha* attacks pineapple stems in Central and South America. Label data indicate that this species has been widely taken at lights, from agave in Colombia, pineapple in Costa Rica, and attacking the roots of African oil palm (*Elaeis guineensis* Jacq.) in Nicaragua.

Distribution.—Mexico through Central America to Colombia west of the Cordillera Orienta and Peru. The single Peruvian record is questionable.

Locality Records (Figs. 7, 9).—126 specimens examined (60 males, 66 females). Specimens were seen from the following collections: AHCC, AMNH, BMNH, CASC, CNCI, FMNH, HAHC, LACM, MCZC, PMNH, UNC, USNM.

COLUMBIA (26).—BOYACA (1): Miraflores; CUNDINAMARCA (2): Bogotá; HUILA (3): Gigante, Neiva; MAGDALENA (2): Aracataca; NORTE DE SANTANDER (3): Bucaramanga, Soata, Velez; VALLE (3): Anchicaya Dam (70 mi. E. Buenaventura); No data (1)). February (2), April (1), May (3), June (3), July (2), December (2).

COSTA RICA (12).—GUANACASTE (1): Finca Jiminez (near Taboga); LIMÓN (9): Guápiles, Las Mercedes, Reventazón, Siguirres; No data (2). April (4), May (5), July (1), September (1), November (1).

ECUADOR (6).—PICHINCHA (3): Santo Domingo; SANTIAGO-ZAMORA (1): no data; No data (2). August (5), October (1).

EL SALVADOR (9).—SAN SALVADOR (3): San Salvador; UNION (6): La Unión, Vol. Conchagua. May (9).

MEXICO (6).—CHIAPAS (1): Tuxtla Gutierrez; JALISCO (1): Casimiro Castillo; SINALOA (3): 6 mi. N. Mazatlán, Venedio, 28 mi. E. Villa Unión; VERACRUZ (1): Puente Nacional. June (3), July (2), August (1).

NICARAGUA (6).—CHONTALES (4): no data; No data (2). July (1), September (1).

PANAMA (60).—CANAL ZONE (38): Corozal, Cristóbal, Las Cascadas, Madden Dam; DARIÉN (16): Sante Fé; PANAMÁ (2): Panamá City; VERAGUAS (1): Santiago; No data (3). May (23), June (31), October (1).

PERU (1).—LORETO (1): Yarina Cocha (Ucayali River).

Remarks.—*Strategus jugurtha* can usually be quickly identified by the short setae on the apices of the elytra in combination with the large punctures behind the humerus. If the setae are worn off, this species may be confused with *S. surinamensis surinamensis,* in which case the key characters and the place of origin should be sufficient to separate the two. The Cordillera Orienta in northern Colombia and the Cordillera do Merida in western Venezuela seem to provide a distinct barrier between the two species.

Strategus longichomperus, new species
(Figs. 7, 63–66, 146–147)

Type Material.—Holotype male, labeled "San Andrés, 6/30/61" (= San Andrés Tuxtla, Vera-

cruz, Mexico); deposited at FMNH. Allotype female, labeled "Guatamala: Petén, Tikal, 18 Apr. 1956, at camp., E. M. Shock"; deposited at FMNH. Also six male and seven female paratypes deposited in the following collections: AMNH, BCRC, BMNH, CNCI, MCZC, SEBO ENDRÖDI, USNM.

Holotype.—Male. Length 45.6 mm; width across humerus 22.4 mm. Color piceous, shining. *Head:* Front behind each tubercle densely punctate; punctures large, shallow, some confluent; middle of front virtually impunctate, surface roughened. Clypeus with apex strongly reflexed, deeply and broadly excised by a triangular notch, lobes either side of emargination triangular; surface aciculate, sparsely punctate; punctures moderately deep, very shallow. Tubercles moderately strong, conical, transverse, weakly separated. Mandibles with basal lobe small, rounded; middle lobe large, elongate, triangular, apex rounded; apical lobe small, triangular. Interocular width 2.25 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow, rugose band; band reduced to basal bead at middle. Disc aciculate, sparsely punctate; punctures small, deep. Sides as disc except lateral margin in basal half with a few large, shallow punctures. Anterior half as disc. Fovea deep, median longitudinal ridge from base of anterior horn very low and broadly rounded, not prominent. *Horns:* Anterior long, subslender, attenuate, curving forward and upward, apex narrowly rounded, dorsal surface rounded. Posterior horns moderate in length, attenuate, robust, laterally compressed, projecting forward subhorizontally, apex rounded; in lateral view horns parallel, bases joined across disc in an arc. *Elytra:* Sutural stria strongly impressed, crenulate. Disc aciculate, sparsely punctate; punctures small, deep. Sides as disc except punctures slightly larger, wrinkling behind humerus, and with 2 short rows of ocellate-umbilicate punctures behind humerus; punctures large, shallow, median row forked. Apex sparsely punctate; punctures small, deep. *Pygidium:* Convex in lateral view. Disc finely granulate, aciculate, moderately punctate; punctures small, shallow, becoming denser apically either side of midline, a few scattered, large, shallow punctures medially. Apex with several moderate-sized, setigerous punctures; setae long. *Genitalia:* Figs. 146–147.

Allotype.—Female. Length 41.7 mm; width across humerus 19.5 mm. As holotype except in the following respects: Color more reddish. *Head:* Front completely rugose. Clypeal apex with a small, triangular notch; surface rugose. Mandibles similar to those of holotype but smaller, especially middle lobe; middle lobe with apex acutely rounded. *Pronotum:* Disc very sparsely punctate; punctures small to minute. Sides rugose; a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior third rugose. Fovea deep. Tubercle very low, conical, transverse. *Elytra:* Disc with punctures very small, extremely shallow to obsolete, some almost in rows. *Pygidium:* In lateral view basal half convex, apical half concave. Disc finely subgranulate, densely and completely setigerously punctate; punctures moderate to large, shallow, setae long; lateral emargination very shallow.

Variation.—Males (6 paratypes): Length 35.4–48.4 mm; width across humerus 16.3–23.3 mm. *Head:* Front as holotype to rugose in minors. Clypeus as holotype except minors with apex weakly and broadly emarginate; surface rugose. Interocular width 3.0 transverse eye diameters in minors. *Pronotum:* As holotype except minors with a narrow, punctate to rugo-punctate band on lateral margin in basal half. Anterior half rugose. *Horns:* Majors (Figs. 63–64) with anterior as holotype to apex weakly and minutely emarginate in 1 paratype. Minors (Figs. 65–66) with anterior a strong, transverse, conical tubercle. Posterior horns virtually effaced. *Elytra:* Disc frequently with 2 feebly impressed, incomplete striae. Sides with a short, median, third row of ocellate-umbilicate punctures; minors with lateral rows of ocellate-umbilicate punctures nearly obsolete. *Pygidium:* Disc on midline with an irregular, longitudinal, narrow to wide band of setigerous punctures, setae long; remainder of disc without setigerous punctures. Apical margins occasionally rugo-punctate to rugose in a wide band, setigerous.

Females (7 paratypes): Length 37.4–43.1 mm;

width across humerus 17.0–20.5 mm. Color as holotype to more reddish as allotype. *Head:* Front densely punctate, punctures large, shallow, confluent. Mandibles as allotype to apex of middle lobe not as acute, more rounded. Interocular width 2.0–2.5 transverse eye diameters. *Pronotum:* Base with rugose band very narrow to obsolete. Sides with basal half as disc except punctures slightly larger and denser, a narrow rugose band on lateral margin. Tubercle very low and rounded to strong and conical. *Elytra:* Disc with punctures minute to small, very shallow to moderately deep, occasionally with 2 feebly impressed, incomplete striae. Sides as allotype to rows of ocellate-umbilicate punctures obsolete in largest specimens. *Pygidium:* Disc with punctures reduced to moderate in density in largest specimens.

Biology.—Unknown.

Distribution.—Central America.

Locality Records (Fig. 7).—15 specimens examined (7 males, 8 females). Specimens deposited in the following collections: AMNH, BCRC, BMNH, CNCI, FMNH, MCZC, SEBO ENDRÖDI, USNM.

GUATAMALA (5).—EL PETÉN (3): Tikal; No data (2). April (3), May (1).

HONDURAS (2).—ATLÁNTIDA (2): La Ceiba. April (1), July (1).

MEXICO (8).—CHIAPAS (2): Palenque; TAMAULIPAS (3): Ciudad Victoria, El Salto Falls (26 mi. W. Antiguo Morelos); VERACRUZ (3): Dos Amates (Catemaco), Lake Catemaco, San Andrés Tuxtla. May (1), June (3), July (1), August (3).

Remarks.—The key characters will serve to separate *S. longichomperus* from all other *Strategus,* although the deeply excised clypeal apex, the very elongate mandibles, and the subvertical posterior horns in the males will be immediately noticed. *S. longichomperus* is the only species in the genus where the female possesses a triangularly notched clypeal apex.

Etymology.—From the Latin *longus,* meaning long, and from the American slang "chompers" meaning teeth; here descriptively named in reference to the very elongate middle lobe of the mandibles.

Strategus mandibularis Sternberg
(Figs. 9, 67–70, 148–149)

Strategus mandibularis Sternberg, 1910: 99. [Holotype male at ZMHU. Type locality: Montes Claros, Minas Gerias, Brazil.]

Male.—Length 51.4–57.5 mm; width across humerus 24.0–27.0 mm. Color piceous, shining. *Head:* Front grossly rugo-punctate to rugose, weakly setigerous above eye in unworn specimens. Clypeus with apex broadly truncate, strongly reflexed; surface rugulose to coarsely punctate; punctures large, confluent, and shallow, or sparsely punctate; punctures small, deep. Tubercles conical, moderately strong, transverse, distinctly (but not widely) separated. Mandibles with basal lobe small, rounded; middle lobe large, triangular, apex rounded; apical lobe small, triangular. Interocular width 2.5 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a wide band of rugosity; band reduced to basal bead at middle. Disc aciculate, feebly roughened to finely granulate, sparsely punctate; punctures small, deep. Sides similar except punctures a little larger and denser laterally; lateral margin with a narrow punctate to rugo-punctate band in basal ⅔; base of posterior horns usually with an irregular, slightly depressed, punctate to rugo-punctate area. Anterior third as disc in majors, rugose in minors. Fovea shallow, median longitudinal ridge from base of anterior horn strong, rounded to keel-like. *Horns:* Majors (Figs. 67–68) with anterior long, slender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface rounded to subcarinate. Posterior horns long, slender, attenuate, laterally compressed, extending forward and upward at about 65–75° from plane of disc, apex narrowly rounded; in dorsal view horns subparallel to strongly curving toward one another, bases not forming a distinct arc across disc. Minors (Figs. 69–70) with anterior similar to majors but very short. Posterior horns reduced to prominent, triangular bosses. *Elytra:* Sutural stria strongly

impressed, crenulate. Disc aciculate, sparsely punctate, punctures small and minute mixed, very shallow to deep, occasionally some slightly raised; 2–3 very feebly impressed striae on lateral half present or not. Sides similar except 2–3 very weak rows of moderate sized, shallow punctures behind humerus, rows occasionally effaced; striae lacking. Apex moderately punctate; punctures small to moderate, shallow. *Pygidium:* Convex in lateral view. Disc finely subgranulate, aciculate, sparsely punctate; punctures minute to small, shallow; occasionally a strong, median band of large punctures present; punctures dense, oval to oblong, shallow, setigerous. Apical margins either side of middle rugo-punctate in a narrow band to moderately densely punctate; punctures small to moderately large, shallow, simple to oblong, sparsely setigerous in unworn specimens; setae long. *Genitalia:* Figs. 148–149.

Female.—Length 51.2–52.2 mm; width across humerus 24.3–24.7 mm. As male except in the following respects: *Head:* Clypeus with apex narrowly truncate; surface rugose. Mandibles similar to those of male but smaller, especially middle lobe. Interocular width 2.75 transverse eye diameters. *Pronotum:* Base with rugose band narrow to wide. Sides rugo-punctate to rugose in basal third, anterior ⅔ rugose; a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior half rugose. Fovea moderately deep. Tubercle conical, strong, slightly transverse. *Elytra:* Disc at base just medial of humerus with 1–4 very short, confused rows of punctures; punctures ocellate-umbilicate, small to large, dense, shallow. Sides behind humerus usually with 4 short, irregular rows of punctures; punctures ocellate-umbilicate, small to large, shallow; rows occasionally reduced or obsolete. *Pygidium:* In lateral view basal half convex, apical half concave. Surface entirely rugose, densely setigerous.

Biology.—Unknown.

Distribution.—Argentina, Brazil, and Paraguay.

Locality Records (Fig. 9).—9 specimens examined (4 males, 5 females). Specimens were seen from the following collections: UC, USP, ZMHU.

ARGENTINA (2).—MISIONES (2): Loreto. December (2).

BRAZIL (5).—GOIAS (2): 20 km. N. São João da Alianca; MINAS GERIAS (1): Montes Claros; SANTA CATARINA (1): Rio Vermhelho; SÃO PAULO (1): Ararquara. March (1), April (1), May (2).

PARAGUAY (2).—BOQUERÓN (1): Gran Choco; GUAIRA (1): Puerto Suayra (Villarrica). June (1).

Remarks.—The male of *S. mandibularis* and *S. validus* are similar, but *S. mandibularis* can be quickly separated by its large, middle mandibular lobe, the wide band of rugosity at the base of the pronotum, and the usually more punctate pygidium. Male minors of *S. mandibularis* might be confused with *S. hipposiderus,* but the genitalia of each are diagnostic. See also the remarks for *S. hipposiderus.* The key characters will adequately separate the females. The females up until this time were apparently unknown and are here recognized and described for the first time.

Strategus mormon Burmeister
(Figs. 6, 71–72, 150–151)

Strategus mormon Burmeister, 1847: 130. [Holotype male at MNHN (Oberthür Collection). Type locality: Texas.]

Male.—Length 25.0–29.2 mm; width across humerus 13.6–15.8 mm. Color dark castaneous, occasionally piceous, shining. *Head:* Front rugo-punctate to coarsely punctate; punctures small to moderately large, dense, shallow, confluent; setigerous above eye. Clypeus with apex very acutely pointed; surface aciculate, weakly rugo-punctate to densely punctate; punctures small to moderately large, shallow, becoming smaller and denser laterally. Tubercles conical, transverse, very weak to virtually effaced. Mandibles with basal lobe small, rounded; middle lobe very long, slender, apex acutely pointed; apical lobe small, triangular. Interocular width 3.0–3.5 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pro-*

notum: Base with a very narrow, sparsely punctate band; punctures small to moderately large, shallow, oval to oblong; band reduced nearly to basal bead at midline. Disc aciculate, sparsely punctate; punctures small and minute mixed, shallow. Sides similar to disc except lateral margin with a narrow band of sparse punctures; punctures small to moderately large, shallow, occasionally setigerous at middle in unworn specimens, becoming rugose in anterior angles; a slightly depressed, rounded, punctate area postero-lateral of fovea; punctures small to moderate, dense to nearly obsolete, shallow. Anterior margins rugose, rugosity frequently extending postero-medially into fovea. Fovea moderately deep, only occasionally weakly divided by a feeble, longitudinal, median carina extending posteriorly from base of anterior horn. *Horns:* anterior conical to very short, slender, attenuate, transverse, curving forward and upward, apex narrowly rounded to minutely emarginate. Posterior horns are weak to very prominent triangular bosses; in lateral view dorsal edge slopes forward and downward *to* apex in undeveloped specimens, and backward and downward *from* apex in developed specimens, anterior edge slopes backward and upward in undeveloped specimens and is subvertical in developed individuals; in dorsal view bosses laterally compressed, parallel, bases joined across disc in an arc. *Elytra:* Sutural stria weakly to moderately impressed, subcrenulate. Disc aciculate, very sparsely punctate; punctures minute and small mixed, shallow; 2–3 very feebly impressed, incomplete striae on lateral half, striae subgranulate. Sides as disc except striae absent. Apex densely punctate; punctures small to moderate, shallow, with very short setae in unworn specimens. *Pygidium:* Convex in lateral view. Disc finely subgranulate, very sparsely punctate; punctures moderate in size, very shallow. Apical margins either side of middle with punctures a little larger, denser, and deeper. *Genitalia:* Figs. 150–151.

Female.—Length 26.0–28.8 mm; width across humerus 13.5–15.0 mm. As male except in the following respects: *Pronotum:* Apical half moderately to densely punctate; punctures small to large, shallow, usually grading to rugo-punctate or rugose in apical third. Fovea shallow. Tubercle conical, weak to strong, transverse, apex usually weakly emarginate. *Pygidium:* In lateral view basal half convex, apical half concave. Disc with punctures occasionally large. Apical margins moderately to densely punctate; punctures simple to oblong, shallow.

Biology.—Knaus (1916) observed *S. mormon* burrows under and adjacent to horse droppings in Kansas and indicated that burrow shafts were vertical or inclined up to 15° and that they varied from 4–12 inches in depth. A mass of dung 1.25–1.50 inches in diameter and several inches long was found in a burrow under 3–4-week-old horse manure; seven white eggs measuring 2–3 mm in diameter were found in the dung. Other similar burrows were found by Knaus who suggested that this species prefers horse droppings 1–3 weeks old; *S. mormon* burrows were never associated with cow manure although Knaus later mentions that he did find a dead female with an associated burrow under cow manure. In a later paper Knaus (1924) concluded, after examining many burrows, that the male appears 5–15 days before the female and prepares a burrow under horse manure, preferably selecting droppings 6–12 months old. The bottom of the burrow is enlarged to contain the larval provisions which consist of horse or cow manure obtained by the attracted female. Several eggs are deposited in the food mass after which the adults leave the burrow. If true, the apparent division of labor and burrow provisioning described (or generalized upon) by Knaus would be remarkable for dynastine scarabs which are not generally known for such behavior. More detailed observations are certainly needed to verify Knaus' conclusions.

Strategus mormon seem to be primarily arenicolous. This species is apparently relatively scarce in numbers, and field collecting and museum collections tend to support this view. In two days of very intense collecting at Medora, Kansas, in late May, 1972, I was able to obtain only one specimen at blacklight even though horse and cattle droppings were examined in large numbers.

Distribution.—Southcentral United States.

Locality Records (Fig. 6).—186 specimens

examined (91 males, 95 females). Specimens were seen from the following collections: AMNH, BCRC, CASC, CNCI, DEUN, FMNH, HAHC, KSUC, LACM, MCZC, OSUC, OSUO, PMNH, SEMC, UMMC, USNM.

UNITED STATES (186).—ARKANSAS (2): *Benton (1):* Bentonville; *Pope (1):* Russelville. KANSAS (142): *McPherson (2):* 18 mi. S. McPherson; *Reno (129):* Medora, Sylvia; *Rice (1):* 8 mi. S. Little River. OKLAHOMA (39): *Delaware (1):* Jay; *Kingfisher (1):* Kingfisher; *Mayes (2);* Chatou; *Murray (1):* Sulphur; *Muskogee (2):* Muskogee; *Oklahoma (1):* Norman; *Pawnee (4):* no data; *Payne (23):* Stillwater; *Pottawatome (2):* Shawnee; *Tulsa (1):* Tulsa; *No data (1).* TEXAS (3): *Bexas (1):* San Antonio; *No data (2).* March (1), April (1), May (29), June (134), July (11).

Remarks.—This species is easily recognized by its very long, slender, acute middle lobe of the mandibles in conjunction with a completely, setigerously punctate mesosternum. The males do not display what could be accurately termed major and minor development of pronotal armature although minor differences in horn length do exist.

Strategus oblongus (Beauvois)
(Figs. 2, 73–76, 152–153)

Scarabaeus oblongus Beauvois, 1807: 74. [Types unknown to me. Type locality: Dominican Republic.]

Scarabaeus quadrifoveatus Beauvois, 1807: 74. [Types unknown to me. Type locality: Dominican Republic.]

Scarabaeus beauvoisi, **New name.** [Replaces *Scarabaeus dubius* Beauvois, 1819: 209, which is a primary junior homonym with *Scarabaeus dubius* Beauvois, 1811: 104 (a *Dyscinetus* sp.) which, in turn, is a primary junior homonym with *Scarabaeus dubius* Olivier, 1789: 32 (also a *Dyscinetus* sp.). Types unknown to me. Type locality: Dominican Republic.] **New synonymy.**

Male.—Length 35.0–58.8 mm; width across humerus 18.0–27.8 mm. Color piceous to black (rarely castaneous), shining. *Head:* Front coarsely rugo-punctate to rugose, occasionally very reduced in especially large individuals. Clypeus with apex strongly reflexed, very broadly truncate, frequently with a very shallow, triangular emargination; surface in majors punctate; punctures moderately dense, small, shallow; surface in minors coarsely rugo-punctate to rugose. Tubercles conical, low, transverse, usually distinctly separated. Mandible with basal lobe small, prominently rounded; middle lobe large, triangular, apex rounded; apical lobe small, subtriangular. Interocular width 2.0–2.5 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow to moderately wide rugose band; band reduced to basal bead at midline. Disc aciculate, sparsely punctate; punctures small, deep. Sides similar except minors usually with a feeble, sparsely punctate band on lateral margin; punctures large, round to oblong. Anterior portion of pronotum as disc in majors; minors with anterior ¼–⅓ rugose or rugose in a band from anterior angles postero-medially into fovea. Fovea deep; longitudinal median carina extending posteriorly from base of anterior horn nearly obsolete. *Horns:* Majors (Figs. 73–74) with anterior long, subslender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface weakly convex to flattened. Posterior horns long, stout, attenuate, laterally compressed, extending forward and upward at about 25–45° from plane of disc, apex narrowly rounded; in dorsal view horns parallel or curving toward one another, bases weakly joined across disc in an indistinct arc. Minors (Figs. 75–76) with anterior as majors except short, stout. Posterior horns nearly obsolete to prominent, acute, laterally compressed, pyramidal bosses; the latter in lateral view with dorsal surface sloping forward and downward *to* apex or backward and downward *from* apex, anterior surface vertical to subvertical; in dorsal view horns subparallel, bases joined across disc in an arc. *Elytra:* Sutural stria strongly impressed, distinctly crenulate to wavy. Disc aciculate, finely subgranulate, sparsely punctate; punctures small and minute mixed, deep, rarely slightly raised; usually 2 feebly impressed, incomplete striae on lateral half. Sides as disc except punctures slightly larger to moderate in size, frequently a short row of 1–10

moderate to large, very shallow punctures behind humerus, and striae absent. Apex moderately punctate; punctures small, deep. *Pygidium:* In lateral view basal ¾ convex, apical ¼ concave. Disc finely subgranulate, sparsely to moderately densely punctate; punctures small to moderate, shallow when sparse, very shallow to nearly effaced when dense. Apical margins rugose either side of middle; lateral emargination shallow. *Genitalia:* Figs. 152–153.

Female.—Length 39.4–48.2 mm; width across humerus 18.3–22.3 mm. As male except in the following respects: *Head:* Front rugose, setigerous above eye in unworn specimens. Clypeus with apex broadly truncate to narrowly rounded. Mandibles similar to those of male but smaller. *Pronotum:* Base with a very narrow rugose band; band reduced at middle almost to basal bead. Sides with a narrow rugo-punctate to rugose band on lateral margin in posterior half; a similar, but very wide, band of rugosity in anterior half; frequently a small, slightly depressed, punctate to rugose patch lateral of base of fovea; punctures moderate to large, sparse to dense, round to oblong to crescent shaped. Anterior third rugose. Fovea moderate in depth. Tubercle conical, transverse, weak to moderately strong. *Pygidium:* In lateral view basal half convex, apical half concave. Apical margins with a wide, rugose band either side of middle.

Biology.—Plank (1945), in a verification and supplement to Smythe (1916, 1920), has given a detailed account of the life history of *S. oblongus* in Puerto Rico as follows: The eggs are large (2.9–3.1 × 3.7–4.0 mm), globular to oblong, with a smooth chorion, and are an opaque, ivory white when newly deposited. During incubation they become somewhat translucent and after 10 days assume a pearly white color which later changes to dull ivory. Eggs may expand while incubating; the largest egg seen was 4.5 × 5.4 mm two days before hatching. A total of 51 eggs were observed to have an incubation period of 13–34 days (average 16.8 days). Eggs with the shortest incubation periods were deposited in June and July; those with the longest were laid in February when temperatures were cooler.

The eggs may be scattered in the softer, decayed parts of loose wood but are more usually concealed in small cases of wood and humus. Wolcott (1948) noted that the eggs are also laid in the rotting trunks of dead palms which quickly collapse after the larvae feed on the interior. The larvae are about 10 mm in length when they hatch and have been seen to consume their egg shells and to eat cast skins. Tables 1 and 2 illustrate larval development.

TABLE 1
INSTAR DURATION IN DAYS FOR *S. oblongus*

Instar	No. Observed	Range	Average
1	48	46–144	73
2	9	90–240	145
3	6	180–240	210

TABLE 2
INSTAR MEASUREMENTS IN MM FOR *S. oblongus*

Instar	No. Observed	Head Capsule Width		Maximum Body Length
		Range	Average	
1	296	2.8–4.0	3.6	28.0
2	176	5.5–7.7	6.7	55.0
3	249	9.6–14.1	12.3	100.0

Larvae became cannibalistic when crowded and were also seen to chew through the bottom of tin-can rearing containers, thus giving some idea as to their mandibular strength. The larvae feed on the roots of deciduous trees and in moist, decaying tree stumps (Wolcott, 1949). Larvae have been taken from the following food hosts: *Cocos nucifera* L., *Citrus sinensis* (L.), *Inga inga* (L.), *Inga laurina* (Sw.), *Spathodea campanulata* Beauv., *Spondias* sp., and other palms. They have also been observed damaging the roots of young cacao trees (*Theobroma cacao* L.) in the Dominican Republic (Wolcott, 1926). Under certain conditions larvae fed on the rind of decaying coconut husks but not on the fibers. Larvae were unable to survive on sugar cane and old manure (Smythe, 1920).

The pre-pupal state in 18 specimens lasted from 12–20 days (average 18 days). The pupal period in 60 specimens ranged from 20–47 days (average 33 days). Newly emerged adults were

observed to remain in the pupal chamber 2–10 days (average four days) after eclosion.

The length of adult life ranged from 53 to 193 days (average 90 days) in 63 beetles. Adult male longevity was 61–128 days (average 96 days) in 29 specimens. Adult female longevity was 53–131 days (average 85 days) in 34 beetles. The total life span in *S. oblongus* may be as long as 16–18 months.

Plank noted that eggs were deposited nine days after the one observed mating, and oviposition continued for nine days; 10 eggs were deposited, and four well-developed eggs remained in the female when she died. All stages, except the egg, have been found in all months of the year.

Feeding habits and gut analyses demonstrated that the adults feed primarily on the juices of the plants they attack. Martorell (1945a) and Wolcott (1923, 1948) observed that adults occasionally burrowed into the stalks of sugar cane and injured young coconut palms by burrowing into the trunk and roots at ground level.

Natural enemies are apparently few in number. Nematodes attacked the eggs in the laboratory but were not seen in the field. The green muscardine fungus, *Metarrhizium anisopliae* (Metschn.), attacked some larvae. Martorell (1945b) observed that both the adults and immature stages are susceptible to attack by the fungus with the pupa being the most susceptable and the egg the least susceptible to attack. Predators include mites of the families Parasitidae and Tyroglyphidae as well as herons, owls, rats, poultry, hogs, and the mongoose. Martorell (1945b) noted that the mongoose, *Herpestes birmanicus* (Thomas), which feeds on the adults, might be the most important enemy of *S. oblongus*, while the Puerto Rican grackel, *Quiscalus niger brachypterus* (Cassin), is very efficient in consuming larvae when they are turned by plows in fields under cultivation.

Known as the coconut rhinoceros beetle, *S. oblongus* was a serious pest of coconuts in Puerto Rico (Martorell, 1945a; Plank, 1945) but was insignificant as a pest of sugar cane (Smythe, 1920). The principal damage results from adults feeding on germinal tissue and the growing point of palms. The adults have been taken a number of times injuring sugar cane; several individuals may congregate on one stool while those nearby are unharmed. Lodging may occur when a beetle bores into the stalk at ground level and tunnels upward 8–14 inches. The attempted use of dead palms for fence posts or anything else is impossible and actually hazardous to the palm groves because they may contain developing beetles within the palm logs. *S. oblongus* may become injuriously abundant a few years after destructive hurricanes unless the dead palms are cleared away (Wolcott, 1948). The regions of greatest wind damage (not necessarily those of the greatest coconut production) have usually been the areas suffering the most insect injury.

The severe cutting of the native forests has driven *Strategus* to live on sugar cane and palm trees and to become economically harmful. Wolcott (1936) lists several economic accounts and illustrates the larvae.

Distribution.—Grand Cayman Island, Hispaniola, Puerto Rico; not established on St. Croix (Miskimen and Bond, 1970). The short series of specimens from Grand Cayman is particulary interesting because they are reasonably disjunct in their distribution. The prevailing winds, currents, and storm paths, however, might easly account for establishment of *S. oblongus* on Grand Cayman from a Hispaniola source.

Locality Records (Fig. 2).—175 specimens examined (75 males, 100 females). Specimens were seen from the following collections: AMNH, BCRC, BMNH, CNCI, HAHC, MCZC, TAMU, USNM.

GRAND CAYMAN ISLAND (5).—GRAND CAYMAN (5): West end of Georgetown. May (1), July (4).

DOMINICAN REPUBLIC (41).—DISTRITO NACIONAL (1): Santo Domingo; LA VEGA (9): Constanza, Convento (12 km. S. Constanza), Jarabacoa, Rio Camu (19 km. NE. Jarabacoa); MONTE CRISTI (1): Monte Cristi; PERAVIA (3): Baní; PUERTO PLATA (2): Puerto Plata, Sosúa; SAMANA (9): Sánchez; SAN PEDRO DE MACORIS (5): San Pedro de Macoris; SANTIAGO (2): Santiago; No data (9). May (4), June (15), July (6), August (7), October (2).

HAITI (40).—OUEST (38): Port-au-Prince; No data (2). February (2), March (1), May (2), August (1), October (31).

PUERTO RICO (89).—AGUADILLA (6): Aquadilla, Anasco, Lares, Las Marias; ARECIBO (4): Arecibo, 5 mi. NE. Jayuya, Manati, Utuado; GUAYAMA (3): Aguirre, Aibonito, Caguas; HUMACAO (4): El Yunque Sta. (Luquillo Forest), Loiza Viejo, Luquillo, Rio Grande; MAYAGUËZ (52): Cabo Rojo, Maricao, Mayaguëz, San German, Yauco; PONCE (2): Adjuntas, Ponce; SAN JUAN (5): Bayamon, Corozal, Rio Piedras, San Juan, Toa-Baja; No data (13). January (6), February (6), March (4), April (3), May (6), June (5), July (7), August (5), September (13), October (10), November (1), December (12).

REMARKS.—The broadly truncate clypeus, narrow band of rugosity on the base of the pronotum, simple horns, and the lack of large, post-humeral or discal punctures will usually separate *S. oblongus* from all other species.

Arrow (1937a), in synonymizing *S. quadrifoveatus* with *S. oblongus,* was apparently not satisfied that *S. quadrifoveatus* was a *Strategus.* Indeed, Beauvois' illustration depicts a specimen lacking a fovea on an otherwise convex pronotum; in addition, the elytra possesses 2–3 striae. Without the type it is difficult to state positively that *S. quadrifoveatus* was a *Strategus,* but it will be so considered here. It is definitely strategid in its affinities and may simply be a female with a nearly obsolete pronotal fovea.

Although *S. quadrifoveatus* was described prior to *S. oblongus,* it is here formally designated that *Strategus oblongus* is the valid name for this taxon in order to maintain nomenclatural stability.

Strategus sarpedon (Burmeister)
(Figs. 2, 77–78, 154–155)

Podalgus sarpedon Burmeister, 1847: 122. [Types unknown to me. Type locality: Cuba.]

Male.—Length 19.9–28.2 mm; width across humerus 10.4–13.9 mm. Color castaneous to piceous, shining. *Head:* Front grossly punctate; punctures confluent, moderately large, shallow, occasionally reduced along midline; setigerous above eye in unworn specimens. Clypeus with apex rounded, moderately reflexed; surface rugo-punctate to weakly or moderately punctate; punctures confluent, shallow. Tubercles conical, very low to nearly effaced, transverse, usually widely separated although occasionally connected by a feeble, transverse carina. Mandibles with basal lobe small, rounded; middle lobe moderate in size, subobtusely to obtusely rounded; apical lobe very small, broadly confluent with middle lobe. Interocular width about 3.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a moderately wide, rugo-punctate to rugose band; band reduced nearly to basal bead medially. Disc aciculate, sparsely punctate; punctures small, moderately deep. Sides similar to disc except punctures slightly larger; lateral margin with a moderately wide, rugo-punctate to rugose band joined to basal band; frequently a rounded, slightly depressed area of moderate to large punctures just postero-lateral of fovea. Anterior ¼–⅓ rugose. Fovea shallow. *Horns:* Anterior a moderate to large, slightly transverse tubercle; apex narrowly rounded or narrowly truncate. Posterior horns completely lacking. *Elytra:* Sutural stria impressed, usually not crenulate. Disc aciculate, medial ⅓–½ sparsely to moderately punctate; punctures ocellate-umbilicate, moderate to large, shallow; lateral ½–⅔ usually with 6 rows of moderate to large, ocellate-umbilicate, shallow punctures, rows 1–2 and 4–5 closely adjacent, rows 3 and 6 sparsely punctate; rows occasionally reduced. Sides usually with 6 confused rows of punctures similar to those of disc. Apex moderately densely punctate; punctures small and moderate mixed, shallow. *Pygidium:* In lateral view basal half strongly convex, apical half weakly concave to nearly flat. Disc very finely granulate, sparsely to moderately punctate; punctures small, very shallow; disc occasionally becoming weakly rugo-punctate. Apical margins frequently rugo-punctate to rugose. *Genitalia:* Figs. 154–155.

Female.—Length 21.2–25.0 mm; width across humerus 10.9–12.5 mm. As male except in the following respects: *Head:* Front as male to weakly rugulose; setae above eye more pronounced. Clypeal apex slightly narrower and less

reflexed than in male. *Pronotum:* Tubercle virtually effaced. *Pygidium:* In lateral view basal half weakly convex.

Biology.—Essentially unknown. *S. sarpedon* has been taken on the roots and seed pieces of sugar cane (Stahl and Scaramuzza, 1929; Valdes, 1951). *Tiphia argentipes* Cresson (Hymenoptera: Tiphiidae) and *Campsomeris trifasciata* (Fabr.) (Hymenoptera: Scoliidae) are two known natural enemies (Valdes, 1951).

Distribution.—Cuba.

Locality Records (Fig. 2).—68 specimens examined (27 males, 41 females). Specimens were seen from the following collections: AMNH, BMNH, CNCI, HAHC, MCZC, SEMC, USNM.

CUBA (67).—CAMAGUEY (25): Baraguá, Jaronú, Jatibonico, Pilar, Santo Tomás Vertientes; HABAÑA (6): Cerro, Habaña, Santiago de Las Vegas, Vedado; LAS VILLAS (22): Cayamas, Cienfuegos; MATANZAS (8): Cárdenas; ORIENTE (1): Cristo; No data (5). March (1), April (3), May (36), June (16), July (3), September (1), October (1).

Remarks.—The partially punctate mesosternum, presence of rows of moderate to large punctures on the elytral disc, the rounded clypeal apex, shining elytra, length of less than 30 mm, and absence of horns on the pronotum will serve to separate this species from all others. *Strategus sarpedon* is the smallest species in the genus. The males are not dimorphic in the sense of having major and minor development of pronotal armature.

Although placed in *Scaptophilus* (= *Bothynus)* by Chevrolat (1865) and questioned by others as to its generic placement, *S. sarpedon* is indeed a true *Strategus.*

Strategus simson (L.)
(Figs. 1, 79–82, 156–157)

Scarabaeus simson L., 1758: 345. [Type material possibly lost; see remarks. Type locality: originally published as "America" but actually Jamaica.]

Scarabaeus titanus Fabr., 1775: 10. [Types unknown to me; they are not in the Hunter Collection at Glasgow. Type locality: originally published as "America" but here restricted to Jamaica.]

Scarabaeus simson Fabr., 1787: 5. [Redescription of Linnaeus' *simson.*]

Scarabaeus titanus Fabr., 1787: 6. [Redescription.]

Male.—Length 29.6–40.0 mm; width across humerus 14.0–20.0 mm. Color piceous, dull, not shining. *Head:* Front just behind tubercles rugose to rugo-punctate to very sparsely punctate; punctures small, shallow. Clypeus with apex slightly reflexed, truncate to subtruncate, occasionally with a feeble, triangular notch medially; surface in majors moderately to densely punctate; punctures small or large and confluent respectively, shallow; surface in minors rugose. Tubercle conical, very low to nearly obsolete, transverse, distinctly separated. Mandibles with basal lobe small, rounded; middle lobe moderate in size, subtriangular; apical lobe small, triangular. Interocular width 2.0–2.33 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Majors with base lacking a transverse band of sculpturing; entire pronotum finely granulate, weakly aciculate, sparsely punctate; punctures small, deep; fovea deep. Minors as majors except base with a very narrow, punctate band; punctures small to moderately large, sparse, oval to oblong, shallow; lateral margin of sides with a similar punctate band; a punctate to rugo-punctate band extending postero-medially from anterior angles; fovea deep. *Horns:* Majors (Figs. 79–80) with anterior long, slender, curving forward and slightly to strongly downward and then upward, apex strongly expanded and forked; horn shaft subrectangular in cross section, dorsal surface flat to slightly concave and longitudinally carinate on each lateral margin. Posterior horns long, slender, laterally compressed, attenuate, projecting forward subhorizontally at about 20° from plane of disc; apex acutely rounded; occasionally a slight ventral flaring just before apex in large individuals; in dorsal view horns subparallel with apices curving toward one another, bases joined across disc in an arc. Minors (Figs. 81–82) with anterior similar to major except short, projecting forward and upward, apex

weakly expanded or not, longitudinal carina on dorsal surface feeble to absent. Posterior horns short to subconical, otherwise as majors. *Elytra:* Sutural stria impressed, crenulate. Disc finely granulate, aciculate, sparsely punctate; punctures simple and ocellate-umbilicate mixed, the former small and minute mixed, deep, and the latter small to moderate, shallow, occasionally obsolete; usually 3 feebly impressed striae on lateral half of disc and usually a poorly defined to strong row of ocellate-umbilicate punctures mesad of each stria; punctures small to moderate, shallow. Sides similar to disc except without striae and usually with 2–3 ill-defined rows of ocellate-umbilicate punctures as on disc. Apex densely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc finely granulate, punctate; punctures sparse to moderate (frequently denser in minors), small, shallow. Apical margins either side of middle rugulose in minors, as disc in majors. *Genitalia:* Figs. 156–157.

Female.—Length 26.0–37.8 mm; width across humerus 13.8–19.0 mm. As male except in the following respects: *Head:* Front rugo-punctate to rugose. Clypeus with apex narrowly truncate in unworn specimens to narrowly rounded in worn specimens; surface rugose. Tubercles frequently a little larger than in male, and then weakly connected by a feeble, transverse carina. Interocular width 2.33–2.66 transverse eye diameters. *Pronotum:* Base with an extremely narrow, punctate to rugo-punctate band; band reduced to basal bead at middle. Sides just postero-lateral of fovea with a slightly depressed, rounded patch of moderately dense punctures; punctures moderate to large, oblong to crescent shaped, shallow; lateral margins usually with a wide, punctate to rugo-punctate band in basal half. Anterior third rugose. Fovea shallow. Tubercle very low, transverse, nearly obsolete. *Elytra:* Ocellate-umbilicate punctures usually less pronounced. *Pygidium:* In lateral view basal ¾ convex, apical ¼ concave; protuberant at middle. Disc completely and moderately densely punctate; punctures small to moderate, shallow. Apical margins rugulose; lateral emargination shallow.

Biology.—Gowdy (1923), in rather simplified and incomplete observations, noted the following life history: The eggs are laid singly in spherical cells of wood fiber formed by the adult in tunnels made by the males. The average number of eggs per female is 15. The average duration of incubation is 18 days. Larval development consists of three instars: the average length of the first instar is 42 days, the second 72 days, and the third 200 days. Larvae are usually found in decaying wood and in woody growth at the base of old sugar cane stools where they feed on rotted stems and other organic matter. Sugar cane may suffer considerable damage because of the underground feeding and cutting of cane roots by the larvae; the underground portion of living cane stems is usually not attacked. Larvae have also been found in manure. Mature larvae form pupal cells of wood fiber or soil and undergo a pre-pupal stage of from several days to two weeks. The average length of pupation is 25 days. After emerging, adults remain in the pupal cells about seven days before burrowing out. Adult food consists of the green parts of trees and occasionally sugar cane.

In addition to damaging sugar cane (Edwards, 1939; Gowdy, 1923), label data indicate that *S. simson* has been taken from banana cargos arriving at New York and Washington, D.C. Chapin (1932b) suggested that they might possibly be of economic interest in connection with the banana industry as specimens apparently enter the United States on bunches of the fruit.

Gosse (1848), in the only available note on natural enemies, found males in the stomachs of *Nyctibius griseus jamaicensis* (Gmelin) (Caprimulgiformes: Nyctibiidae).

Distribution.—Jamaica. Howden (1970) mentioned that this species was limited largely to lowland areas.

Locality Records (Fig. 1).—68 specimens examined (20 males, 48 females). Specimens were seen from the following collections: AMNH, BMNH, CNCI, FMNH, HAHC, MCZC, USNM.

JAMAICA (68).—CORNWALL (5): Balaclava, Malverne, Montego Bay, Munro College; MIDDLESEX (32): Brown's Town, Mandeville, Moneagne, Springfields; SURREY (19): Bath, Kingston, Port Antonio; No data (12). January (3), March (10), May (2), June (5), July (13), August (3), Sep-

tember (6), October (7), November (2), December (6).

Remarks.—*Strategus simson* is similar to *S. caymani, S. aenobarbus,* and *S. ajax,* but it is the only species of this group with well-developed posterior horns in the majors. Minors may be confused with these other species, but the key characters will separate them.

The type material for *S. simson* is apparently unknown. Chapin (1932b) was apparently of the belief that Linnaeus described *S. simson* based solely on the works of Browne (1756) and Sloane (1725) in which the beetle is figured (thus bringing up the interesting possibility that the current name is invalid because it was based on a hypothetical concept, i. e., the illustrations in Browne and Sloane; since there is no way to prove this, I believe the current name should remain valid). Landin (1956) reported three unlabeled specimens in the collection of the Linnaean Society in London, but there is no way of knowing whether these specimens are the original types. Although it is possible that these specimens may be the types, the lack of evidence dictates that the types remain unknown. I do not feel that a neotype is necessary.

Westwood (1837) placed *S. simson* in junior synonymy with *S. titanus* but in the genus *Dynastes;* his figured specimens are clearly labeled Jamaica. *S. titanus auct.* most commonly referred to *S. talpa* in the literature up to the 1930s in reference to specimens from Puerto Rico or the Virgin Islands.

***Strategus splendens* (Beauvois)**
(Figs. 4, 83–84, 158–159)

Scarabaeus splendens Beauvois, 1809: 89. [Types unknown to me. Type locality: South Carolina, United States.]

Scarabaeus boscii Beauvois, 1809: 89. [Types unknown to me. Type locality: South Carolina, United States.]

Anastrategus cognatus Casey, 1915: 236. [Holotype female at USNM. Type locality: Kissimmee, Florida, United States.]

Anastrategus carolinensis Casey, 1915: 237. [Holotype female at USNM. Type locality: Southern Pines, North Carolina, United States.]

Male.—Length 25.0–31.5 mm; width across humerus 12.0–16.1 mm. Color castaneous, shining. *Head:* Front rugo-punctate to rugose, setigerous above eye. Clypeus with apex slightly reflexed, moderately to broadly truncate, occasionally with a weak, medial notch; surface feebly rugulose to rugulose-punctate. Tubercles conical, low to moderate, very transverse, occasionally connected by a weak, transverse carina. Mandibles with basal lobe small, rounded; middle lobe large, triangular, apex rounded; apical lobe small, triangular. Interocular width 3.5–4.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a narrow rugose band; band reduced at middle to basal bead. Disc finely roughened, aciculate, sparsely punctate; punctures small to moderate, shallow to deep. Sides in basal half similar to disc except punctures a little larger; apical half grading from crescent and oblong-shaped punctures to rugo-punctate anteriorly; a slightly depressed, rounded, rugo-punctate to rugose area just postero-lateral of fovea, this area occasionally obsolete. Anterior half rugo-punctate. Fovea shallow. *Horns:* Anterior a strong, erect, transverse tubercle, apex usually minutely emarginate. Posterior horns absent. *Elytra:* Sutural stria impressed, subcrenulate. Disc finely roughened to feebly subgranulate, aciculate, sparsely punctate; punctures small, shallow. Sides as disc except punctures slightly larger and more dense. Apex subrugose to very densely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc finely granulate, sparsely punctate; punctures small, shallow to extremely shallow, occasionally with a few sparse, moderate-sized punctures. *Genitalia:* Figs. 158–159.

Female.—Length 25.2–36.0 mm; width across humerus 11.5–18.1 mm. As male except in the following respects: *Head:* Front usually more strongly sculptured than in male. Clypeus as in male to apex broadly rounded. Mandibles similar to those of male except middle lobe smaller, apical lobe usually larger. *Pronotum:* Tubercle very low to nearly obsolete. *Pygidium:* In lateral view

basal ⅓ convex, apical ⅔ weakly concave to nearly flat. Apical margins either side of middle frequently with sparse, moderate sized punctures.

Biology.—Unknown. Label data indicate specimens have been taken on palms in Florida and injuring young palms in nursery stock. Ritcher (1944, 1966) has described the larva.

Distribution.—Southeastern United States.

Locality Records (Fig. 4).—137 specimens examined (56 males, 81 females). Specimens were seen from the following collections: AMNH, BCRC, BMNH, CASC, CNCI, FMNH, INHS, KSUC, MCZC, OSUC, OSUO, PMNH, SEMC, UMMC, USNM.

UNITED STATES (137).—ALABAMA (7): *Baldwin (1):* No data; *Lee (1):* Auburn; *Mobile (5):* Mobile. FLORIDA (99): *Alachua (2):* Gainesville; *Brevard (8):* Melbourne; *Broward (2):* Ft. Lauderdale; *Charlott (2):* Punta Gorda; *Collier (1):* Marco; *Dade (2):* Miami; *Duval (3):* Jacksonville; *Hardee (1):* Zolfo Springs; *Highlands (5):* Archibald Biol. Stat.; *Hillsborough (8):* Lutz, Tampa; *Holmes (1):* Smyrna; *Lee (10):* Ft. Myers; *Manatee (1):* Oneco; *Okeechobee (1):* Okeechobee; *Orange (1):* Winter Park; *Palm Beach (8):* Lake Worth, 9 mi. W. Lake Worth, West Jupiter; *Pinellas (24):* Cabbage Key, Dunedin, Gulf Port, St. Petersburg; *Polk (2):* Lakeland; *Sarasota (3):* Englewood, Sarasota; *Volusia (4):* Daytona Beach, Enterprize; *No data (10).* GEORGIA (4): *Liberty (1):* Hinesville; *Macon (1):* Oglethorpe; *Thomas (1):* Thomasville; *No data (1).* MISSISSIPPI (4): *Greene (1):* Leakesville; *Harrison (1):* no data; *Jackson (2):* Biloxi. NEW YORK (1): *No data.* NORTH CAROLINA (16): *Moore (16):* Southern Pines. SOUTH CAROLINA (6): *Charleston (2):* McClellanville; *Georgetown (1):* Georgetown; *Horry (1):* Myrtle Beach; *Richland (1):* Columbia; *No data (1).* January (7), February (6), March (23), April (37), May (15), June (11), July (12), August (3), September (4), November (2).

Remarks.—The partially punctate mesosternum, absence of rows of moderate to large punctures on the elytral disc or behind the humerus, the simple and short anterior horn, shining elytra, presence of a narrow rugose band at the base of the pronotum, length of less than 35 mm, and lack of posterior horns will easily separate *S. splendens* from all other species.

Although Gemminger and Harold (1869) synonymized *S. bosci* with *S. mormon,* I believe the description of *S. bosci* clearly indicates that it is *S. splendens.* Arrow (1937a), Casey (1915), and Horn (1875) suspected *S. bosci* was synonymous with *S. splendens* also, but they remained undecided. Although *S. bosci* was described prior to *S. splendens* on the same page (and more thoroughly as well), it is here formally designated that *Strategus splendens* is the correct valid name for this taxon in order to maintain nomenclatural stability.

The males do not possess major and minor forms of pronotal development, but some differences in horn size can be observed.

Strategus surinamensis surinamensis Burmeister

(Figs. 9, 85–88, 160–161)

Strategus surinamensis Burmeister, 1847: 135. [Holotype male at MNHN (Oberthür Collection). Type locality: Guyana.]

Male.—Length 32.0–40.0 mm; width across humerus 16.2–18.0 mm. Color piceous (rarely castaneous), feebly shining. *Head:* Front moderately rugose to rugo-punctate, especially behind tubercles; setigerous above eye. Clypeus with apex very narrowly truncate, nearly subacute, moderately reflexed; surface weakly rugose to rugo-punctate or frequently reduced to sparse punctures; punctures small, shallow; when punctures sparse, surface also finely subgranulate and aciculate. Tubercles conical, low to strong; tubercles when low are transverse, occasionally weakly connected by a transverse carina; tubercles when strong usually not transverse and are distinctly separated. Mandibles with basal lobe small, prominently rounded; middle lobe large, subtriangular; apical lobe small, triangular. Interocular width 2.0–2.33 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pronotum:* Base with a narrow to obsolete, rugo-punctate to rugose band; band reduced at middle to basal

bead. Disc finely subgranulate, aciculate, sparsely punctate; punctures very small, deep. Sides as disc to punctures slightly larger. Anterior half as disc in majors; smallest minors not seen but presumably with typical increase in sculpturing. Fovea deep; usually a low, broadly rounded, longitudinal ridge extending posteriorly from base of anterior horn. *Horns:* Majors (Figs. 85–86) with anterior long, subslender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface rounded or weakly to strongly carinate longitudinally down middle. Posterior horns long, stout, laterally compressed, attenuate, apex narrowly rounded; in lateral view horns project upward at about 65° from plane of disc and are frequently recurved slightly; in dorsal view horns curve toward one another; bases joined across disc in an arc; arc slightly produced at middle. Minors (Figs. 87–88): smallest individuals not seen but presumably with typical reduction. *Elytra:* Sutural stria impressed, weakly to distinctly crenulate; rarely reduced to large, deep, irregularly shaped, nearly confluent punctures. Disc finely subgranulate, aciculate, sparsely punctate; punctures minute to very small, shallow; 1–3 very feebly impressed striae present or not. Sides as disc except striae lacking, lateral margin with punctures slightly larger to moderate; 2–3 short rows of large punctures behind humerus; punctures usually ocellate, simple to umbilicate (even on same specimen), moderately deep. Apex densely punctate; punctures small to moderate, shallow. *Pygidium:* In lateral view basal half convex, apical half weakly convex to nearly flat. Disc finely subgranulate, aciculate, sparsely punctate; punctures minute, shallow, occasionally a few moderate in size. Apical margins either side of middle with punctures larger or occasionally weakly rugulose in a narrow band. *Genitalia:* Figs. 160–161. Parameres slightly variable in degree of curvature.

Female.—Length 31.8–40.7 mm; width across humerus 14.7–19.0 mm. As male except in the following respects: *Head:* Front coarsely rugose. Clypeus with surface weakly to strongly rugose. Mandibles similar except middle lobe a little smaller, apical lobe a little larger. *Pronotum:* Base with a narrow to moderate, rugose band. Sides in basal half with lateral margin rugopunctate to rugose in a moderately wide band; a slightly depressed, rounded patch of rugosity just postero-lateral of fovea. Anterior half of pronotum rugose. Fovea shallow. Tubercle strong, conical, slightly transverse. *Elytra:* Disc with punctures slightly larger than in male. *Pygidium:* In lateral view basal half convex, apical half weakly to moderately concave. Surface completely and setigerously punctate to rugopunctate; punctures small to moderate, very shallow, moderately dense; setae sparse to moderate, occasionally worn completely off. Apical margins rugulose in a narrow band.

Biology.—Unknown.

Distribution.—Amazon River north to Venezuela.

Locality Records (Fig. 9).—90 specimens examined (35 males, 55 females). Specimens were seen from the following collections: AHCC, AMNH, BCRC, BMNH, CNCI, FMNH, JDG, HAHC, MCZC, UC, UMMC, USNM.

BRAZIL (1).—RIO BRANCO (1): Limão (Rio

SURINAM (1).—No data (1).

ECUADOR (1).—NAPO PASTAZA (1): Tena. January (1).

FRENCH GUIANA (2).—No data (2).

GUYANA (2).—BERBICE (1): Ituni; ESSEQUIBO (1): Bartica. July (1).

SURINAM (1).—No data (1).

TRINIDAD (37).—CARONI (2): Caparo; MAYARO (1): Mayaro Beach; ST. GEORGE (28): Arima Valley, Maracas Bay, Morne Bleu, Orange Grove, Port-of-Spain, St. Augustine; ST. PATRICK (3): Fyzabad; No data (3). February (2), March (2), April (4), May (3), June (10), August (9), September (1).

VENEZUELA (46).—ARAGUA (7): Guayas, La Providencia, Maracay, Rancho Grande; DISTRITO FEDERAL (11): Caracas, El Valle; FALCON (15): Cerroda Mision (El Alzo), Los Taques, 60 mi. SE. Maracaibo, Palma Sola; MONAGAS (1): Caripito; PORTUGUESA (1): Guanare; SUCRE (1): Guanoca; TRUJILLO (1): Trujillo; ZUILA (1): no data; No data

(8). April (2), May (24), June (4), July (5), August (1), October (1).

Remarks.—This species may be distinguished by the key characters. Although very similar to *S. jugurtha*, *S. surinamensis surinamensis* lacks the setae on the elytral apices, possesses stouter, more erect horns, and is apparently allopatric. The genitalia are nearly identical in the two species, but in *S. jugurtha* the parameres are usually slightly more elongate.

Strategus surinamensis surinamensis may be distinguished from *S. surinamensis hirtus* by the following combination of characters: In the males, the base of the pronotum has a narrow to obsolete band of sculpturing in *surinamensis* and a narrow to moderate band in *hirtus;* the discal punctures of the pronotum are usually small in *surinamensis* and very small in *hirtus;* the posterior horns in *surinamensis* are frequently recurved posteriorly whereas in *hirtus* they are usually not; the discal punctures of the elytra are small in *surinamensis* and very small in *hirtus;* the pygidium in *surinamensis* is sparsely and minutely punctate and occasionally with a few moderate-sized punctures, whereas in *hirtus* the pygidium is sparsely to moderately densely punctate with the punctures small to moderate in size, and there is usually a small median band or triangular patch of large, setigerous punctures on the apical portion on the disc.

In the females the pygidium of *surinamensis* is moderately punctate to rugo-punctate whereas in *hirtus* the pygidium is densely rugo-punctate to subrugose.

I believe that the creation of an Amazonian inland sea during the Pleistocene is probably directly responsible for the isolation and subsequent subspeciation in *S. surinamensis* (see section on zoogeography).

Strategus surinamensis hirtus Sternberg
(Figs. 9, 89–92, 162–163)

Strategus hirtus Sternberg, 1910:100. [Holotype female at ZMHU. Type locality: here designated as Reyes, Bolivia.]

Strategus kolbeanus Prell, 1934: 164. [Types unknown to me. Type Locality: São Paulo, Brazil.] **New synonomy.**

Male.—Length 18.5–40.3 mm; width across humerus 13.0–19.6 mm. Color piceous (rarely castaneous), shining. *Head:* Front strongly rugose to rugo-punctate, setigerous above eye. Clypeus with apex very narrowly truncate, nearly subacute, usually feebly emarginate in unworn specimens; weakly to strongly reflexed; surface varies from weakly (rarely strongly) rugose to feebly rugo-punctate to moderately or densely punctate; punctures moderate in size, very shallow. Tubercles conical, moderate to strong, transverse, usually widely separated. Mandibles with basal lobe small, prominently rounded; middle lobe large, subtriangular; apial lobe small, triangular. Interocular width 2.0–2.5 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pronotum:* Base with a narrow to moderate rugose to rugo-punctate band; band reduced to basal bead at middle. Disc finely subgranulate, aciculate, sparsely punctate; punctures small, deep. Sides as disc to punctures slightly larger in majors; minors with a moderately wide, rugo-punctate to rugose band on lateral margin in basal half; a slightly depressed, rounded, rugo-punctate to rugose area just postero-lateral of fovea in minors, at base of posterior horns in majors. Anterior half as disc in majors; minors with a rugo-punctate to rugose band extending postero-medially from anterior angles or with anterior half completely rugose. Fovea deep; usually a low, rounded, longitudinal ridge extending posteriorly from base of anterior horn. *Horns:* Majors (Figs. 89–90) with anterior long, subslender, attenuate curving forward and upward, apex narrowly rounded, dorsal surface rounded or weakly to strongly carinate longitudinally down middle. Posterior horns long, stout, laterally compressed, attenuate, apex narrowly rounded; in lateral view horns project upwards at about 45–65° from plane of disc, only rarely recurved; in dorsal view horns subparallel to curving toward one another, bases joined across disc in an arc, arc slightly produced at middle. Minors (Figs. 91–92) with anterior short, conical, transverse. Posterior horns low and rounded, or laterally compressed triangular bosses; in lateral view dorsal surface subhorizontal to sloping slightly forward and downward, anterior edge vertical to subvertical; in dorsal view horns subparallel, bases joined across disc in an arc.

Elytra: Sutural stria impressed, weakly to distinctly crenulate. Disc finely subgranulate, aciculate, sparsely punctate; punctures small, shallow; 1–3 very feebly impressed striae present or not. Sides as disc except striae lacking, lateral margin with punctures slightly larger to moderate; 2–3 short rows of large punctures behind humerus; punctures usually ocellate, simple to umbilicate (even on same specimen), moderately deep (4 specimens seen where these punctures are nearly obsolete). Apex densely punctate; punctures small to moderate, shallow. *Pygidium:* In lateral view basal half convex, apical half weakly convex to nearly flat. Disc finely subgranulate, aciculate, sparsely to moderately densely punctate; punctures usually small, occasionally moderate, shallow; usually a small, median band or triangular patch of moderately large, setigerous punctures on apical portion of disc, occasionally reduced or obsolete. Apical margins either side of middle weakly rugo-punctate to rugulose. *Genitalia:* Figs. 162–163. Parameres slightly variable in relative width and degree of curvature.

FEMALE.—Length 30.0–38.1 mm; width across humerus 13.8–18.0 mm. As male except in the following respects: *Head:* Front coarsely rugose. Clypeus with surface weakly to strongly rugose. Mandibles similar to those of male except middle lobe a little smaller, apical lobe a little larger. Interocular width 2.0–2.66 transverse eye diameters. *Pronotum:* Sides in basal half with lateral margin rugo-punctate to rugose in a moderately wide band. Anterior half of pronotum rugose. Fovea moderately deep. Tubercle strong, conical slightly transverse. *Pygidium:* In lateral view basal half convex, apical half weakly to moderately concave. Surface completely, densely, and setigerously rugo-punctate to subrugose; setae dense. Apical margins rugose.

Biology.—Unknown. Specimens have been taken in coconut nurseries in Brazil (Vayssierre, 1965) and at lights.

Distribution.—Amazon River south to Argentina.

Locality Records (Fig. 9).—191 specimens examined (68 males, 123 females). Specimens were seen from the following collections: AHCC, AMNH, BCRC, BMNH, CASC, CNCI, FMNH, HAHC, LACM, MCZC, PMNH, SEMC, UC, UMMC, USNM, USP, ZMHU.

ARGENTINA (19).—CHACO (1): R. S. Peña, CORRIENTES (3): Bella Vista; JUJAY (1): Jujay Ciudad; MISIONES (13): Puerto Bemberg, Rio Alto, Paraná; SALTA (1): Salta. January (3), February (4), December (12).

BOLIVIA (13).—CHUQUIBACA (2): Yhancaroinza; SANTA CRUZ (10): San José de Chiquitos, Santa Cruz; No data (1).

BRAZIL (138).—AMAZONAS (1): Tefé; DISTRITO FEDERAL (5): Brasilia; GOIAS (7): Dianópolis, Fazenda Nova Orlandia (Jatai), Goiatuba, Leopoldo de Bulhoes, Vianópolis; MATO GROSSO (13): Campo Grande, Corumba, Mato Verde (Rio Araguaia), Rio São Domingos, Xavantina; PARÁ (1): Cachibbo; PARANÁ (3): Caviuna, Curitiba, Rolandia; SANTA CATARINA (71): Nova Teutonia, Rio Natal, Sao Francisco do Sul; SÃO PAULO (30): Bilac, Castilho, Divinolandia, Fazenda Campininas (Mogi Guacu), Neves Paulista, Piracicaba, Ribeirão Preto (Tamandua and Fazenda Medicina), São Paulo; No data (7). January (54), February (24), March (2), April (1), September (2), October (10), November (13), December (23).

PARAGUAY (16).—ALTO PARANA (2): Puerto Bertoni; CAAGUAZU (3): Estancia Primera, Puerto Central; CONCEPCION (1): Horqueta; GUAIRA (1): Puerto Suaryro (Villarrica); LA CORDILLERA (2): Ascuncion, San Bernardino; No data (7). January (1), February (1), March (2), May (1), July (1), October (1), November (1), December (6).

PERU (5).—HUÁNUCO (2): Tingo Maria; LIMA (1): M. Sani Beni; LORETO (1): Nauta; SAN MARTIN (1): vicinity of Rioja. November (3).

Remarks.—This species was commonly known as *Strategus tridens* Burm. prior to this study, primarily because of Kolbe's (1906) complete description of what he thought Burmeister's (1847) *S. tridens* to be. Recourse to the supposed "type" of Burmeister's *S. tridens* (MNHN) showed it to be *S. validus*. The "type" of *S. tridens* was apparently designated later by someone other than Burmeister and is not actually a type at all. Furthermore, the name *S. tridens* is

here declared a *nomen nudum* because Burmeister himself stated that he did not consider Dupont's unpublished manuscript *tridens* to be any different from *S. aloeus;* the name was not proposed as describing a new taxon by Burmeister but merely mentioned in textual discussion and does not meet the requirements of Articles 12 and 16 of the 1961 Code. Subsequent authors, however (Arrow, 1937a; Blackwelder, 1944; Kolbe, 1906), credited Burmeister for validly describing *S. tridens* although he did not do so. Sternberg's *S. hirtus,* as the available senior synonym, replaces *S. tridens* as the correct name for this taxon.

I think it is interesting to note that Kolbe was first to accurately describe the taxon *S. surinamensis hirtus,* but he was apparently unaware of the status of Burmeister's so-called type and its name, and, therefore, overlooked the opportunity of naming the species which he, in fact, first described.

Sternberg described the type of *S. surinamensis hirtus* as being from Reyes, but he did not know whether the Reyes in Mexico or in Bolivia was referred to. Reyes, Bolivia, is here designated as the type locality, since *S. surinamensis hirtus* is unquestionably South American and not Mexican.

This species may be distinguished from other species by the key characters and from *S. surinamensis surinamensis* by those characters listed in the remarks for that subspecies.

Strategus symphenax, new species
(Figs. 2, 93–94, 164–165)

Type Material.—Holotype male, labeled "Las Martinas, P. de R., Cuba, Jun 24/40, J. Acuña"; deposited at USNM. Also one male paratype deposited in BCRC.

Holotype (Figs. 93–94).—Male. Length 35.0 mm; width across humerus 17.0 mm. Color piceous, shining. *Head:* Front densely rugo-punctate to rugose; a longitudinal, smooth area medially; setigerous above eye. Clypeus with apex broadly truncate, moderately reflexed; surface transversely rugose. Tubercles conical, very low (nearly effaced), slightly transverse, widely separated. Mandibles with basal lobe small, prominently rounded; middle lobe small, broadly rounded at nearly a right angle; apical lobe very small, subtriangular. Interocular width 2.66 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base with a moderately wide, rugose band, band reduced at midline to basal bead. Disc very finely subgranulate, aciculate, sparsely punctate; punctures small and minute mixed, shallow. Sides as disc except lateral margin with a wide, punctate to rugo-punctate band; punctures large, shallow, some crescent shaped. Anterior half as disc. Fovea moderately deep. *Horns:* Anterior long, slender, attenuate, curving forward and upward, apex narrowly rounded, dorsal surface rounded. Posterior horns long, subslender, attenuate, laterally compressed, apex rounded; in lateral view horns project forward and upward at about 60° from plane of disc; in dorsal view horns curve toward one another. *Elytra:* Sutural stria impressed, feebly crenulate. Disc weakly subgranulate, aciculate, sparsely punctate; punctures small, moderately deep; medial third with moderately dense, ocellate-umbilicate punctures; punctures irregular, large, shallow; lateral ⅔ with 6 rows of moderate to large, ocellate-umbilicate, shallow punctures. Sides with similar background sculpturing as disc and with 6 confused rows of ocellate-umbilicate punctures; punctures moderate to large, shallow, occasionally confluent. Apex densely punctate to rugo-punctate. *Pygidium:* Convex in lateral view. Disc finely granulate, sparsely punctate medially; punctures minute, small, and moderate mixed, shallow; a few moderate, oval to oblong, punctures at apex; punctation laterally very dense to rugo-punctate. Apical margins strongly rugo-punctate in a wide band. *Genitalia:* Figs. 164–165.

Female.—Unknown.

Variation.—Single male paratype as holotype except in the following respects: Length 37.5 mm; width across humerus 17.6 mm. *Head:* Setae above eye apparently worn off. Mandibles with middle lobe obtusely rounded. Interocular width 3.0 transverse eye diameters. *Pronotum:* Lateral margin with punctures moderate to large. *Horns:* Posterior horns project at about 70° from plane of disc. *Elytra:* Sutural stria strongly crenu-

late. Disc on lateral ⅔ with 6 rows of punctures as in holotype, but rows 3 and 6 confused. *Pygidium:* Disc densely punctate medially.

Biology.—Unknown.

Distribution.—Cuba.

Locality Records (Fig. 2).— 2 male specimens examined (BCRC, USNM).

CUBA (1).—PINAR DEL RIO (1): Las Martinas; No data (1). June (1).

Remarks.—The partially punctate mesosternum, presence of rows of moderate to large ocellate-umbilicate punctures on the elytral disc and adjacent to the sutural stria, the broadly trunctate clypeus, shining elytra, length greater than 30 mm, and pronotum with three simple horns will distinguish this species.

Although *S. symphenax* is very similar to *S. anachoreta,* the form of the horns and body shape differs, and *S. anachoreta* is without large ocellate-umbilicate punctures adjacent to the sutural stria. In addition, the genitalia of *S. anachoreta* are more stout than those of *S. symphenax.*

Etymology.—From the Greek *symphenax* meaning a partner in deceit; so named because, until very late in this study, I believed the specimens belonged to *S. anachoreta,* hence the two species were partners in deceit.

Strategus syphax (Fabr.)
(Figs. 3, 104–107, 172–173)

Scarabaeus syphax Fabr., 1775: 9. [Holotype male at BMNH (Banks Collection). Type locality: originally published as America but here restricted to Guadeloupe.]

Scarabaeus syphax Fabr., 1787: 6. [Redescription.]

Scarabaeus vulcanus Fabr., 1792: 11. [Type apparently lost. Type locality: Guadeloupe.]

Male.—Length 33.6–42.8 mm; width across humerus 16.6–21.5 mm. Color piceous, moderately shining. *Head:* Front in majors very finely subgranulate, aciculate, sparsely punctate; punctures small, moderately deep; area just posterior of tubercles usually densely punctate; punctures small to moderately large, shallow, often confluent; front in minors finely rugulose. Clypeus with apex moderately reflexed, strongly and narrowly bidentate in unworn specimens, narrowly truncate or feebly emarginate in worn specimens; surface in majors very finely subgranulate, aciculate, sparsely punctate; punctures small, moderately deep; surface in minors moderately to densely punctate; punctures small to moderately large, shallow, often confluent. Tubercles conical, very low or virtually effaced, transverse, widely separated. Mandibles with basal lobe small, prominently rounded; middle lobe moderate in size, triangular to subtriangular, apex narrowly rounded; apical lobe small, subtriangular. Interocular width 2.66–3.0 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base in majors without a rugose band; base in minors with a narrow, medially reduced, punctate band; punctures small to large, shallow, oblong to crescent shaped. Disc in majors very finely granulate, aciculate, very sparsely punctate; punctures minute to small, deep; disc in minors similar except frequently with an irregular band of sparse punctures extending from base of posterior horns postero-medially to center base of disc; punctures moderate to large, shallow, oval to oblong to crescent shaped. Sides in majors as disc. Sides in minors similar except lateral margin more punctate; punctures large, shallow, crescent shaped; base of posterior horn usually with a slightly depressed punctate area; punctures sparse, small to moderately large, crescent shaped. Anterior half in majors as disc; anterior half in minors usually with a band of rugosity extending posteromedially from anterior angle or else variably rugose. Fovea deep. *Horns:* Majors (Figs. 104–105) with anterior very long, slender, attenuate, curving forward and upward, apex narrowly rounded, dorsal surface usually rounded (occasionally almost flat). Posterior horns very long, subslender, attenuate, laterally compressed, apex narrowly rounded; in lateral view horns slightly enlarged ventrally about ⅓ total distance from apex and extending forward and upward at about 35° from plane of disc; in dorsal view horns curve toward one another. Minors (Figs.

106–107) with anterior short, slender, attenuate, apex narrowly rounded. Posterior horns reduced to prominent, triangular bosses; in lateral view dorsal edge slopes forward and downward, anterior edge vertical to subvertical; in dorsal view horns laterally compressed, parallel, bases joined across disc in an arc. *Elytra:* Sutural stria a row of close-set, moderate to large, umbilicate punctures; punctures not forming an impressed line. Disc finely granulate, aciculate, sparsely to moderately punctate; punctures minute to small, shallow, mixed with moderate to large, shallow, ocellate-umbilicate punctures; some ocellate-umbilicate punctures in distinct rows. Sides similar except ocellate-umbilicate punctures greatly reduced in number. Apex densely punctate; punctures small to moderately large, shallow, usually confluent. *Pygidium:* In lateral view basal half convex, apical half nearly flat to feebly concave. Disc aciculate, finely granulate, roughened, moderately densely punctate; punctures minute to small, very shallow; majors frequently with a subapical, median, longitudinal, shallow depression. Apical margins either side of midline rugose; lateral emargination shallow. *Genitalia:* Figs. 172–173.

Female.—Length 32.0–40.5 mm; width across humerus 15.5–20.3 mm. As male except in the following respects: *Head:* Front punctate to rugo-punctate; punctures moderate to dense, small to large, shallow, often confluent. Clypeus with surface as front. Mandibles similar to those of male except middle lobe slightly smaller. *Pronotum:* Base with a narrow, punctate to rugo-punctate band; punctures sparse to dense, small to large, oval to oblong. Disc sparsely punctate; punctures small, deep; an irregular band of moderately dense punctures extending from lateral base of fovea postero-medially to center base of disc; punctures moderate to large, shallow, oval to oblong. Sides in basal half punctate to rugo-punctate; punctures moderate in density, small to large, shallow, frequently crescent shaped; a slightly depressed, rounded patch of rugosity postero-lateral of fovea. Anterior half rugo-punctate. Fovea shallow. Tubercle conical, transverse, strong. *Pygidium:* Convex in lateral view. Disc moderately densely punctate; punctures small to moderate, shallow. Apical margins rugo-punctate to rugulose; lateral emargination shallow.

Biology.—Unknown.

Distribution.—Guadeloupe.

Locality Records (Fig. 3).—10 specimens examined (5 males, 5 females). Specimens were seen from the following collections: BCRC, BMNH, MNHN. F. Chalumeau (personal communication) provided 14 additional records.

GUADELOUPE (24).—GRANDE TERRE (2): Grands Fonds, Pointe-á- Pitre (Chalumeau, *in litt.,* and Paulian, 1947, respectively); GUADELOUPE (15): Goyave (Chalumeau, *in litt.*), IFAC (Chalumeau, *in litt.),* Petit-Bourg, Sainte Rose, Sofaïa (Chalumeau, *in litt.*), Trois Rivierés (Paulian, 1947), Vernou (Chalumeau, *in litt.*); No data (7). April (1), May (1), June (7), July (1), September (1), October (1).

Remarks.—The bidentate clypeal apex, punctate sutural "stria," and large discal punctures on the median third of the elytral disc are diagnostic for this species.

Verill's (1906) *S. tricornis* was questionably synonymized with *S. vulcanus* by Arrow (1911, 1937a) and positively by Leng and Mutchler (1917), but it is here removed from synonymy; it is definitely not *S. syphax.*

Fleutiaux and Sallé (1889) may have applied the name *S. syphax* to *S. vulcanus* although their checklist differentiates between a *S. syphax* and a *S. vulcanus.* Lacordaire (1856) considered *S. vulcanus* a variety of *S. syphax* thus accurately placing *S. vulcanus* in synonymy with *S. syphax.*

Illustrations of the type of *S. syphax* were not seen until very late in this study and after the plates had been prepared, hence the interruption in alphabetical sequence in the habitus figures.

***Strategus talpa* (Fabr.)**
(Figs. 3, 95–97, 166–167)

Scarabaeus talpa Fabr., 1792: 32. [Lectotype male, labeled *"talpa,"* and lectoallotype female, labeled *"talpa,"* here designated; deposited at UZM with my lectotype labels. Type locality: St. Barthélemy (West Indies).]

Strategus barbigerus Chapin, 1932b; 455. [Holotype male and 24 paratypes at USNM; 20 paratypes at AMNH. Type locality: Aguirre, Puerto Rico.] **New synonymy.**

Male.—Length 27.0–37.0 mm; width across humerus 13.3–19.0 mm. Color piceous, dull, not shining. *Head:* Front of majors sparsely punctate; punctures small to moderate, shallow, becoming denser and larger just behind tubercles, setigerous above eye in unworn specimens; minors with front coarsely punctate to rugo-punctate, also setigerous above eye in unworn specimens. Clypeus with apex narrowly subtruncate to truncate, weakly reflexed; surface in majors moderately to moderately densely punctate; punctures moderate to large, shallow; surface in minors rugo-punctate to rugose. Tubercles conical, very low, slightly transverse, widely separated. Mandibles with basal lobe small, rounded; middle lobe moderate in size, subtriangular, apex narrowly rounded; apical lobe very small, triangular. Interocular width 3.0 transverse eye diameters in minors grading to 4.0 transverse eye diameters in majors. *Mesosternum:* Anterior ½—¾ setigerously punctate. *Pronotum:* Base with a very narrow to nearly obsolete rugo-punctate band; band reduced at middle to basal bead. Disc aciculate, punctate; punctures moderate in density, small, shallow; occasionally a few moderate to large punctures along midline. Sides as disc except majors with a few moderate to large, crescent-shaped punctures at base of posterior horns; minors with a slightly depressed, rounded, punctate to rugose patch just postero-lateral of fovea; lateral margin in majors with a band of sparse punctures; punctures moderate to large, simple to oblong, shallow; lateral margin in minors varies from densely punctate to rugo-punctate to rugose. Anterior third as disc in majors; minors with a postero-medial, rugo-punctate to rugose band extending from anterior angles or else with anterior third of pronotum rugose. Fovea deep in majors, moderate to very shallow in minors. *Horns:* Majors (Figs. 95–96) with anterior long, stout, dorso-ventrally compressed, apex strongly expanded and bifid, curving forward and upward; dorsal surface flat, lateral margins delineated by a small, longitudinal carina. Posterior horns are large, pyramidal bosses; in lateral view dorsal surface slopes downward and backward, anterior surface subvertical; in dorsal view horns parallel, laterally compressed, bases joined across disc in an arc. Minors (Fig. 97) with anterior short to tuberculate; when short the anterior is stout, sides subparallel, apex bifid but not expanded, dorsal surface rounded. Posterior horns vary from low, pyramidal bosses to completely absent; when low, bosses are similar to majors except much reduced. *Elytra:* Sutural stria impressed, crenulate. Disc very finely granulate, aciculate, sparsely punctate (rarely moderately dense); punctures simple and umbilicate mixed, small (rarely small and minute mixed), shallow; disc on lateral ⅔ with 6 rows of moderate to large, umbilicate, shallow punctures, rows 1–2 and 4–5 regularly punctate and closely adjacent, rows 3 and 6 irregular and more sparsely punctate; rows of punctures and size of larger punctures occasionally reduced so that rows become confused and difficult to define. Sides similar to disc except row 3 usualy reduced to only a few irregular punctures, row 6 sparsely and irregularly punctate. Apex sparsely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc finely subgranulate to granulate, sparsely punctate (especially in majors); punctures small to moderate, very shallow to effaced. *Genitalia:* Figs. 166–167. Paramere just before apex may or may not be slightly flared laterally.

Female.—Length 25.8–38.0 mm; width across humerus 12.0–21.0 mm. As male except in the following respects: *Head:* Front rugose. Clypeus with apex rounded; surface rugose. Tubercles conical, low, strongly transverse, connected by a weak transverse carina. Mandibles similar to those of male but middle lobe smaller. Interocular width 2.66–3.0 transverse eye diameters. *Pronotum:* Sides with lateral margins punctate to rugo-punctate to rugose in a wide band or sides completely punctate to rugo-punctate; punctures moderate to large, moderately dense, shallow. Anterior third rugose. Fovea shallow to nearly obsolete. Tubercle conical, very low, transverse. *Elytra:* Umbilicate punctures frequently less pronounced. *Pygidium:* In lateral view basal ¾ convex, apical ¼ slightly concave;

protuberant at middle. Disc aciculate, very finely subgranulate, sparsely to moderately densely punctate; punctures small to large, shallow, frequently elongate in lateral emarginations. Apical margins rugo-punctate to rugose with a few short setae medially in unworn specimens; lateral emargination very shallow.

Biology.—Smythe (1920) conducted rearing experiments in Puerto Rico and established the following life history: The eggs are pearly white, opaque, and oblong-oval in shape. When first deposited they averaged 2.8–3.0 × 3.5–3.8 mm; during incubation eggs expanded and just prior to hatching averaged 4.0–4.5 × 5.3–5.5 mm. The duration of incubation in 207 eggs was 15–19 days (average 17.5 days). The eggs are laid singly in spherical cells of soil or fiber which are 2–3 times larger than the newly deposited egg. Preferred deposition sites for the eggs are in the chewed-up fiber in which the adult has been tunneling or in the excavated interior of buried sugar cane stalks.

Larvae are about 8 mm in length when they hatch. Tables 3 and 4 indicate larval development.

TABLE 3
INSTAR DURATION IN DAYS FOR *S. talpa*

INSTAR	NO. OBSERVED	RANGE	AVERAGE
1	115	24–72	40.5
2	67	43–85	72.0
3	55	137–282	199.0

TABLE 4
INSTAR MEASUREMENTS IN MM FOR *S. talpa*

INSTAR	NO OBSERVED	HEAD CAPSULE WIDTH		MAXIMUM BODY LENGTH
		RANGE	AVERAGE	
1	20	3.25–3.90	3.54	25.0
2	91	—	5.64[2]–6.24[3]	45.0
3	—	—	—	—

[2]Less than one week in age.
[3]Over nine weeks in age.

The first instar is apparently able to subsist with no more organic materal present than the humus in black soil although it begins to feed on rotten wood near the end of the stadium. Larvae demonstrated a preference for feeding on rotting wood and were most commonly found in decaying tree stumps. Unlike *S. oblongus* with which it is sympatric, larvae of *S. talpa* can survive on manure and are frequently found there. The grubs also show a preference for the rotten stems in the stool of sugar cane; they do not usually attack living stems. However, the underground portions of living stems will be attacked if the available dead stems are entirely consumed by the developing larvae before they reach maturity. Larvae have been observed to sever completely a cane stalk underground and then to tunnel upward within the stalk a distance of several inches. Pupae have been found within the excavated underground base of the stalk.

A pupal cell is usually constructed just prior to pupation near where the grub stops feeding. The pupal cell is oblong and somewhat larger than the pupa. A quiescent pre-pupal stage lasts from several days to several weeks, and during this stage the pre-pupa is very susceptable to attack by fungi, bacteria, mites, and nematodes. The pupal period ranged from 22 to 29 days (average 24 days). Newly emerged adults became active within a week after eclosion and then immediately dug their way out of their chamber.

Adult female longevity in 11 individuals averaged 37.5 days (maximum 93 days). The total life span averages about one year. The preoviposition period for five females ranged from 20 to 27 days (average 24 days). The average number of eggs laid per female was 13, the maximum number 43. The oviposition period lasted 1–21 days (average eight days).

The adults feed largely on the green parts of shrubs and trees but not on foliage. They rarely damage sugar cane, and then only incidentally as they penetrate the cane to deposit eggs or occasionally to feed on underground stems.

Natural enemies are few in number (see biology for *S. oblongus*). The green muscardine fungus, *Metarrhizium anisopliae* (Metschn.), is particularly virulent and attacks the adults as well as the immature stages. The pupa appears to be the most susceptable to attack, and the egg the least susceptable. Larvae in the laboratory frequently became diseased and died due to the bacterium *Micrococcus nigrofasciens* which caused shining, black, hardened areas to form on the body,

head, and legs. *Campsomeris atrata* (Fabr.) (Hymenoptera: Scoliidae) is parasitic on the larvae of *S. talpa* (Wolcott, 1936, 1948). An undetermined species of predatory mite was observed to feed on the adults; another undetermined species was seen to feed on the eggs of the beetle resulting in the death of the egg. Other predators include the Puerto Rican grackle, *Quiscalus niger brachypterus* (Cassin), which feeds on the larvae; the mongoose, *Herpestes birmanicus* (Thomas), which feeds on the adults; and the American Giant Toad, *Bufo marinus* (L.), which also feeds on the adults. In a detailed study in Puerto Rico, Dexter (1932) found seven *Strategus* (probably *S. talpa*) in 301 toads for a total of 0.6% of the total bulk found in all toad samples. Wolcott (1948, 1950) noted that *Bufo marinus* was a very effective predator of *S. talpa* in Puerto Rico and that the beetles nearly disappeared when the toads were numerous and vice versa. Miskimen and Bond (1970) indicated that *S. talpa* did not reach economic levels of importance on St. Croix because of the toad. On the other hand, Simmonds (1969) stated that there was no definite evidence as to the degree of reduction of any specific pest by the toad.

Strategus talpa is known as the sugar cane rhinoceros beetle in Puerto Rico. It is not, and probably never has been, a serious pest of sugar cane even though the larvae were previously found in cane fields. As Smythe (1920) pointed out, the larvae of the rhinoceros beetle were often blamed for the damage caused by *Phyllophage* spp. (Scarabaeidae) which were more numerous (but not so readily found) than the larvae of *Strategus*. *Strategus* larvae were found among the underground stems of sugar cane because of the large amount of organic food material that occurs there; the larvae do not feed on cane roots, and damage that does occur is caused largely by inadvertent severing of the roots during feeding. Wolcott (1948) noted that "*Strataegus* (sic) grubs primarily feed on rotten wood, especially the roots and stumps of trees in the soil, but when these have been consumed in recently cleared land, readily attack old cane stalks and decaying cane seed, and may eventually attack live cane root-stalks and rootlets when other more acceptable sources of organic matter are lacking."

Distribution.—Puerto Rico, Virgin Islands, St. Barthélemy, Antigua, and probably other islands in the Leeward Islands.

Locality Records (Fig. 3).—98 specimens examined (41 males, 57 females). Specimens were seen from the following collections: AMMH, BCRC, BMNH, CASC, CNCI, HAHC, MCZC, USNM, UZM.

LEEWARD ISLANDS (16).—ANTIGUA (1); ST. BARTHÉLEMY (2); ST. CROIX (7): Christiansted, Const. Hill, no data (Beatty, 1944); ST. JOHN (1); ST. THOMAS (3); TORTOLA (2). May (1), June (2), August (3), October (3).

PUERTO RICO (82).—AGUADILLA (3): Aguadilla, Isabela, Las Marias; ARECIBO (2): Dorado, Vega Baja; GUAYAMA (11): Aguirre, Aibonito, Caguas; HUMACAO (2): El Verde Camp (Rio Grande) (Wolcott, 1941), Fajardo (Wolcott, 1936); ISLA MONA (3): Sardinera (Ramos, 1946); MAYAGUËZ (17): Guanica, Mayaguëz, Route 334 (Guanica Forest), San Germán; PONCE (16): Como Springs, 5 mi. NE. Jayuya, Ponce, Santa Isabel; SAN JUAN (7): Bayamón, Corozal, Rio Piedras, San Juan; VIEQUES ISLAND (2) (Wolcott, 1923, 1936); No data (19). January (1), February (3), March (1), April (7), May (11), June (9), August (5), September (3), October (14), November (4), December (6).

Remarks.—The partially punctate mesosternum, rows of moderate to large umbilicate punctures on the elytral disc, narrowly subtruncate to truncate clypeal apex, dull elytra, absence of a well-developed angular prominence on the lateral margin near the apex of the male genitalia, and the distinctly expanded and forked apex of the anterior horn will serve to separate this species from all others.

Chapin (1932b) described *S. barbigerus* without seeing the type of *S. talpa*.

Strategus tarquinius, new species
(Figs. 3, 98–99, 168–169)

Type Material.—Holotype male, labeled "Granada (sic), May, 1918"; deposited at AMNH. Allotype female, labeled "Chantilly Est. (Windward side), Grenada, W. I., H. H. Smith, 60" and

"W. Indies, 1900.40"; deposited at BMNH. Also one male paratype (Figs. 98–99) and one female paratype deposited in BCRC.

Holotype.—Male. Length 32.6 mm; width across humerus 16.2 mm. Color castaneous, shining. *Head:* Front very feebly rugose behind tubercles; setigerous above eye. Clypeus with apex very narrowly truncate, moderately reflexed; surface sparsely punctate; punctures small, shallow. Tubercles low, transverse, distinctly separated. Mandibles with basal lobe small, prominently rounded; middle lobe moderate in size, triangular, apex rounded; apical lobe small, subtriangular. Interocular width 2.33 transverse eye diameters. *Mesosternum:* Completely and setigerously punctate. *Pronotum:* Base without sculpturing. Disc very finely subgranulate, aciculate, very sparsely punctate; punctures very small, shallow. Sides and anterior half as disc. Fovea deep. *Horns:* Anterior very long, slender, attenuate, curving forward and downward and then upward, apex narrowly rounded, dorsal surface rounded. Posterior horns very long, slender, attenuate, laterally compressed, apex narrowly rounded, projecting forward and upward at about 20° from plane of disc; in dorsal view horns diverge, bases joined across disc in an arc. *Elytra:* Sutural stria impressed, subcrenulate. Disc very finely subgranulate, very sparsely punctate; punctures minute, shallow; lateral half with 3 very feebly impressed, incomplete striae. Sides similar except punctures slightly larger and striae absent. Apex moderately punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Disc subgranulate, very sparsely punctate; punctures minute, shallow. *Genitalia:* Figs. 168–169.

Allotype.—Female. Length 33.3 mm; width across humerus 15.4 mm. As holotype except in the following respects: *Head:* Front feebly rugose. Mandibles similar to those of holotype except middle lobe smaller. *Pronotum:* Base with a very narrow band of sparse punctures and rugae; band reduced at middle to basal bead. Sides in basal half as disc except margin with a feeble, narrow, punctate band; a rounded, slightly depressed, rugo-punctate patch just postero-lateral of fovea. Anterior half of pronotum rugo-punctate grading to rugose anteriorly. Fovea shallow. Tubercle conical, low, transverse. *Pygidium:* In lateral view basal half weakly convex, apical half nearly flat. Disc very finely subgranulate, virtually impunctate medially, sparsely punctate on apical margins and lateral emargination; punctures moderate in size, shallow; lateral emargination shallow.

Variation.—Males (1 paratype): Length 33.7 mm; width across humerus 16.5 mm. *Head:* Middle lobe of mandible subtriangular, apex narrowly rounded. Interocular width 3.0 transverse eye diameters. *Pronotum:* Disc not aciculate. *Horns:* Anterior curves forward and upward (not downward). Posterior horns in lateral view extend forward and upward up about 35° from plane of disc; in dorsal view horns curve toward one another. *Elytra:* Disc with 1 feebly impressed stria.

Females (1 paratype): Length 26.9 mm; width across humerus 11.8 mm. *Head:* Interocular width 2.0 transverse eye diameters. *Pronotum:* Base with a narrow, feeble, punctate band; punctures moderate in size, shallow. Sides with marginal punctate band narrow; punctures moderate in size, shallow. *Pygidium:* Disc moderately punctate; punctures small to moderate, shallow.

Biology.—Unknown. Found in rotting wood (Arrow, 1900).

Distribution.—Grenada (West Indies).

Locality Records (Fig. 3).—4 specimens examined (2 males, 2 females). Specimens deposited in the following collections: AMNH, BCRC, BMNH.

GRENADA (4).—Chantilly Est. (Windward side) (1), Grenville (Windward side) (1), No data (2). May (1).

Remarks.—The completely punctate mesosternum, absence of rows of punctures on the disc of the elytra and behind the humerus, narrowly truncate clypeal apex, and the lack of sculpturing at the base of the pronotum will easily separate *S. tarquinius* from all other species. It has the least amount of sculpturing of any species in the genus as well as being lighter in color. It seems to be closely related to *S. jugurtha.*

Arrow (1900), in referring to the two female described here, speculated that they were *S. fascinus* or a closely related species and that males were needed to place them definitely; he was apparently unaware that he was dealing with a new species.

The male paratype illustrated here (Figs. 98–99) was reared from a larva collected by John Glaser who first provided me with an example of this new species.

Etymology.—From the Latin *tarquinius* meaning proud; here named in reference to the magnificent set of horns on the males.

Strategus validus (Fabr.)

(Figs. 8, 100–103, 170–171)

Scarabaeus validus Fabr., 1775: 6. [Holotype female at BMNH (Banks Collection). Type locality: Brazil].

Scarabaeus tricornis Jablonsky (not Herbst), 1785: 269. [Types unknown to me. Type locality: unknown, but here presumed to be east-central South America.]

Scarabaeus validus Fabr., 1787: 4. [Redescription.]

Oryctes faunus Billberg, 1820: 383. [Types unknown to me. Type locality: originally published as Barbary (erroneous), but here presumed to be east-central South America.]

Strategus tridens Burmeister, 1847: 133. [**Nomen nudum.** See remarks for *S. surinamensis hirtus.*]

Male.—Length 31.0–49.6 mm; width across humerus 15.0–24.3 mm. Color piceous, shining. *Head:* Front rugo-punctate to rugulose, sculpturing usually reduced at midline. Clypeus with apex broadly truncate, occasionally very weakly notched medially, strongly reflexed; surface in majors moderately punctate; punctures small, shallow, or surface rugo-punctate; punctures large, shallow; surface in minors usually feebly rugulose. Tubercles conical, strong, widely separated. Mandibles with basal lobe small, prominently rounded; middle lobe large, subtriangular, apex narrowly rounded; apical lobe small, triangular. Interocular width 2.0–2.25 transverse eye diameters. *Mesosternum:* Anterior half setigerously punctate. *Pronotum:* Base without sculpturing (primarily in majors) or with a very narrow, rugo-punctate to rugose band; band reduced at middle to basal bead. Disc acciculate, sparsely punctate; punctures small, deep. Sides in majors as disc except punctures slightly denser and larger along margin; sides in minors with lateral margin punctate to rugo-punctate in a moderate to very wide band in basal 2/3; punctures moderate to dense, small to large, shallow to deep, simple to crescent shaped; a rounded, slightly depressed rugo-punctate to rugose area at base of posterior horn. Anterior half of pronotum as disc in majors; minors with anterior third variably rugose. Fovea moderate in depth. *Horns:* Majors (Figs. 100–101) with anterior very long, slender, attenuate, curving forward and upward, apex narrowly rounded; dorsal surface usually with 1 median and 2 lateral parallel, longitudinal, feeble carinae. Posterior horns long, subslender to stout, attenuate, laterally compressed, apex rounded; in lateral view horns extend forward and upward at about 70–90° from plane of disc, occasionally recurving slightly; in dorsal view horns slightly diverging to curving toward one another. Minors (Figs. 102–103) with anterior short to conical, suberect, apex acutely rounded, dorsal surface rounded. Posterior horns very short and triangular or weak to strong triangular bosses or obsolete; in lateral view dorsal edge horizontal to sloping forward and downward or sloping backward and downward, anterior edge vertical to sloping upward and backward; in dorsal view horns or bosses laterally compressed, subparallel, bases joined across disc in an arc. *Elytra:* Sutural stria strongly impressed, crenulate. Disc aciculate, frequently feebly and finely subgranulate, sparsely punctate; punctures small to moderate and minute mixed, shallow to deep; lateral half of disc usually with 1–3 very feebly impressed, incomplete striae; occasionally a short longitudinal row of small to large punctures at base just medial of humerus. Sides similar to disc except 1–5 short, confused rows of punctures behind humerus; punctures usually sparse, moderate to large, frequently ocellate-umbilicate, moderately deep. Apex moderately densely punctate; punctures small, shallow. *Pygidium:* Convex in lateral view. Surface acicu-

late, finely subgranulate, sparsely punctate; punctures minute to small, shallow. *Genitalia:* Figs. 170–171. Parameres vary from subslender to stout and from subparallel to slightly arcuate.

Female.—Length 32.0–47.0 mm; width across humerus 15.0–25.0 mm. As male except in the following respects: *Head:* Front coarsely rugo-punctate to rugose. Clypeus with apex broadly subtruncate to truncate, but not so broadly as in male; surface coarsely rugo-punctate to rugulose. Mandibles similar to those of male except middle lobe smaller, usually subequal with apical lobe. Interocular width 2.0–2.5 transverse eye diameters. *Pronotum:* Base with a narrow to moderate rugo-punctate to rugose band; band reduced at middle to basal bead. Sides in basal 1/2–2/3 moderately to densely punctate; punctures moderate to large, shallow, frequently crescent shaped; a slightly depressed, rounded, rugo-punctate to rugose area postero-lateral of fovea, lateral margin with a moderate to wide, rugo-punctate to rugose band in basal half. Anterior 1/3–1/2 rugose. Fovea shallow. Tubercle conical, low, transverse. *Elytra:* Disc as in male to lateral half more strongly punctate with 1–5 incomplete, confused rows of punctures; punctures moderate to large, simple to ocellate-umbilicate, deep. Sides behind humerus with 3–6 incomplete, confused rows of similar punctures. *Pygidium:* Weakly convex in lateral view. Disc aciculate, finely subgranulate, sparsely to moderately punctate; punctures moderate to large, simple to oval to oblong, shallow. Lateral emargination very shallow.

Biology.—*Strategus validus* has been taken from the base of wax palms in Brazil (Goncalves, 1946) and from sugar cane, bananas, pineapples, and coconut palms in Argentina and Brazil (Costa Lima, 1953; Hayward, 1942). Costa Lima also indicated that this species is an intermediate host for *Macracanthorhynchus hirudinaceus* (Pallas) (Archiacanthocephala: Oligacanthorhynchidae).

Distribution.—Argentina, Brazil, Paraguay, Uruguay.

Locality Records (Fig. 8).—362 specimens examined (155 males, 207 females). Specimens were seen from the following collections: AHCC, AMNH, BCRC, BMNH, CASC, CNCI, FMNH, HAHC, LACM, MCZC, PMNH, UC, UMMC, URU, USNM, USP.

ARGENTINA (3).—BUENOS AIRES (1): Buenos Aires; JUJUY (Hayward, 1942); MISIONES (1): Puerto Aguirre; RIO NEGRO (1): Negro Muerto; SALTA (Hayward, 1942); TUCUMAN (Hayward, 1942). November (1), December (1).

BRAZIL (348).—AMAZONAS (6): Ipiranga; CEARA (Goncalves, 1946); ESPIRITO SANTO (3): Corrego do Ita, Fazenda Corrego Alto (C. Itape Mirim); GOIAS (1): Goias; MATO GROSSO (3): Albuquerque, Guape, Km. 100 (Br. 55); MINAS GERIAS (4): Belo Horizonte, Vicosa; PARÁ (2): Belém, Fazenda Santa Maria (Monte Alegre); PARANÁ (37): Banhados, Caviuna, Curitiba, Ponte Grossa, R.R. from Curitiba to Parangua, Rolandia; PIAUI (Goncalves, 1946); RIO DE JANEIRO (2): Sarada Carioca; RIO GRANDE DO SUL (17): Pelotas, Rio Grande, S. Lorenzo; SANTA CATARINA (130): Corupa, Joinville, Nova Teutonia, Pinhal, Rio Verhelo; SÃO PAULO (124): Alto de Serra, Barveri, Campininas (Mogi Guacu), Cantareira, Caraguatatuba, Cipo, Divinolandia, Est. Biol. Boracea (Salesópolis), Fazenda Medicina (Ribeirão Prêto), Fazenda Paul D'Alho (Itu), Itu, Pindamonhangaba, Piracicaba, Rio Claro, São José dos Campos, São Paulo, Serra Negre; No data (19). January (62), February (50), March (9), April (4), June (1), July (1), September (11), October (4), November (30), December (99).

PARAGUAY (1).—CAAGUAZU (1): Estancia Primera. January (1).

URUGUAY (10).—ARTIGAS (1): Rio Cuareim; MALDONADO (3): Maldonado; RIVERA (3): Arroyo de la Aurora (Sierra de la Aurora), Camino a Tranqueras, Rivera; TACURAREMBO (3): Puntas Arroyo Laureles.

Remarks.—The key characters will distinguish *Strategus validus* from all other species although the erect horns, general absence of basal sculpturing on the pronotum, and the broadly truncate clypeus will usually be sufficient to separate this species. *S. validus* is closely related to *S. mandibularis*, but the greater degree of basal sculpturing on the pronotum and the much

larger middle lobe of the mandibles of the latter will easily separate the two.

Based on the description only, Arrow (1914) was probably correct in synonymizing *Oryctes faunus* Billberg with *S. validus.*

Strategus verrilli, new name
(Fig. 3)

Strategus verrilli, New name. [Replaces *Strategus tricornis* (Verrill), 1906: 317, which is a secondary junior homonym of *Strategus tricornis* (Jablonsky), 1785: 269, which is, in turn, a junior subjective synonym of *Strategus validus* (Fabr.), 1775. Type locality: Dominica (West Indies).]

Remarks.—Arrow (1911, 1937a) questionably synonymized Verrill's new Dominican species with *S. vulcanus (= syphax)* (see remarks for *S. syphax*). All of Verrill's type material has been lost or destroyed (Kirby Brown, personal communication), and apparently no male specimens resembling this species have been taken from Dominica since. I do have one female specimen from Dominica which does not really seem to fit any other species, but I currently have no reliable way of placing it in *S. verrilli.* Verill indicated that the female was unknown when he described the species in 1906. This specimen shall be retained until additional specimens are taken. *Strategus verrilli* is definitely not *Strategus syphax* of neighboring Guadeloupe because Verrill's original description (1906) and subsequent photographs (1907) clearly show very smooth, shining elytra as opposed to the sculptured elytra of *S. syphax. S. verrilli* is also not *S. tarquinius* for the following reasons: the body shape of *S. tarquinius* is proportionately more oblong; the posterior horns of *S. tarquinius* are considerably more erect; the body and legs of *S. tarquinius* are light reddish brown and *S. verrilli* is a deep black; the head tubercles of *S. tarquinius* are distinctly separated whereas they form a transverse ridge in *S. verrilli;* the measurements given for *S. verrilli* indicate that it is at least 10–20% larger than *S. tarquinius.*

Other than *S. syphax* and *S. tarquinius* and perhaps *S. jugurtha* (which has easily distinguishable post-humeral punctures), there are no other species that *S. verrilli* might be confused with, and so I feel confident in renaming the taxon now during this revision rather than waiting until additional specimens are taken. I believe, based on the description and photographs, that this species is valid and may be closely related to *S. jugurtha* or *S. tarquinius.* The lack of more specific knowledge regarding certain character states prevents it from being included in the key to the species. The precipitous terrain of Dominica has undoubtedly aided in delaying the rediscovery of *S. verrilli,* and even the Bredin-Archibald-Smithsonian Biological Survey of Dominica failed to yield any specimens.

Etymology.—The species is renamed after A. Hyatt Verrill who originally described the species.

ZOOGEOGRAPHY

This section will attempt to sketch briefly the distribution of the species of *Strategus* primarily within the framework of an historical analysis where geology and chorology are the principal parameters. The model proposed here is based largely on logical inferences drawing upon what I believe to be sufficient circumstantial evidence; it may serve for testing the distributional patterns of other groups.

Wickam's (1914) single Miocene (actually Oligiocene) fossil from Colorado places the genus at least 12–25 million years B.P., but if the fossil is indeed a true *Strategus* (which it appears to be), then the age of the genus is certainly older.

In the absence of any hard evidence, it is here suggested that Mexico-Central America is the place of origin for the genus because this area contains a modest number (four) of primitive species whereas all other areas (excluding the Antilles) contain more of the derived species (see Table 6). Kolbe (1906) also proposed the northern subtropics as the area of origin for the genus because most of the hornless (primitive) species occurred there. The Antilles are ruled out as a center of origin for the genus despite the high number (eight) of primitive species occurring there. The Greater Antilles were not even emergent until the early Miocene (Woodring, 1954), and it would therefore be impossible to have an

earlier Oligocene fossil in Colorado as is the case with *S. cessatus.* I believe the majority of more primitive Caribbean species is indicative of a longer and continued isolation as will be mentioned later. Minor supporting evidence for a Mexican-Central American origin is the fact that this area is about the center of the range for the genus, thus allowing for radial expansion; in addition, the second largest number of species occurs in this region which tends to indicate that the genus may have been here longer than in any other area (the larger number of endemic species in the Antilles is a misleading number clue and has been explained by greater isolation due to fragmented populations cut off from one another by water barriers). Darlington (1957) and Müller (1973) have accurately observed that it is poor methodology to assume that the center of range of a group or its center of greatest diversity is necessarily its center of origin; therefore, the use of number clues and center of range are, at best, tenuous avenues of approach for determining a center of origin. This is the rationale for employing relative proportions of primitive and derived species in any given area in conjunction with geologic history, as well as the number clues.

From the Mexican-Central American center of origin *Strategus* then extended its range northward into the United States, southward into South America, eastward into the Greater Antilles, and northward from South America into the Lesser Antilles.

NORTH AMERICA

Howden (1966, 1969) has stated that most North American scarabaeid genera were established by Miocene times. *Strategus cessatus* Wickham, the fossil from the Oligocene shale deposits at Florissant, Colorado, tends to support this view. *S. cessatus* is very closely related to *S. cessus* which occurs in the mountain chain from Durango in Mexico northwards into southern Arizona and New Mexico. *Strategus cessatus* indicates that this group, expanding from the south, followed the Rockies as far north as the 39th parallel during warmer Oligocene-Miocene times. With the subsequent formation of the major deserts in southwestern North America by the mid-Pliocene (Axelrod, 1948, 1950; Cohn, 1965; Darrow, 1961), *Strategus* probably became isolated in the more humid mountain areas. Their ecological valency has undoubtedly allowed for adaptation to the cooler temperatures of the slightly higher elevations (especially during the Pleistocene glaciations), but as Dillon (1956) and Howden (1963, 1966) have pointed out, the desert areas had by this time formed impassable barriers to further dispersal.

On the other hand, Martin and Mehringer (1965), using extensive and more recent data on Southwestern pollen profiles, have decisively shown a direct pollen correlation with the Wisconsin glaciation, starting about 70,000 years B.P., which indicates a 900–1,200 m lowering of biotic zones. They state that a "belief that the present biota of the Southwest attained, and has retained, its present geographic distribution since the end of the Pliocene was based on certain biogeographic inferences now largely invalidated by the Pleistocene fossil record. To be more specific, the fossil pollen record of Wisconsin-age pine parkland with spruce south of the Colorado Plateau means sufficient downward displacement of plant communities to allow several invasions of 'Arcto-Tertiary geofloras' into the desert mountains during the Pleistocene." Thus, I believe that the more highly derived *S. aloeus,* which is often sympatrically isolated with *S. cessus* on the more equable mountain islands in a sea of desert in the Southwest, also expanded northward from a Mexican refugium during pluvial periods of the Pleistocene when the Southwestern grasslands were invaded by pine-parkland. Isolation of the *S. aloeus* line then occurred with the rapid recovery of post-glacial vegetation about 12,000 B.P. In the American Southwest, then, there have been at least two invasions of *Strategus:* once in the Miocene-Oligocene with the old *S. cessus-cessatus* line and again during the Pleistocene with the *S. aloeus* line. The more optimum conditions of Louisiana, eastern Texas, etc., have permitted *S. aloeus* to become quite common there.

The two species in the southeastern United States, *S. antaeus* and *S. splendens,* have Antillean affinities and possibly came from this area originally. There is good geologic evidence that a rather large land mass has been in existence in northern Florida since the Middle Miocene (Clench and Turner, 1956; Howden, 1963; Hub-

bell, 1954; Vernon, 1951) that was not submerged during the Pleistocene (Altschuler and Young, 1960). Goin (1958), Neill (1957), and Ross (1965) have shown that there has been continuous evolution influenced by recurrent isolation in this region from the Miocene to Recent time. The ancestors of these two species could have arrived at this Floridian land mass at any time since the Middle Miocene, but Young (1954) suggested Florida received the ancestors of the species of Antillean-Caribbean affinities during the last part of the Pleistocene or during the warm interglacial periods, and this seems more plausible in view of Antillean paleogeography. During the Pleistocene glaciations Florida was undoubtedly serving as a refugium (Howden, 1969), and *S. antaeus* and *S. splendens,* or their immediate ancestors, expanded northward and westward from this area when the climate ameliorated. I do not believe these ancestors originated in Mexico and moved east to Florida during the interglacials as has been shown for some prairie or semi-desert orthopterans (Hubbell, 1960).

The presence of *S. mormon* in the southcentral United States might best be explained by a westward movement of ancestral stock after introduction into the southeastern United States from the Caribbean. The development of mesic conditions could have then isolated the present surviving populations of *S. mormon* from its parent stock.

SOUTH AMERICA

Strategus probably spread into South America east of the Andes during Tertiary times after the formation of the Panamanian land bridge. Postulating inferences for the historical dispersal of the South American members of the genus is highly problematical in view of the lack of additional extensive specimen locality data, absence of fossils, and a lack of well-documented geologic history for some parts of the continent. Haffer (1969) has convincingly demonstrated that during the several dry climatic periods of the Pleistocene and post-Pleistocene the Amazonian forest was restricted to a number of smaller, disjunct forests which served as refugia for numerous populations of forest animals which then differentiated from one another during these periods of geographic isolation. The isolated forest areas re-expanded during periods of humid climatic conditions permitting the refuge area populations to extend their ranges. Haffer proposed that this rupturing and rejoining of the various forests was repeated several times and led to a rapid differentiation of the Amazon forest fauna in geologically very recent times. Vuilleumier (1971) has elaborated upon Haffer's conclusions and shown that the chances were indeed very good for speciation in successive periods of ecological isolation: "These biological data, combined with supportive geological evidence, show that climatic events during the last million or so years have affected the biota of South America as much as the Pleistocene glacial changes affected the biotas of Eurasia and North America. Since most of South America lies within tropical latitudes, it is suggested here that part of the diversity of species in the tropical areas of this continent is due to two historical factors: the lack of wholesale elimination of species (compared with northern and high latitudes), and ample opportunity for speciation in successive periods of ecological isolation. The apparent paradox of the wealth of species in the 'stable tropics' is partially explained by the fact that the tropics have probably been quite unstable, from the point of view of their biotas, during the Pleistocene and perhaps part of the Tertiary." These events undoubtedly influenced the evolution of *Strategus* in South America although to what extent is largely speculative due to the lack of certain aforementioned information.

During the warmer interglacial periods of the Pleistocene, the Amazon basin apparently became a rather large inland sea when water levels were raised about 50 m higher than today's level (Haffer, 1969; Vuilleumier, 1971). I believe that this interglacial sea transgression into the Amazon basin was directly responsible for the subspeciation of *S. surinamensis* into *S. surinamensis hirtus* south of the Amazon and *S. surinamensis surinamensis* north of the Amazon. The interglacial inland sea barrier may also have been an isolating mechanism for the ancestors of other South American species of *Strategus,* and this might explain, in part, the seeming isolation of the species found exclusively south of the Amazon. The relative lack of *Strategus* species diversity in the Amazon region itself is indicative

of a re-colonization pattern from both the north and the south. As Ross (1965) has noted, when species or species groups of reasonably low vagility have disjunct ranges, there is a good likelihood that the disjunctions are the result of disruptions by ecological changes in a once continuous range.

THE ANTILLES

According to Chace and Hobbs (1969) and Woodring (1954), conclusions on pre-Tertiary Caribbean history are only tentative, but a number of insular land masses probably existed in the Caribbean during the Cretaceous and, except for a chain of volcanic islands in the area now encompassed by Cuba, most, if not all, of the extant islands, northern South America, and parts of Central America were submerged during this period. They state further that most of the islands are probably not older than late Oligocene or early Miocene, and that there is no geological evidence to support the continuous existence of land masses in the Caribbean prior to the Eocene. Geologically and faunistically, the Greater and Lesser Antilles have separate origins and so will be discussed separately.

Lesser Antilles

The main Lesser Antillean chain has been emergent for no more than 11 million years (K–Ar dating), and Barbados probably emerged only ½ million years ago (Yang *et al.*, 1974). Barbados is not more than 300 m in elevation, receives less rainfall than many of the higher islands, and is not known to support any *Strategus.* Little is known of Pliocene paleoclimates of the Caribbean, but climates were known to be considerably drier during the low temperature periods of the Pleistocene glaciations. Bonatti and Gartner (1973) have shown that these dry periods are compatible with other data indicating ice age aridity in the western equatorial Atlantic as well as in tropical South America. They suggested that one factor contributing to this phenomenon was the decreased temperature of surface water in tropical and temperate oceans which would have significantly reduced the amount of water vapor in the atmosphere above these areas. Using these data, Yang *et al.* (1974) convincingly proposed that the rainforests of the high islands were probably much less extensive then they are today and that the more desert-like vegetation which presently characterizes the low islands and the rain shadow areas of high islands was at times the dominant or even the only cover on large islands: "Only high islands produce their own rain by adiabatic cooling, so only on high islands could conditions have been favorable for the persistence and continuing evolution of forest lizards during the periodic Pleistocene droughts." I believe these conclusions apply equally well to *Strategus,* and this might help to explain their absence or presence on many of the islands.

Simpson (1956) has succinctly noted that the Lesser Antilles are a highly attenuated extension of the recent fauna of Trinidad and Venezuela; the 3–4 endemic species of *Strategus* represented in the Lesser Antilles seem to bear this out. Trinidad is a recently separated continental island and is not considered to be part of the Lesser Antilles. *S. aloeus* and *S. surinamensis surinamensis* occur commonly in Trinidad and on the mainland ten miles distant. The Lesser Antilles have probably never been connected north of St. Vincent (Darlington, 1938) although all those islands within a single bank south of St. Vincent that are separated by shallow channels (i.e., the Grenadines) were presumably joined during the last glaciation (15,000 B.P.) when sea levels were about 100 m lower than today (Yang *et al.*, 1974). Yang *et al.* have demonstrated that *Anolis* lizards are virtually the same within the same bank of islands and different between banks. Matthews (1966) has shown, with the Scarabaeinae, that an immigrant pattern of distribution characterizes those species which are common to more than one island or to the continent and one or more islands. Distance from the continent and island size are among the most important factors determining the number of species present on an island and, as a consequence, there is usually a gradual reduction in the number of species as one progresses outward from the mainland. Matthews demonstrated that the Scarabaeinae of the Lesser Antilles were clearly derived from South American forms or identical with them and that a fair amount of divergence has occurred among the outermost species. The species of *Strategus* in the Lesser Antilles display an identical pattern. Grenada would be the most likely landfall for

rafting dispersal from the mainland; *S. tarquinius* is found here, and it is nearly identical with *S jugurtha* and very similar to *S. surinamensis surinamensis* in northern South America. *Strategus verrilli* is found on Dominica, and, from all accounts, it is also very similar to the preceding three species. *S. syphax* occurs on Guadeloupe and represents the northernmost penetration of the Lesser Antilles from South America. *S. syphax* possesses several derived characters but, at the same time, retains some important ancestral ones which tend to indicate peripheral divergence as noted by Matthews as well as longer isolation from the parent stock. The data seem to indicate secondary colonization at least up to Dominica because of the close phenetic (and presumably genetic) similarities between *S. verrilli, S. tarquinius, S. surinamensis surinamensis,* and *S. jugurtha* as opposed to the more primitive *S. syphax.*

Strategus species have not been recorded from the three remaining large islands, Martinique, St. Lucia, and St. Vincent. This is not surprising since there has probably been little collecting there, but I would be willing to guess that these islands do contain *Strategus,* and, considering the high degree of insular speciation in the Antilles, there is a good likelihood that these species may be new. Ballou (1914) reported that *Strategus* species do not occur on Antigua or St. Kitts.

S. talpa has expanded into some of the Leeward Islands from the east and is not part of the "normal" colonization sequence of the Lesser Antilles as previously discussed. More will be said regarding *S. talpa* later.

Greater Antilles

The paleogeography of the Greater Antilles remains the subject of considerable controversy among geologists and particularly biogeographers. Much of the fauna and flora of the Greater Antilles has unquestionable Central American affinities. Attempts to explain the methods of animal dispersal to the Greater Antilles fall into two basic schools of thought: (1) most of the fauna came from Central America by way of a land bridge along the Nicaraguan swell to Jamaica and Hispaniola (Allen, 1911; Anthony, 1925, 1926; Barbour, 1914, 1916; Bond, 1933; Dunn, 1932, 1934; Forbes, 1930; Martorell, 1945a; Osborn, 1932; Pilsbry, 1930; Rivas, 1958; Scharff, 1922; Schuchert, 1935; Schmidt, 1928), and (2) most of the fauna arrived by waif dispersal from Central and South America (Baskin and Williams, 1966; Darlington, 1938, 1957; King, 1962; Koopman, 1958; Matthew, 1915, 1916, 1918; Myers, 1938; Rosen and Bailey, 1963; Ruibal, 1967; Simpson, 1956). The equally impressive arguments of the proponents of both factions have been well documented and will not be repeated here.

Although Heatwole and Levins (1972) and King (1962) provided valuable and significant data to the idea of flotsam transport, I remain unconvinced that waif dispersal alone can account for the distribution pattern of *Strategus* in the Greater Antilles (Simpson, 1956, notwithstanding), but, on the other hand, there does not appear to be any positive geologic evidence for a continuous land bridge. Therefore, rather than advocate the conclusions of one camp over the other, I have tried to utilize the reasoning of both approaches so as to best explain the current distribution of *Strategus* in the Greater Antilles.

Khudoley and Meyerhoff (1971), in a rather definitive work on the geologic history of the Greater Antilles, have demonstrated that the volcanic history of these islands suggests in-place development, that is, a period of long stability as opposed to the younger, independent Lesser Antilles tectonic unit. They state further that the Miocene was a time of active vertical uplift and considerable basinal or coastal subsidence, and that this was the last time during which important thicknesses of sediments accumulated on the existing Greater Antilles islands, with the exceptions of west-central Cuba, possibly the younger Cauto basin of southeastern Cuba, and locally within the grabens of Hispaniola. After Miocene times most deposition was confined to present coastal and offshore areas—reefs, estuaries, and river mouths. The distribution of Miocene marine deposits shows that numerous large and small islands were present on the site of the modern Greater Antilles. However, none of the islands was as large as today's major islands until the middle or late Miocene when most of the existing land areas emerged. Khudoley and Meyerhoff observed that the faunal and floral similarities between Central America and the Greater Antilles suggests that direct land con-

nections existed perhaps via western Cuba or via the Cayman ridge and Nicaraguan rise. Most importantly, they state that this connection was possibly in the form of fairly closely spaced island "stepping stones." I do not believe that the concept of closely spaced island stepping stones falls within the realm of the land bridge theory *per se*, but it does reasonably enable the mechanisms of a land bridge *and* waif dispersal to function. The major difficulty of time and distance with respect to delicate, dessication-prone, or salt-sensitive animals rafting across large water barriers is eliminated as sequential colonization is now possible across smaller bodies of water by rafting or being carried by storm winds (see Darlington, 1938, for an in-depth discussion of the latter).

Utilizing the island "stepping stone" theory to which I adhere means that Jamaica would be the first island invaded from the Central American mainland followed by Hispaniola and then Cuba and Puerto Rico (the linear sequence of dispersal of Simpson, 1956). According to Matthews (1966) and Simpson (1956) the last two islands would be the last to be affected by new invasions and so would preserve early elements for the longest time. This appears nearly to be the case with *Strategus* (see Tables 5 and 6 and Fig. 175). Among the Greater Antillean *Strategus*, the Cuban *S. sarpedon* (1) is the most primitive, followed in order by *S. inermis* (2) (Hispaniola), *S. talpa* (2) (Puerto Rico), *S. atlanticus* (3) (San Salvador), *S. ajax* (3) and *S. symphenax* (3) (Cuba), *S. aenobarbus* (3) (Hispaniola), *S. simson* (4) (Jamaica), *S. caymani* (5) (Cayman Islands), *S. anachoreta* (5) (Cuba), and finally *S. oblongus* (6) (Puerto Rica and Hispaniola). The solid arrows in the figure indicate the probable island "stepping stones" route which is partially supported by the geology of the region. Furthermore, Darlington (1938) has shown that faunal relationships among the islands are definitely from Jamaica to Hispaniola to Cuba and not directly from Jamaica to Cuba, and that the Greater Antilles are faunistically more closely related to one another than is any one of the islands to the mainland. Figure 175 shows the proposed major routes of dispersal, and that, in general, the most primitive species are indeed peripherally located among the Greater Antilles due to their longer isolation from the source of continued gene flow; *Strategus oblongus* and *S. anachoreta* are the only two species that do not fit the hypothetical pattern well.

Ruibal (1967) observed that if inter-island colonizations were an important factor in the evolution of a group, it is logical to expect more common species between islands. The high level of endemicity and differentiation shown by *Strategus* in the Greater Antilles indicates a reasonably long separation from the mainland as well as among the islands and among themselves. Only *S. oblongus* occurs on three islands (Grand Cayman, Hispaniola, and Puerto Rico) while all the other species are strictly endemic to a single major island.

The occurrence of *S. atlanticus* on San Salvador in the southern Bahamas is almost certainly the result of its ancestors being fortuitously rafted or windblown from Cuba, Hispaniola, or Puerto Rica where it has close relatives in *S. aenobarbus, S. ajax,* and *S. talpa.* In spite of favorable currents for waif dispersal from the Greater Antilles, the Bahamas in general are probably not inhabited by *Strategus* because they are too low and dry.

The extreme similarity between *S. aenobarbus* and *S. ajax* suggests a fairly recent separation and isolation of these two species. Both species are most closely related to *S. caymani* and *S. simson.*

S. oblongus of Hispaniola and Puerto Rico is probably a recent introduction to Grand Cayman Island, arriving there by rafting or being blown by storm winds; currents and strom tracks for this region agree well with this hypothesis. The affinities of *S. oblongus* to the Central American *S. aloeus* and *S. longichomperus* present a somewhat confusing situation zoogeographically.

S. talpa occurs in Puerto Rico, the Virgin Islands, and on some of the Leeward Islands. The Virgin Islands are geologically a part of the Greater Antilles and may have once been loosely joined with Puerto Rico, and so it is not surprising that *S. talpa* occurs there. On the other hand, the occurrence of *S. talpa* in the Leewards indicates either a flotsam-jetsam dispersal to these islands or else introduction by the activities of man prior to 1790 (since the types were taken from St. Barthélemy and described in 1792). *S.*

talpa is closely related to *S. aenobarbus* (Cuba) and *S. ajax* (Hispaniola), and its ancestors undoubtedly came from Hispaniola.

Strategus simson (Jamaica) and *S. caymani* (Cayman Islands) are closely related and are both highly derived, with *S. simson* occupying the "port of entry" island of the Greater Antilles dispersal route from the mainland. I suspect the ancestors of *S. caymani* originally came to the Cayman Islands fairly recently from Jamaica by waif or windblown dispersal. A previous island connection from Jamaica to Grand Cayman is not possible because of the intervening, very deep Barlett trough.

Belkin (1962) believes that the Caribbean was an important center of evolution of new mosquitoes and other organisms rather than a barrier to dispersal and that during island formation through fragmentation of a land area, great environmental stress would come to bear on the reduced and isolated surviving populations. Under these possibly rigorous conditions new adaptive types would have an ideal opportunity to become quickly fixed. Bram (1967) reported that 47 of 61 American species of the subgenus *Culex (Culex)* (Diptera: Culicidae) are found in the Caribbean which was apparently their main center of origin. The relict pattern of dispersal displayed by *Strategus* in the Caribbean is very similar to that situation found in the Scarabaeinae by Matthews (1966) who believed that the high degree of endemicity of the Scarabaeinae in the Antilles is a reflection, not of special insular evolution, but of the continued survival of an ancient fauna for which the islands have become a refuge.

PHYLOGENY

INTRODUCTION

The following is a computer-assisted cladistic reconstruction of the presumed phylogeny or evolutionary history of the lineage of the genus based on the tenets of Hennig (1966) and Brundin (1966, 1972). Cladistic relationships refer to the branching sequence among the species in a phylogenetic tree (cladogram) regardless of any time scale or of phenetic similarities among the taxonomic units. It is a logical, repeatable system which offers an alternative to the phenetic system espoused by numerical taxonomy and to the classical system of intuitively derived reconstructions. I believe the objectivity of this approach and especially its repeatability enable the results to be clearly substantiated and arrived at by other systematists.

ASSUMPTIONS

Strategus is considered to be monophyletic and, as such, includes all the species assumed to have descended from the hypothetical ancestor. As Cracraft (1973) notes, this type of approach only assumes a relationship of hypothetical common ancestry but cannot recognize and identify specific ancestors. All of the conclusions presented here, therefore, are based on neontological data, and these data consist of the morphological character states and the inferred evolutionary directions of those characters.

Primitive characters are termed plesiomorphous, and derived characters are apomorphous (after Hennig, 1966). "Evolutionary (primitive-derived) sequences of the character states are hypothesized and taxa are clustered on the basis of shared derived character states. There is general agreement among systematists of very different persuasions that reliable evolutionary sequences can be constructed for many character states" (Cracraft, 1973).

Table 5 shows the presumed states for the 19 characters used in this analysis. The following combinations of parameters were used to ascertain plesiomorphy and apomorphy: (1) Simple to complex—as a general trend (that is not without exceptions), less derived species generally possess simpler or less elaborate modifications in their morphological character states. Thus, the absence of horns is usually a less derived state than the presence of horns, and a simple horn is generally less derived than a horn with a forked or modified apex; similarly, an excised clypeal apex is more derived than an entire (simple) apex, and an enlarged mandibular lobe is more derived than undeveloped lobes. It must be emphasized that this parameter cannot be used in and of itself as incorrect conclusions will result. For instance, elytral and pygidial punctation (a more complex state) is here considered to be more primitive than a smooth or impunctate elytra or pygidium based on the information pro-

vided by the remaining parameter. In general, however, the other characters used in this study tend to fit the pattern of simple to complex as it is correlated with primitive to derived. (2) In-group and ex-group comparisons—similar character states which occur in closely related groups are probably ancestral; this is based on the inference that different lineages arising from a common ancestor diverge with regard to their characters; in other words, a shared or common character is ancestral. The genus *Strategus* belongs to the tribe Oryctini which, along with the very closely related Pentodontini, contains just over a hundred genera, and of these roughly 35 are monotypic. Comparisons of *Strategus* character states were made with the following 35 pentodontine and oryctine genera: *Pentodon, Alissonotum, Heteronychus, Metanastes, Pycnoschema, Dilobderus, Coelosis, Ligyrus, Philoscaptus, Oxyligyrus, Bothynus, Aphonides, Papuana, Anoplognathus, Aphonus, Euetheola, Oxygrylius, Orizabus, Pimelopus, Dipelicus, Phyllognathus, Calicnemis, Thronistes, Pericoptus, Cyphonistes, Xyloryctes, Heterogomphus, Enema, Oryctes, Podischnus, Scapanes, Semanopterus, Megaceras, Licnostrategus,* and *Trichogomphus.*

The shared character states possessed by many of these genera and *Strategus* suggest what is pleisomorphous and apomorphous with regard to all the characters being used, with the possible exceptions of the tubercles on the head and the punctation on the mesosternum. The presence of tubercles on the head (like the presence of horns) would normally be considered a more complex and derived state, but the occurrence of tubercles in such a wide array of oryctine genera also suggests that this condition might be primitive. It was decided to call the presence of tubercles on the head a derived condition which most of the genera in this tribe have attained; this conclusion was based on a wider ex-group comparison between the tribe Oryctini and the less-derived tribes Hexodontini and Cyclocephalini and with the more advanced Dynastini. Similarly, a completely punctate mesosternum might probably be considered plesiomorphous as compared to a partially punctate (loss of punctures) mesosternum because of the commonness of punctation in general on the elytra and pygidium in the majority of the less-derived genera observed; in other words, the punctation of the mesosternum would follow the same trend as the other punctation characters, i.e., loss of punctures being apomorphic. However, in-group and ex-group comparisons indicate that this is not the case. The partially punctate mesosternum is here considered a less-derived condition than a completely punctate mesosternum because the large majority of oryctine genera share this partially punctate state, and, more importantly, because the more highly derived Dynastini show increased or complete punctation of the mesosternum. In this case, the wider ex-group comparisons provided more information than would the Oryctini alone.

Fossil sequences could not be used in this study because they do not exist. The single Oligocene elytron available exhibits gross punctation, but the single fossil by itself cannot reliably prove that this state is primitive. The punctation of the elytra *is* considered primitive in this analysis based on in-group and ex-group comparisons and commonness, and the fossil evidence tends to corroborate this conclusion.

METHODS

Table 6 shows, in a conventional data matrix, the scoring of the characters used in the analysis of this genus where 0 is the primitive state, and 1, 2, etc. indicate an increasingly derived condition. The %D column in the table suggests, in a very general way, the relative degree of primitiveness or derivedness of each taxonomic unit, and, as Edmonds (1972) and others have observed, the frequency of synapomorphy is a valid measure of inferred phyletic (cladistic) relationship. The %D is arrived at by dividing the number of derived characters by the total number (19) of characters being employed.

The method of arriving at a phylogeny is that of Camin and Sokal (1965), but because of the size of the data matrix and the subsequent operations required of the data, the three sequential CLADN programs written in FORTRAN IV by Bartcher (1966) for estimation of cladistic relationships were used and adapted to an IBM 360 computer. The data were processed at the Lin-

coln Computing Facility of the University of Nebraska Computer Network.

"The proposed method does not weight characters equally in the construction of the cladogram, since compatible characters are preferred over those that are incompatible. Characters with few states tend to be more compatible than those with many. Since evolutionary steps are equally weighted, those with more states will be more heavily weighted. However, the weighting procedure agrees with the principles of numerical taxonomy (Sokal and Sneath, 1963); it is automatic and *a posteriori*, based on the entire available evidence rather than on *a priori* or character-by-character weighting as employed in conventional phylogenetic procedures" (Camin and Sokal, 1965). In view of the above statements, I have some doubts as to whether characters seven and eight should be maintained as separate characters or joined to form one multistate character, but they are here retained as two characters. It is assumed that the cladogram with the minimum number of evolutionary steps (most parsimonious) is the best inference of the correct cladistic relationships.

"The first program, CLADN1, computes a compatibility matrix from the original data matrix. The compatibility matrix reveals which characters provide 'good' patterns that are relatively close to the presumed correct cladogram. It also points out 'bad' characters which appear to be miscoded or not to fit the assumptions of the method and should, therefore, be removed from consideration before proceeding with the analysis.

"The second program, CLADN2, applies the monothetic clustering procedure to the data matrix to yield a relatively parsimonious cladogram as a basis for further studies. The monothetic procedure is applied to a data matrix from which the 'bad' characters have been deleted.

"The third program, CLADN3, takes as input the procladogram produced by the monothetic procedure and by performing a number of operations it improves its structure to yield a simpler or more 'parsimonious' tree. The following operations are performed: (1) Program removes all empty internodes, (2) Program moves all common steps of branches with a common origin to the base stem of these branches, (3) It moves branches by one or two branching points closer to the base, and tries to rearrange the various branches into clusters that are more parsimonious in terms of the number of evolutionary steps" (Bartcher, 1966).

RESULTS

Table 7 shows the compatibility matrix resulting from CLADN1. Characters and patterns are listed at the left and upper margins of the table, the right and lower margins list compatibilities and the extra evolutionary steps required for rows and columns respectively. Although there are several row characters lacking compatibilities, none of the characters was considered "bad," and so all were retained for the CLADN2 analysis.

The CLADN2 program resulted in a basically non-parsimonious procladogram upon which CLADN3 is to act. The summary table at the end of this program indicated that 161 evolutionary steps were required in the procladogram. A goal of the CLADN3 program is to reduce this number of evolutionary steps by as many as possible in order to arrive at the most parsimonious solution.

Fig. 176 shows the proposed phylogeny for the genus *Strategus* as generated by the CLADN3 program. The level numbers of successive furcations are given at the left-hand margin, and the four-letter abbreviations for each taxonomic unit are given at the top of the figure. Evolutionary changes in character states are shown on each branch of the cladogram. The left number is the character number, and the right number indicates the number of evolutionary steps required for that character in the indicated branch. Successive stages in clustering of CLADN3 (in this case four were needed) has reduced the total number of evolutionary steps required from the original 161 to 116.

The results in Fig. 176 agree fairly well with my preconceived, intuitively derived conclusions which were based largely on phenetic evidence. The cladogram illustrates species clusters in a fashion which tends to receive support from the zoogeographical analysis and vice versa. It should probably be pointed out that the zoogeography was done independently and before the phylogenetic analysis so that the resul-

tant phylogeny would not unduly influence any zoogeographic considerations. The cladogram also tends to support the premise stated earlier that the frequency of synapomorphy is indeed a valid measure of cladistic relationship.

ERRONEOUS RECORDS

The following records are erroneous or extremely unlikely. In certain instances they may reflect mislabeling, inadvertent conveyance by man to the place of capture, or are the result of being substantially displaced by storm activity (in which case, if proven, the data would be valuable for zoogeographic considerations).

Strategus ajax.—BRAZIL: CEARÁ (1): Fortaleza. COSTA RICA: ALAJUELA (1): San Carlos. JAMAICA: No data (1).

Strategus aloeus.—CUBA: No data (2). UNITED STATES. CALIFORNIA (3): No data. FLORIDA (28): *Alachua (27):* Gainesville; *Orange (1):* No data. These specimens by F. W. Walker are mislabeled; they provide another example and corroboration to a similar case discussed by Woodruff (1973: 38). Woodruff has informed me (personal communication) that this species probably occurs in the panhandle and far west but that it has never been taken east of the Apalachicola River in Florida.

Strategus anachoreta.—TRINIDAD (Ballou, 1914; Smythe, 1920).

Strategus antaeus.—UNITED STATES: MICHIGAN (1): no data. NEBRASKA (2): *Lancaster:* Malcolm. *S. antaeus* is not established in either of these states.

Strategus argentinus.—BOLIVIA (Endrödi, 1973b). I am not convinced of the correct determination of these specimens.

Strategus centaurus.—VENEZUELA: MERIDA (1): Merida.

Strategus cessus.—UNITED STATES: CALIFORNIA (1): *San Diego:* Cuyamaca.

Strategus hipposiderus.—BRAZIL: BAHIA (1): Bahia.

Strategus mormon.—UNITED STATES: UTAH (Saylor, 1946).

Strategus sarpedon.—BRAZIL: No data (1).

Strategus syphax.—CUBA, GRENADA, HISPANIOLA (Blackwelder, 1944).

Strategus jugurtha.—VENEZUELA: ARAGUA: La Providencia (Martorell, 1939).

TABLE 5
PRIMITIVE AND DERIVED CHARACTER STATES IN *Strategus*.
Conclusions based on in-group comparisons, comparisons with related genera, commonness, and simple versus complex states.

No. CHARACTER	PRIMITIVE	DERIVED
(1) apex on clypeus	entire	emarginate or excised
(2) tubercles on head	reduced or obsolete	distinct
(3) middle lobe of mandible	small	large
(4) setae above eye	absent	present
(5) eye size	interocular width less than 3.0 transverse eye diameters	interocular width greater than 3.0 transverse eye diameters
(6) punctation on mesosternum	anterior half setigerously punctate	entirely and setigerously punctate
(7) development of anterior horn	not devloped; tuberculate	developed
(8) apex of anterior horn	simple	forked
(9) development of posterior horns	not developed	developed
(10) punctation of elytral disc	large, ocellate punctures present	large, ocellate punctures absent
(11) apex of elytra	without setae	setae present
(12) shape of parameres	simple	angulate or spined
(13) punctation of pygidium	densely and coarsely punctate	sparsely punctate
(14) setae on pygidium	absent	present
(15) body length	less than 35 mm	greater than 35 mm
(16) post-humeral punctation	present	absent
(17) color	dark, piceous	light, castaneous
(18) punctation on base of pronotum	present	absent
(19) elytral luster	dull	shining

TABLE 6
SCORING OF CHARACTER STATES IN *Strategus*
and % frequency of derived states (%D). 0 = primitive; 1+ = increasingly derived

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	%D
adolescens	0	1	0	0	0	0	1	0	0	1	0	0	1	0	0	2	0	0	2	0.316
aenobarbus	0	0	0	0	1	0	2	1	1	0	0	1	1	0	1	0	0	0	0	0.368
ajax	0	0	0	0	1	0	2	1	1	0	0	1	1	0	1	0	0	0	0	0.368
aloeus	1	1	2	1	1	0	2	0	2	1	0	0	1	1	1	2	0	0	2	0.648
anachoreta	0	1	2	1	1	0	2	0	2	0	0	0	1	0	1	0	1	0	2	0.526
antaeus	0	1	3	1	0	0	2	0	2	1	0	0	1	0	1	2	0	0	2	0.526
argentinus	1	1	1	0	0	0	1	0	1	1	0	0	0	1	1	2	0	0	2	0.526
atlanticus	0	1	0	1	1	1	0	0	0	0	0	1	1	0	0	0	1	0	0	0.368
caymani	1	0	0	0	1	0	2	1	0	1	0	1	1	0	1	0	1	0	1	0.526
centaurus	1	0	2	0	1	0	2	0	2	0	0	0	0	0	2	0	0	0	2	0.368
cessus	0	1	0	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	2	0.263
craigi	0	1	0	0	0	0	0	0	0	1	0	0	0	1	1	2	0	0	2	0.316
fallaciosus	0	1	1	1	0	0	0	0	0	1	0	0	0	1	1	0	0	0	2	0.368
fascinus	1	1	1	1	1	1	2	1	2	1	0	0	1	0	1	1	0	0	2	0.737
hipposiderus	1	1	2	0	1	0	1	0	1	1	0	0	1	0	1	1	0	0	2	0.579
howdeni	0	1	0	1	1	0	1	0	1	1	0	0	0	1	1	2	0	0	2	0.526
inermis	0	0	0	1	1	0	0	0	0	1	0	0	0	1	0	0	1	0	2	0.316
jugurtha	0	1	1	1	1	1	2	0	2	1	1	0	1	0	1	1	1	0	2	0.737
longichomperus	1	1	2	0	1	0	2	0	2	1	0	0	1	1	1	1	0	0	2	0.631
mandibularis	0	1	2	1	1	0	2	0	2	1	0	0	0	1	1	1	0	0	2	0.579
mormon	0	0	3	1	0	1	1	0	1	1	1	0	1	0	0	2	1	0	2	0.579
oblongus	0	1	2	1	1	0	2	0	2	1	0	0	1	0	1	1	0	0	2	0.579
sarpedon	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0.158
simson	1	0	0	0	1	0	2	1	2	0	0	1	1	0	1	0	0	0	1	0.474
splendens	0	1	1	1	0	0	0	0	0	1	0	0	1	0	0	2	1	0	2	0.421
surinamensis	0	1	1	1	1	1	2	0	2	1	0	0	1	0	1	1	0	0	2	0.631
symphenax	0	0	0	1	1	0	2	0	2	0	0	0	1	0	1	0	0	0	2	0.368
syphax	1	0	0	0	1	0	2	0	2	0	0	1	0	0	1	0	0	0	2	0.368
talpa	0	0	0	0	0	0	2	1	1	0	0	1	1	0	1	0	0	0	0	0.316
tarquinius	0	1	1	1	1	1	2	0	2	1	0	0	1	0	1	2	1	1	2	0.737
validus	0	1	0	0	1	0	2	0	2	1	0	0	1	0	1	1	0	0	2	0.474

TABLE 7
CLADN1 COMPATIBILITY MATRIX OF THE 19 CHARACTERS

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19		
1	0	1	2	1	1	1	1	1	2	1	0	1	1	1	1	2	1	0	1	2	19
2	1	0	3	1	1	1	2	1	2	1	1	1	1	1	1	2	1	1	1	0	23
3	2	3	0	2	2	3	4	1	4	2	3	0	2	2	5	4	3	1	0	2	43
4	1	1	3	0	1	1	2	1	2	1	1	1	1	1	1	2	1	1	1	0	23
5	1	1	2	1	0	1	2	1	2	1	1	1	1	1	2	2	1	1	2	0	24
6	1	1	2	0	1	0	2	1	2	1	1	1	0	0	1	2	1	1	1	3	19
7	2	2	5	2	2	2	0	2	3	2	2	2	2	2	3	4	2	2	4	0	45
8	1	1	1	1	1	1	0	0	2	1	0	1	0	0	0	1	1	0	2	6	14
9	2	2	5	2	2	2	1	2	0	2	2	2	2	2	3	4	2	2	3	0	42
10	1	1	3	1	1	1	2	1	2	0	1	1	1	1	1	1	1	1	1	0	22
11	0	1	1	0	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	11	7
12	1	1	0	1	1	1	1	1	2	1	0	0	1	0	1	0	1	0	2	5	15
13	1	1	3	1	1	1	2	1	2	1	1	1	0	1	1	2	1	1	2	0	24
14	1	1	2	1	1	0	2	0	2	1	0	0	1	0	1	2	1	0	0	6	16
15	1	1	3	1	1	1	2	1	2	1	1	1	1	1	0	2	1	1	2	0	24
16	2	2	6	2	2	2	4	1	4	0	2	0	2	2	2	0	2	2	0	3	37
17	1	1	3	1	1	1	2	1	2	1	1	1	1	1	1	2	0	1	2	0	24
18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	18	0
19	2	2	2	2	2	2	4	2	4	2	2	2	2	2	4	2	2	2	0	0	42
	2	1	2	3	1	3	2	3	1	3	5	5	4	5	2	2	2	5	5		
	21	23	46	20	22	21	34	18	40	19	19	16	19	18	29	35	22	17	24		

ALPHABETICAL LIST OF VALID SPECIES AND SYNONYMS OF *STRATEGUS*

Valid Species	Synonyms
adolescens Kolbe, 1906,	
aenobarbus (Fabr.), 1775	= *eurytus* (Fabr.), 1775 = *aenoburbns* (Fabr.), 1787 (misprint) = *eurytus* (Fabr.), 1787 (redescription) = *fossula* (Beauvois), 1819 **(new synonymy)** = *laterispinus* Chapin, 1932b
ajax (Olivier), 1789	
aloeus (L.), 1758	= *semiramis* (Fabr.), 1801 **(new synonymy)** = *aesalus* (Laporte), 1840 = *julianus* Burmeister, 1847 **(new synonymy)** = *piosomus* Kolbe, 1906 **(new synonymy)** = *roosevelti* Casey, 1915 **(new synonymy)** = *frontalis* Casey, 1915 **(new synonymy)** = *tarsalis* Casey, 1915 **(new synonymy)** = *gaillardi* Casey, 1915 **(new synonymy)**
anachoreta Burmeister, 1847	
antaeus (Drury), 1773	= *maimon* (Fabr.), 1775 = *maimon* (Fabr.), 1787 (redescription) = *divergens* Casey, 1915 = *atrolucens* Casey, 1915 = *pinorum* Casey, 1915 = *septentrionis* Casey, 1915 = *sinuatus* Casey, 1915 = *semistriatus* Casey, 1915 = *antaeus houstonensis* Knaus, 1925
argentinus Kolbe, 1906	
atlanticus, **new species**	
caymani, **new species**	
centaurus Kolbe, 1906	
cessatus Wickham, 1914 (fossil)	
cessus LeConte, 1866	= *beckeri* Kolbe, 1906 **(new synonymy)** = *cessus cavicauda* (Casey), 1915 = *durangoensis* (Casey), 1915 = *inflatus* (Casey), 1915 = *tantalus* (Casey), 1915
craigi, **new species**	
fallaciosus Kolbe, 1906	
fascinus Burmeister, 1847	
hipposiderus, **new species**	
howdeni, **new species**	
inermis Arrow, 1947	
jugurtha Burmeister, 1847	
longichomperus, **new species**	
mandibularis Sternberg, 1910	
mormon Burmeister, 1847	

oblongus (Beauvois), 1807	= *quadrifoveatus* (Beauvois), 1807 = *beauvoisi* **(new name; new synonymy)**
sarpedon (Burmeister,), 1847 *simson* (L.), 1758	= *titanus* (Fabr.), 1775 = *simson* (Fabr.), 1787 (redescription) = *titanus* (Fabr.), 1787 (redescription) = *boscii* (Beauvois), 1809 = *cognatus* (Casey), 1915 = *carolinensis* (Casey), 1915
splendens (Beauvios), 1809	= *tridens* Burmeister, 1847 *(nomen nudum)* = *kolbeanus* Prell, 1934 **(new synonymy)**
surinamensis surinamensis Burmeister, 1847 *surinamensis hirtus* Sternberg, 1910	= *syphax* (Fabr.) 1787 (redescription) = *vulcanus* (Fabr.), 1792 = *barbigerus* Chapin, 1932b **(new synonymy)**
symphenax, **new species** *syphax* (Fabr.), 1775	= *tricornis* Jablonsky, 1785 = *validus* (Fabr.), 1787 (redescription) = *faunus* (Billberg), 1820
talpa (Fabr.), 1792 *tarquinius,* **new species** *validus* (Fabr.), 1775	
verrilli, **new name**	

REFERENCES

Allen, G. M. 1911. Mammals of the West Indies. Bull. Mus. Comp. Zool. Harvard 54:175–263.

Altschuler, Z. S., and E. J. Young. 1960. Residual origin of the "Pleistocene" sand mantle in central Florida uplands and its bearing on marine terraces and Cenozoic uplift. U.S. Geol. Surv. Prof. Pap. 400–B: 202–207.

American Geographical Society. 1943a. Index to map of Hispanic America, 1: 1,000,000. Vol. 1: Geographical names in Central America. U.S. Gov't. Print. Off., Washington. 58 pp.

_____. 1943b. Index to map of Hispanic America, 1:1,000,000. Vol. III: Geographical names in the West Indies. U.S. Gov't. Print. Off., Washington. 46 pp.

_____. 1943c. Index to map of Hispanic America, 1:1,000,000. Vol IV: Geographical names in the Guinas. U.S. Gov't. Print. Off., Washington. 27 pp.

_____. 1944a. Index to map of Hispanic America, 1:1000,000. Vol. II: Geographical names in Mexico. U.S. Gov't. Print. Off., Washington. 181 pp.

_____. 1944b. Index to map of Hispanic America, 1:1,000,000. Vol. V: Geographical names in Brazil. U.S. Gov't. Print. Off., Washington. 286 pp.

_____. 1944c. Index to map of Hispanic America, 1:1,000,000. Vol. VI: Geographical names in Bolivia. U.S. Gov't. Print. Off., Washington. 33 pp.

_____. 1944d. Index to map of Hispanic America, 1:1,000,000. Vol. VII: Geographical names in Ecuador and Peru. U.S. Gov't. Print. Off., Washington. 65 pp.

_____. 1944e Index to map of Hispanic America, 1:1,000,000. Vol. VIII: Geographical names in Paraguay and Uruguay. USS. Gov't. Print. Off., Washington. 32 pp.

_____. 1944f. Index to map of Hispanic America, 1:1,000,000. Vol. IX: Geographical names in Chile. U.S. Gov't. Print. Off., Washington. 68 pp.

_____. 1944g. Index to map of Hispanic America, 1:1,000,000. Vol. X: Geographical names in Argentina. U.S. Gov't. Print. Off., Washington. 111 pp.

_____. 1944h. Index to map of Hispanic America, 1:1,000,000. Vol. XI: Geographical names in Venezuela. U.S. Gov't. Print. Off., Washington. 47 pp.

_____. 1944i. Index to map of Hispanic America, 1:1,000,000. Vol. XII: Geographical names in Colombia. U.S. Gov't. Print. Off., Washington. 62 pp.

Anthony, H. E. 1925–26. Mammals of Porto Rico, living and extinct. New York Acad. Sci., Sci. Surv. Porto Rico & Virgin Isl. 9:1–238.

Arnett, Jr., Ross H., and G. Allan Samuelson (eds.). 1969. Directory of Coleoptera collections of North America (Canada through Panama). Dept. Ent., Purdue Univ., Lafayette. 123 pp.

Arrow, Gilbert J. 1900. On pleurostict lamellicorns from Grenada and St. Vincent (West Indies). Trans. Ent. Soc. London 1900: 175–182.

_____. 1911. Notes on the coleopterous subfamily Dynastinae, with descriptions of new genera and species. Ann. Mag. Nat. Hist. (series 8) 8:151–176.

_____. 1914. Some further notes on lamellicorn beetles of the subfamily Dynastinae. Ann. Mag. Nat. Hist. (series 8) 14:257–276 and 360.

_____. 1937a. Scarabaeidae: Dynastinae. Coleopterorum Catalogus 21 (pars 156): 1–124. W. Junk, Berlin.

_____. 1937b. Systematic notes on beetles of the subfamily Dynastinae, with description of a few new species in the

British Museum collection (Coleoptera). Trans. Roy. Ent. Soc. London 86:35–37.

———. 1947. A few notes on West Indian dynastine beetles and descriptions of two new species. Ann. Mag. Nat. Hist. (series 11) 14: 221–224.

———. 1951. Horned Beetles. W. Junk, The Hague. 154 pp.

Axelrod, Daniel I. 1948. Climate and evolution in western North America during Middle Pliocene time. Evol. 2: 127–144.

———. 1950. Evolution of desert vegetation in western North America. Carnegie Ins. Publ. 590: 217–306.

Ballou, H. A. 1914. Sugarcane pests in the Leeward Islands. Imp. Dept. Agric. West Indies, pamphlet ser. 75: 1–45.

Barbour, T. H. 1914. A contribution to the zoogeography of the West Indies, with especial reference to amphibians and reptiles. Mus. Comp. Zool. Mem. 44(2): 209–346.

———. 1916. Some remarks upon Matthew's "Climate & Evolution" with supplementary note by W. D. Matthew. Ann. New York Acad. Sci. 27: 1–15.

Bartcher, Ronald L. 1966. FORTRAN IV program for estimation of cladistic relationships using the IBM 7040. Comp. Contr. 6: 1–54.

Bartholomew, John (ed.). 1957. The Times atlas of the world. Mid-century edition. Vol. V: The Americas. Times Publ. Co. Ltd., London. 57 pp., 120 plates.

Baskin, J. N., and E. E. Williams. 1966. The Lesser Antillean *Ameiva* (Sauria, Teiidae). Re-evaluation, zoogeography and the effects of predation. Stud. Fauna Curacao & other Carib. Isl. 23: 144–176.

Bates, Henry W. 1886–1890. Pectinicornia and lamellicornia. *IN* Godman and Salvin (eds.), Biologia Centrali-Americana. Insecta, Coleoptera, vol. 2, part 2: 1–432.

Beatty, Harry A. 1944. Fauna of St. Croix, V. I., J. Agric. Univ. Puerto Rico 28(3–4): 103–185.

Beauvois, Palisot de, A.M.F. J. 1805–1821. Insects recueillis Afrique et en Amérique. Paris. 276 pp., 90 plates.

Beebe, William. 1944. The function of secondary sexual characters in two species of Dynastidae (Coleoptera). Zoologica 29(2): 53–58.

Belkin, J. N. 1962. Mosquitoes of the South Pacific (Diptera, Culicidae), vol. 1. Univ. California Press, Berkeley. 608 pp.

Billberg, G. J. 1820. Novae insectorum species descriptae. Mem. Akademiia Nauk S.S.S.R. (ser. 5)7: 381–395.

Blackwelder, Richard E. 1944. Checklist of the coleopterous insects of Mexico, Central America, the West Indies, and South America, part 2. Bull. U.S.N.M. 185: 189–341.

Bodkin, G. E. 1919. Notes on the Coleoptera of British Guiana. Ent. Month. Mag. 55: 210–219.

Bonatti, Enrico, and Stefan Gartner, Jr. 1973. Caribbean climate during Pleistocene ice ages. Nature 244: 563–565.

Bond, J. 1933. The distribution and origin of the West Indian avifauna. Proc. American Philos. Soc. 72: 341–349.

Bram, R. A. 1967. Classification of *Culex* (sugenus *Culex*) in the New World (Diptera: Culicidae). Proc. U.S.N.M. 120: 1–222.

Browne, Patrick. 1756. The civil and natural history of Jamaica. T. Osborne and J. Shipton, London. 428 pp.

Bruch, Carlos. 1911. Catalogo sistematico de los coleopteros de la republica Argentina, pars IV. Revista Museo La Plata 17 (series 2) 4: 185–225.

Brundin, L. 1966. Transantarctic relationships and their significance, as evidenced by chironomid midges. Kungl. Svenska Vetenskap. Handl. 11(1): 1–472.

———. 1972. Evolution, causal biology, and classification. Zool. Scripta 1: 107–120.

Burges, N. A. 1965. Biological processes in the decomposition of organic matter. *IN* Hallsworth, E. G., and D. V. Crawford (eds.), Experimental Pedology. Butterworths, London. 413 pp.

Burges, N. A., H. M. Hurst, and B. Walkden. 1964. The phenolic constituents of humic acid and their relation to the lignin of the plant cover. Geochim. Cosmochim. Acta 28: 1547–1554.

Burmeister, Herman. 1847. Handbuch der entomologie, vol. 5. Berlin. 584 pp.

Camin, Joseph H., and Robert R. Sokal. 1965. A method for deducing branching sequences in phylogeny. Evol. 19(3): 311–326.

Casey, Thos. L. 1915. A review of the American species of Rutelinae, Dynastinae, and Cetoniinae. Memoirs of the Coleoptera. 6: 1–394.

Chace Jr., Fenner A., and Horton H. Hobbs, Jr. 1969. The freshwater and terrestrial decapod crustaceans of the West Indies with special reference to Dominica. Bull. U.S.N.M. 292: 1–258.

Chapin, Edward A. 1932a. Revision of the pleurostict Scarabaeidae of Cuba and Isle of Pines. II. Rutelinae, Dynastinae, and Cetoniinae. Ann. Ent. Soc. Amer. 25(2) 282–314.

———. 1932b. *Strategus simson* L. and related West Indian species (Coleoptera: Scarabaeidae). J. Washington Acad. Sci. 22(15): 449–456.

Chevrolat, A. 1865. Coléoptères de l'ile Cuba. Notes, synonymies et descriptions d'espéces nouvelles. Ann. Soc. Ent. France. (series 4) 5: 21–36.

Clench, W. J., and R. D. Turner. 1956. Fresh-water mollusks of Alabama, Georgia, and Florida from the Escambia to the Suwannee River. Bull. Florida St. Mus. 1: 97–239.

Cockerell, T. D. A. 1906. *Strategus* injuring date-palms. Ent. News 17(1): 34.

Cohn, T. J. 1965. The arid-land katydids of the North American genus *Neobarrettia*: their systematics and a reconstruction of their history. Misc. Publ. Univ. Michigan Mus. Zool. 126: 1–179.

Costa Lima, A. D. 1953. Insectos do Brasil. vol. 8. Coleópteros, 2ª parte. Escola Nacional de Agronomia, Série Didática 10: 1–223.

Cracraft, Joel. 1974. Phylogenetic models and classification. Syst. Zool. 23: 71–90.

Darlington, Jr., P. G. 1938. The origin of the fauna of the Greater Antilles, with discussion of dispersal of animals over water and through the air. Quart. Rev. Biol. 13 (3): 274–300.

———. 1957. Zoogeography: The geographical distribution of animals. John Wiley and Sons, Inc., New York. 675 pp.

Darrow, R. A. 1961. Origin and development of the vegetational communities of the Southwest. *IN* Shields, L. M., and L. H. Gardner (eds.), Bioecology of the arid and semi-arid lands of the Southwest. New Mexico Highl. Univ. Bull.: 30–47.

Dejean, Pierre F. M. A. 1836. Catalogue des coléoptéres de la collection de M. le comte Dejean. Troisième édition, revue, corrigée et augmentée. Paris 468 pp.

Dexter, R. R. 1932. The food habits of *Bufo marinus*. Internat. Soc. Sugar-cane Tech. 4th Congress, part 2, Bull. 74:1–6.

Dillon, Elizabeth S., and Lawrence S. Dillon. 1961. A manual of common beetles of eastern North America. Row, Peterson & Co., Evanston, Ill. 884 pp.

Dillon, L. W. 1956. Wisconsin climate and life zones in North America. Sci. 123: 167–176.

Drury, Dru. 1773. Illustrations of natural history, wherein are exhibited upwards of two hundred and forty figures of exo-

tic insects, according to their different genera, very few of which have hitherto been figured by any author, being engraved and coloured from nature, with the greatest accuracy, and under the authors own inspection; on fifty copper plates; with a particular description of each insect, interspersed with remarks and reflections on the nature and properties of many of them. Vol. 2. London. 90 pp., 50 plates.

Duges, D. Eugenio. 1876. Metamórfosis de un coleóptero de la familia de los lamelicórneos y del genero *Strategus*. Naturaleza. Mexico. Museo Nacional de Historia Natural. 3:49–52.

———. 1886. Métamorphoses de quelques coléoptères Mexicains. Ann. Soc. Ent. Belgique 30: 27–45.

Dunn, E. R. 1932. The colubrid snakes of the Greater Antilles. Copeia 1932: 89–92.

———. 1934. Physiography and herpetology in the Lesser Antilles. Copeia 1934 (3): 105–111.

Edmonds, W. D. 1972. Comparative skeletal morphology, systematics and evolution of the phanaeine dung beetles (Coleoptera: Scarabaeidae). Univ. Kansas Sci. Bull. 59(11): 731–874.

Edwards, W. H. 1939. Annual report of the entomologist for the year 1938. *IN* Jones, G. A., Annual Report of the Department of Agriculture for the Year Ended 31st December 1938. Jamaica. 98 pp.

Endrödi, Sebo. 1959. Neue Käfer. 4. Melolonthiden (Dynastinen). Bonner Zool. Beitr. 10(1–2): 116–125.

———. 1973a. Designation von Lectotypen aus der Sammlung von H. Burmeister: Oryctini und Dynastini (Coleoptera: Melolonthidae). Acta Zool. Acad. Sci. Hungaricae 19(1–2): 11–17.

———. 1973b. Einige Dynastinen-Arten (Coleoptera: Melolonthidae) aus Bolivien. Opusc. Zool. Budapest 12(1–2): 57–61.

Entwhistle, P. F. 1972. Pest of cocoa. Longman Group Ltd., London. 779 pp.

Fabricius, Johann C. 1775. Systema entomologiae. Lipsiae. 382 pp.

———. 1787. Mantissa Insectorum, vol. 1. Hafniae. 382 pp.

———. 1792. Entomologia systematica, vol. 1. Hafniae. 538 pp.

———. 1801. Systema eleutheratorum, vol. 1. Kiliae. 506 pp.

Fall, H. C. and T. D. A. Cockerell. 1907. The Coleoptera of New Mexico. Trans. American Ent. Soc. 33: 145–218.

Feeny, P. P. 1968. Effects of oak leaf tannins on larval growth of the winter moth *Operophtera brumata*. J. Insect Physiol. 14: 805–817.

———. 1969. Inhibitory effect of oak leaf tannins on the hydrolysis of proteins by trypsin. Phytochem. 8: 2119–2126.

Fleutiaux, E., and A. Sallé. 1889. Liste des coléoptères de la Guadeloupe et descriptions d'espéces nouvelles. Ann. Soc. Ent. France (series 6) 9: 351–484.

Forbes, W. T. M. 1930. Insects of Porto Rico & Virgin Islands. Heterocera or moths (excepting the Noctuidae, Geometridae and Pyralidae). New York Acad. Sci., Sci. Surv. Porto Rico & Virgin Isl. 12(1) 1–171.

Gemminger, M., and B. de Harold. 1869. Catalogus coleopterorum hucusque descriptorum synonymicus et systematicus. Vol. 4. Scarabaeidae. Monachii. pp. 979–1346.

Goin, J. C. 1958. Comments upon the origin of the herptofauna of Florida. Quart. J. Florida Acad. Sci. 21: 61–70.

Goncalves, Cincinato R. 1946. Males de carnaúba no Ceará e no Piauí. Bol. Fitossanit. 3(3/4): 145–170.

Gosse, Philip Henry. 1848. On the insects of Jamaica. Ann. Mag. Nat. Hist. (series 2) 1: 109–115, 197–202, 268–270, 349–352.

Gowdy, C. C. 1923. Principal agricultural pests of Jamaica. Jamaica Dept. of Agric. Ent. Bull. 2: 1–80.

Gruner, L. 1971. Scarabaeidae Melolonthinae, Dynastinae, Rutelinae, Cetoniinae (Coleoptera) récoltés in Guyane Francaise par la mission du Muséum National d'Histoire Naturelle (1). Ann. Soc. Ent. France (N.S.) 7 (4): 843–848.

Haffer, Jurgen. 1969. Speciation in Amazonian forest birds. Sci. 165(3889): 131–137.

Harshberger, J. W. 1916. The vegetation of the New Jersey pine-barrens. C. Sower, Philadelphia. 329 pp.

Hayward, K. J. 1942. El escarabajo o cascarudo rinocerante (*Strategus validus* (Fabricius)) y la cana de azucar. Rev. Indust. Agric. Tucuman 32(10/12): 333–335.

Heatwole, Harold, and Richard Levins. 1972. Biogeography of the Puerto Rican Bank: flotsam transport of terrestial animals. Ecol. 53(1): 112–117.

Hennig, W. 1966. Phylogenetic systematics. Univ. Illinois Press, Urbana. 263 pp.

Henshaw, Samuel. 1885. List of the Coleoptera of America, north of Mexico. American Ent. Soc., Philadelphia. 160 pp.

Hope, Frederick W. 1837. The coleopterist's manual, containing the lamellicorn insects of Linneus and Fabricius. Vol. 1. 121 pp.

Horn, Geo. H. 1875. Synonymical notes and descriptions of new species of North American Coleoptera. Trans. American Ent. Soc. 5: 126–162.

Howden, Henry F. 1963. Speculations on some beetles, barriers, and climates during the Pleistocene and pre-Pleistocene periods in some non-glaciated portions of North America. Syst. Zool. 12(4): 178–201.

———. 1966. Some possible effects of the Pleistocene on the distributions of North American Scarabaeidae (Col.). Canadian Ent. 98(11): 1177–1190.

———. 1969. Effects of the Pleistocene on North American insects. Ann. Rev. Ent. 14: 39–56.

———. 1970. Jamacian Scarabaeidae: notes and descriptions (Coleoptera). Canadian Ent. 102(1): 1–15.

Hubbell, Theodor H. 1954. Relationships and distribution of *Mycotrupes*. *IN* Olson, Ada L., T. H. Hubbell, and H. F. Howden, The burrowing beetles of the genus *Mycotrupes* (Coleoptera: Scarabaeidae: Geotrupinae). Misc. Publ. Mus. Zool., Univ. Michigan, No. 84: 1–59.

———. 1960. Endemism and speciation in relation to Pleistocene changes in Florida and the southeastern coastal plain. Proc. 11th Intern. Cong. Ent. 11(1): 466–469.

Hurpin, B., and D. Mariau. 1966. Contribution a la lutte contre les *Oryctes* nuisibles aux palmiers. Mise au point d'un élevage permanent en laboratoire. C. R. Acad. Agric. France. (1966): 178–186.

Jablonsky, Carl Gustav. 1785. Natursystem aller bekannten in- und ausländischen Insecten. J. Pauli, Berlin. 310 pp.

Janzen, Daniel H. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. Biotropica 6(2): 69–103.

Khudoley, K. M., and A. A. Meyerhoff. 1971. Paleogeography and geological history of the Greater Antilles. Geol. Soc. America Mem. 129: 1–199.

King, W. 1962. Systematics of Lesser Antillean lizards of the genus *Sphaerodactylus*. Bull. Florida St. Mus. 7: 1–52.

Kirby, William, and William Spence. 1828. An introduction to entomology, vol. 4 (5th ed.). London. 683 pp.

Knaus, Warren. 1916. Notes on *Strategus mormon*. Bull. Brooklyn Ent. Soc. 11(4): 79–81.

———. 1924. Collection and life history notes on *Strategus*

mormon. J. New York Ent. Soc. 32(3): 124–125.
———. 1925. Three new forms of Coleoptera. Pan-Pacific Ent. 1(4): 182–183.
Kolbe, H. 1906. Ueber die Arten der amerikanischen Dynastidengattung *Strategus*. Berliner Ent. Zeit. 51: 1–32.
Koopman, K. F. 1958. Land bridges and ecology in bat distribution on islands off the northern coast of South America. Evol. 12: 429–439.
Lacordaire, Jean T. 1856. Histoire naturelle des insects. Genera des coléoptères ou expose methodique et critique de tous les genres proposes jusqu'ici dans cet odre d'insectes. Vol. 3. Libraire Encyclopedique de Roret, Paris. 594 pp.
Lamb, K. P. 1974. Economic entomology in the tropics. Academic Press, London. 195 pp.
Landin, Bengt-Olof. 1956. The Linnean species of Lamellicornia described in "Systema Naturae" ed. X (1758). (Col.). Entomol. Tidsk. 77(1): 1–18.
Laporte, Francois L. (Comte de Castelnau). 1840. Histoire naturelle des insectes coléopterès. Avec une introduction renferment l'anatomie et la physiologie des animaux articulés, par M. Brullé. Vol. 2. P. Duménil, Paris. 564 pp.
LeConte, John L. 1861–62. Classification of the Coleoptera of North America. Part 1. Smiths. Misc. Coll., pp. 1–285.
———. 1866. Additions to the coleopterous fauna of the United States. No. 1. Proc. Acad. Nat. Sci. Philadelphia 18: 361–394.
———. 1873. Classification of the Coleoptera of North America. Part 2. Smiths. Misc. Coll., pp. 286–348.
Leng, Charles W., and Andrew J. Mutchler. 1914. A preliminary list of the Coleoptera of the West Indies as recorded to January 1, 1914. Bull. American Mus. Nat. Hist. 33: 391–493.
———. 1917. Supplement to preliminary list of the Coleoptera of the West Indies. Bull. American Mus. Nat. Hist. 37: 191–220.
Leng, Charles W. 1920. Catalogue of the Coleoptera of America, north of Mexico. John D. Sherman, Mount Vernon, New York. 470 pp.
Lever, R. J. A. W. 1969. Pests of the coconut palm. FAO Agric. Stud. No. 77: 1–190.
Linnaeus, Carolus. 1758. Systema naturae, edito decima. Lipsiae. 824 pp.
Manee, Abraham H. 1908. Some observations at Southern Pines, N. Carolina Ent. News 19(6): 286–289.
Manter, H. W. 1928. Notes on the eggs and larvae of the thorny-headed worm of hogs. Trans. American Microsc. Soc. 48(3): 342–347.
Martin, P. S. and P. J. Mehringer, Jr. 1965. Pleistocene pollen analysis and biogeography of the Southwest. *IN* Wright, Jr., H. E., and D. G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press, Princeton, New Jersey, 922 pp.
Martorell, Luis F. 1939. Insects observed in the state of Aragua, Venezuela, South America. J. Agric. Univ. Puerto Rico 23(4): 177–232.
———. 1945a. A survey of the forest insects of Puerto Rico. Part 1. J. Agric. Univ. Puerto Rico 29(1): 70–354.
———. 1945b. A survey of the forest insects of Puerto Rico. Part 2. J. Agric. Univ. Puerto Rico 29(4): 355–608.
Matthew, William Diller. 1915. Climate and evolution. Ann. New York Acad. Sci. 24: 171–318.
———. 1916. Supplemental note (See Barbour, 1916). Ann. New York Acad. Sci. 27: 11–15.
———. 1918. Affinities and origin of the Antillean mammals. Bull. Geol. Soc. America 29: 657–666.
Matthews, Eric G. 1966. A taxonomic and zoogeographic summary of the Scarabaeinae of the Antilles (Coleoptera: Scarabaeidae). Mem. American Ent. Soc. No. 21: 1–134.
Miles, P. W. 1969. Interaction of plant phenols and salivary phenolases in the relationship between plants and Hemiptera. Entom. Exp. Appl. 12: 736–744.
Miskimen, George W., and Richard M. Bond. 1970. The insect fauna of St. Croix, United States Virgin Islands. Sci. Surv. Puerto Rico and Virgin Islands 13(1): 1–114.
Myers, George S. 1938. Fresh-water fishes and West Indian zoogeography. Ann. Report Smith. Instit. 1937: 339–364.
Müller, P. 1973. The dispersal centres of terrestrial vertebrates in the Neotropical realm. Dr. W. Junk, N. V., The Hague. 244 pp.
Neave, Sheffield Airey (ed.). 1940. Nomenclator Zoologicus, vol. 4 (Q–Z). Zool. Soc. London, London. 758 pp.
Neill, W. T. 1957. Historical biogeography of present-day Florida. Florida St. Mus. Bull. 2: 175–220.
Nevermann, F. 1933. Beobachtungen über die Lebensweise einiger Lamellicornier und einer Chrysomelidae. Ent. Blätter Fuer Biol. Syst. Käfer 29: 179–183.
Olivier, Antoine Guillaume. 1789. Entomologie, ou histoire naturelle des insectes, avec leurs caractères géneriques et specifiques, leur description, leur synonymie, et leur figure enluminée. Coléopéres. Vol. 1. Paris. Genera separately paged.
Osborn, H. 1932. Geographic and ecologic factors in distribution of neotropic Homoptera. 5th Cong. Intern. d'Ent., Paris: pp. 461–468.
Paulian, Renaud. 1947. Scarabaeoidea. Coléoptères de Antilles, vol. 1. Faune de L'Empire Francais 7: 17–84.
Pilsbry, H. A. 1930. Land mollusks of the Caribbean Islands. Proc. Acad. Nat. Sci. Philadelphia 82: 221–261.
Plank, H. K. 1945. Life history, habits and control of the coconut rhinoceros beetle in Puerto Rico. Bull. Federal Exp. Sta., Mayaguez 45: 1–35.
Prell, Heinrich. 1934. Beiträge zur Kenntnis der dynastinen (XII). Beschreibungen und bemerkungen. Ent. Zietsch. 47: 162–164, 186–188, 194–195.
Ramos, J. A. 1946. The insects of Mona Island (West Indies). J. Agric. Univ. Puerto Rico 30(1): 1–74.
Ritcher, P. O. 1944. Dynastinae of North America with descriptions of the larvae and keys to genera and species (Coleoptera: Scarabaeidae). Bull. Kentucky Agric. Exp. Sta. 467: 1–56.
———. 1966. White grubs and their allies. Oregon State Univ. Press, Corvallis. 219 pp.
Rivas, L. R. 1958. The origin, evolution, dispersal, and geographical distribution of the Cuban poeciliid fishes of the tribe Girardinini. Proc. American Philos. Soc. 102(3): 281–320.
Rosen, Donn Eric, and Reeve M. Bailey. 1963. The poeciliid fishes (Cyprindontiformes), their structure, zoogeography, and systematics. Bull. American Mus. Nat. Hist. 126: 1–176.
Ross, Herbert H. 1965. Pleistocene events and insects. *IN* Wright, Jr., H. E., and David G. Frey (eds.), The Quaternary of the United States. Princeton Univ. Press. Princeton. 922 pp.
Ruibal, R. 1967. Evolution and behavior in West Indian anoles. *IN* Milstead, William W. (ed.), Lizard ecology, a symposium. Univ. Missouri Press, Columbia. 300 pp.
Saylor Lawrence W. 1946. Synoptic revision of the United States scarab beetles of the subfamily Dynastinae, No. 2: tribe Oryctini (part). J. Washington Acad. Sci. 36(1): 16–21.
Schaeffer, Charles. 1915. New Coleoptera and miscellaneous

notes. J. New York Ent. Soc. 23(1): 47–55.
Scharff, Robert Francis. 1922. On the origin of the West Indian Fauna. Bijdr. Tot de Dierkunde, Leiden 22:65–72.
Schmidt, K. P. 1928. Amphibians and land reptiles of Porto Rico, with a list of those reported from the Virgin Islands. New York Acad. Sci., Sci. Surv. Porto Rico & Virgin Isl. 10(1): 1–160.
Schuchert, Charles. 1935. Historical geology of the Antillean-Caribbean region. John Wiley & Sons, Inc., New York. 811 pp.
Schufeldt, R. W. 1884. Observations upon a collection of insects made in the vicinity of New Orleans, Louisiana, during the years 1882 and 1883. Proc. U.S.N.M. 7(22): 331–338.
Simmonds, F. J. 1969. Biological control of sugar cane pests: a general survey. *IN* Williams, J. R., J. R. Melcalfe, R. W. Mungomery, and R. Mathes (eds.), Pests of sugar cane. Elsevier Publ. Co., Amsterdam. 568 pp.
Simpson, George Gaylord. 1956. Zoogeography of West Indian land mammals. American Mus. Novit. No. 1759: 1–28.
Sloane, Hans. 1725. A voyage to the islands Madera, Barbados, Nieves, S. Christophers, and Jamaica, with the natural history of the herbs and trees, four-footed beasts, fishes, birds, insects, reptiles, & c. of the last of those islands; to which is prefix'd. an introduction, wherein is an account of the inhabitants, air, waters, diseases, trade & c. of that place, with some relations concerning the neighboring continent, and islands of America. Illustrated with figures of the things described, which have not been heretofore engraved; in large copper-plates as big as the life. Vol. 2. British Museum, London. 205 pp.
Smythe, Eugene G. 1916. Report of the South Coast Laboratory. *IN* Fourth Rep. Board Commis. Agric. Porto Rico, Gov't. Porto Rico, Rio Piedras. 53 pp.
———. 1920. The white-grubs injuring sugar cane in Porto Rico. J. Dept. Agric. Porto Rico 4(2): 3–29.
Sokal, R. R., and P. H. A. Sneath. 1963. Principles of numerical taxonomy. W. H. Freeman and Co., San Francisco. 359 pp.
Stahl, C. F., and L. C. Scaramuzza. 1929. Soil insects attacking sugar cane in Cuba. Tropical Plant Res. Found. Bull. No. 10: 1–19.
Staig, Robert A. 1931. The Fabrician types of insects in the Hunterian collection at Glasgow University, part I. Coleoptera. Cambridge Univ. Press, Cambridge. 110 pp.
Sternberg, Chr. 1910. Neue Dynastiden-Arten II. Ann. Soc. Ent. Belgique 54: 91–102.
Torre-Bueno, J. R. de la. 1937. A glossary of entomology. Brooklyn Ent. Soc., Brooklyn. 336 pp.
Valdes, Barry R. 1951. Control de gusanos blancos. Mem. Asoc. Tecn. Azucareros Cuba 25: 51–56.
Van Dinther, J. B. M. 1956. Insects of the coconut palm in Suriname. Landbouwproefstation in Suriname Bull. No. 69: 1–27.
Vayssiere, P. 1965. Sur quelques insectes des palmiers en Amérique de Sud. Mededel Landouwhogesch Opzoekingssta Ghent 30(3): 1571–1576.
Vernon, R. O. 1951. Geology of Citrus and Levy counties, Florida. Bull. Florida Geol. Surv. 33: 1–256.
Verrill, A. Hyatt. 1906. Descriptions of two remarkable new species of goliath beetles (*Dynastes*) from Dominica Island, Antilles. Brief contributions to zoology from the museum of Yale University, no. LXVI. American J. Sci. (4th series) 21(124): 317–320.
———. 1907. Description of a new species or sub-species of hercules beetles from Dominica Island, B. W. I., with notes on the habits and larvae of the common species and other beetles. Brief contributions to zoology from the museum of Yale University, no. LXVII. American J. Sci. (4th series) 24(142): 305–308.
Vuilleumier, Beryl Simpson. 1971. Pleistocene changes in the fauna and flora of South America. Sci. 173: 771–780.
Westwood, John O. 1837. Illustrations of exotic entomology, containing upwards of six hundred and fifty figures and descriptions of foreign insects, interspersed with remarks and reflections on their nature and properties. By Dru Drury. A new edition, brought down to the present state of the science, with the systematic characters of each species, synonyms, indexes, and other additional matter. Vol. 1. Henry G. Bohn, London. 123 pp.
Whitehead, D. C. 1964. Identification of *p*-hydroxbenzoid, vanillic, *p*-coumaric and ferulic acids in soils. Nature 202: 417–418.
Wickham, H. F. 1914. New Miocene Coleoptera from Florissant. Bull. Mus. Comp. Zool. 58(11): 423–494.
Wolcott, George N. 1923. Insectae Portoricensis. A preliminary annotated checklist of the insects of Porto Rico, with descriptions of some news (sic) species. J. Dept. Agric. Porto Rico 7(1): 1–312.
———. 1926. Las plagas del cacao en Santo Domingo, y algunas indicaciones para combatirlas. Rev. Agric. Puerto Rico 6: 11–12.
———. 1936. "Insectae Borinquenses." A revised annotated check-list of the insects of Puerto Rico. J. Agric. Puerto Rico 20(1): 1–600.
———. 1941. A supplement to "Insectae Borinquenses." J. Agric. Univ. Puerto Rico 25(2): 33–158.
———. 1948. Insects of Puerto Rico. J. Agric. Univ. Puerto Rico 32(1): 1–748.
———. 1950. The sugar-cane rhinoceros beetle. J. Econ. Ent. 43(3): 385.
Woodring, W. P. 1954. Caribbean land and sea through the ages. Bull. Geol. Soc. America 65: 719–732.
Woodruff, Robert Eugene. 1973. The scarab beetles of Florida, part 1. Arthropods of Florida and Neighboring Land Areas 8: 1–220.
Yang, Suh Yung, Michael Soulé, and George Gorman. 1974. *Anolis* lizards of the eastern Caribbean: a case study in evolution. 1. Genetic relationships, phylogeny, and colonization sequence of the *roquet* group. Syst. Zool. 23: 387–399.
Young, Frank N. 1954. The water beetles of Florida. Univ. Florida Studies, Biol. Sci. Ser. 5(1): 1–238.
Zimsen, Ella. 1964. The type material of I. C. Fabricus. Munksgaard, Copenhagen. 656 pp.

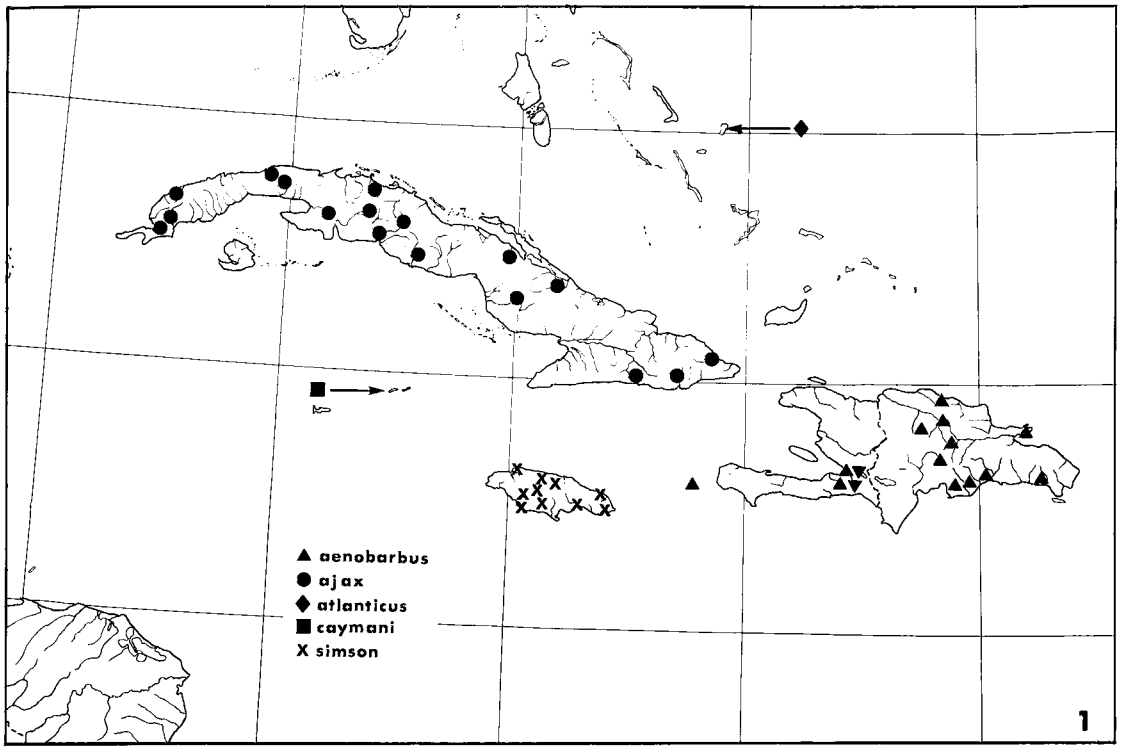


Fig. 1.—Distribution map for *S. aenobarbus, S. ajax, S. atlanticus, S. caymani, S. simson.*

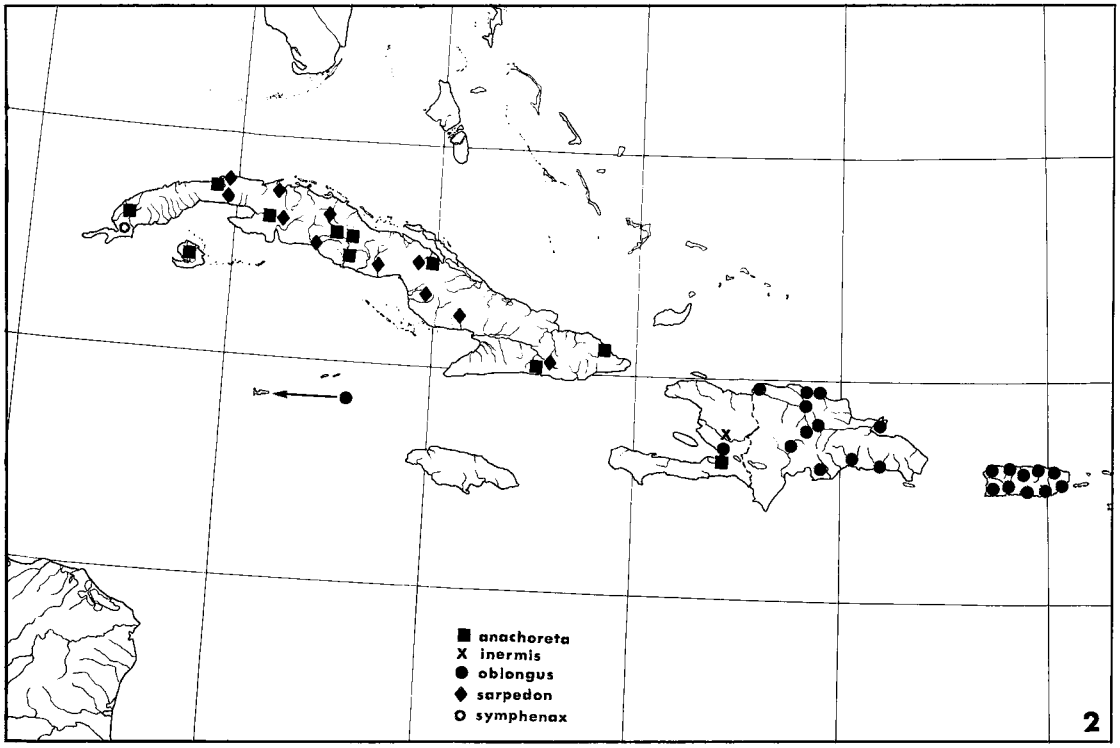


Fig. 2.—Distribution map for *S. anachoreta, S. inermis, S. oblongus, S. sarpedon, S. symphenax.*

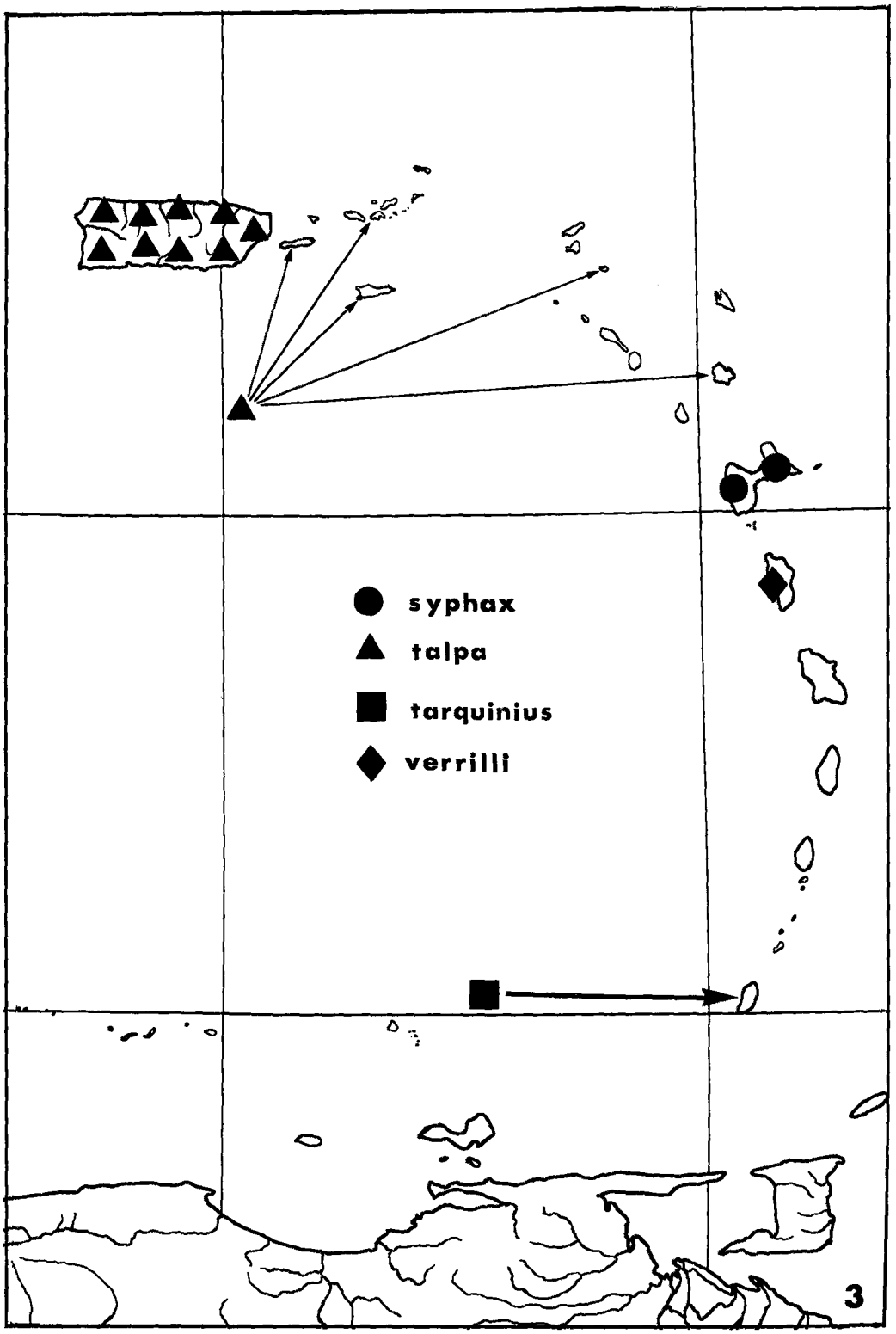


Fig. 3.—Distribution map for *S. syphax, S. talpa, S. tarquinius, S. verilli.*

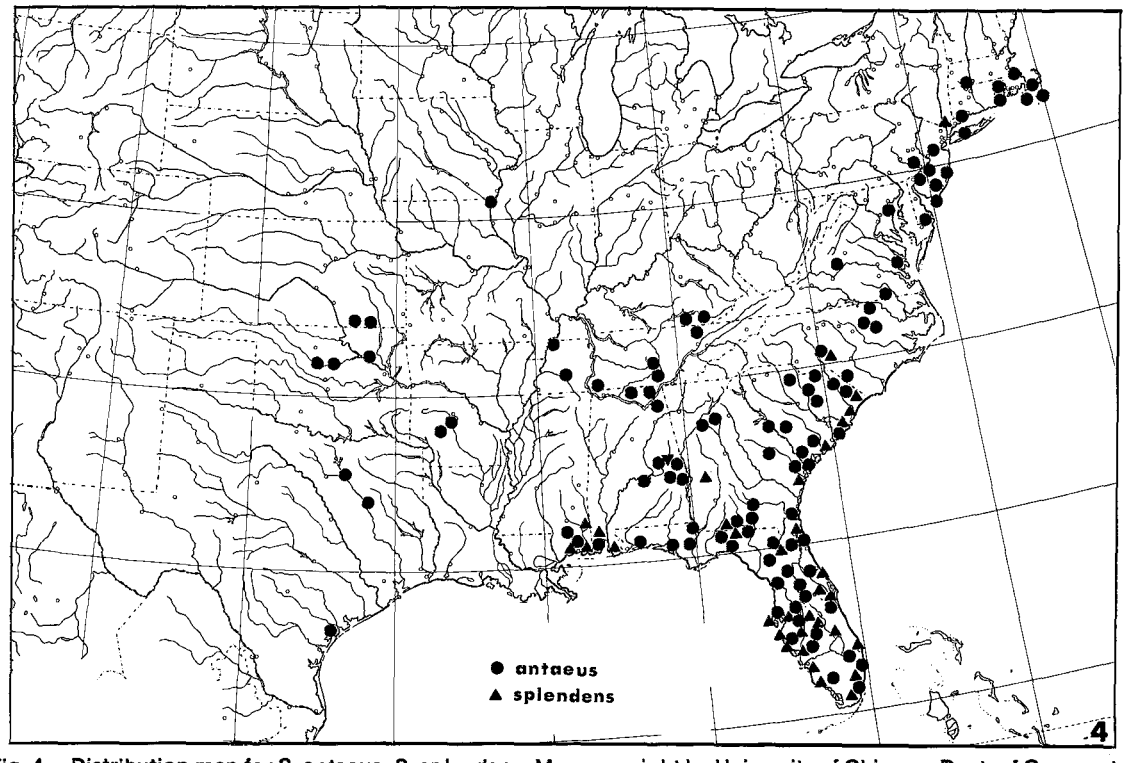


Fig. 4.—Distribution map for *S. antaeus, S. splendens.* Map copyright by University of Chicago, Dept. of Geography.

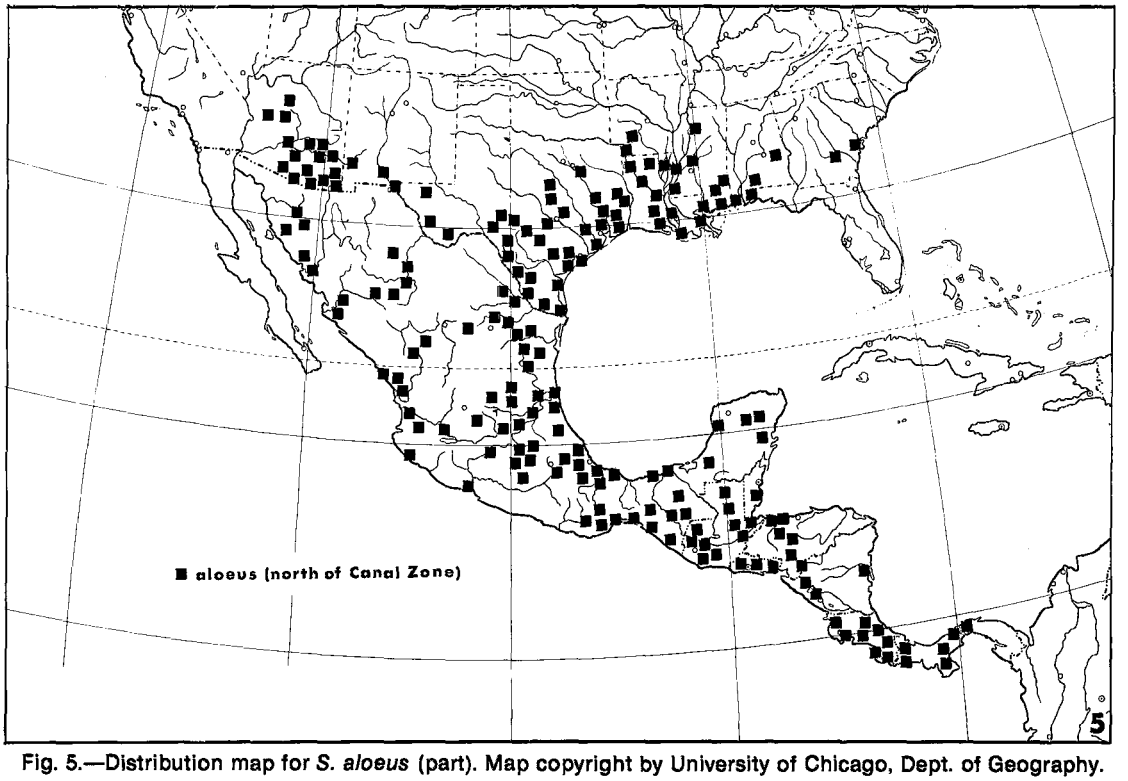


Fig. 5.—Distribution map for *S. aloeus* (part). Map copyright by University of Chicago, Dept. of Geography.

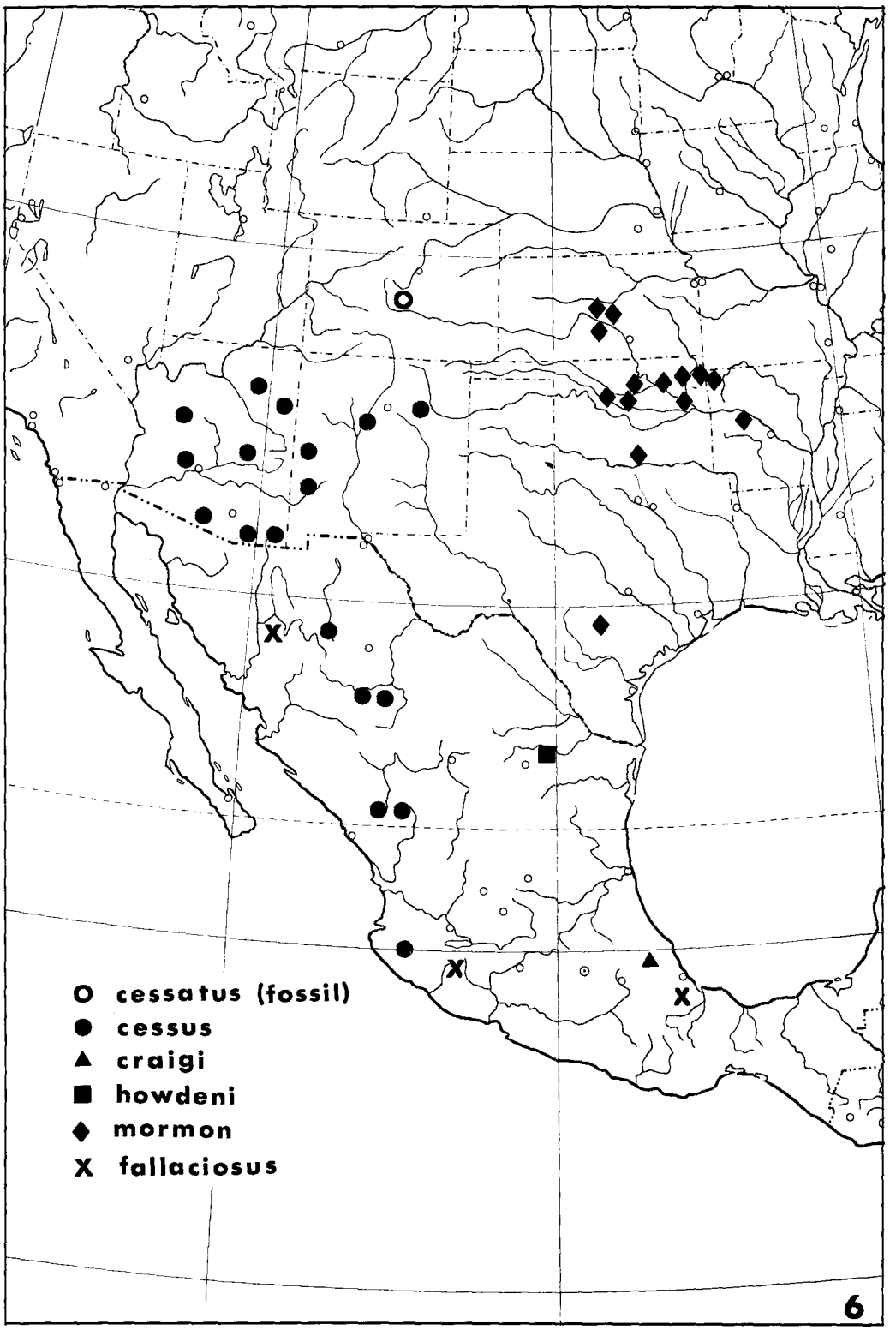


Fig. 6.—Distribution map for *S. cessatus, S. cessus, S. craigi, S. fallaciosus, S. howdeni, S. mormon.* Map copyright by University of Chicago, Dept. of Geography.

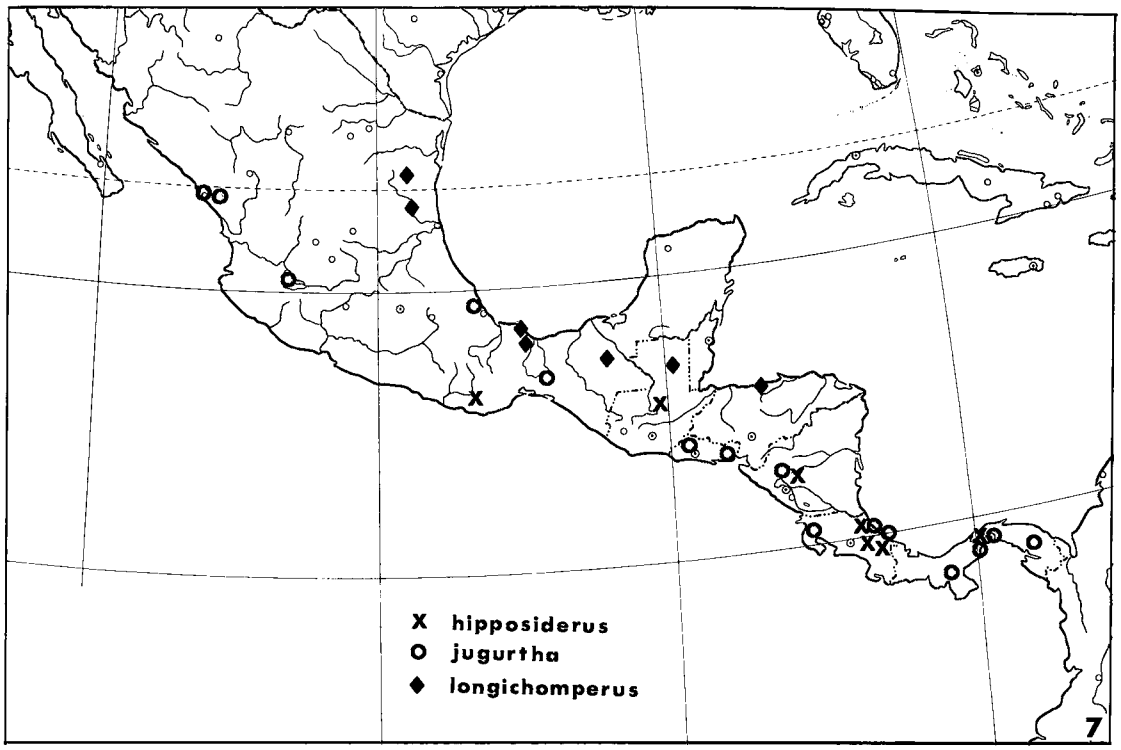


Fig. 7.—Distribution map for *S. hipposiderus* (part), *S. jugurtha* (part), *S. longichomperus*. Map copyright by University of Chicago, Dept. of Geography.

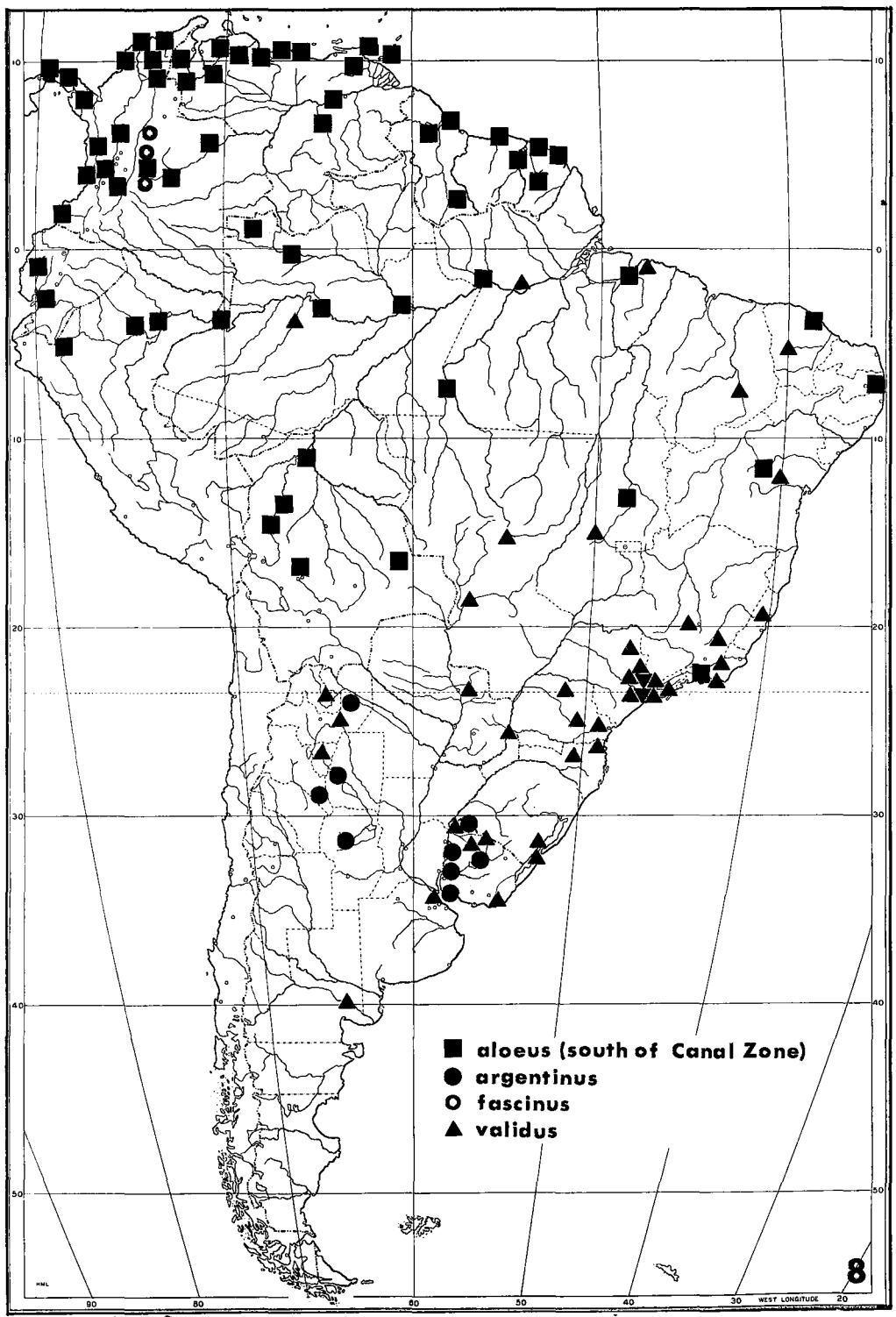


Fig. 8.—Distribution map for *S. aloeus* (part), *S. argentinus*, *S. fascinus*, *S. validus*. Map copyright by University of Chicago, Dept. of Geography.

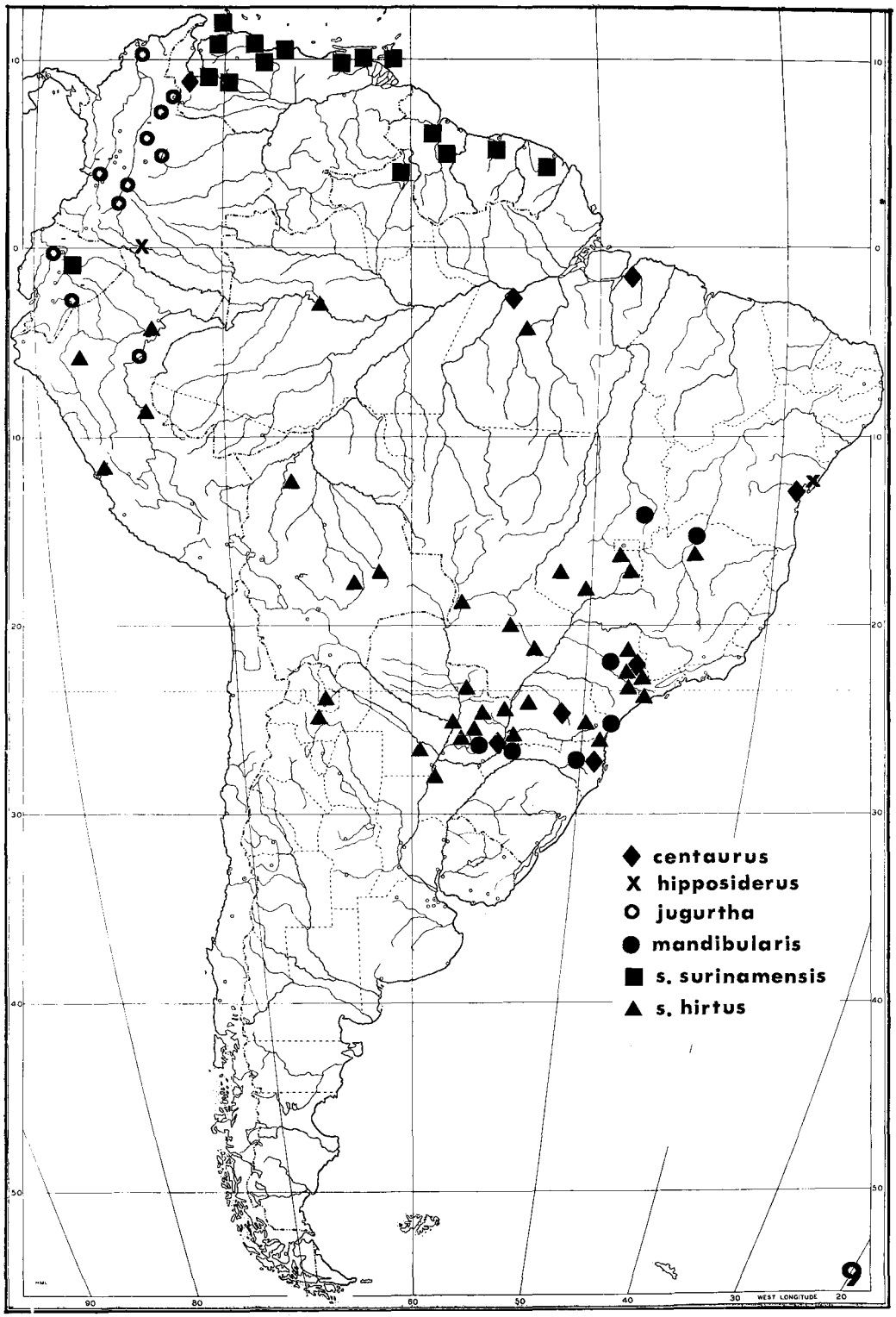
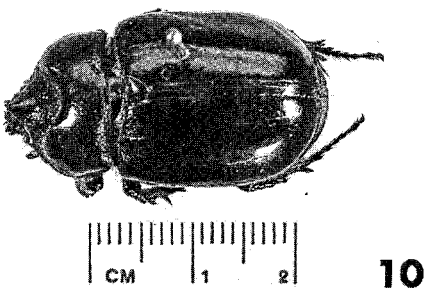


Fig. 9.—Distribution map for *S. centaurus, S. hipposiderus* (part), *S. jugurtha* (part), *S. mandibularis, S. surinamensis surinamensis, S. surinamensis hirtus.* Map copyright by University of Chicago, Dept. of Geography.



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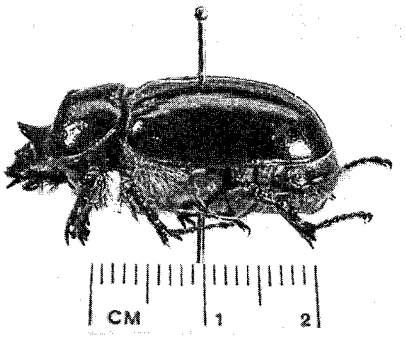

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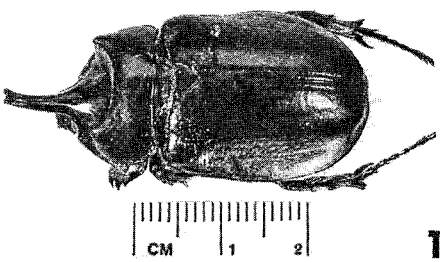

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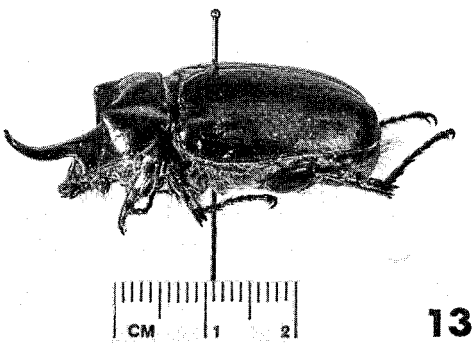

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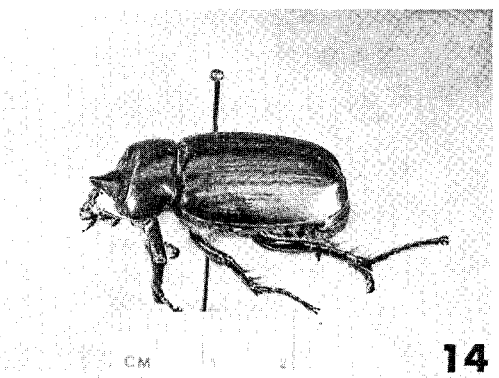

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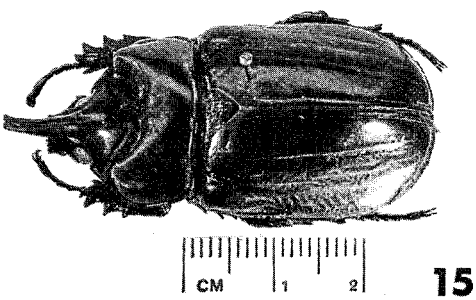

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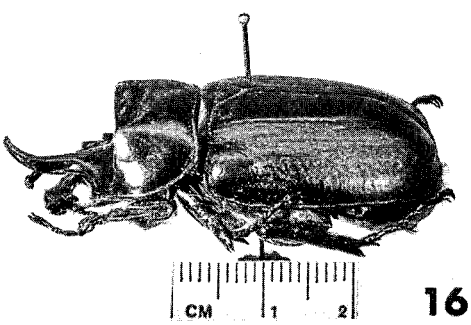

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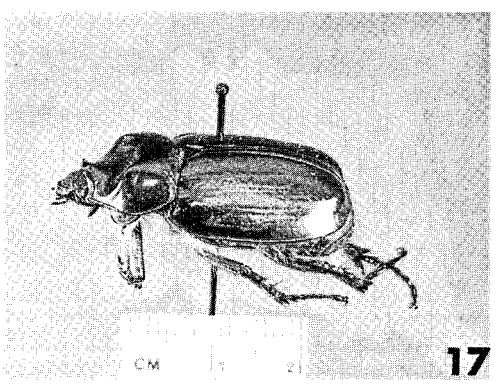

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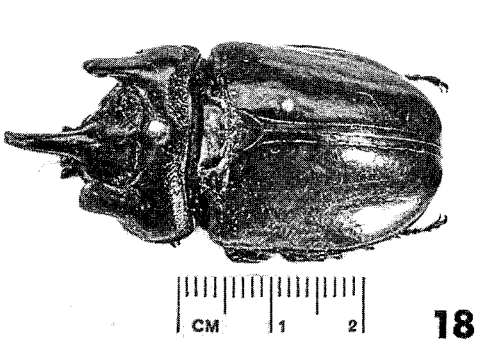
Figs. 10–11.—*S. adolescens* (lectotype). Figs. 12–13.— *S. aenobarbus* (major development). Fig. 14.—*S. aenobarbus* (minor development). Figs. 15–16.—*S. ajax* (major development). Fig. 17.—*S. ajax (minor development).*



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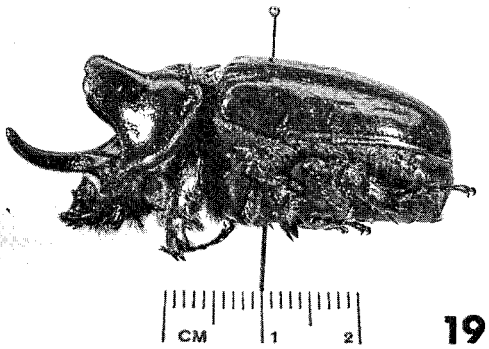

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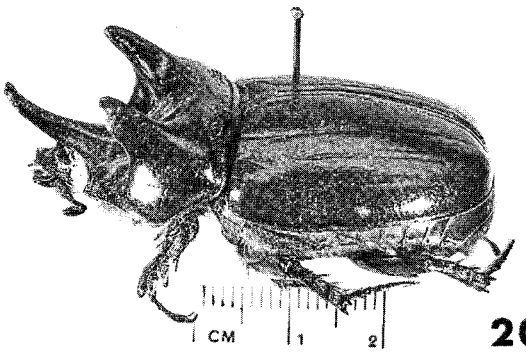

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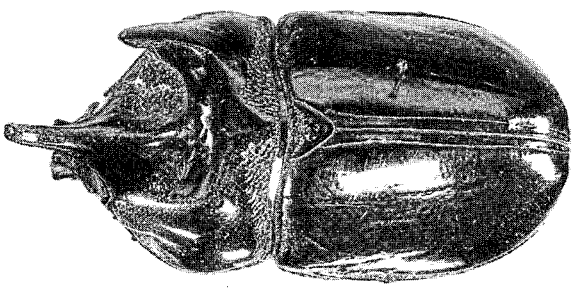

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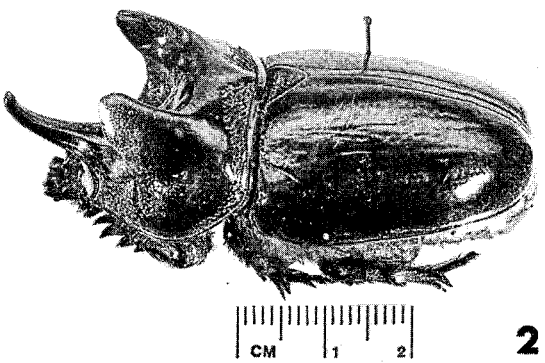

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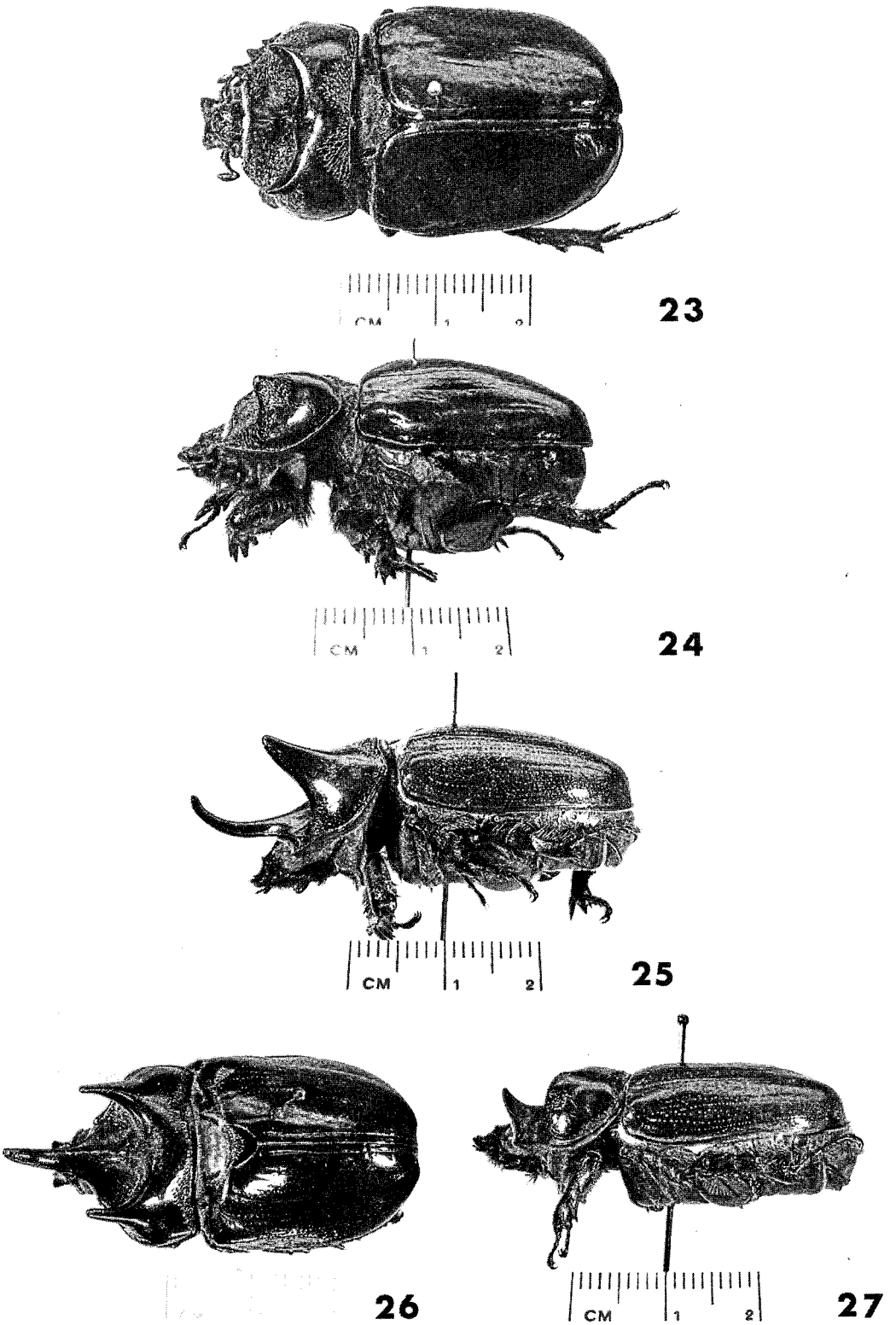
Figs. 18–20.—*S. aloeus* (North America). Figs. 21–22.—*S. aloeus* (South America).



Figs. 23–24.—*S. aloeus* (minor development; South America). Figs. 25–26.—*S. anachoreta* (major development). Fig. 27.—*S. anachoreta* (minor development).

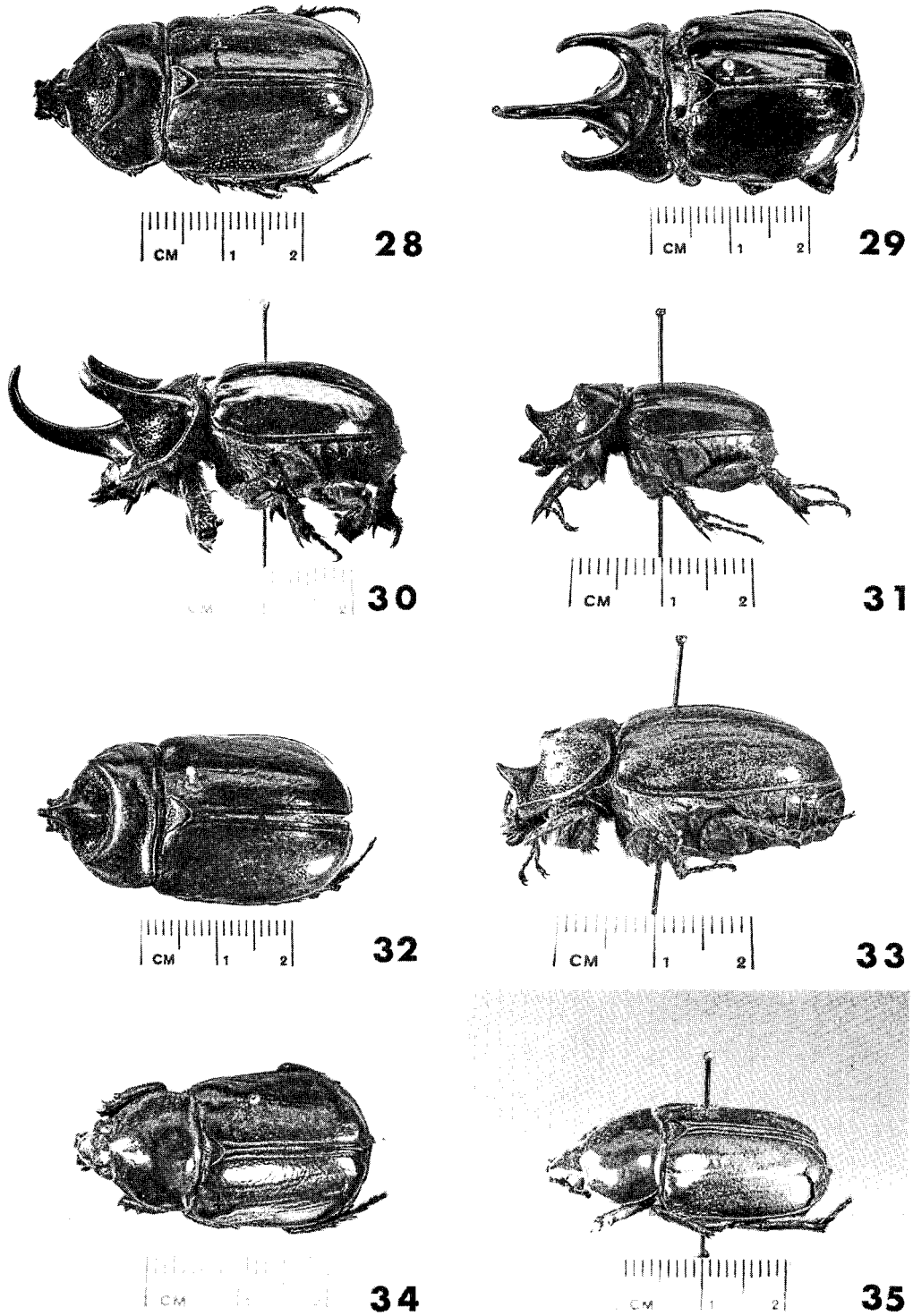
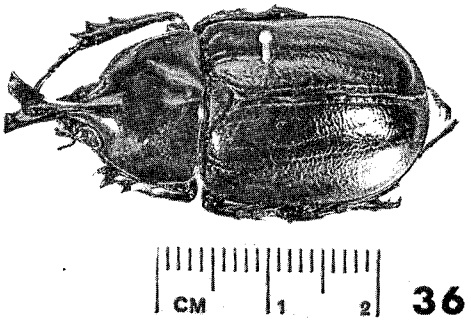


Fig. 28.—*S. anachoreta* (minor development). Figs. 29–30.— *S. antaeus* (major development). Fig. 31.—*S. antaeus* (minor development). Figs. 32–33.—*S. argentinus*. Figs. 34–35.—*S. atlanticus* (holotype).



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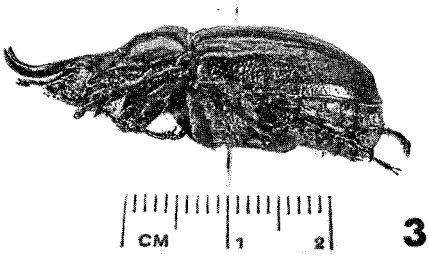

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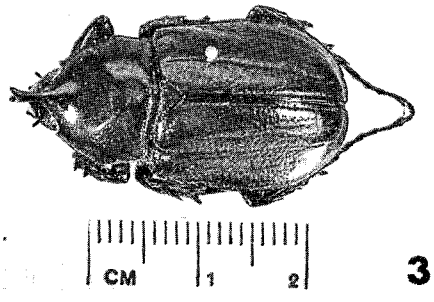

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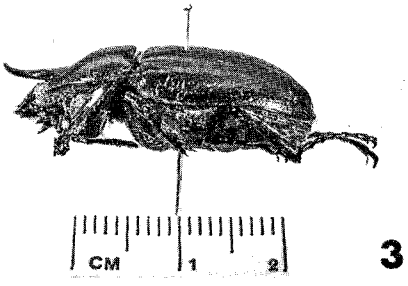

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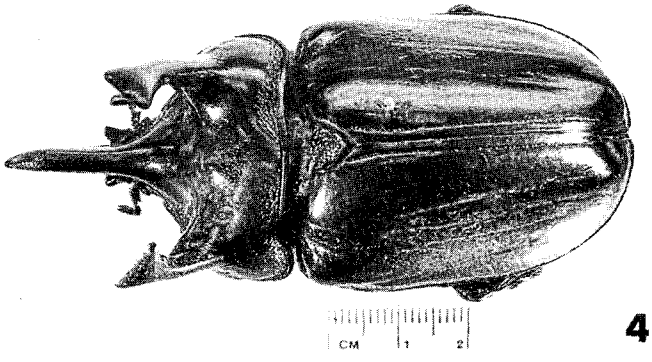

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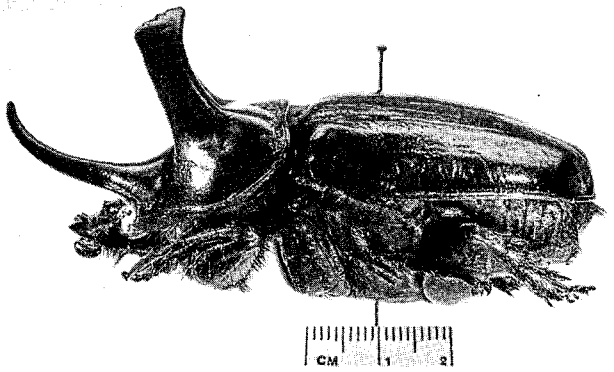

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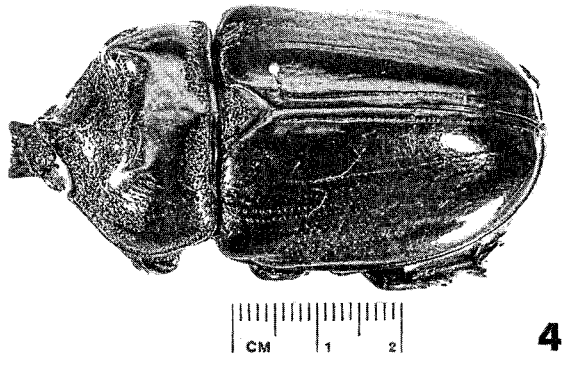
Figs. 36–37.—*S. caymani* (major development; paratype). Figs. 38–39.—*S. caymani* (minor development; paratype). Figs. 40–41.—*S. centaurus* (major development).



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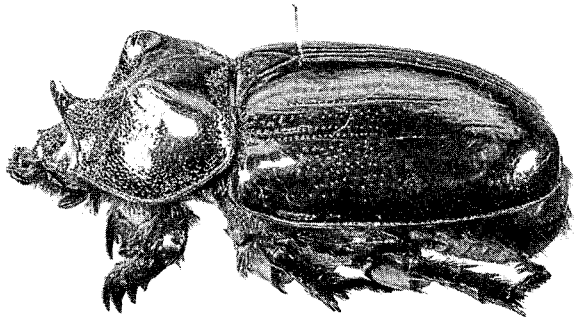

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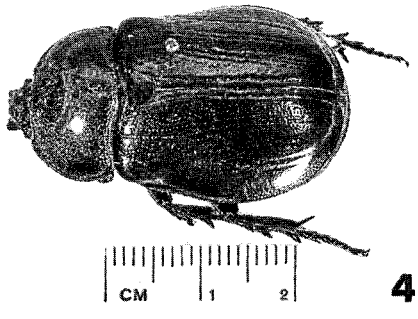

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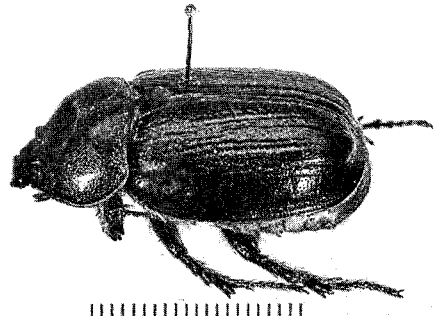

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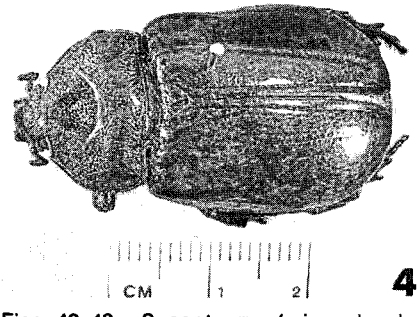

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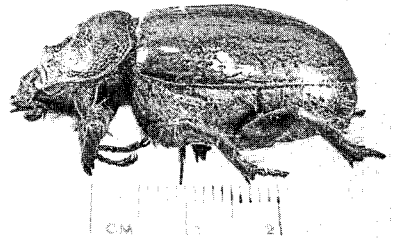

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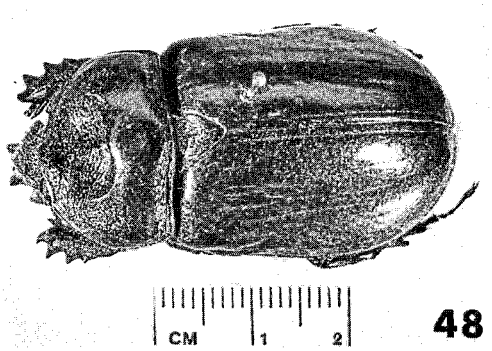
Figs. 42–43.—*S. centaurus* (minor development). Figs. 44–45.—*S. cessus*. Figs. 46–47.—*S. craigi* (holotype).



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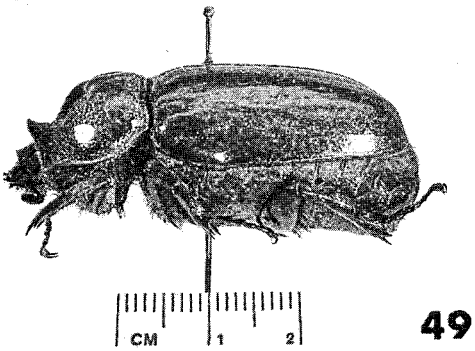

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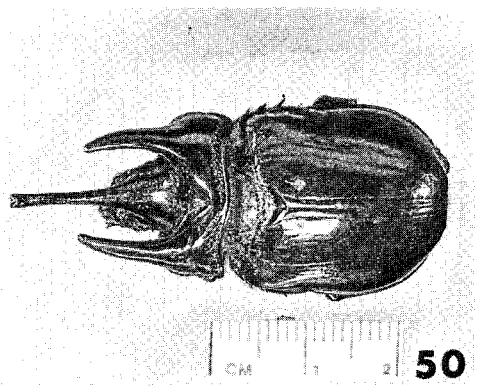

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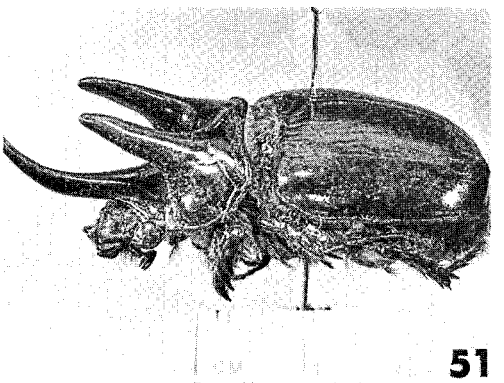

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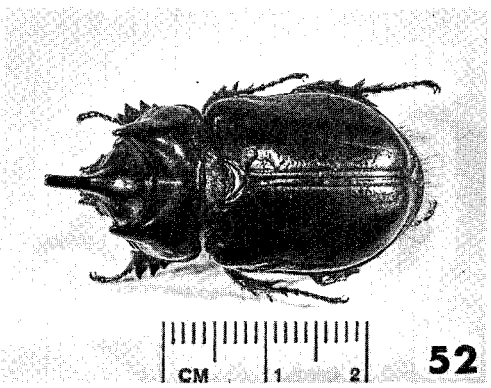

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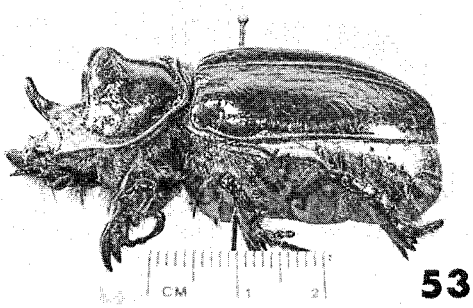

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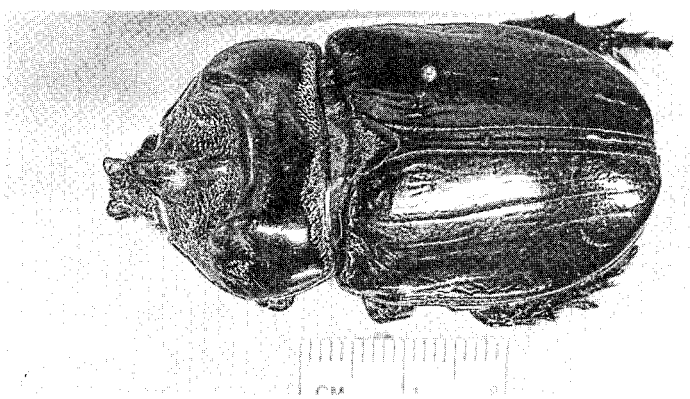

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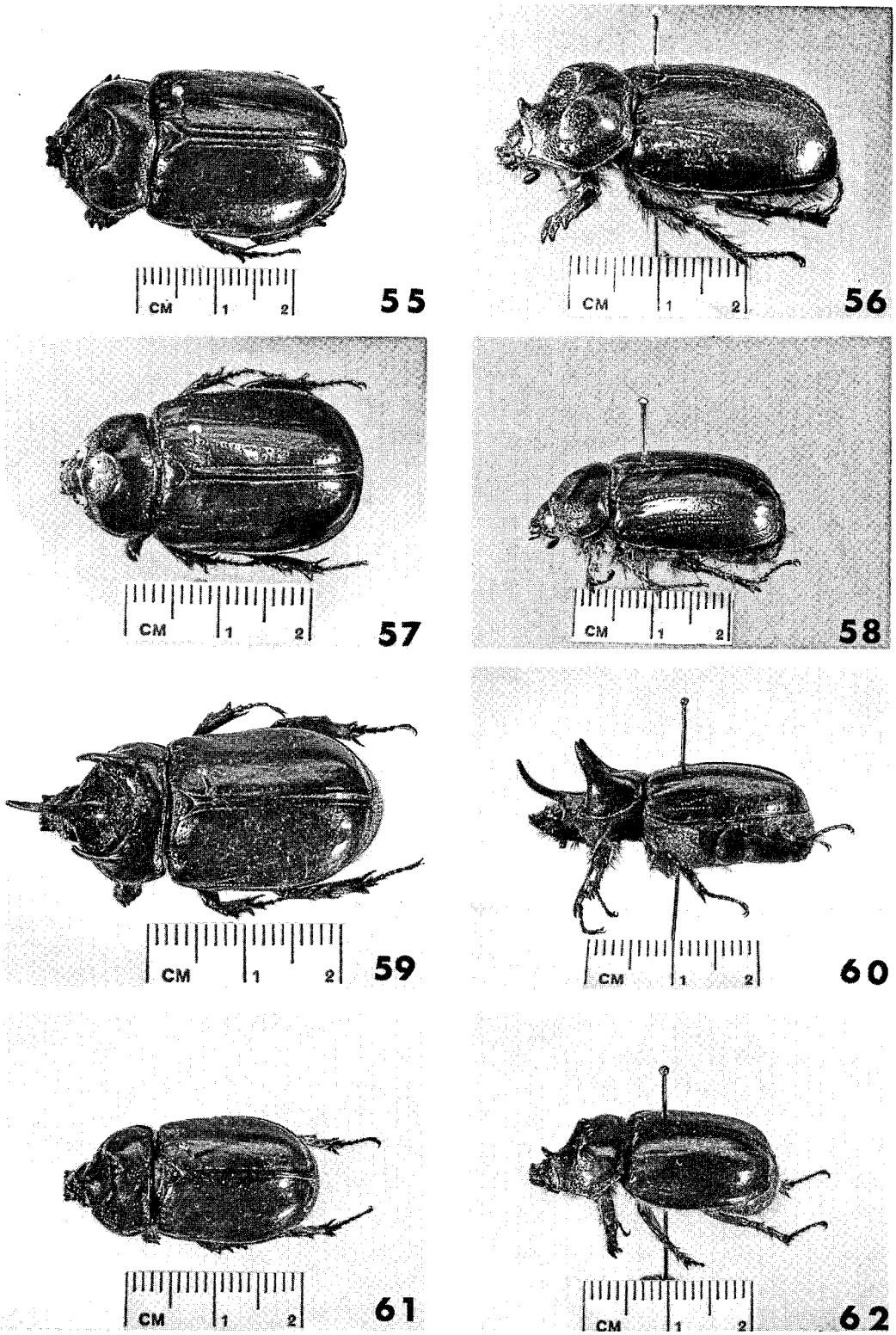
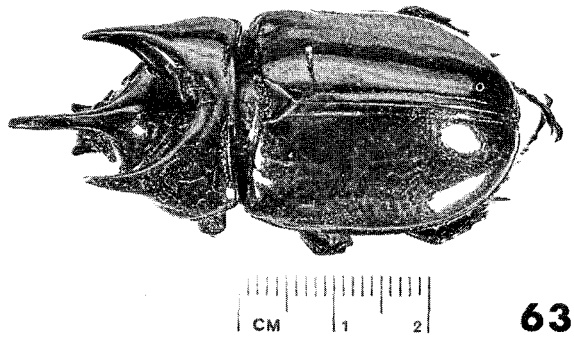
Figs. 48–49.—*S. fallaciosus*. Figs. 50–51.—*S. fascinus* (major development). Fig. 52.—*S. fascinus* (minor development). Figs. 53–54.—*S. hipposiderus* (holotype).



Figs. 55–56.—*S. howdeni* (paratype). Figs. 57–58.—*S. inermis* (holotype). Figs. 59–60.—*S. jugurtha* (major development). Figs. 61–62.—*S. jugurtha* (minor development.)



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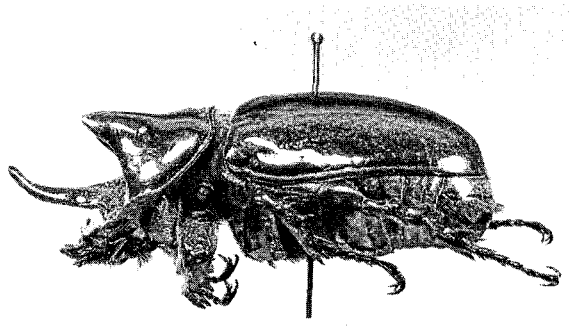

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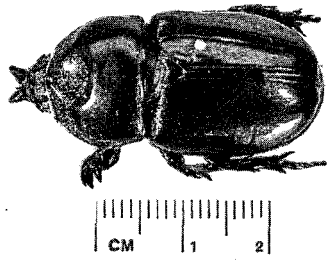

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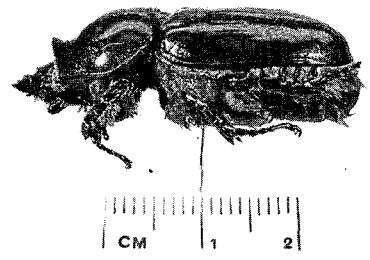

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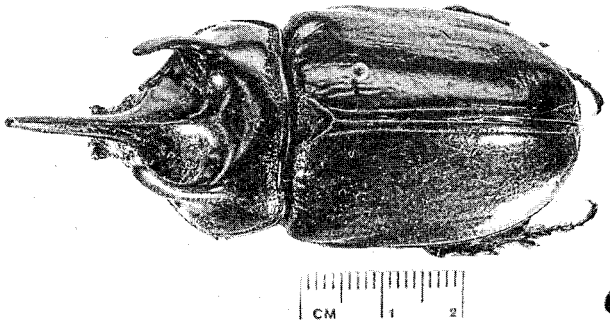
Figs. 63–64.—*S. longichomperus* (major development; paratype). Figs. 65–66.—*S. longichomperus* (minor development; paratype).



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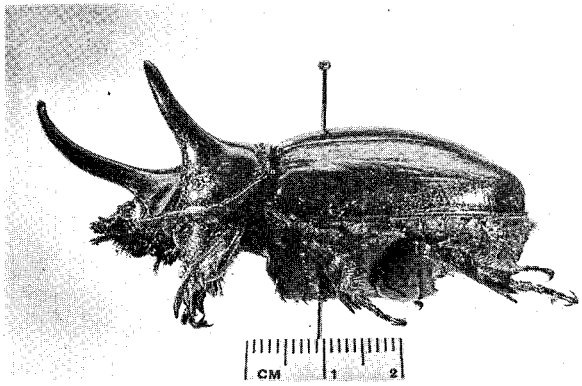

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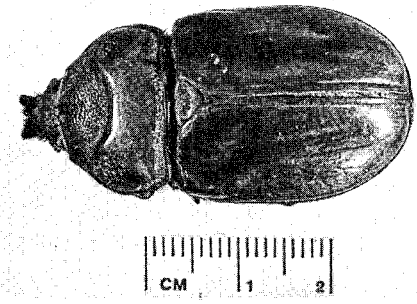

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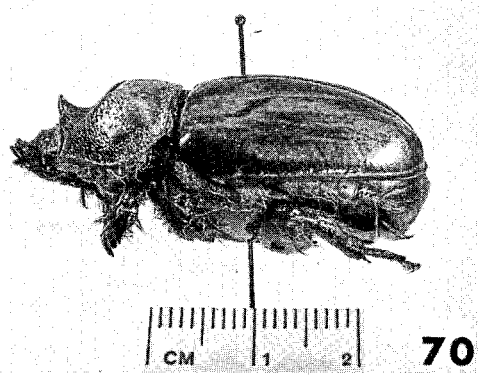

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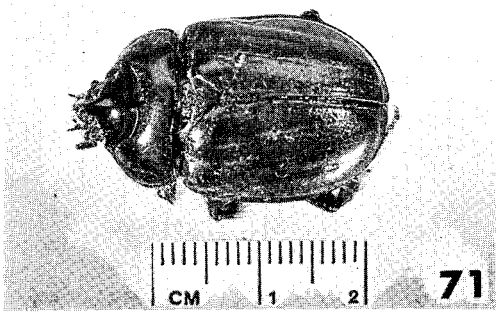

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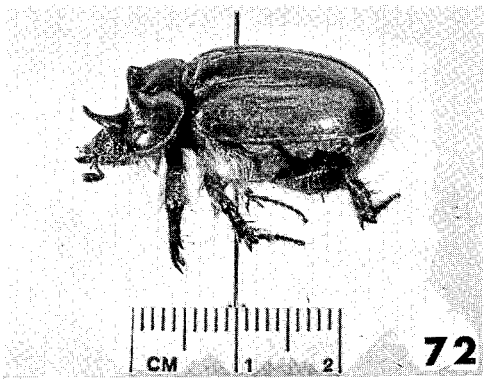
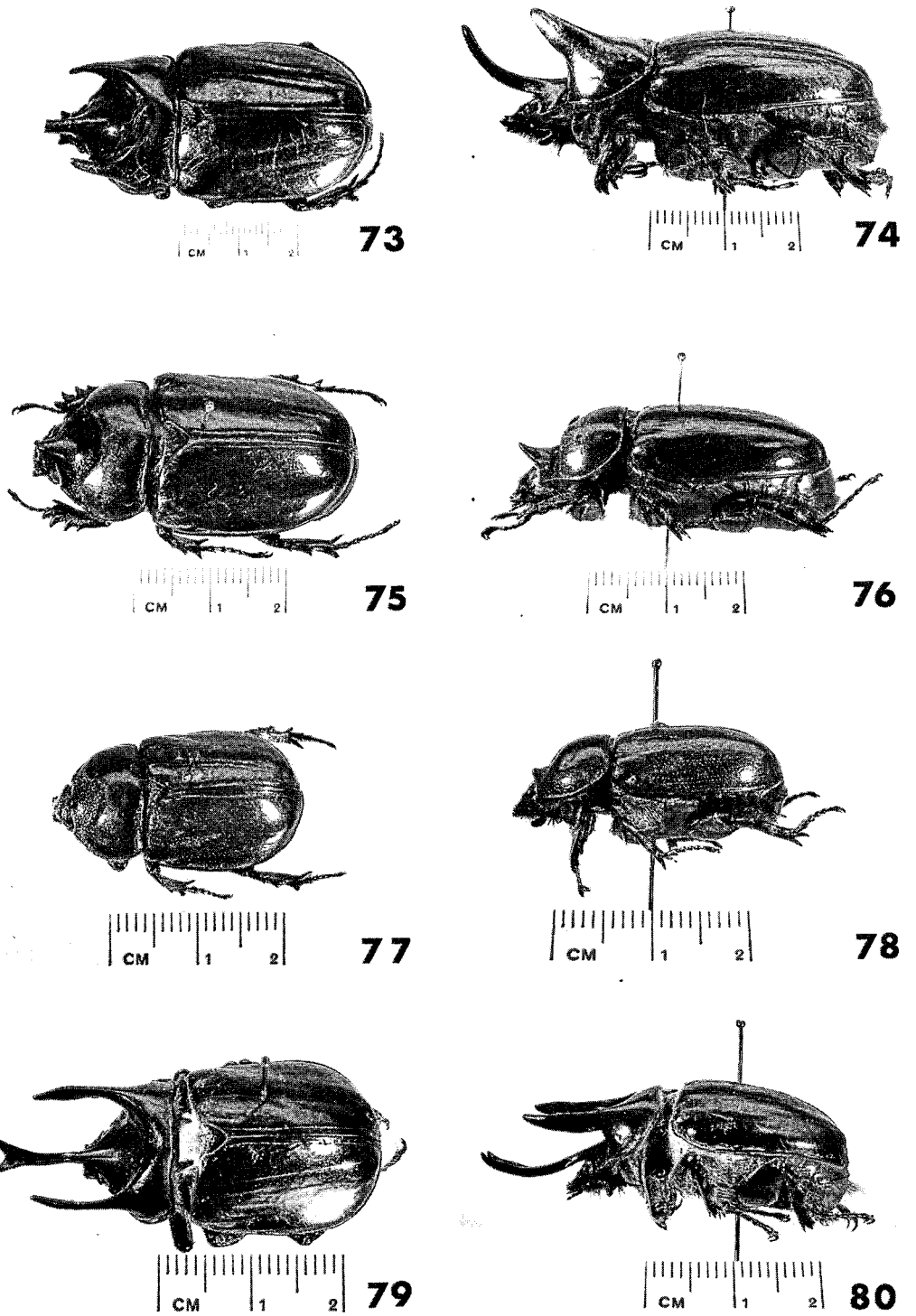
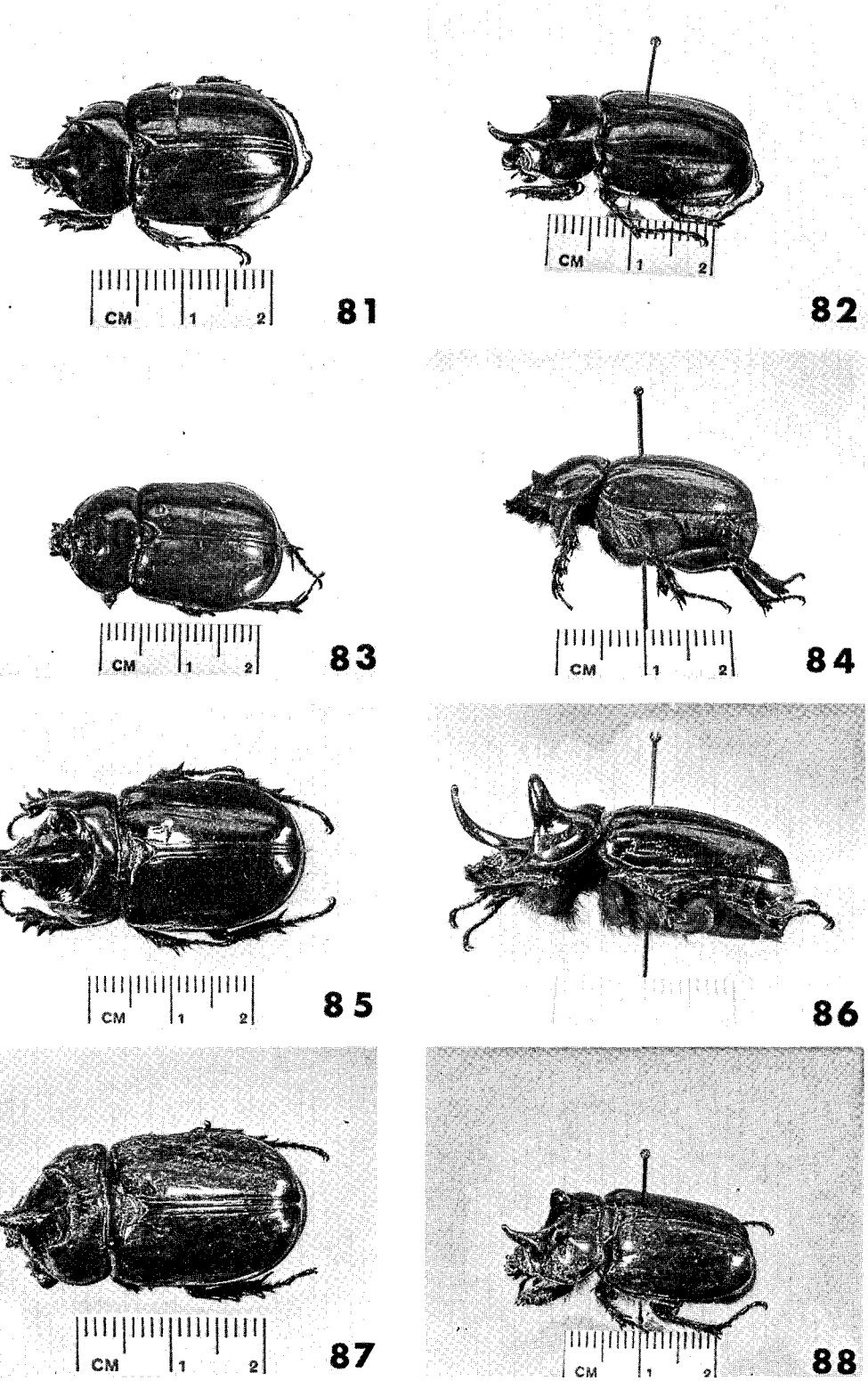


72

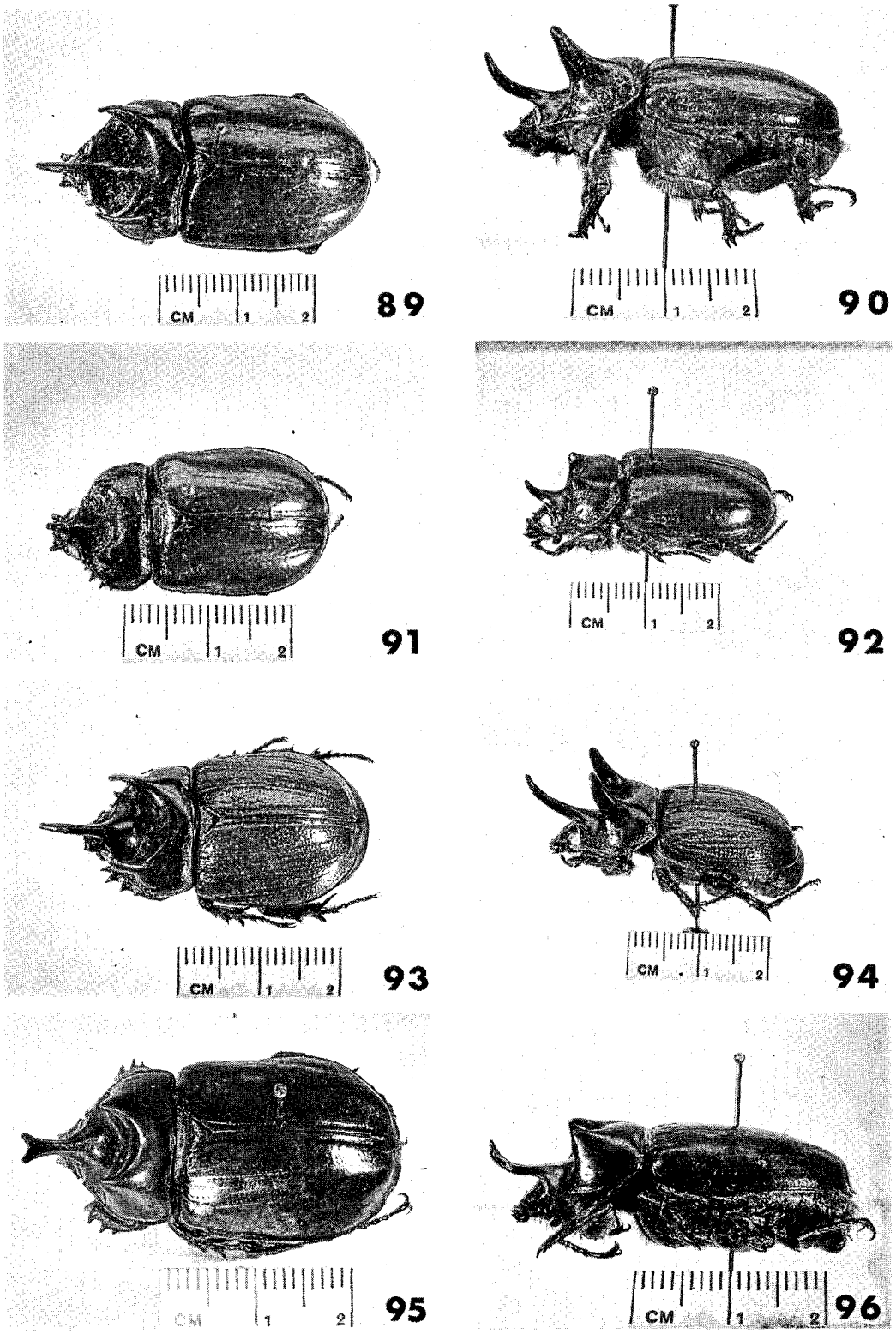
Figs. 67–68.—*S. mandibularis* (major development). Figs. 69–70.—*S. mandibularis* (minor development). Figs. 71–72.—*S. mormon.*



Figs. 73–74.—*S. oblongus* (major development). Figs. 75–76.—*S. oblongus* (minor development). Figs. 77–78.—*S. sarpedon*. Figs. 79–80.—*S. simson* (major development).



Figs. 81–82.—*S. simson* (minor development. Figs. 83–84.—*S. splendens.* Figs. 85–86.—*S. surinamensis surinamensis* (major development). *Figs. 87–88.—S. surinamenis surinamensis* (minor development).



Figs. 89–90.—*S. surinamensis hirtus* (major development). Figs. 91–92.—*S. surinamensis hirtus* (minor development). Figs. 93–94.—*S. symphenax* (holotype). Figs. 95–96.—*S. talpa* (major development).

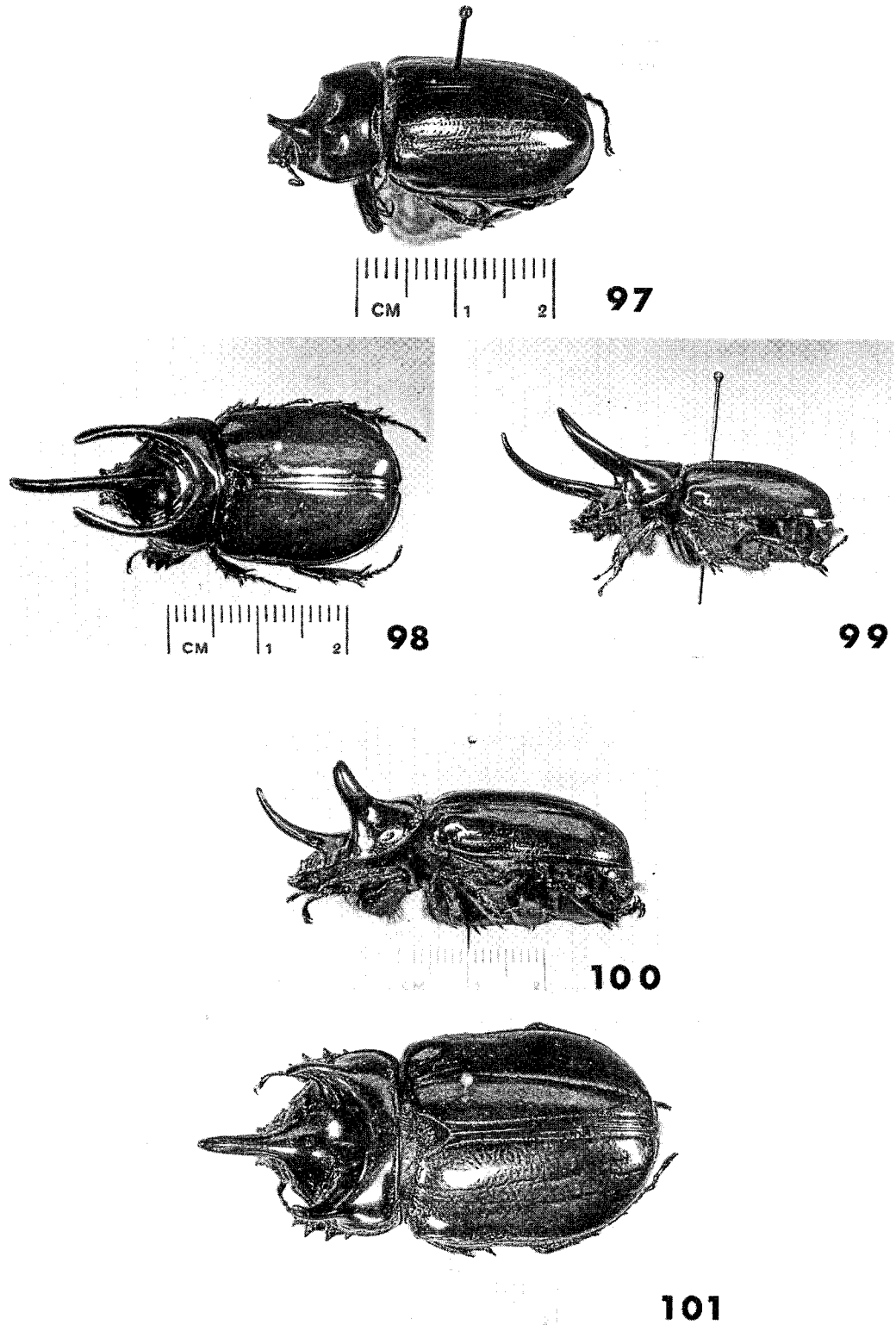
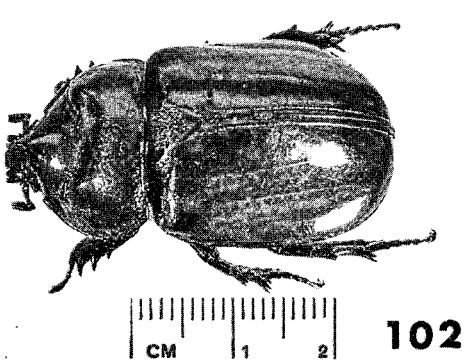


Fig. 97.—*S. talpa* (minor development). Figs. 98–99.—*S. tarquinius* (paratype). Figs. 100–101.—*S. validus* (major development).



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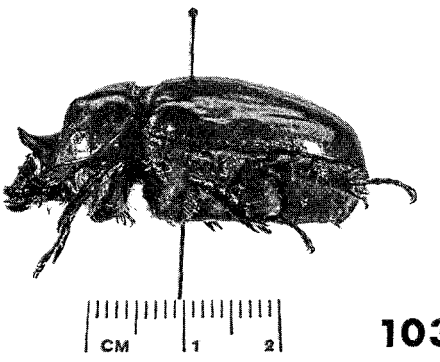

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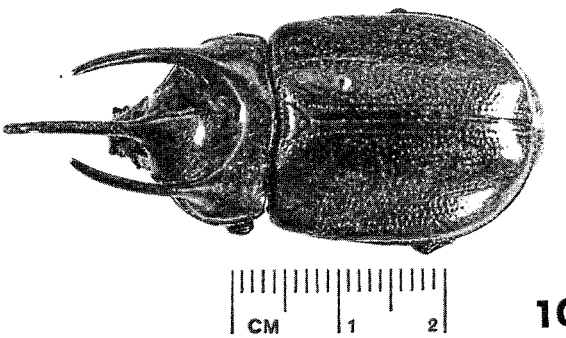

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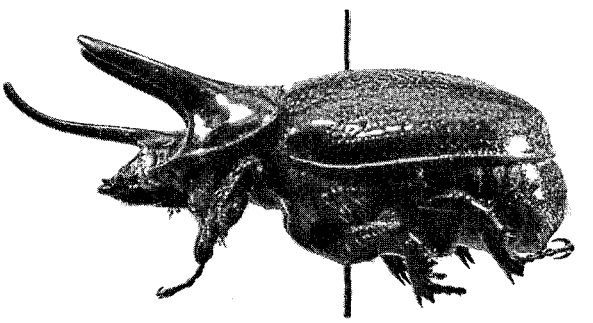

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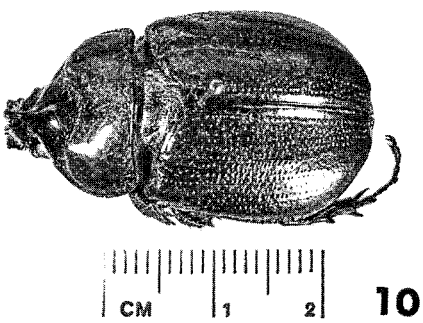

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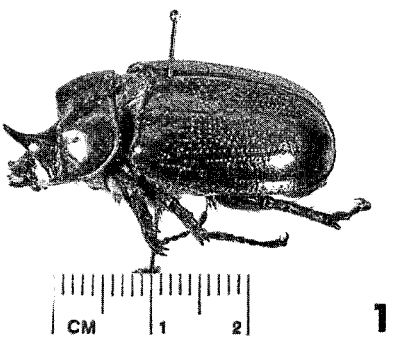

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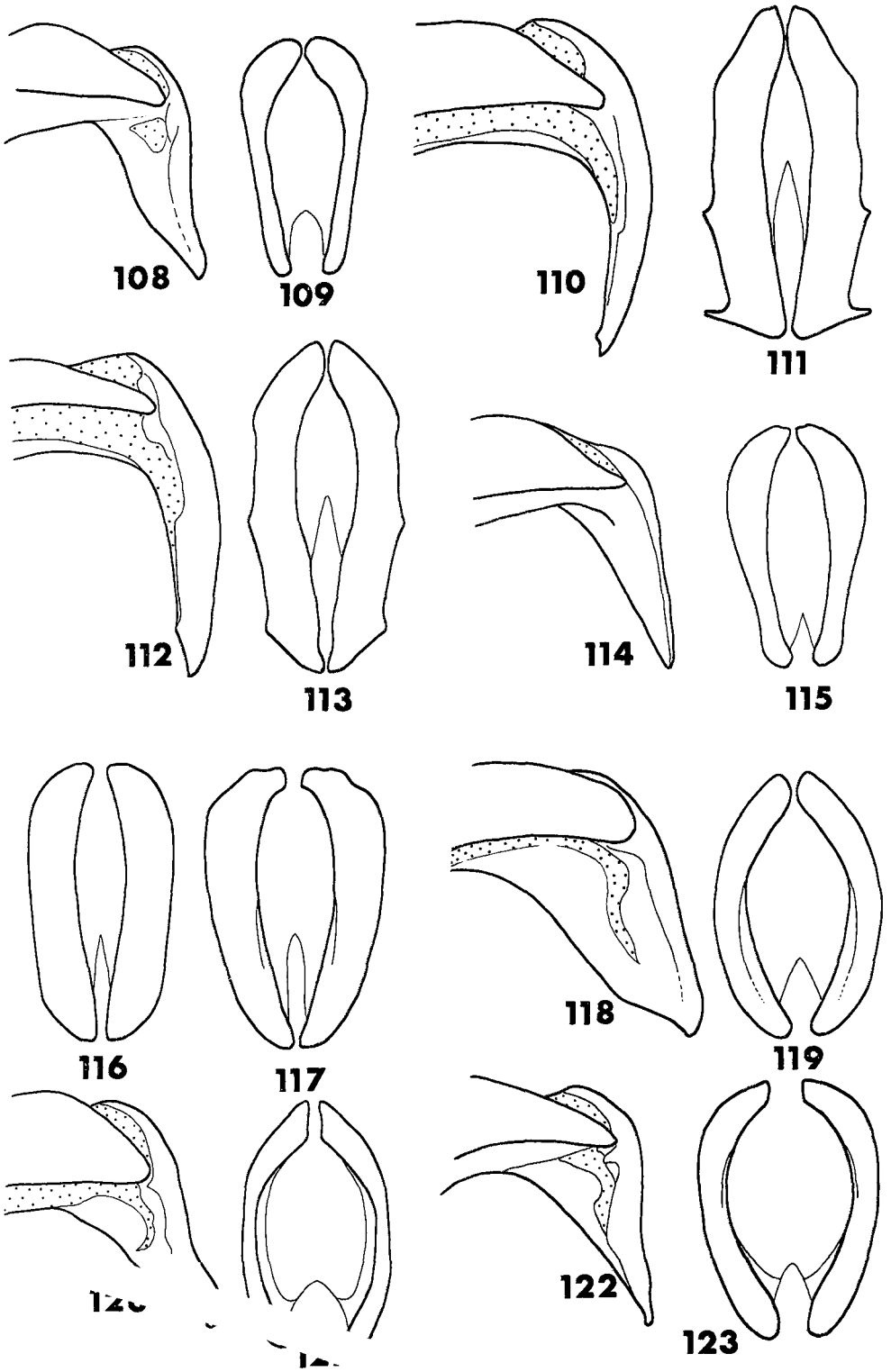
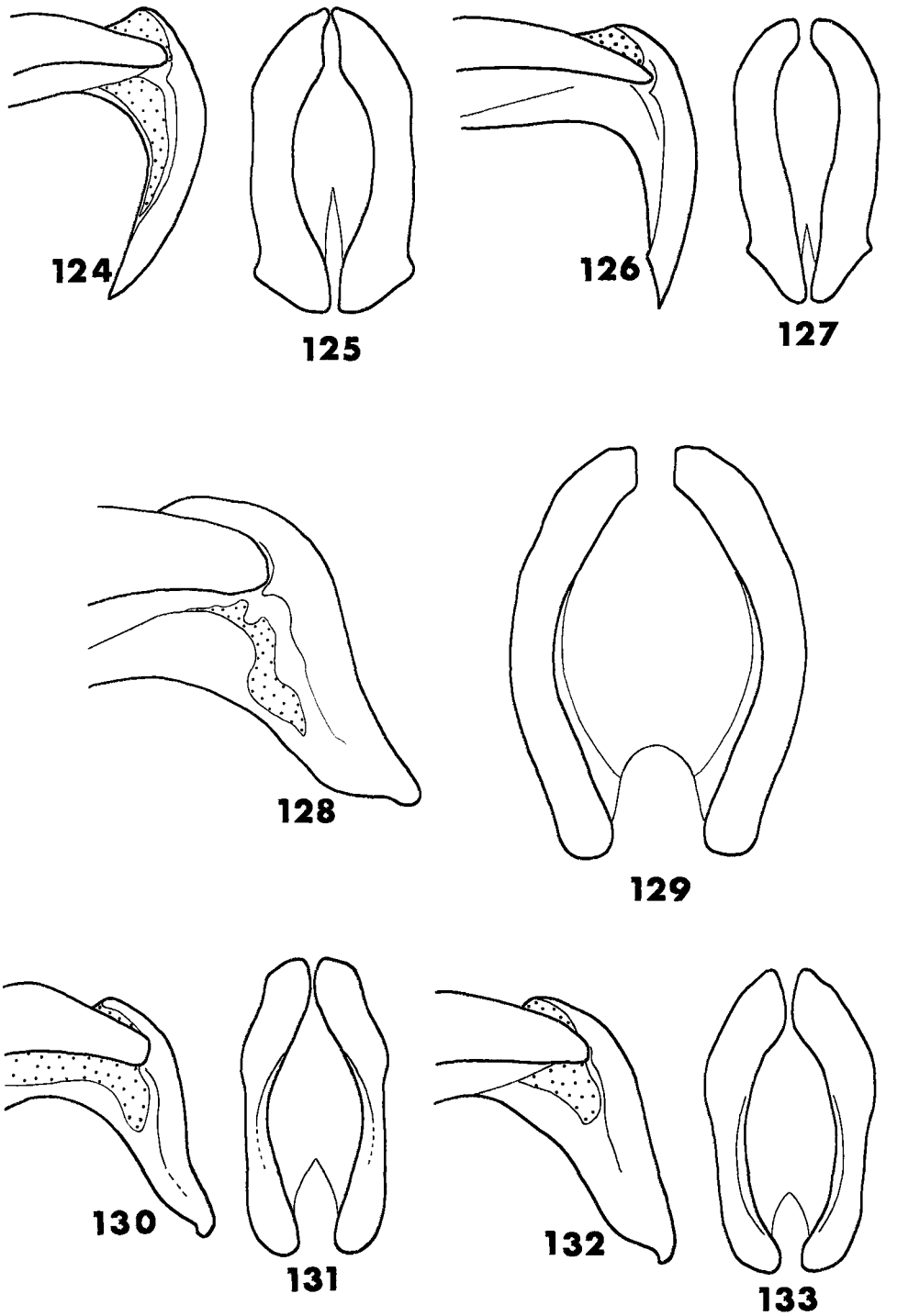
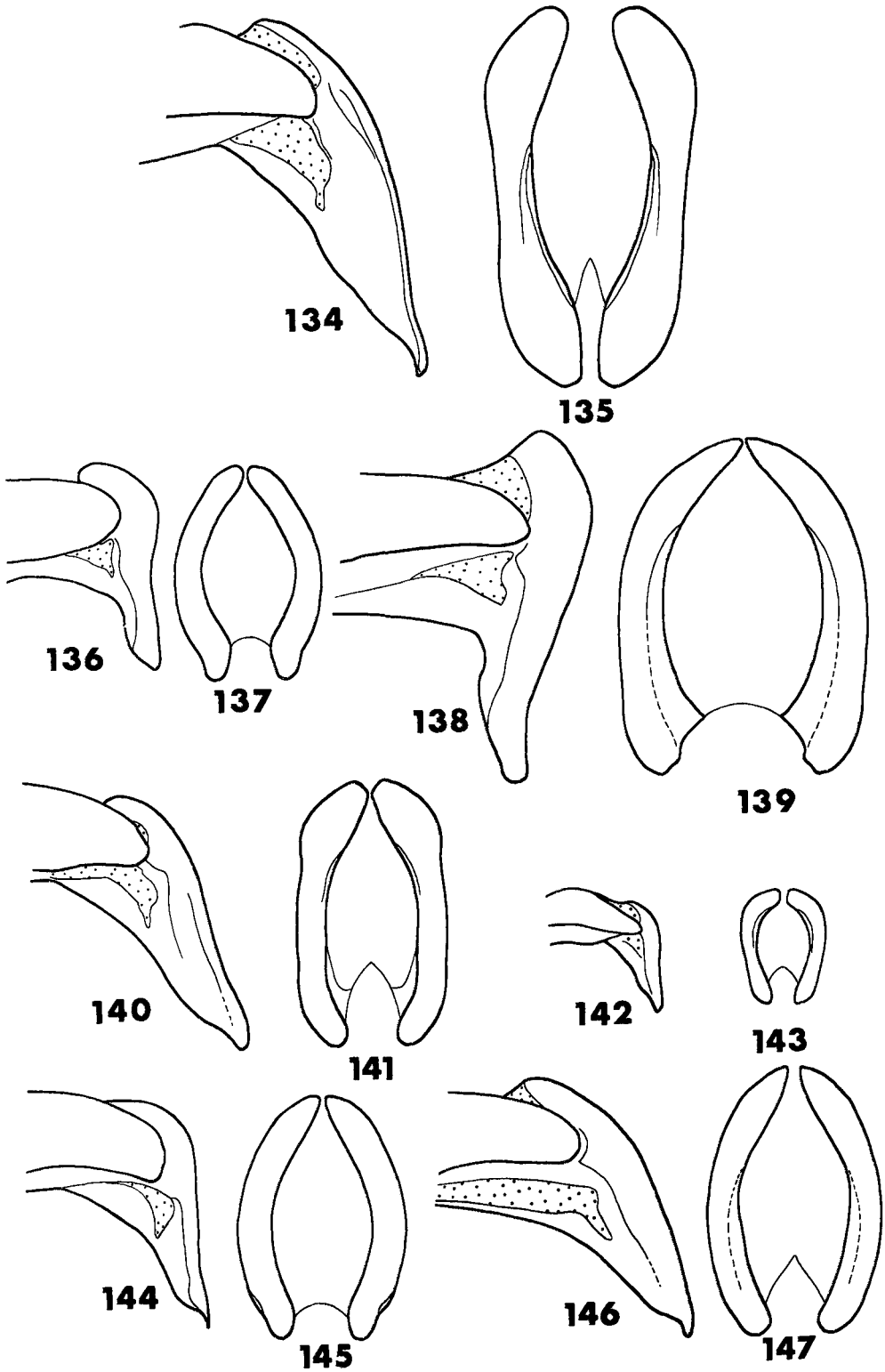
Figs. 102–103.—*S. validus* (minor development). Figs. 104–105.—*S. syphax* (major development). Figs. 106–107. (minor development).



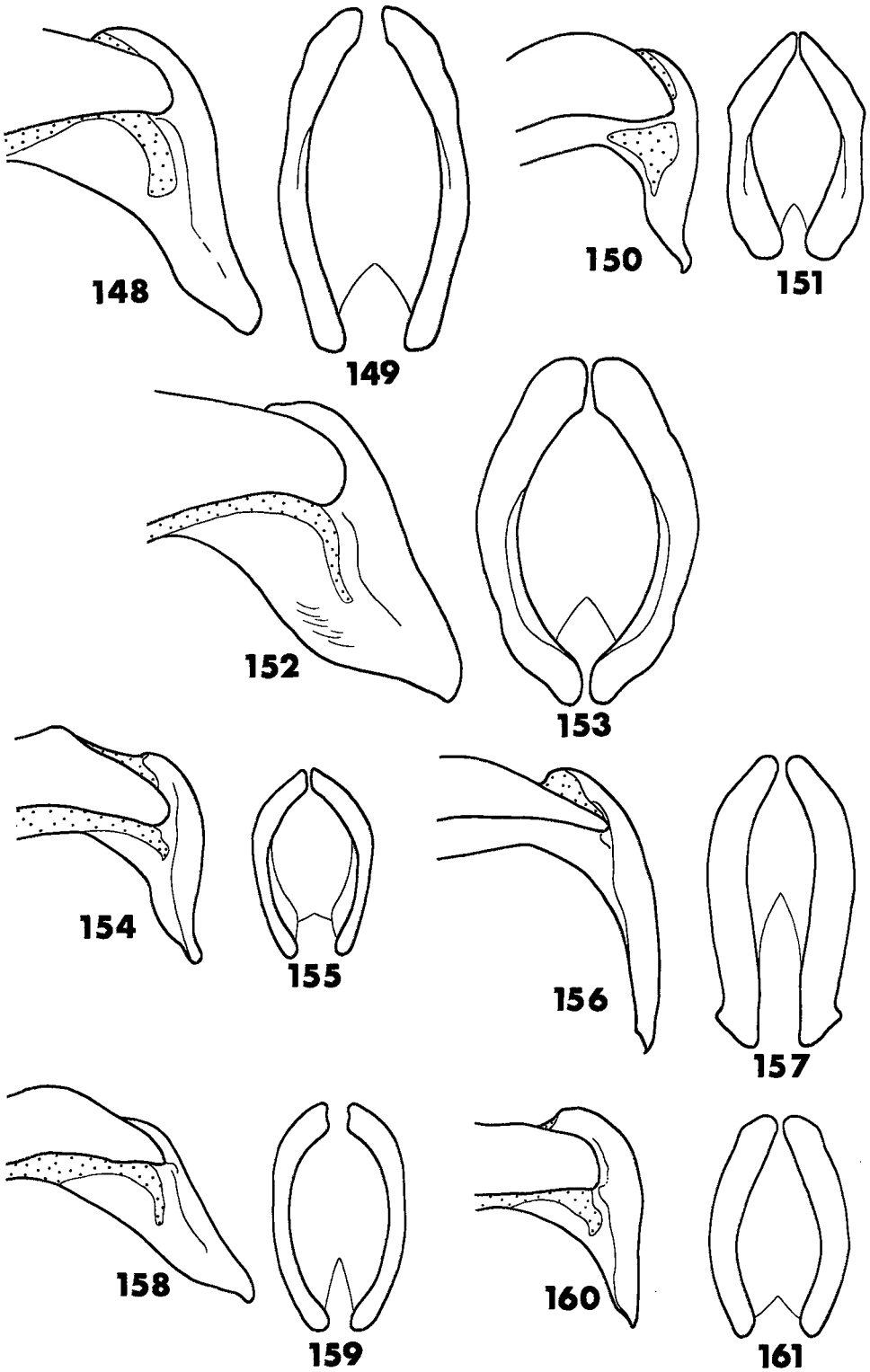
Figs. 108–123.—Lateral and caudal views of male genitalia. [illegible]–109.—*S. adolescens*. Figs. 110–111.—*S. aenobarbus*. Figs. 112–113.—*S. ajax*. Figs. 114–115.—*S. aloeus* (North Amer[illegible] 116–117.—*S. aloeus* (Colombia, Venezuela). Figs. 118–119.—*S. anachoreta*. Figs. 120–121.—*S. antaeus*. Figs. 122–123.—[illegible]*us*.



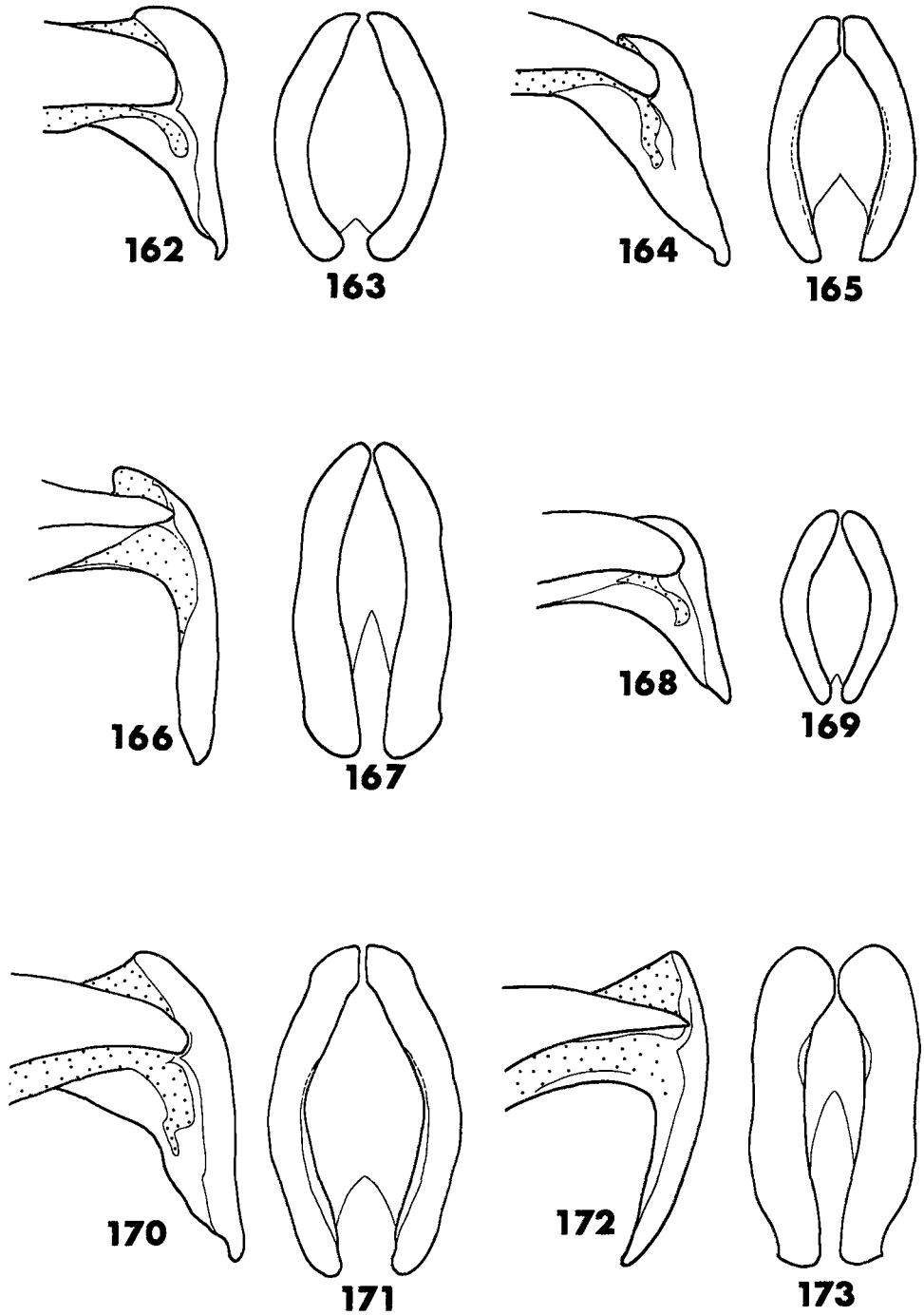
Figs. 124–133.—Lateral and caudal views of male genitalia. Figs. 124–125.—*S. atlanticus*. Figs. 126–127.—*S. caymani*. Figs. 128–129.—*S. centaurus*. Figs. 130–131.—*S. cessus*. Figs. 132–133.—*S. craigi*.



Figs. 134–147.—Lateral and caudal views of male gentalia. Figs. 134–135.—*S. fallaciosus.* Figs. 136–137.—*S. fascinus.* Figs. 138–139.—*S. hipposiderus.* Figs. 140–141.—*S. howdeni.* Figs. 142–143.—*S. inermis.* Figs. 144–145.—*S. jugurtha.* Figs. 146–147.—*S. longichomperus.*



Figs. 148–161.—Lateral and caudal views of male genitalia. Figs. 148–149.—*S. mandibularis*. Figs. 150–151.—*S. mormon*. 152–153.—*S. oblongus*. Figs. 154–155.—*S. sarpedon*. Figs. 156–157.—*S. simson*. Figs. 158–159.—*S. splendens*. Figs. 160–161.—*S. surinamensis surinamensis*.



Figs. 162–173.—Lateral and caudal views of male genitalia. Figs. 162–163.—*S. surinamensis hirtus.* Figs. 164–165.—*S. symphenax.* Figs. 166–167.—*S. talpa.* Figs. 168–169.—*S. tarquinius.* Figs. 170–171.—*S. validus.* Figs. 172–173.—*S. syphax.*

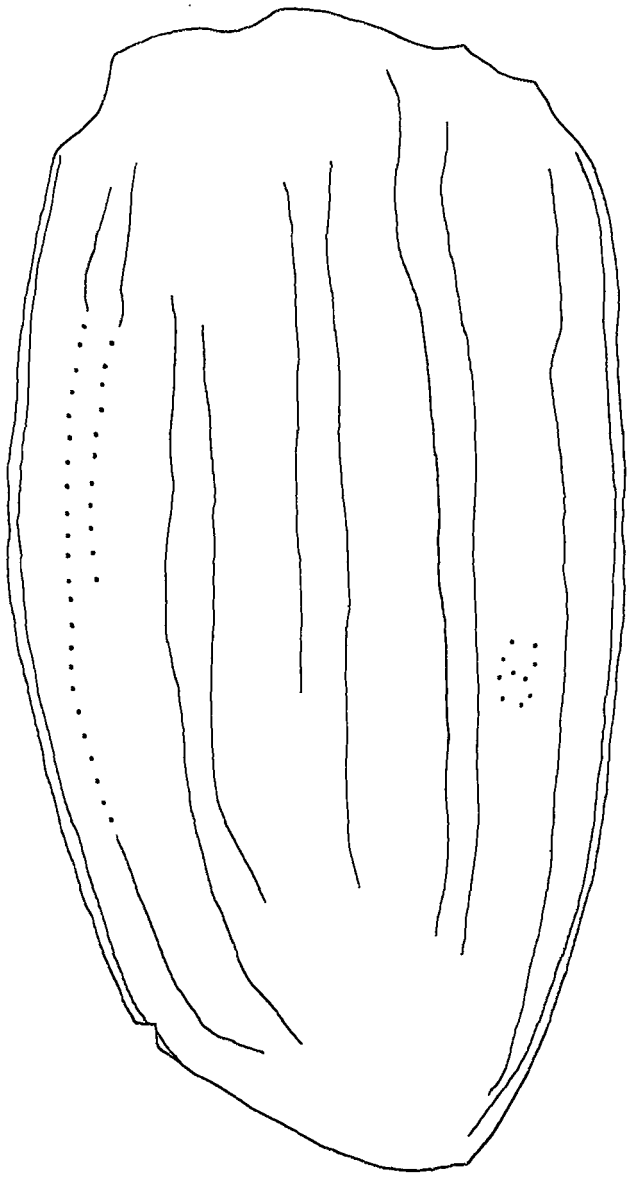


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Fig. 174.—Fossil elytron of *Srategus cessatus* Wickham (after Wickam 1914).

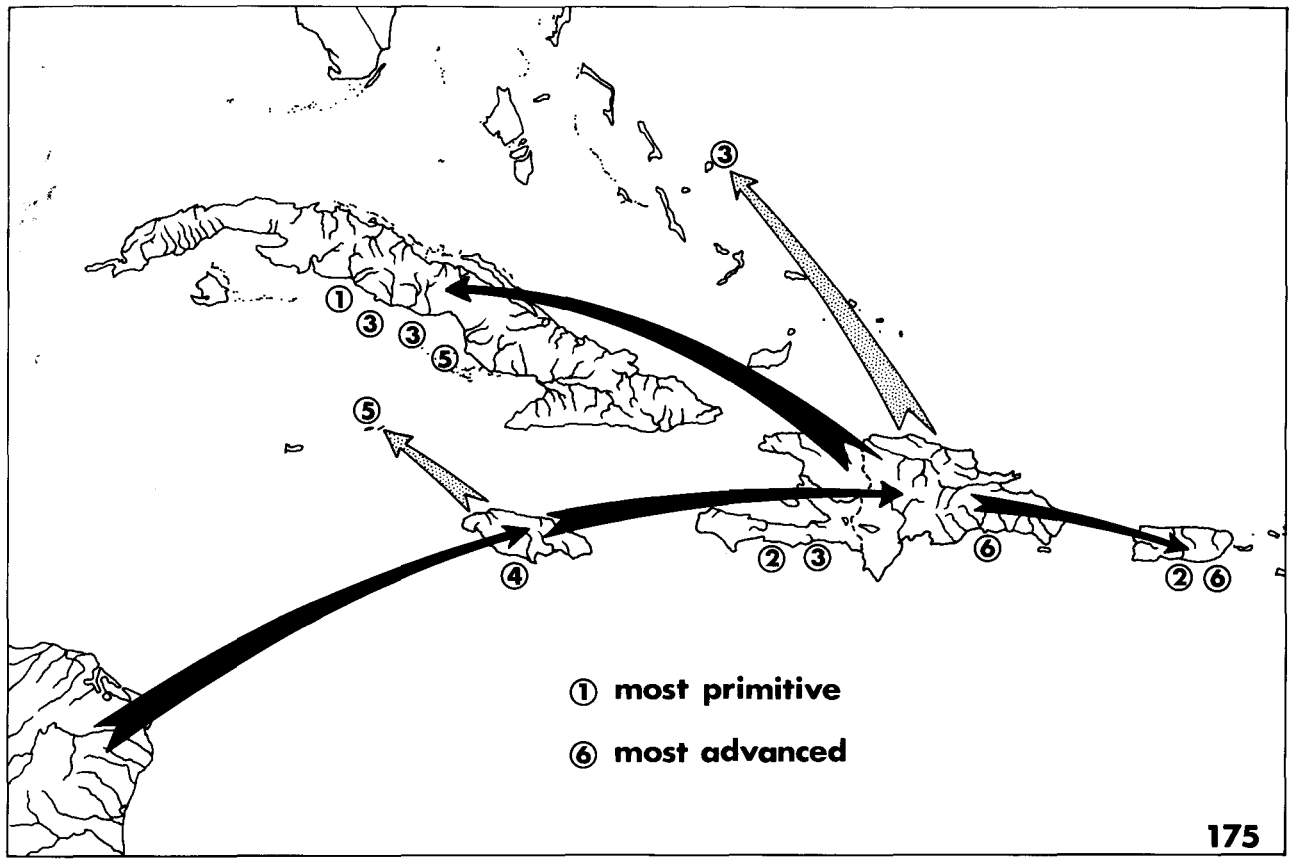

Fig. 175.—Proposed Greater Antillean dispersal routes of ancestral *Strategus*. Each number indicates the present occurrence of a species and its relative derivedness rating. 1 = most primitive; 5 = most advanced. Solid arrows = possible land connections or a closely spaced island "stepping stones" route. Dotted arrows = a probable flotsam dispersal route.

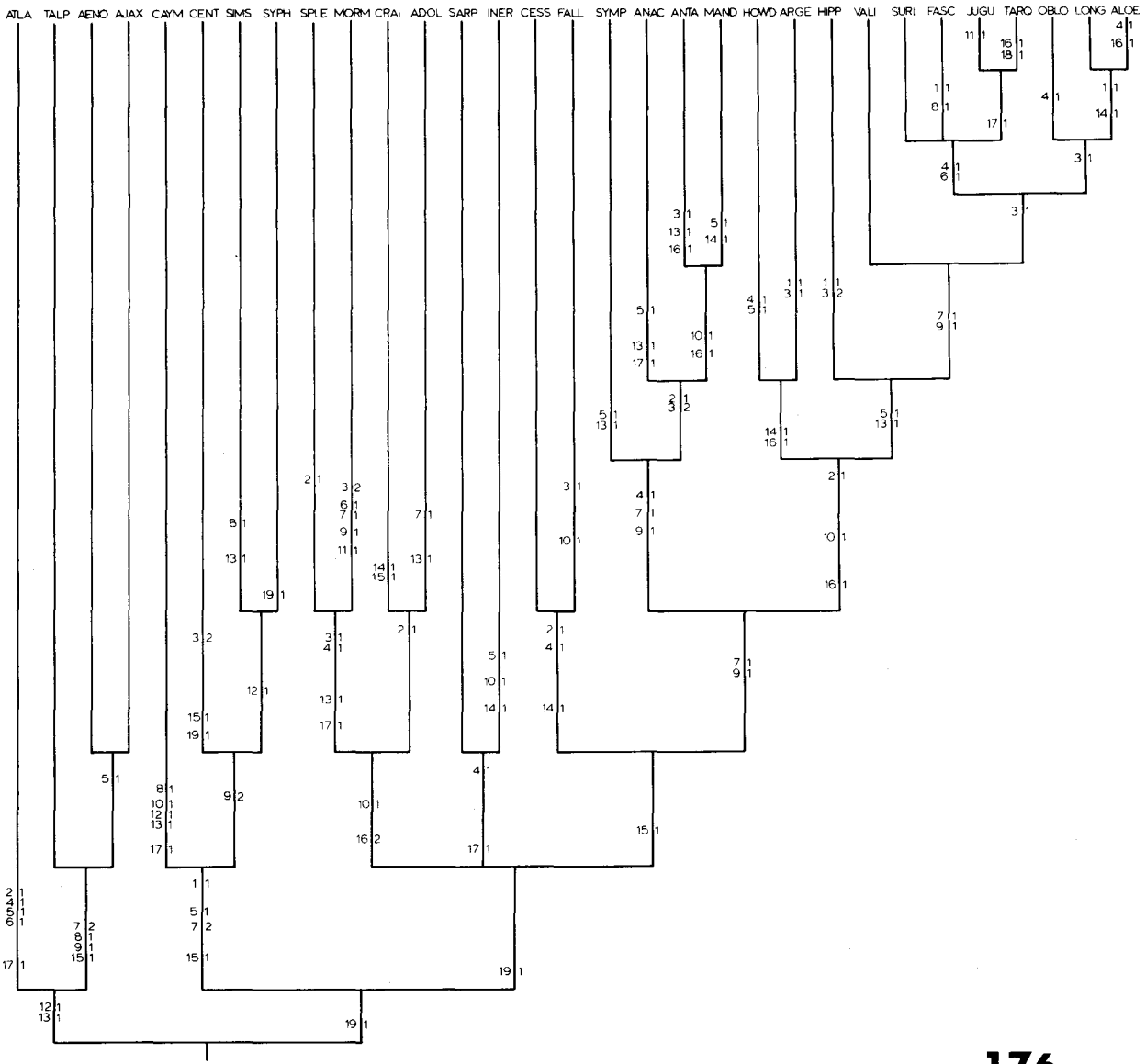

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Fig. 176.—Computer-generated cladistic reconstruction of the presumed phylogeny of the genus *Strategus*. See text for explanation.