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STUDIES ON THE GENUS *APHODIUS* OF THE UNITED STATES AND CANADA (COLEOPTERA: SCARABAEIDAE). VII. FOOD AND HABITAT; DISTRIBUTION; KEY TO EASTERN SPECIES

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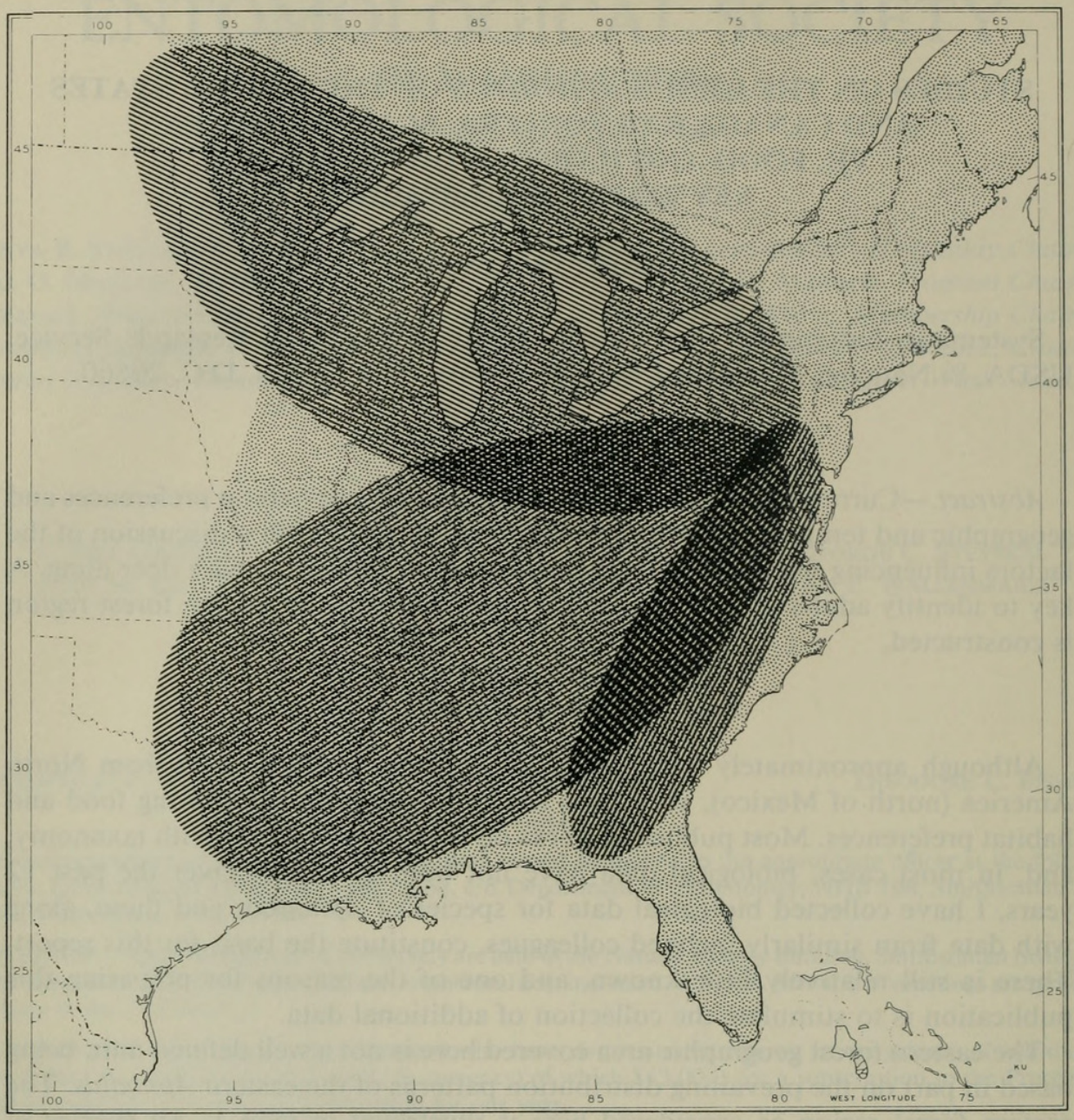
Abstract.—Currently available information on food and habitat preferences and geographic and temporal distribution is presented, along with a discussion of the factors influencing the distribution of those species associated with deer dung. A key to identify adults of *Aphodius* species that occur in the eastern forest region is constructed.

Although approximately 210 species of *Aphodius* are described from North America (north of Mexico), very little has been published concerning food and habitat preferences. Most published works on the genus deal only with taxonomy, and, in most cases, biological data have not been available. Over the past 12 years, I have collected biological data for species of *Aphodius,* and these, along with data from similarly inclined colleagues, constitute the basis for this report. There is still relatively little known, and one of the reasons for preparing this publication is to stimulate the collection of additional data.

The eastern forest geographic area covered here is not a well defined unit, being based in part on the prevailing distribution patterns of the eastern *Aphodius.* The eastern forest region as considered here is illustrated in map 1. All species of *Aphodius* having primary distributions within these limits are treated even though some extend into the Midwest and West. Those species whose primary distributions lie west of the limits but extend into the eastern forest region are not treated except in the key to species. All of the imported or holarctic species in the region are included even though the distribution patterns often extend across the continent.

Most of the data presented here are previously unpublished and are the result of personal field work and information supplied by fellow workers such as the late O. L. Cartwright (Department of Entomology, Smithsonian Institution, Washington, D.C.), Henry Howden (Carleton University, Ottawa, Canada), and Robert Woodruff (Florida Department of Agriculture, Gainesville, Florida). Published information has been obtained from Cartwright (1957), Robinson (1948), Sim (1930), Brown (1927), Hubbard (1894), and Woodruff (1973). I thank D. R. Whitehead for critical comments and suggestions, and W. Steiner for testing the key to species.



Map 1. Eastern forest region. Ellipses indicate the three major areas of species distribution.

Food and Habitat

The eastern species of native *Aphodius* can be divided into five categories based on food and habitat preference as indicated in Tables 1–5. Category I is the most important in terms of numbers of species and biological significance.

Category I: Species associated with deer dung (Table 1).—Seventeen species of eastern *Aphodius* are associated with deer dung, either in an obligate fashion or in showing a strong preference for deer dung when it is available. *Aphodius odocoilus* Robinson and *A. robinsoni* Cartwright are examples of the former; *A. ruricola* Melsheimer and *A. rubripennis* Horn are examples of species that show a preference for deer dung, but which will utilize other dung (horse, cow, etc.) if available.

A very thorough study of the ecology of *Aphodius* species occurring on the island of Faro in the Baltic sea was done by Landin (1961). The factors Landin

Table 1. Category I, species associated with deer dung.

Species	Geographic distribution	Temporal distribution
Spring:		
Aphodius odocoilis Robinson	New Jersey	March–May
Aphodius brimleyi Cartwright	North Carolina	April–July
Aphodius abusus Fall	East Texas	March–April
Winter:		
Aphodius crassulus Fall	Virginia to Florida	October–February
Aphodius floridanus Robinson	Florida	January–May
Aphodius silvanus Cartwright	Maryland (Eastern Shore)	October–April
Aphodius windsori Cartwright	South Carolina to Florida	November–March
Aphodius bicolor Say	New York to Florida, west to Kansas and Texas	September–April
Aphodius terminalis Say	Pennsylvania to Florida, west to Kansas and Texas	November–April
Aphodius lodingi Cartwright	South Carolina and Florida, west to Texas	November–April
Aphodius leopardus Horn	North Carolina north to Ontario and west to British Columbia and Alaska	August–June
Fall:		
Aphodius robinsoni Cartwright	New Jersey, West Virginia, North Carolina, South Carolina	September–November
Aphodius stupidus Horn	New Jersey and Pennsylvania to Florida, west to east Texas	October–December
Aphodius lutulentus Haldeman	Maryland and Virginia south to Florida, west to Texas and Oklahoma	October–February
Aphodius manitobensis	Northeastern U.S. and eastern Canada west to Manitoba	September–December
Summer:		
Aphodius rubripennis Horn	Southeastern Canada to North Carolina	June–October
Aphodius ruricola Melsheimer	Ontario to Florida, west to Manitoba and Texas	May–August (most months of year)

found, that influence the selection of dung by *Aphodius* species are, in large part, the factors discussed herein. Landin studied only dung of domestic animals, and perhaps because of that, some of his conclusions differ somewhat from my own observations. For example, Landin states that "it is not the kind of dung, but the climatic conditions of the environment (particularly the microclimatic conditions of the droppings) which restrict dung-beetles to a certain habitat." I find that the obligate deer dung species will not utilize horse or bovine dung even when it occurs in appropriately shaded areas. They will utilize sheep dung, but there

Table 2. Category II, species associated with rodent burrows or nests, or burrows of the gopher tortoise.

Species	Geographic distribution	Temporal distribution
Aphodius aegrotus Horn (pocket gopher)	North Carolina, Florida	March–September
Aphodius laevigatus Haldeman (pocket gopher)	Florida	February–November
Aphodius badiceps Fall (squirrel nests)	Southeastern Canada to South Carolina, west to Minnesota, Kansas and Arkansas	February–November
Aphodius troglodytes Hubbard (gopher tortoise)	South Carolina, Florida	May–December

appears to be very little difference between the dung of deer and sheep. Therefore I conclude that, under natural conditions with dung of native animals, it is often the *kind* of dung that restricts the beetles to a certain habitat.

The moisture content and exposure of deer dung are of paramount importance in regard to selection by beetles. Very few species will use dung that is dry, and, obviously, if eggs are laid in pellets without sufficient moisture content, the larvae will not be able to mature before complete drying occurs. Whether the dung is in shade or exposed to the sun is correlated with moisture. Dung exposed to the sun will dry more quickly than if shaded, and an obvious bias is for shaded dung.

The fact that deer dung normally is in the form of a pile of small pellets makes rapid drying inevitable, especially when precipitation is infrequent, making the moisture factor much more important than when horse or bovine dung is the resource. Very few species are associated with deer dung in the arid regions of western North America, and lack of reliable precipitation is probably the reason. The fact that most deer dung species occur in fall, winter, and spring is another result of moisture supply; the pellets maintain moisture much longer in cool weather. Only two deer dung species of *Aphodius* are classified as summer species (Table 1), and both of these are capable of utilizing a variety of dung resources. In contrast, eight are classified as "winter" species, four as "fall" species, and three as "spring" species. This breakdown is based on available label data for adults. Several species occur in fall, winter, and spring, but the period of peak abundance usually occurs in one season. That is the season used to classify the species treated here. *Aphodius leopardus* Horn is an extreme example, with adults active through all except the hottest months but with peak activity in the winter.

Latitude is, of course, an important factor for those species having a wide north–south distribution. For instance, *A. leopardus* occurs as an adult from August to June; in the southern portions of the range it is most abundant in winter, but in the northern portions of the range the population peaks in the fall. Southern winters have warm periods during which flight activity, etc., can take place, but northern winters normally remain too cold for such activity; therefore, "winter" active species do not occur in the north.

The thermal factor must also be considered. The species that live in deer dung during fall and winter exhibit a "restricted thermal resistance" (Landin, 1961)

Table 3. Category III, native generalists.

Species	Geographic distribution	Temporal distribution
Aphodius cuniculus Chevrolat	South Carolina to Texas (primarily a Caribbean species)	All months of year
Aphodius vittatus Say	Southern Holarctic—North America; southern Canada, U.S. from Maine to South Carolina, west to Washington and Mexico	All months of year
Aphodius femoralis Say	Pennsylvania to South Carolina, west to Nebraska and east Texas	April–June
Aphodius campestris Blatchley	New Jersey to Florida and Mississippi	All months of year
Aphodius stercorosus Melsheimer	Southeastern Canada to Florida, west to Kansas and Texas	May–October
Aphodius rubeolus Beauvois	Southeastern Canada to Florida, west to Nebraska and Texas	April–August
Aphodius lentus Horn	Ontario to Georgia, west to North Dakota and Texas	June–July
Aphodius borealis Gyllenhal	Holarctic, in North America primarily boreal forest	April–July

while the summer species and the majority of the competitor species exhibit "intermediate thermal resistance." This may be very important when attempting to explain partitioning of the resource in terms of winter versus summer. "Thermal resistance" refers to the degree of tolerance for high temperature.

Wind is another factor since dung beetles search for droppings with their olfactory organs. A light wind would aid in the location of droppings, while a strong wind would tend to prevent flight activity. A forested area would tend to favor the search for droppings because strong wind would not be a normal occurrence.

Vagility may be an important factor, but data on this subject are very limited. Location of the food supply is accomplished by a searching flight. Most species are capable fliers and the search mode consists of an erratic, rapid flight close to the ground, a pattern very similar to that observed in many Diptera. Personal observations indicate that flights usually take place on overcast days, or in late afternoon, not when it is sunny and hot.

A conclusion reached by Landin (1961) with which I agree entirely, is that two or more species can occupy the same "niche," in this case the dung heap. In fact this is the rule rather than the exception. Landin summarized this as follows: "Interspecific as well as intraspecific fluctuations occurring in natural populations of dung-beetles in the dung heaps depend on abiotic factors rather than on the competition factor." However, competition possibly is a factor when food resources are limited, as is often the case with deer dung. This competition may come from other species of *Aphodius* or other species of Scarabaeidae that are not *Aphodius*. Table 7 lists the major competition from non-*Aphodius* by season. Note that of the ten species on the list, five are in the summer category and three are found all year, leaving only one species in direct competition with winter

Table 4. Category IV, native detritivores.

Species	Geographic distribution	Temporal distribution
Aphodius paleroides Horn	New York to South Carolina (coastal sand areas)	June–July
Aphodius parcus Horn	Florida	May–September
Aphodius pinguis Haldman	Quebec to New York, west to Alberta and Montana	May–September
Aphodius hyperboreus LeConte	Quebec to New York, west to British Columbia	May–September

Aphodius and one in direct competition with spring *Aphodius*. The temporal distribution of these competitors is almost a complete reversal of the temporal distribution of *Aphodius* species. The first six names on the list are members of the Aphodiinae, the last four are in the Coprinae. Table 8 lists the species of deer dung *Aphodius* on the left and non-*Aphodius* competitors on the right, broken down by season. Where groupings can be indicated by brackets this has been done—where this was not possible lines are drawn directly between the species of *Aphodius* and the competitor. The brackets on the extreme left group those species of *Aphodius* that may compete with each other. For example, the two summer species of *Aphodius* compete with each other whenever they occur together, and all of the competitor species can compete with both *Aphodius* species.

Category II: Species associated with rodent burrows or nests, or burrows of gopher tortoise (Table 2).—In the midwestern and western United States, about 60 species, or approximately 43% of the North American species whose habitats are known, are in this category. However, only four eastern species belong here, presumably because the harsh climatic changes during the Miocene in the western part of North America did not cause the same radical vegetation changes in eastern North America. *Aphodius badiceps* Fall is found in tree squirrel nests, usually those of the flying squirrel; *A. troglodytes* Hubbard only in burrows of the gopher tortoise; and *A. aegrotus* Horn and *A. laevigatus* Haldeman in pocket gopher burrows. The three burrow inhabiting species are restricted to sand areas of the southeastern United States.

Category III: Native generalists (Table 3).—The eight species in this category are general surface dung feeders, some of which are habitat restricted, but are not known to have distinct dung preferences except that they rarely utilize deer dung. Two possible exceptions to this statement are *Aphodius lentus* Horn and *A. borealis* Gyllenhal. I have taken *A. lentus* in sheep dung, and most species that will utilize sheep dung are also capable of living in deer dung. *Aphodius borealis* is a northern holarctic species which may use deer dung, but probably also occurs in dung of moose, elk, caribou, and possibly in ground squirrel pellets.

Category IV: Native detritivores (Table 4).—The eastern forest fauna in this category is analogous to the fauna of the rodent associated category in that the eastern fauna is comparatively depauperate in both. The native detritivores comprise about 23% of the North American fauna, but only four species occur in the eastern forest region. *Aphodius parcus* Horn and *A. phaleroides* Horn occur in sand areas along the Atlantic seaboard, including Florida; *A. pinguis* Haldeman

Table 5. Category V, native species, habits unknown.

Species	Geographic distribution	Temporal distribution
Aphodius serval Say	Pennsylvania to South Carolina, west to Kansas and Texas	September–April
Aphodius guttatus Escholtz	Newfoundland to New England, west to Alaska	May–November
Aphodius fordi Gordon	Georgia	July
Aphodius macdonaldi Robinson	Pennsylvania	April

and *A. hyperboreus* LeConte occur in marshy, grassy situations in southern Canada and northern United States.

Category V: Native species, habits unknown (Table 5).—Obviously little can be said about these species, but probable habits can be predicted from knowledge of the majority of the fauna. *Aphodius mcdonaldi* Robinson may be an early spring deer dung species; *A. guttatus* Escholtz probably utilizes the dung of moose, elk, and possibly deer; *A. serval* Say is probably a detritivore in sandy riverine situations; *A. fordi* Gordon is an enigma, all specimens having been taken at light, but the species is morphologically most similar to the European *A. scrofa* (F.) which is a surface dung feeder. It is possible that this is a recent immigrant because of its apparently restricted distribution (coastal Georgia), but this is pure speculation at present.

Table 6: Imported species of *Aphodius*; mostly generalists.—These species have the same surface dung feeding habits as the native species in Category III, but have been imported from Europe and have become established. Most are widespread in North America; but three species, *A. scrofa* (F.) and *A. subterraneus* (L.) are restricted to eastern seaboard localities, and *A. rufipes* (L.) occurs in the forested mountain regions from New York to Virginia. With the exception of *A. rufipes*, all of the imports prefer open pastures and bovine dung.

Species Identification

The standard reference for determining species of North American *Aphodius* has been Horn (1887), which is still the only publication dealing solely with the

Table 6. Imported species of *Aphodius*, mostly generalists.

Aphodius fimetarius (L.)
Aphodius granarius (L.)
Aphodius haemorrhoidalis (L.)
Aphodius fossor (L.)
Aphodius erraticus (L.)
Aphodius lividus (Olivier)
Aphodius distinctus (Mull.)
Aphodius rufipes (L.)
Aphodius prodromus (Brahm)
Aphodius scrofa (F.)
Aphodius subterraneus (L.)

Table 7. Competitors for deer dung other than species of *Aphodius*: geographic and temporal distribution.

Species	Geographic distribution	Temporal distribution
Dialytellus humeralis (LeConte)	Southeastern Canada to North Carolina	October–May (winter)
Dialytellus dialytoides (Fall)	Eastern Canada to North Carolina	May–October (summer)
Dialytes ulkei Horn	Eastern Canada to South Carolina	June–October (summer)
Dialytes striatulus (Say)	Eastern Canada to Georgia, west to Manitoba and Iowa	June–October (summer)
Dialytes truncatus (Melsheimer)	Southeastern Canada to South Carolina, west to Wisconsin and Illinois	July–October (summer)
Aphotaenius carolinus (Van Dyke)	Maryland to Florida, west to Indiana	June–August (summer)
Onthophagus concinnus	Pennsylvania to Florida, west to Mississippi	April–December (all year)
Onthophagus subaeneus (P. de B.)	Pennsylvania to Florida, west to Kansas and Texas	February–June (spring)
Onthophagus tuberculifrons Harold	Connecticut to Florida, west to Wisconsin and east Texas	February–December (all year)
Copris minutus (Drury)	Vermont to Florida, west to Kansas and Texas	February–December (all year)

North American fauna as a whole. Schmidt (1922) published descriptions and keys to subgenera and species of the *Aphodius* fauna for the world, and included several North American species unknown to Horn in 1887. Since 1922, a few papers dealing with segments of North American *Aphodius* have appeared (Brown, 1927, 1928, 1929; Saylor, 1940; Cartwright, 1972; Gordon, 1976, 1977a, 1977b), as have two significant regional publications dealing with the fauna of the Pacific Northwest (Hatch, 1972) and Florida (Woodruff, 1973). In addition, several new species descriptions also have appeared since 1922.

The following key to eastern North American *Aphodius* includes those species restricted to, or centered in, the eastern forest region. In addition to those species, several species of primarily midwestern occurrence are included because they penetrate the eastern forest to a significant degree; these species are indicated by an asterisk (*). The key is arranged to facilitate identification, regardless of phylogenetic relationships. One species, *A. rotundiceps* Fall (in Fall and Cockerell, 1907) (type locality, Highlands, North Carolina) is not included in the key nor in the foregoing discussion. The species is apparently known only from the holotype which I examined several years ago. I seriously doubt that *A. rotundiceps* is a member of the American fauna; more likely, the type is a mislabeled Old World specimen.

Most species of *Aphodius* have been assigned to various subgenera, most notably by Schmidt (1922). Most of these "subgenera" are of questionable merit. However,

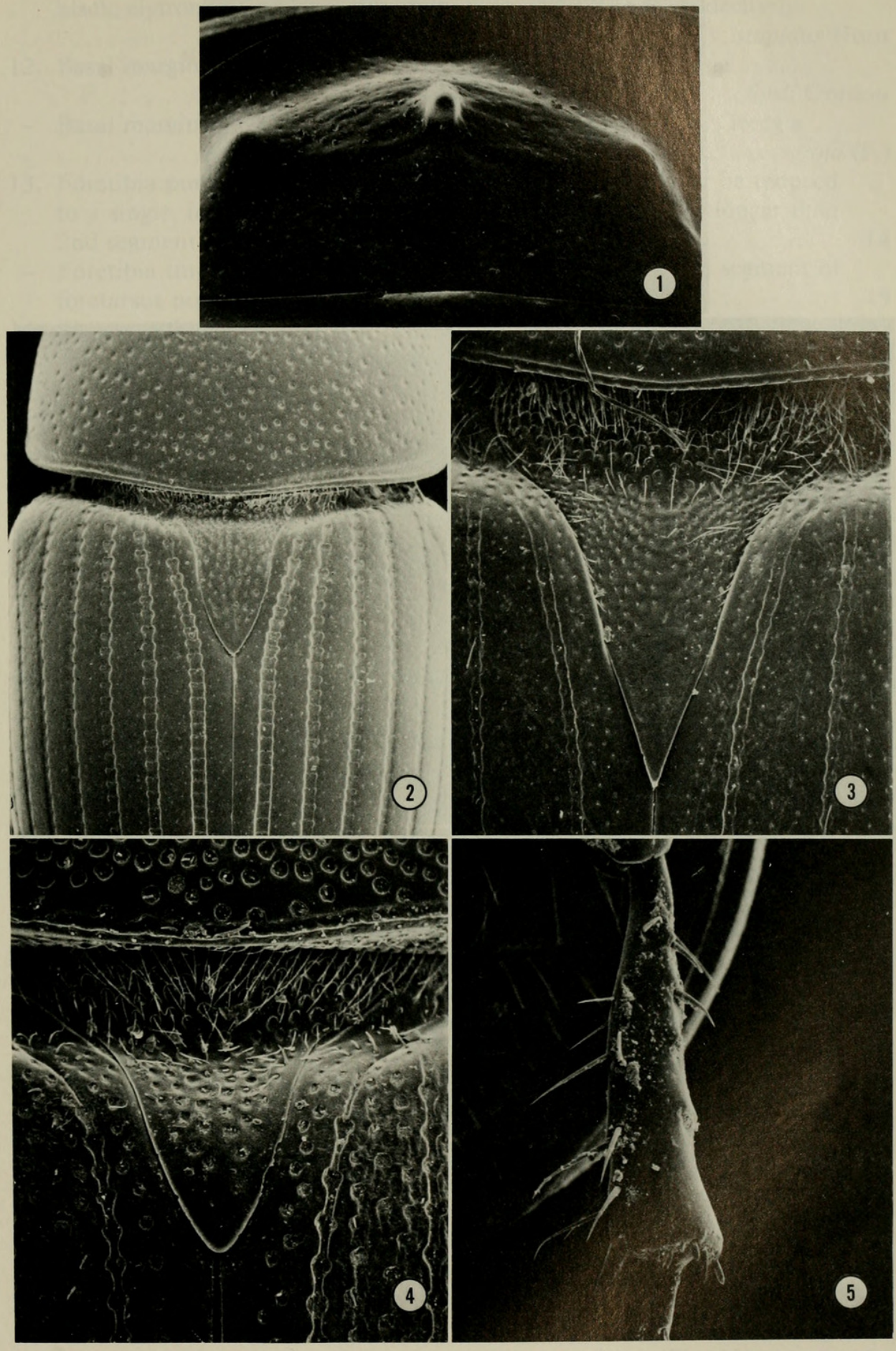
Table 8. Competition among species utilizing deer dung as an energy resource.

Species	Actual and probable competitors
Spring species:	
Aphodius odocoilis Robinson *Aphodius brimleyi* Cartwright *Aphodius abusus* Fall	*Onthophagus tuberculifrons* Harold *Onthophagus subaeneus* (P. de B.) *Onthophagus concinnus* LaPorte *Copris minutus* (Drury) *Dialytellus humeralis* (LeConte)
Summer species:	
Aphodius rubripennis Horn *Aphodius ruricola* Melsheimer	*Dialytellus dialytoides* (Fall) *Dialytes ulkei* (Horn) *Dialytes striatulus* (Say) *Dialytes truncatus* (Melsheimer) *Aphotaenius carolinus* (Van Dyke) *Onthophagus subaeneus* (P. de B.) *Onthophagus concinnus* LaPorte *Onthophagus tuberculifrons* Harold
Fall species:	
Aphodius robinsoni Cartwright *Aphodius stupidus* Horn *Aphodius lutulentus* Haldeman *Aphodius manitobensis* Brown	*Onthophagus tuberculifrons* Harold *Onthophagus concinnus* LaPorte *Onthophagus subaeneus* (P. de B.) *Copris minutus* (Drury)
Winter species:	
Aphodius leopardus Horn *Aphodius terminalis* Say *Aphodius bicolor* Say *Aphodius silvanus* Cartwright *Aphodius crassulus* Fall *Aphodius windsori* Cartwright *Aphodius lodingi* Cartwright *Aphodius floridanus* Robinson	*Dialytellus humeralis* (LeConte) *Onthophagus tuberculifrons* Harold *Onthophagus concinnus* LaPorte *Copris minutus* (Drury)

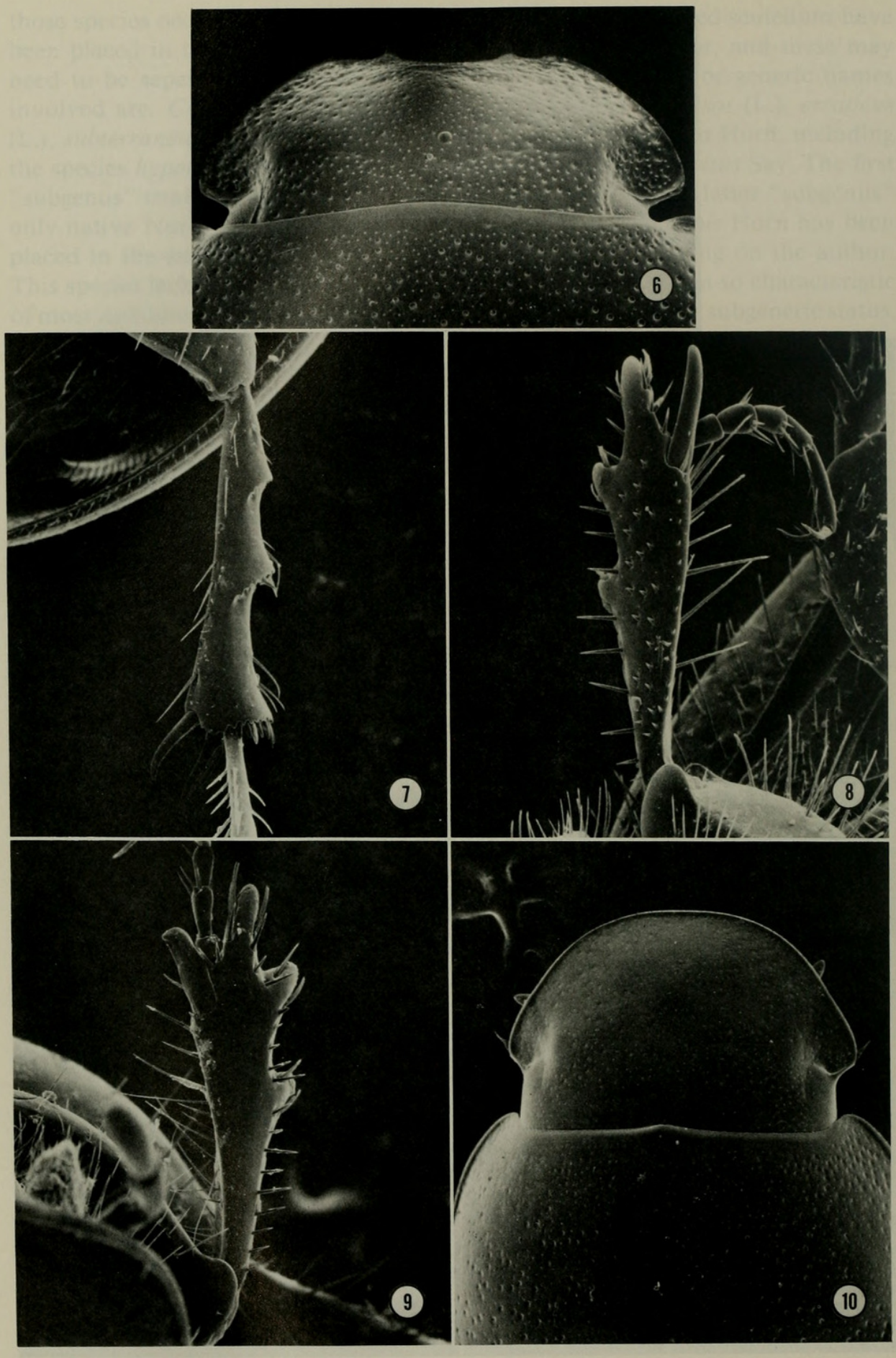
those species occurring in North America that have an elongated scutellum have been placed in two subgenera, or genera, depending on author, and these may need to be separated from *Aphodius* proper. The subgeneric or generic names involved are: *Colobopterus* Mulsant, including the species *fossor* (L.), *erraticus* (L.), *subterraneus* (L.), and *haemorrhoidalis* (L.); and *Diapterna* Horn, including the species *hyperboreus* LeConte, *pinguis* Haldeman, and *hamatus* Say. The first "subgenus" contains species introduced from Europe, and the latter "subgenus" only native North American species. Similarly *Aphodius parcus* Horn has been placed in the subgenus or genus *Didactylia* Orbigny, depending on the author. This species lacks the oblique, transverse ridges on the hindtibia so characteristic of most *Aphodius* species. This species probably deserves at least subgeneric status, but I have followed the same conservative course here in key couplet 9, of treating it as "*Aphodius*."

Key to Eastern North American Species of *Aphodius*

1. Scutellum large, 1/5 to 1/3 as long as elytron (Figs. 2, 3) 2
– Scutellum small, 1/10 to 1/8 as long as elytron (Fig. 4) 8
2. Head with at least one median tubercle, usually with 3 tubercles (Fig. 1); surface of head roughened or densely punctured 3
– Head without trace of tubercles; surface of head smooth 6
3. Small species, less than 6.0 mm long; elytron black except apical 1/3 always red or yellow, humerus often red or yellow ..... *haemorrhoidalis* (L.)
– Species longer than 6.0 mm; elytron not as described above 4
4. Elytron entirely yellow or yellowish brown except sutural margin black; surface of pronotum dull, densely punctured ..... *erraticus* (L.)
– Elytron entirely black or dark brown; surface of pronotum shiny, not densely punctured 5
5. Intervals on elytron flat; length 9.0 mm or more ..... *fossor* (L.)
– Intervals on elytron convex; length 8.0 mm or less ..... *subterraneus* (L.)
6. Elytron yellow or yellowish brown with obscurely defined brown blotch medially ..... *hamatus hamatus* Say
– Elytron entirely brown or black 7
7. Mid- and hindfemora and median area of mesosternum coarsely punctured ..... *pinguis* Haldeman
– Mid- and hindfemora and median area of mesosternum finely punctured, appearing impunctate ..... *hyperboreus* LeConte
8. Hindtibia without oblique, transverse ridges (Fig. 5) ..... *parcus* Horn
– Hindtibia with oblique, transverse ridges (Fig. 7) 9
9. Elytron pubescent throughout; dorsal color uniformly dark brown or uniformly light brown, obscurely defined reddish areas may be present 10
– Elytron lacking pubescence, or if pubescent, then pubescence not present throughout, or if so, then pronotum and head entirely or partially brown or black, elytron red or yellow, or uniformly dull gray (*lutulentus*) 13
10. Pronotum lacking pubescence on dorsal surface 11
– Pronotum pubescent on dorsal surface 12
11. Mesosternum carinate between coxae; dorsal surface reddish brown .. .. *lentus* Horn
– Mesosternum not carinate between coxae; dorsal surface dark brown to



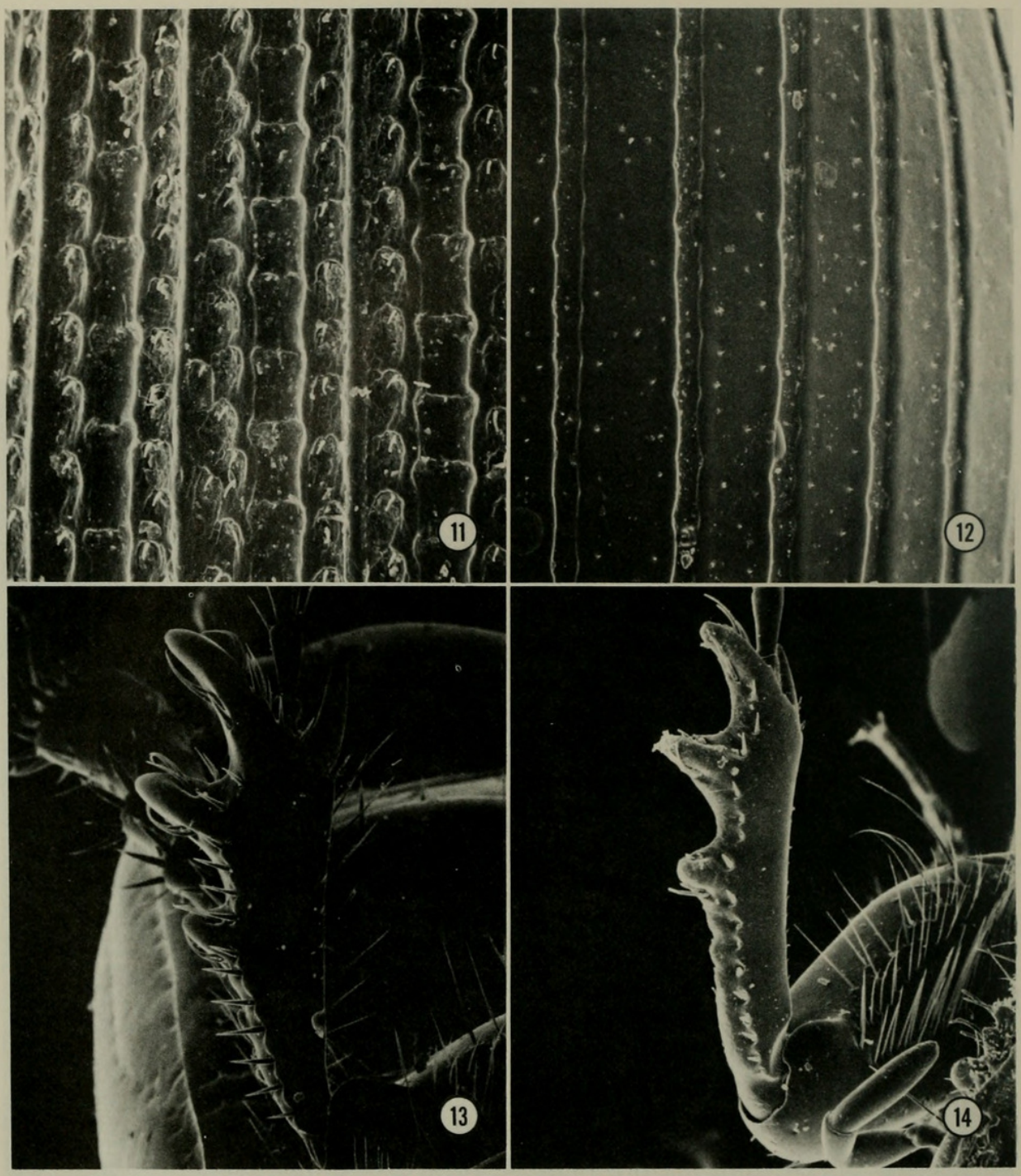
Figs. 1–5. 1, *Aphodius fossor,* head (×44). 2, *A. haemorrhoidalis,* scutellum (×44). 3, *A. erraticus,* scutellum (×60). 4, *A. lutulentus,* scutellum (×100). 5, *A. parcus,* hindtibia (×120).



Figs. 6–10. 6, *Aphodius badiceps,* head with clypeal teeth (×40). 7, *A. distinctus,* hindtibia (×70). 8, *A. campestris,* foretibia (×110). 9, *A. prodromus,* foretibia (×80). 10, *A. rubripennis,* clypeus (×35).

black, elytron with obscure red areas, particularly on apical declivity... ..... *stupidus* Horn

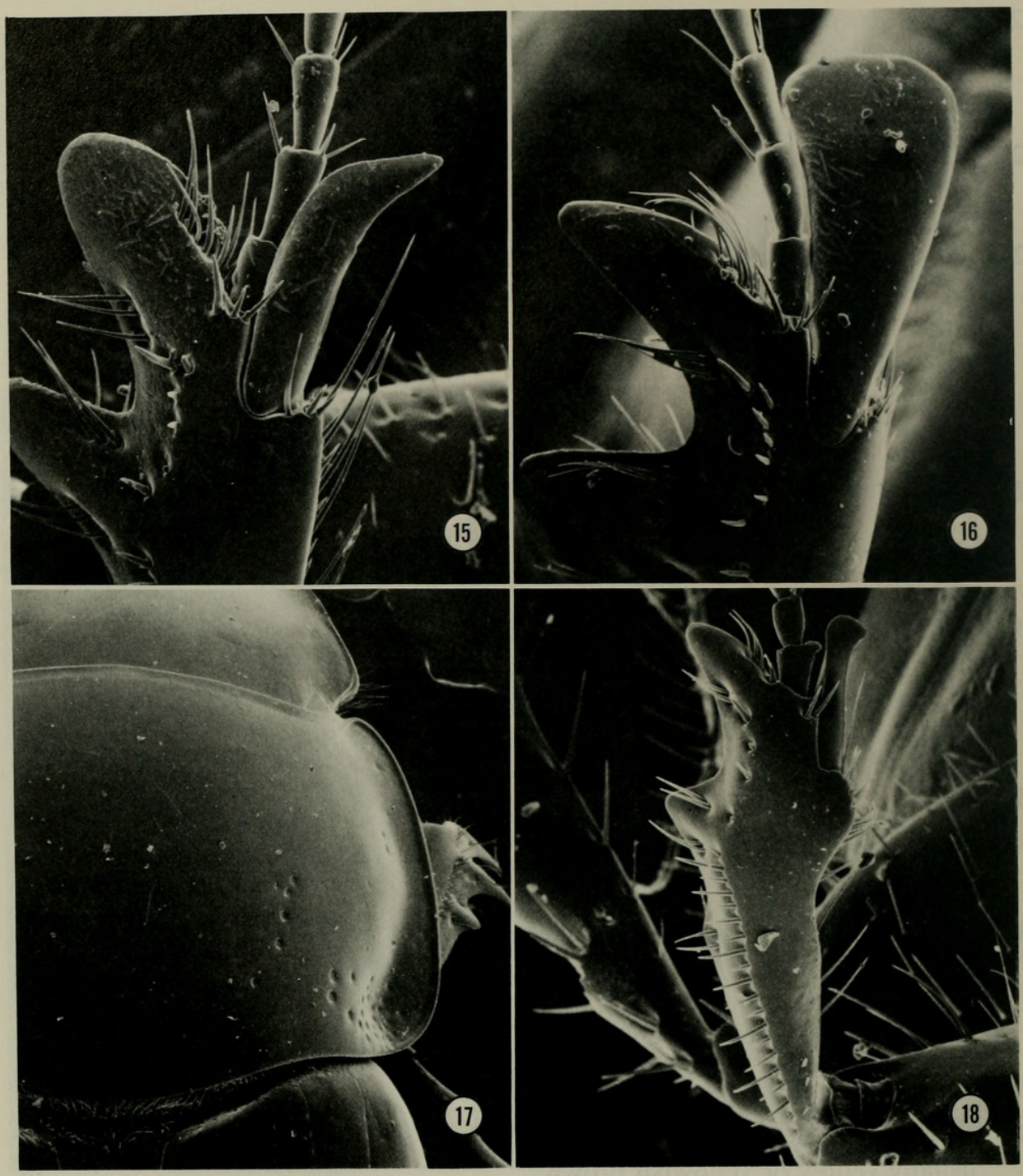
12. Basal marginal line of pronotum strongly impressed; Georgia .... *fordi* Gordon
– Basal marginal line of pronotum obsolete; not known from Georgia .. .. *scrofa* (F.)
13. Foretibia punctate on front surface (Fig. 8), punctures may be reduced to a single, irregular row (*sallei*); 1st segment of foretarsus longer than 2nd segment (except *sallei*) 14
– Foretibia impunctate, smooth on front surface (Fig. 9); 1st segment of foretarsus not longer than 2nd segment 19
14. Elytron pubescent in apical ⅓ near lateral margin 15
– Elytron without trace of pubescence except hairs on lateral margin may be present 16
15. First segment of hindtarsus shorter than next 3 segments; color uniformly reddish brown ..... *rubeolus* Beauvois
– First segment of hindtarsus as long as next 3 segments; pronotum reddish brown, elytron pale brownish yellow ..... *campestris* Blatchley
16. Head tuberculate; elytron with intervals convex, striae deeply impressed; south Texas; punctures on foretibia arranged in irregular row .... *sallei* Harold
– Head smooth; elytron with intervals flat, striae finely impressed; not known from south Texas (except *stercorosus*) 17
17. Pronotal punctures very fine, nearly invisible; lateral margin of elytron with widely spaced, long hairs, burrows of gopher tortoise .... *troglodytes* Hubbard
– Pronotum with dense, coarse punctures in lateral ⅓, discal area impunctate or with fine punctures; lateral margin of elytron without hairs 18
18. Basal margin of pronotum slightly projecting medially, pronotal disc with distinct, fine punctures; in surface dung ..... *stercorosus* Melsheimer
– Basal margin of pronotum evenly rounded, pronotal disc appearing impunctate; in pocket gopher burrows ..... *aegrotus* Horn
19. Each anterior angle of clypeus with short, triangular or spiniform tooth (Fig. 6); dorsal color uniformly black, brown, or dull gray 20
– Each anterior angle of clypeus rounded or obtusely prominent (Figs. 10, 19) dorsal color variable, but if anterior angle of clypeus appears strongly angulate, then elytron pale red, or dark with pale maculation 29
20. Length 8.0 mm or more; clypeal teeth somewhat spiniform (Fig. 6); in squirrel nests ..... *badiceps* Fall
– Length less than 8.0 mm; clypeal teeth more or less triangular 21
21. Dorsal surface dull, with grayish cast; elytron roughened with carinae or alutaceous sculpture 22
– Dorsal surface shiny, uniformly black or brown 23
22. Length 5.0 mm or more; intervals on elytron roughened, alutaceous, flat ..... *lutulentus* Haldeman
– Length 4.50 mm or less; intervals on elytron carinate (Fig. 11) .... *robinsoni* Cartwright



Figs. 11–14. 11, *Aphodius robinsoni,* elytron (×200). 12, *A. odocoilus,* elytron (×130). 13, *A. windsori,* foretibia (×130). 14, *A. lodingi,* foretibia (×85).

23. Intervals on elytron concave (Fig. 12); middle of metasternum pubescent in male; New Jersey Pine Barrens ..... *odocoilis* Robinson
– Intervals on elytron flat or convex; metasternum not pubescent in male; New Jersey Pine Barrens and elsewhere 24
24. Last abdominal sternum concave medially, apex of sternum acuminate; mountains of North and South Carolina ..... *brimleyi* Cartwright
– Last abdominal sternum not concave medially, apex of sternum rounded 25
25. Striae on elytron wider over apical declivity than on disc 26
– Striae on elytron not wider over apical declivity than on disc 27

26. Intervals on elytron convex on disc to strongly convex over apical declivity; Virginia to Florida ..... *crassulus* Horn
– Intervals on elytron flat on disc, barely convex over apical declivity; Maryland ..... *silvanicus* Cartwright
27. Entire clypeus strongly rugose-punctate; east Texas ..... *abusus* Fall
– Clypeus with small, rounded, well-separated tubercles, or wrinkled in apical ½ only; not occurring in east Texas 28
28. Basal tooth of foretibia nearer base than apex (Fig. 13); dorsal surface of clypeus strongly wrinkled; surface of pronotum smooth, polished throughout; South Carolina to Florida ..... *windsori* Cartwright
– Basal tooth of foretibia nearer apex than base (Fig. 14); dorsal surface of clypeus with distinct, dense tubercles; surface of pronotum smooth, polished except lateral ⅛ weakly alutaceous, somewhat dull ..... *lodingi* Cartwright
29. Elytron red, head and pronotum black; elytron pubescent in apical ⅓; head smooth between punctures; pronotum lacking basal marginal line ..... *rubripennis* Horn
– Combination of characters not as described above 30
30. Head and pronotum smooth, punctation nearly invisible; length 9.0 mm or more; mountains from New York to North Carolina ..... *rufipes* (L.)
– Head usually with at least some visible punctures; pronotum always punctate, at least laterally; length less than 9.0 mm, or if longer, then pronotum distinctly punctate 31
31. Foretibia with apical spur long, abruptly hooked and acuminate (Fig. 15), or broadly expanded, spatulate (Fig. 16) 32
– Foretibia with apical spur variably modified, but never as described above 33
32. Pronotum with lateral margin broadly explanate (Fig. 17); surface of pronotum smooth, shiny, impunctate medially; Florida and Great Plains; in pocket gopher burrows ..... **haldemani* Horn
– Pronotum with lateral margin slightly explanate; surface of pronotum densely punctate; Iowa and Great Plains; in pocket gopher burrows ..... **russeus* Brown
33. Elytron pubescent throughout, or only in apical ⅓ and lateral ⅛; elytron usually yellow or yellowish brown 34
– Elytron without pubescence 36
34. Foretibia with basal tooth reduced, nearly absent (Fig. 18); lateral margin of elytron fringed with hairs as long as scutellum ..... **walshi* Horn
– Foretibia with basal tooth prominent; lateral margin of elytron fringed with hairs much shorter than scutellum 35
35. Pronotum impunctate medially, or with some scattered, coarse punctures; elytron yellow with large, yellowish-brown, central cloud not extending to base or apex ..... *prodromus* (Brahm)
– Pronotum punctate medially, punctures dense, fine; elytron yellowish brown except basal ⅕ often yellow ..... *femoralis* Say
36. Surface of head smooth, without trace of tubercles; clypeus nearly truncate, anterior clypeal angle broadly rounded; color completely yellow or elytron with some small, brown spots, median ⅓ of pronotum usually



Figs. 15–18. 15, *Aphodius haldemani,* female, foretibial spur (×100). 16, *A. haldemani,* male, foretibial spur (×100). 17, *A. haldemani,* pronotum (×35). 18, *A. walshi,* foretibia (×110).

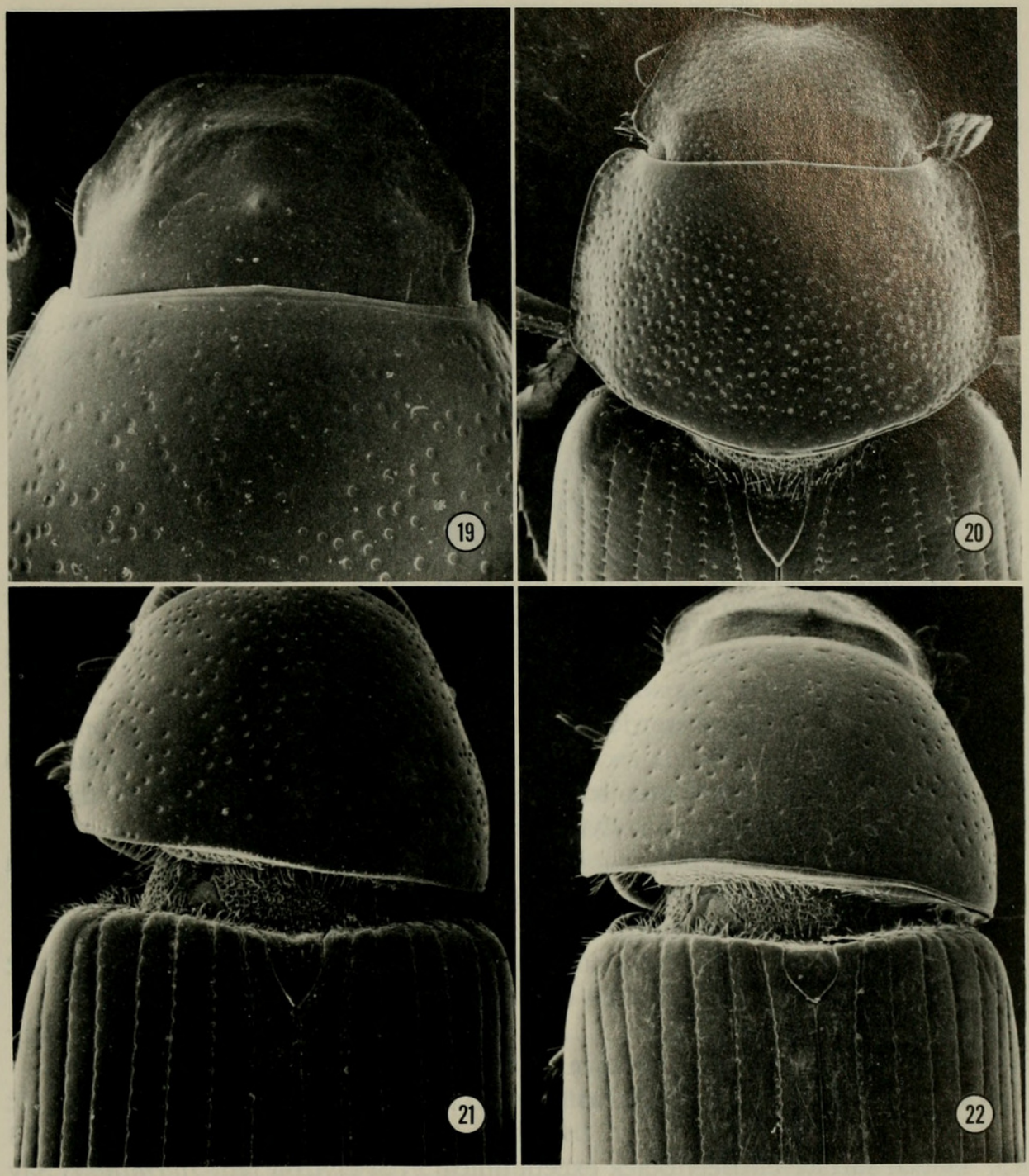
indistinctly yellowish brown; Atlantic coastal sand areas .....
..... *phaleroides* Horn

– Description not as above; not restricted to Atlantic coastal sand areas 37

37. Dorsal color uniformly red or reddish brown; length 7.0 mm or more 38

– Dorsal color not uniformly red or reddish brown, if elytron red, then pronotum black or brown; length 6.0 mm or less, if longer than 6.0 mm, then pronotum darker than elytron 39

38. Surface of pronotum smooth, punctures extremely fine, appearing impunctate; Florida, Georgia, Alabama; in pocket gopher burrows .....
..... *laevigatus* Haldeman



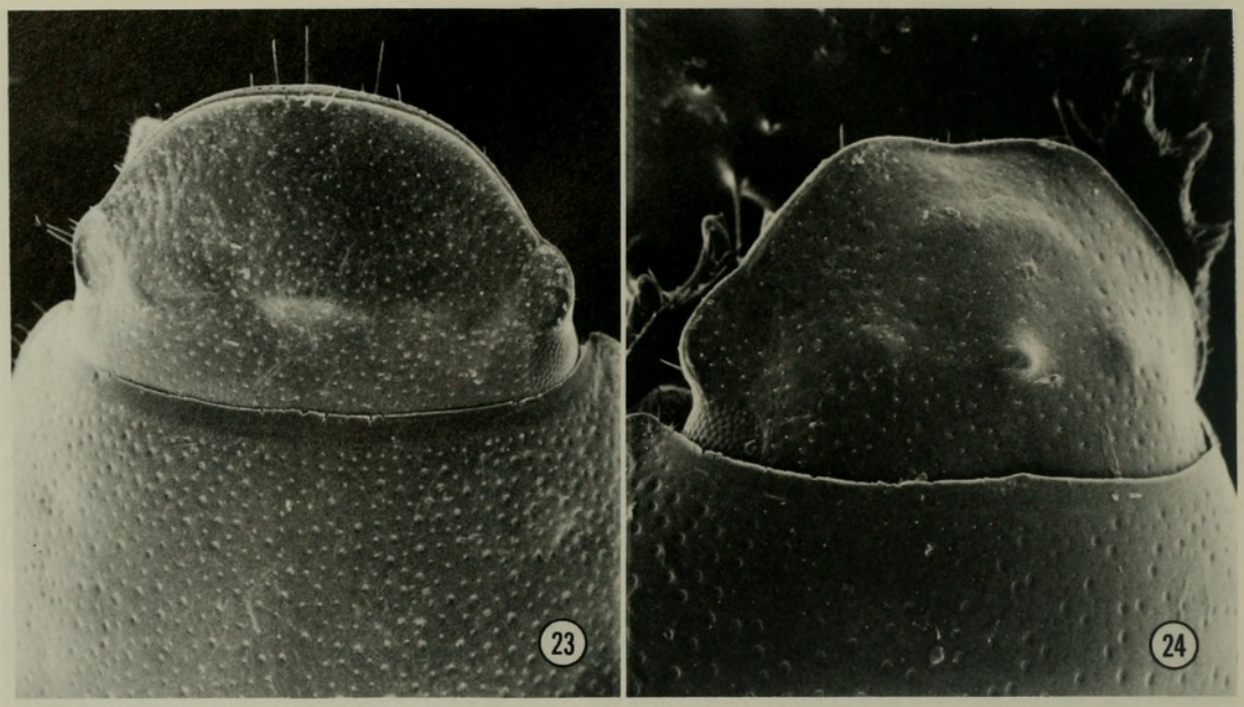
Figs. 19–22. 19, *Aphodius fimetarius,* head (×35). 20, *A. leptotarsis,* pronotum (×42). 21, *A. cuniculus,* pronotum without basal marginal line (×55). 22, *A. granarius,* pronotum with basal marginal line (×45).

– Surface of pronotum densely, coarsely punctured; Indiana, Illinois, Iowa, Great Plains; in rodent burrows ..... **concavus* Say

39. Elytron entirely red; pronotum black except lateral margin or anterior angle pale 40

– Elytron never entirely red, often partially red or yellow; pronotum entirely black or dark brown, often with lateral margin and/or anterior angle pale 41

40. Length less than 6.0 mm; head without prominent tubercles .. *tenellus* Say



Figs. 23, 24. 23, *Aphodius vittatus*, head (×70). 24, *A. borealis*, head (×80).

– Length more than 7.0 mm; head with 3 prominent tubercles and strong clypeal ridge (Fig. 19) ..... *fimetarius* (L.)

41. Lateral margin of pronotum strongly flared outward, explanate (Fig. 20); hindtarsus as long as tibia; elytron entirely brown; in rodent burrows or nests ..... *leptotarsis* Brown

– Lateral margin of pronotum not flared outward, or only feebly so; elytron black or brown, or variably marked; not known to occur in rodent burrows or nests 42

42. Elytron entirely black; meso- and metasterna, and abdomen reddish yellow ..... *bicolor* Say

– Elytron entirely black or brown, or variably marked; meso- and metasterna, and abdomen brown to black, if appearing reddish yellow, then elytron not entirely black 43

43. Dorsal surface entirely black except apical ⅓ of elytron red . *terminalis* Say

– Dorsal surface entirely black or brown, or variably marked, but never with only apical ⅓ of elytron red 44

44. Elytron appearing speckled or mottled, either with pale spots on dark background, or vice versa (see couplet 52, *borealis*) 45

– Elytron not appearing speckled or mottled 48

45. Propleuron with few short hairs, hairs not visible in dorsal view; clypeus with anterior angle sharp, nearly dentate ..... *serval* Say

– Propleuron with dense, long hairs, usually visible beyond lateral margin of pronotum in dorsal view; anterior clypeal angle rounded 46

46. Elytron yellow with elongate, black spots varying in pattern; legs dark brown ..... *distinctus* (Muller)

– Elytron brownish yellow, mottled with dark brown spots, or dark brown with pale spots, legs red or reddish brown 47

47. Surface of elytron dull, strongly alutaceous; median area of metasternum flat to slightly convex, midline distinct ..... *leopardus* Horn
– Surface of elytron shiny, feebly alutaceous; median area of metasternum concave, midline nearly obliterated ..... *guttatus* Escholtz
48. Pronotum without basal marginal line (Fig. 21) 49
– Pronotum with basal marginal line (Fig. 22) 50
49. Elytron yellow with large, yellowish brown, median cloud; pronotum yellow in lateral ⅓, median area brown ..... *lividus* (Olivier)
– Elytron uniformly brown; pronotum piceous except apical and lateral margin brown ..... *cuniculus* Chevrolat
50. Scutellum depressed below level of elytron; pronotal punctures coarse, widely, erratically scattered ..... *granarius* (L.)
– Scutellum not depressed below level of elytron; pronotal punctures coarse or fine, but not widely scattered, more or less evenly spaced 51
51. Clypeus dull, strongly alutaceous; apex of elytron below declivity dull, strongly alutaceous; elytron usually with at least small, red, basal and apical areas 52
– Clypeus mostly shiny, never extremely dull; apex of elytron below declivity as shiny as rest of elytron; elytron uniformly black or brown .. 53
52. Anterior clypeal angle rounded, apex appearing almost semicircular (Fig. 23); elytron usually mostly red except sutural margin, lateral ⅓ obscurely or distinctly darkened, red area often variably reduced ..... *vittatus* Say
– Anterior clypeal angle obtusely angulate, apex appearing broadly emarginate (Fig. 24); elytron usually with small red area on humerus and apical declivity ..... *borealis* Gyllenhal
53. Basal segment of hindtarsus longer than long tibial spur ..... *manitobensis* Brown
– Basal segment of hindtarsus shorter than long tibial spur 54
54. Head essentially impunctate except for fine punctures across vertex and around inner margin of eye; intervals on elytron nearly flat ..... *mcdonaldi* Robinson
– Head distinctly punctured; intervals on elytron convex 55
55. Elytron with many fine punctures on interval, strial punctures strongly impressed; pronotal punctures separated by 1–2× the diameter of a puncture; Ontario to South Carolina, west to Manitoba and east Texas ..... *ruricola* Melsheimer
– Elytron with some scattered, fine punctures on interval, strial punctures weakly impressed; pronotal punctures separated by 2–4× the diameter of a puncture; Florida ..... *floridanus* Robinson

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