

MISCELLANEOUS PUBLICATIONS
MUSEUM OF ZOOLOGY, UNIVERSITY OF MICHIGAN, NO. 84

**The Burrowing Beetles of the
Genus *Mycotrupes*
(Coleoptera: Scarabaeidae: Geotrupinae)**

BY

ADA L. OLSON, T. H. HUBBELL, AND H. F. HOWDEN

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Part II. Relationships and Distribution of *Mycotrupes*

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**Part III. Habits and Life History of *Mycotrupes*, with
a Description of the Larva of *Mycotrupes gaigei***

By HENRY F. HOWDEN

ANN ARBOR
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PLATE I

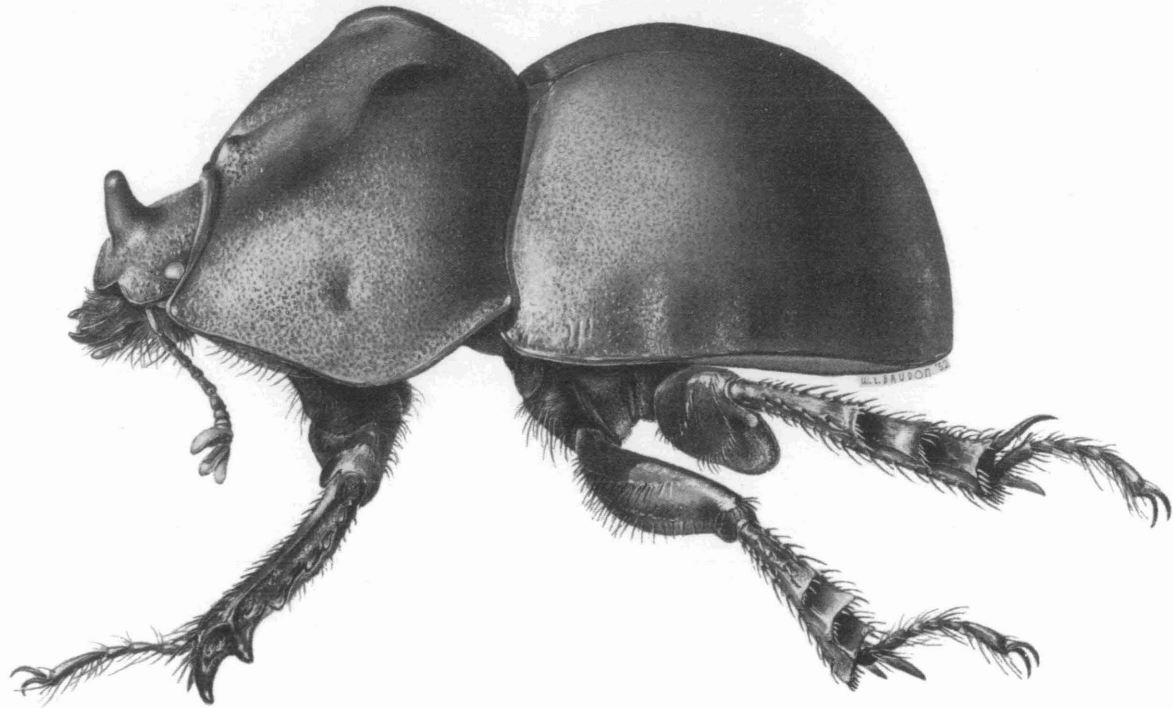


Fig. 1. *Mycotrupes lethroides* (Westwood). Male, Augusta, Georgia.

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THE BURROWING BEETLES OF THE GENUS *MYCOTRUPES*

(Coleoptera: Scarabaeidae: Geotrupinae)

By Ada L. Olson, T. H. Hubbell, and H. F. Howden

THE genus *Mycotrupes* was erected as a subgenus of *Geotrupes* by J. L. LeConte in 1866 to receive his *Geotrupes retusus* of the same date, and no other valid species has since been described. In 1911 Boucomont placed *retusus* as a synonym of *Geotrupes lethroides* Westwood 1837, an assignment that has gone unchallenged for forty-three years. In this paper Olson and Hubbell raise *Mycotrupes* to generic rank, show that *retusus* is distinct from *lethroides*, and describe two new species; Hubbell discusses the relationships and distribution of the genus and its species; and Howden describes one new species and presents data on the habits and life history of two species.

Unlike most other North American Geotrupini, the beetles of this genus have lost the power of flight. The species occupy restricted ranges in the southeastern Coastal Plain of the United States and show a pattern of endemism comparable to that of many other animal groups of low vagility in this region — for example the flightless grasshoppers and the crayfishes.

Mycotrupes beetles spend much of their lives in deep burrows which they dig in sandy soil. In consequence they are seldom seen, and specimens are rare in museums. The first considerable series was obtained by Hubbell in the course of field studies on the camel-crickets of the genus *Ceuthophilus*. The beetles are attracted by the same baits used for collecting *Ceuthophilus*, and many specimens were taken in trap-jars containing dilute fermenting molasses, buried to the brim in the ground. Upon studying this series Olson found that more than one species was represented and undertook a revision of the genus. Material was borrowed by her from various other collections, and after the specific entities had been worked out she visited the Museum of Comparative Zoology at Harvard University to study the type series of *Geotrupes retusus* in the LeConte collection. Various circumstances caused her work to be interrupted, and a number of years later she invited Hubbell to collaborate with her in finishing the revision. Before this joint project was completed, it was learned that Henry F. Howden had also been engaged upon a revision of *Mycotrupes*, as a part of his studies on the Scarabaeidae of the southeastern Coastal Plain. He kindly offered to contribute the results of his work, and this paper has resulted from the pooling of the contributions of the three authors; its final form is that in which it has been cast by Hubbell. It is reassuring to find that three students, working independently, have come to essentially the same taxonomic conclusions regarding the species of this genus.

At Howden's request Dr. F. I. van Emden of the British Museum (Natural History) compared material sent him as *lethroides* (but which was in fact *retusus*) with Westwood's type of *lethroides* borrowed from the Hope Museum at Oxford. He pointed out the differences between the two, and subsequently Olson and Hubbell sent him specimens of two other species for comparison with Westwood's type. One of these proved to be true *lethroides* — and incidentally, it was not the anticipated one. Without Dr. van Emden's help an error would have been made in the identification of Westwood's species, and we wish to thank him for his generous co-operation.

We wish also to express our gratitude to O. L. Cartwright and Frank N. Young for their contributions of specimens and data, and to mention the help given to Olson by the late Nathan Banks, who made available the materials in the Museum of Comparative Zoology (MCZ). Specimens were also lent to us by the following institutions: American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Carnegie Museum (CM), Chicago Natural History Museum (CNHM), Florida Agricultural Experiment Station (FAES), North Carolina State Museum (NCSM), and Snow Entomological Museum, University of Kansas (UK). Paratypes and other material will be deposited in the following additional collections: British Museum (Natural History) (BMNH), Florida State Museum (FSM), Henry F. Howden (HFH), O. L. Cartwright (OLC), Mark Robinson (MR), Hope Museum of Oxford University (HMOU), Canadian National Collection (CNC), and U.S. National Museum (USNM). The types, allotypes, and many of the paratypes of the species here described are in the University of Michigan Museum of Zoology (UMMZ).

The drawings on Plate VIII were made by Howden, the camera lucida sketches for those on Plates IV-VI by Hubbell. Otherwise, all the illustrations in this paper are the work of William L. Brudon, artist of the Museum of Zoology, whose skillful help we gratefully acknowledge.

PART I. A REVISION OF THE GENUS *MYCOTRUPES*

by Ada L. Olson and T. H. Hubbell

The genus *Mycotrupes*, as now understood, comprises five species of geotrupine scarab beetles that together form a distinctive, easily defined generic unit. Although LeConte's original description, with Horn's 1868 additions, will differentiate *Mycotrupes* from other Geotrupinae, it is inadequate by modern standards. The genus is here redefined, taking into account hitherto unremarked characteristics and the features encountered in the new species.

MYCOTRUPES LeConte

Geotrupes (Mycotrupes) LeConte, 1866, *Proc. Acad. Nat. Sci. Phila.*, 1866:381; Horn, 1868, *Trans. Amer. Ent. Soc.*, 1:314; Blanchard, 1888, *Psyche*, 5:105, 109 [in key]; Boucomont, 1912, *Coleopterorum Catalogus*, (Junk), 46:33; Leng, 1920, *Catalogue Coleoptera Amer. N. of Mex.*, p. 252; Bradley, 1944, *Bull. Brooklyn Ent. Soc.*, 39:112 [in key].
Thorectes (Mycotrupes) Boucomont, 1902, *Genera Insectorum* (Wytsman), 7:15.
Geotrypes (Mycotrypes) Boucomont, 1911, *Ann. Soc. ent. France*, 79 (1910): 349 [unwarranted emendations].

GENERITYPE: *Geotrupes (Mycotrupes) retusus* LeConte, by monotypy.

DIAGNOSIS: Small to medium-sized Geotrupini. Dorsum dull black, finely granulate, almost or wholly impunctate (except pronotum in *gaigei*). Elytra fused, almost or entirely nonstriate; hind wings absent. Pronotum and conjoined elytra each strongly convex both transversely and longitudinally, the dorsal profile of body in side view deeply and broadly notched at their junction. Caudolateral angles of pronotum overlying elytral humeri, the marginal carina of humeral angle of elytron engaging with a shallow groove on ventral face of pronotal angle; caudal border of pronotum non-marginate, strongly bisinuate; lateral angles of exposed surface of scutellum acuminate. Sexual dimorphism moderate to pronounced; female having distal tooth of fore tibia of usual Geotrupine form, male having this tooth deeply and broadly divided, the mesal branch forming a slender, elongate, sharp-pointed prong. Caudal part of clypeus horned or tuberculate in male, in female merely tuberculate or callose. Mesocephalic surface of male pronotum weakly to strongly impressed or excavate, the margins of the concavity forming polished and sometimes gibbous crests following a U- or V-shaped course and faintly grooved to distinctly interrupted at meson; corresponding part of female pronotum faintly grooved mesad to moderately impressed, without well-defined polished crests (except in *lethroides*).

OTHER GENERIC FEATURES: Although when dry the body surface appears dull and brown or black, when cleaned and wet with ammonia or alcohol it usually shows brighter colors with metallic glints. The wet dorsal surface may be metallic coppery, bluish, or lavender, and when worn by abrasion the pronotal callosities under bright illumination often glow ruby-red. The minute surface granulations diagnostic of the genus are unique in the Geotrupinae though very like those of the genus *Canthon* in the Coprinae. They are closely and somewhat irregularly spaced, and on the elytra and the margins or whole surface of the pronotum are mostly discrete except in *M. gaigei*, in which they become irregularly confluent on the dorsum. Except for the low rounded summits of these granules, the clypeal tubercle or horn, the pronotal margination, and the smooth pronotal callosities, the entire dorsal surface has a sericeous sheen. This is caused by a dense reticulation of minute polygonal pits with elevated partitions, visible at a magnification of about 200x. All of this surface sculpture is superimposed upon a pattern of obsolete punctae, which are nearly invisible upon the outer surface, but are clearly revealed on the inner elytral surface as a multitude of small round light spots, each with a minute central pore. These spots (Fig. 19) are rather evenly dispersed, without definite alignment, except for a single (cubital) row along the suture and two double rows, one pair (radial) along the midline of the elytron and the other (medial) midway between the cubital and radial rows. The dorsal surface of the elytron shows traces of striae above these rows of punctae — weak but evident in *gaigei*, in the other species very faint to indistinguishable. The labrum and normally concealed base of the head are coarsely punctate, the dorsum otherwise nearly or quite impunctate except in *gaigei*, which has fairly numerous and distinct punctae on the pronotal disk, where there are few or none in the other species.

Head (Figs. 2-6, 43-52): Lateral canthi broad, prominent, lateral margins slightly reflexed, anterior margins not reflexed but in cephalic view somewhat downbent and rising mesad to junction with clypeus, in dorsal aspect forming with clypeus an abrupt and somewhat obtuse re-entrant angle. **Clypeus:** Subtriangular, its cephalic margin a nearly even arc or one that is less convex mesad than laterad ("subtruncate"); halves of fronto-clypeal suture straight or sinuate, convergent caudad at slightly less to slightly more than a right angle; breadth of clypeus 1.2-1.6 times its length. Caudal apex of clypeus angulate in females and in "weak" males, but in "strong" males with a large clypeal horn the bounding suture curving around caudal base of horn. **Antennae:** Middle segment of antennal club uniformly thick, and when club is contracted uniformly exposed all around; surface of funicle polished, of club segments sericeous and often paler than general coloration. **Mandibles** (Figs. 41,42): Distinctive, with one more distal tooth than is usual in the tribe; short, broad, outer margin explanate and strongly arcuate, the dorsal surface excavate within the elevated outer rim, distal part of mandible abruptly narrowed and inbent, with a rounded or subangulate dentiform prominence on outer edge just before point of narrowing; distal inbent part conspicuously tridentate, having an acute distolateral tooth, a longer and sharper apical tooth, and an apically

oblique-truncate ventromesal tooth that is dorsally flattened or grooved. In related genera only the marginal dentation, the apical tooth, and the ventromesal tooth are developed.

Pronotum (Figs. 2-6, 53-62): Width about twice median length; cephalic and lateral borders marginate, caudal border immarginate; cephalic margin strongly and evenly concave or (rarely) with faint mesal convexity; laterocephalic angles extending to or cephalad of caudal margins of eyes and (when head is retracted) in contact with flattened facets on caudal faces of canthi of head, bluntly to rather sharply rounded or subacuminate, dorsally a little flattened and upbent ("explanate"); sides of pronotum thence strongly divergent caudad and straight or weakly sinuate to the broad curve around widest part of pronotum (at or slightly behind midlength), the curve continuing inward in caudal third; caudolateral angles bluntly obtuse, a little upbent, received in shallow depressions on upper surfaces of elytral humeri; ventral face of each pronotal angle with an oblique ridge that forms (with the angle) a shallow groove articulating with the humeral carina of the elytron; caudal margin of pronotum moderately to strongly convex caudad in dorsal aspect, becoming concave as it approaches the caudolateral angles. Pronotal dorsum with a faint to distinct, shallow fovea on each side slightly cephalad of widest point; a weakly impressed median groove often present caudad, or percurrent, or confluent with a more or less extensive mesocephalic excavation. Pronotal form differing in the two sexes. *Male pronotum*: Greatest height at or caudad of midlength; cephalic slope gradual, with surface gently convex or (normally) mesally flattened or impressed to varying degrees; caudal slope moderately to strongly convex-declivent. Cephalomesal depression or excavation varying specifically in size and form, and heterogonically within the species; when well developed bounded (except cephalad) by a distinct and sometimes tumid rim, continuous behind or more or less distinctly divided into arcuate halves separated by a median groove or impression. *Female pronotum*: Less elevated than in male, greatest height usually at or near midlength; cephalomesal impression varying specifically and heterogonically from a faint flattening or hollowing of surface along middle to a well-defined though reduced counterpart of the male specialization.

Sternal characters (Fig. 38): *Prosternum* projecting back from between anterior coxae as a small tumid lobe with broadly convex or convex-tectate surface and arcuate or bluntly obtuseangulate caudal margin. *Mesosternum* distinctive; mesofurcal pit open and shallow, its caudal face not subvertical or overhanging as in most Geotruperini, but sloping up between the mesothoracic coxae; the intercoxal part of the mesosternum acuminate, longitudinally convex, and transversely flat or shallowly concave, its margins scarcely elevated and its surface without mesal keel or point.¹

¹Of related genera, *Pelotrupes* shows the closest approach to this condition of the intercoxal part of the mesosternum, but in it the mesofurcal pit is deeper and has a more vertical caudal face. In *Typhoeus* (*T. typhoeus*, Fig. 36, and *T. momus*) the pit is deep with subvertical caudal face, and the intercoxal piece is narrower, with strongly elevated margins that form a pair of abruptly rounded and slightly divaricate angulations adjacent to the caudal face of the pit. In *Thorectes* and most species of *Geotrupes* the pit is also much deeper than in *Mycotrupes*, and the intercoxal piece is tumid and either carinate,

Mesal part of mesosternum cephalad of pit planate, horizontal, set off from sloping sides by nearly straight, bluntly angulate margins which are scarcely elevated save where they merge with the sides of the pit.

Scutellum: Small, lying wholly upon declivity at elytral base and level with or depressed slightly below adjacent elytral surfaces, somewhat wider than long, with acuminate lateral angles and with sides gently convergent caudad to the appreciably acute apex; surface sparsely granulate.

Elytra: In dorsal aspect together subcordate and about as wide as long,² slightly to distinctly narrower than maximum pronotal width; elytral bases together subtruncate, distinctly emarginate mesad; humeral angles prominent, narrowly rounded; lateral margins gently convex and subparallel in proximal half, in distal half strongly and almost evenly convex-convergent to apex, where they meet in an unbroken curve or with slight angulation. Elytra in side view with dorsal outline strongly convex, becoming subvertical toward apex, highest point cephalad of midlength; lateral (ventral) margins subhorizontal proximad, moderately to strongly decurved distad to apex; marginal (lateral) carina beginning on basal margin opposite edge of mesonotum, becoming prominent on humerus, thence percurrent to apex, this carina in dorsal aspect narrowly but distinctly explanate throughout or at least in middle two-thirds of its course from humerus to apex. Epipleuron very broad at humerus and there sloping strongly inward, thence narrowing to apex and soon taking a position at right angles to dorsal face of lateral carina, its ventral margin narrowly reflexed-carinate, its surface planate to weakly concave and bearing a single row of minute setigerous tubercles. In caudal aspect lateral (ventral) margins of elytra convergent ventrad at an angle of about 120°, meeting at immediate apex in a narrow unbroken curve or with their distal angles slightly blunted so as to form a faint notch; dorsum of conjoined elytra in transverse profile approximating an arc of one-third of a circle.

Abdominal venter: Black to brown, with metallic green or bluish glints that are more evident when the surface is wet. The six visible sternites (II-VII) recessed within elytral margins; the first (II) very narrow, its caudal margin forming a sharp-edged rasp that plays on the stridulatory ridge of the caudal coxa.

Legs: *Fore tibia* (Figs. 21-27) with 5-7 distinguishable lateral teeth, the proximal ones obscure, their size increasing distad except that in the male the subdistal tooth is longest. Distal tooth of male distinctively modified as described in diagnosis. Ventral surface of tibia tectate, forming a sharp-edged ridge evanescent distad and setose along crest, margins of setal sockets becoming dentiform proximad; distal spur in male short, straight or weakly sinuate, acuminate, reaching to about

or mesally ridged, or elevated to form a more or less pointed mesal prominence above the caudal face of the pit.

²All measurements were made optically, those of the smaller parts with a calibrated grid in the eyepiece of a binocular microscope, of the larger ones with the measuring microscope devised by Hubbell for his work on *Ceuthophilus*. Pronotal length was measured along the midline, elytral length from the apex to a line connecting the humeri. As indices of body size we have used the combined lengths of pronotum and elytra, measured separately, and pronotal width.

middle or distal third of second tarsal segment, in female longer, surpassing end of second tarsal segment and with its tip more or less strongly incurved; dorsal setigerous groove of tibia extending into base of distal tooth (not normally interrupted by median carina of subdistal tooth as in some species of *Geotrupes* and in *Thorectes*, Fig. 28), narrow to moderately broad, its surface not conspicuously sculptured, bearing a single row of setae inserted close to its mesal (cephalic) margin. *Middle* and *hind tibiae* each with three strongly elevated transverse dorsal carinae (Figs. 1, 31-35) which are distal, subdistal, and submedian in position and are separated by smooth, rounded-excavate, transverse dorsal grooves; carinae armed with heavy marginal bristles differing specifically in average number and disposition; mesal (caudal) margins of grooves with long hairs alternating with shorter bristles, outer margins of grooves bare except in *gaigei*; proximal half of hind tibia with 4-6 pairs of dorsal marginal bristles some of which may be backed by transversely carinate denticles. Distal spurs of hind tibia acuminate, somewhat surpassing proximal tarsal segment, the dorsal spur a little the longer and weakly bisinuate, the ventral gently curved in distal third. *Tarsi* of all legs relatively elongate and moderately stout. Fore tarsus about half tibial length, its proximal segment very short, next three segments subequal and each longer than broad, distal segment a little shorter than combined lengths of preceding three. Middle tarsus about four-fifths tibial length, hind tarsus more than two-thirds tibial length; in both these tarsi the proximal and distal segments are subequal to each other and to the combined lengths of the remaining three segments. *Tarsal claws* (Figs. 29, 30) of all legs slightly shorter than the segment to which they are attached, rather strongly curved, especially proximad. *Hind femur* and *trochanter* unarmed, the latter (Figs. 63, 64) blunted acute or (in *gaigei*) narrowly truncate at tip. Oblique stridulatory ridge on dorsocaudal surface of *hind coxa* narrow, transversely gently convex, and so finely strigose as to appear smooth at magnifications of less than 20-30x.

Male genitalia (Figs. 7-18): The terminal abdominal segments are retracted as in other Geotrupinae, the tergite and concealed sternite of segment VIII forming the genital capsule (the genital vestibule of Snodgrass). The elongate, heavily sclerotized *phallus* lies, convex side up, in a membranous sac to which it is attached at its inner end. When, by the use of a hook-tipped insect pin or similar instrument, the phallus is extruded from a fresh or relaxed specimen, the sac evaginates, and the phallus usually rotates so that its morphological orientation is no longer obvious.

Much confusion has existed in the morphological interpretation and terminology of the coleopterous phallus and its parts. Sharp and Muir (1912) and most later taxonomists have called the whole organ the *aedeagus*; they recognized in it a large sclerotized *tegmen* composed of a more or less tubular *basal piece* bearing a distal pair of *lateral lobes*, and a *median lobe* supported by *median struts* and bearing the external orifice of the seminal duct (now generally called the *gonopore*) at its tip. Hayes (1922) called the basal piece the *telum* and the lateral lobes the *claspers* in the scarabaeid beetle *Lachnosterna*. Snodgrass (1935), Michener (1944), and Wood (1953) agree in restricting the term *aedeagus* to the median lobe

of Sharp and Muir. Snodgrass refers to the whole organ as the *phallus* and designates the tubular "basal piece" the *theca*. He interprets the latter as a modified *phallobase* developed medially as a support around the aedeagus, and the appended "lateral lobes" as *parameres*. Butt (1944) adopted this terminology in his study of *Amphimallon majalis*. Both Michener and Wood, however, present strong evidence that the theca actually represents the fused *gonocoxites* of segment IX and that the "lateral lobes" are the *gonostyli* of those *gonocoxites*. In the present paper we shall follow Snodgrass in calling the whole organ the *phallus* and the fused *gonocoxites* the *theca*; Michener and Wood have proposed no alternative names.

The parts of the phallus visible without dissection or clearing are the theca and the gonostyli. These show characters of taxonomic value, while no differences have been observed in the concealed aedeagus. Fusion of the *gonocoxites* is complete in the proximal part of the theca, which has an oblique basal opening with much expanded ventral lip and with aperture turned slightly or distinctly toward the right. The axis of the theca is, in lateral aspect, strongly decurved at the immediate base and much more gently concave ventrad in the distal three-quarters; in dorsal aspect the axis is a little concave to the right throughout its length. Distad the theca has the appearance of a large single sclerite rolled into a tube with its edges nearly meeting ventrad and there connected by membrane, the dorsal surface smoothly convex or with a variably distinct median groove. Distodorsad the thecal sclerotization is more or less deeply emarginate, the space thus formed being occupied by the right and left gonostyli ("lateral lobes" or "parameres") and by membranous connections between the gonostyli and the edges of the theca. The gonostyli are asymmetrical lobes hinged to the inner faces of the thecal apices and differing in form from species to species. The distoventral apices of the theca (the ventral lips of the fused *gonocoxites*) are narrowed and separated by an asymmetrically V-shaped, membrane-filled emargination. The sinistral apex is simply rounded; the dextral is abruptly narrowed to form a slender tip, which in the three more southern species (*gaigei*, *cartwrighti*, *pedester*) is acutely pointed, while in the two more northern ones (*retusus*, *lethroides*) it has a mesally directed laminate tooth just before the apex (Plate III).

KEY TO THE SPECIES AND SUBSPECIES OF *MYCOTRUPES*

All the members of this genus vary greatly in size and show correlated differences in development of the heterogonic secondary sexual characters. This makes it hard to construct a satisfactory short key for their identification. Another source of difficulty lies in the fact that old individuals are usually much worn by sand abrasion. They may have the clypeal horn ground down to a stub, the outer mandibular and tibial teeth worn away, and the surface sculpture of the pronotum smoothed; one female studied had nothing left of the fore tibiae but slender, pointed, awl-shaped stumps. The key here given, which takes the known distribution into account, will separate most specimens correctly; but all doubtful ones should be compared with the full descriptions.

1. Dorsum of elytra with a dense, confused pattern of confluent granulations, and with two faint but evident double striae extending at least half the elytral length and often nearly to apex; pronotum with numerous shallow but distinct punctae; phallic theca with ventrodextral apical process simply acuminate (Fig. 9). Northwestern peninsular and adjacent mainland Florida..... *gaugei*, new species.
- 1'. Dorsum of elytra densely and evenly covered with small, mostly separate granulations, striae not evident or just appreciably indicated proximad..... 2
- 2 (1'). Distal tooth of fore tibia deeply and widely emarginate, its mesal (cephalic) branch a slender acuminate prong. Males..... 3
- 2'. Distal tooth of fore tibia of usual form, entire. Females..... 6
- 3 (2). Phallic theca with ventrodextral apical process simply acuminate (Fig. 15). Southern Georgia, Florida..... 4
- 3'. Phallic theca with ventrodextral apical process produced near tip into a mesally directed laminate tooth, giving its outline the shape of a bird's head (Figs. 12, 18). Inner coastal plain of eastern Georgia, central South Carolina..... 5
- 4 (3). Pronotal excavation subcircular or broadly U-shaped in outline, bounded at sides and rear by an evenly arcuate polished crest that subtends an angle of 120-170°; polished summit of crest notched mesad but not prolonged caudad on either side of mesal groove; cephalomedian pronotal tubercle very rarely absent; anterior pronotal angles subacute, briefly explanate; clypeal margin usually evenly arcuate; thecal spine curved slightly or distinctly mesad; elytral tips usually meeting without notch. Southern Georgia, northern Florida east of Apalachicola River, south along east coast to Miami..... *cartwrighti*, new species.
- 4'. Pronotal excavation open in front, bounded at rear by a shorter polished crest that is widely V-shaped, crescentic, or slightly bracket-shaped and subtends an angle of 50-90°; polished summit of crest notched mesad and briefly prolonged caudad on either side of a faintly impressed, median, wedge-shaped tuberculate area, the outline butterfly-like; cephalomedian tubercle rarely present; anterior pronotal angles bluntly rounded-angulate, scarcely explanate; clypeal margin much more strongly convex laterad than mesad; thecal spine directed distad or sometimes slightly laterad; elytral tips usually meeting in a small but distinct notch. Southwestern peninsular Florida..... *pedester* Howden, new species.
- 5 (3'). Clypeus 1.2-1.3 times as broad as long, its cephalic margin strongly convex, subsemicircular to parabolic, its caudal apex bluntly acute-angulate (Figs. 2, 3, 46); clypeal horn laterally compressed, its cephalic face strongly sloped and its base extending far forward (Fig. 51); area of pronotal excavation at maximum slightly smaller than head, the rim forming a rounded V with a narrow and shallow groove mesad; cephalomesal pronotal tubercle absent or indicated as a linear or subtriangular callus confluent with cephalic margination (Fig. 59); smaller, length of

- pronotum+elytra 7-16.5 mm., breadth pronotum 4.5-11 mm. Inner coastal plain of South Carolina *retusus* (LeConte).
- 5'. Clypeus 1.4-1.6 times as broad as long, its cephalic margin much less convex mesad than laterad, its caudal apex bluntly obtuse-angulate (Figs. 4, 47); clypeal horn³ tall, erect, with axis curved slightly caudad, rising abruptly from base which is not extended far forward (Figs. 1, 52); area of pronotal excavation at maximum as large as or larger than head, the bounding ridges prominent, arcuate, their mesal ends separated by a lowered portion of rim nearly as broad as scutellum; cephalomesal pronotal tubercle a prominent, laterally compressed carina with sharply angulate apex at mid-length (Figs. 4, 61); larger, length pronotum+elytra 13.5-18 mm. [predicted extremes 10-18.5 mm.], breadth pronotum 9-12 mm. [predicted extremes 7-12.5 mm.]. Vicinity of Augusta, Georgia [and probably the Fall Line Hills between the Savannah and Altamaha Rivers] *lethroides* (Westwood).
- 6 (2'). Cephalomedian pronotal tubercle³ large, heavy, tetrahedral or subconical, its base involving cephalic margin of pronotum, its tip subacute (Fig. 62); pronotum shallowly but distinctly excavate cephalomesad in reduced counterpart of male specialization, and clypeus as in male [see 5']; large, length pronotum+elytra 16-18.5 mm. [predicted extremes 11-19 mm.], breadth pronotum 11-13 mm. [predicted extremes 7.5-13.5 mm.]. Vicinity of Augusta, Georgia [and see 5'] *lethroides* (Westwood).
- 6'. Cephalomedian pronotal tubercle absent, or not as in alternative; pronotum not or only weakly impressed cephalomesad 7
- 7 (6'). Clypeus 1.2-1.3 times as broad as long, its cephalic margin strongly convex, subsemicircular to parabolic, its caudal apex rectangulate or acuteangulate, its surface weakly tectate except for narrow intramarginal impression cephalad, the ridge crest a smooth line (rarely granulate) and scarcely more elevated caudad than cephalad; cephalomedian pronotal tubercle absent or represented by a small subtriangular widening of cephalic margination (Fig. 60); length pronotum+elytra 11.5-17 mm., breadth pronotum 7.5-11 mm. Inner coastal plain of South Carolina *retusus* (LeConte).
- 7'. Clypeus 1.4-1.6 times as broad as long, its caudal apex obtuseangulate, its surface widely impressed within cephalic margin, centrally tumid and granulate to base of low conical or subcarinate tubercle in caudal angle, a short smooth median crest sometimes extending a short distance forward from base of tubercle; cephalomedian pronotal tubercle usually a flattened callus or rounded nodule attinent to or confluent with cephalic margination. Southern Georgia, Florida 8
- 8 (7'). Cephalomedian pronotal callus or nodule variable but often rather conspicuous, its outline linear, oval or round, or if subtriangular

³The remainder of this rubric applies to large specimens; much smaller ones with lesser development of the secondary sex characters probably exist.

then its apex directed caudad and base confluent with cephalic margination (Fig. 56); larger, length pronotum+elytra 14-18.5 mm., breadth pronotum 9-12 mm.; pronotal angles, clypeal margin, elytral apices, and range as in rubric 4 *cartwrighti*, new species.

- 8'. Cephalomedian pronotal callus or nodule small, sometimes linear or round, but commonly wedge-shaped or heart-shaped with apex attingent to cephalic margination (Fig. 58); smaller, length pronotum+elytra 12-14.5 mm., breadth pronotum 7.5-9.5 mm.; pronotal angles, clypeal margin, elytral apices, and range as in rubric 4' *pedester* Howden, new species.

MYCOTRUPES GAIGEI, new species⁴

(Figs. 5, 7-9, 19, 25, 34, 38, 41-43, 48, 53, 54, 63; Pls. VII and VIII.)

Type: Male, Columbia County, Florida, 3.9 miles north of Santa Fe River bridge on U.S. Highway 41, Oct. 26, 1929 (T. H. Hubbell, Field Cat. No. 94); *allotype* a female with the same data; both in UMMZ.

Diagnosis: This species stands apart from the others in having faint but appreciable elytral striae, partial confluence of the dorsal granules on elytra and pronotum into minute irregular rugulae, distinct pronotal punctae, minutely oblique-truncate hind trochanters, and more numerous fossorial bristles on the middle and hind tibiae, with some present on the outer margins of the grooves between the carinae. In the first three of these features *gaigei* seems more generalized than the remaining species. It is further characterized in both sexes by the subtruncate clypeal margin, the distinctive pronotal modifications, the shape of the fossorial carinae of the middle and hind tibiae, and, in the male, by the sloping clypeal horn and the characters of the phallus, which has the ventrodextral thecal process simply spinose at the tip.

Description of male type: Robust and large for the species, with nearly maximal development of the secondary sexual characters; body length approximately 12.7 mm., breadth of pronotum 7.3 mm. Dorsum when dry dull bronzy black, when wet metallic violaceous brown; venter, legs, and appendages of head reddish brown to dark brown; antennal club sericeous, paler than funicle. *Head*: Length from clypeal margin to occipital plica 2.5 mm., breadth across lateral canthi 3.8 mm., distance from anterior angle of eye to outer edge of canthus 0.50 mm., to lateral angle of clypeus 0.53 mm. Clypeus 2.42 mm. broad, 1.75 mm. long, its cephalic margin gently convex mesad, much more strongly rounded at sides, distance from center of margin to a line drawn between lateral angles 0.75 mm. Clypeal horn well developed, stout, subconical, laterally compressed, its axis

⁴Named in honor of Frederick M. Gaige, former curator of Insects and director of the University of Michigan Museum of Zoology, for whose friendship and guidance during many years we are deeply grateful.

inclined caudad and slightly curved, cephalic face strongly sloping, caudal face slightly overhanging, apex in side view rising 0.8 mm. above clypeal-occipital plane. Antennal scape gradually enlarged distad, dorsal surface slightly flattened and bearing 7 (left) or 8 (right) large and small setae on distal portion (exclusive of those at apex), not grouped but irregularly distributed. *Pronotum* (Figs. 5, 53, 54): Mesal portion strongly tumid; mesocephalic excavation well impressed, U-shaped in outline, smaller in area than head and extending not quite to middle of pronotum, its margins low and indefinite cephalad, becoming more abrupt where excavation cuts into the smoothly tumid central area, a shallow but distinct mesal groove extending from excavation across crest and down the caudal slope, not reaching hind margin; granulation of surface distinct and granules discrete on sides and in excavation, becoming indistinct and confluent toward the central smooth areas, the latter extensive and distinctly and rather coarsely punctate except on rim of excavation. Cephalomedian tubercle (Figs. 5, 53) represented by a small, smooth, slightly raised elongate callus confluent with cephalic margination of pronotum, its apex 0.6 mm. from anterior margin. *Legs*: Fore tibia (Fig. 25) narrow, its distal breadth (inner margin to base of notch between the two distal teeth) 0.17 times its length; dorsal setigerous groove and impressed areas in angle between the two distal teeth very narrow, the groove with a small jog just distad of base of carina of subdistal tooth. Fossorial carinae on dorsal faces of hind and middle tibiae with terminal lobes less produced, central part of carina less emarginate, and marginal bristles more numerous and more evenly spaced than in the other species, bristles of subdistal carina of hind tibia numbering 14 (left) and 16 (right) and distributed along whole carina, outer edge of groove between subdistal and distal carinae with three (left) and four (right) bristles in addition to those on marginal extension of carina. Hind trochanter (Fig. 63) narrowly but sharply oblique-truncate at tip, its outer margin with a few widely spaced setae. *Elytra*: Densely granulose, the granules distinct and discrete on sides, and subdistad partly aligned in three indistinct supramarginal rows, granules on dorsum irregularly confluent to form a confused, subrugulose pattern of very low relief; disc of each elytron with two double striae, faint but easily visible under oblique illumination, extending distad from base and fading out toward apex, each consisting of two parallel, adjacent, weakly impressed and minutely irregular grooves, separated and bordered by faintly tumid ridges. *Phallus* (Figs. 7-9): Theca similar to those of *cartwrighti* and *pedester* in having the tip of the ventrodextral apical process simply spinose, but different in being broader, shorter, not grooved along the mid-dorsal line proximad, less abruptly narrowed at base of the broader and heavier ventrodextral process, and in having differently shaped gonostyli.

Description of female allotype: Large for the species, body length approximately 14.8 mm., breadth of pronotum 7.6 mm. Like the male except as follows: Clypeal tubercle a very low, bluntly rounded, smooth, faintly conical elevation; central area of clypeus gently convex; caudal angle of clypeus rounded-rectangulate and frontoclypeal sutures sinuate. Pronotum with mesocephalic impression small, shallow but distinct, scarcely longer than broad, extending mesocaudad as a narrowing groove

into the large, smoothly tumid, multipunctate central area, the groove ending slightly cephalad of highest part of pronotum, which is at about caudal third; hind surface of pronotum steeply convex-declivent, with shallow median groove which does not reach either summit or caudal margin; cephalomedian tubercle (Fig. 54) a small but distinctly raised blunt-conical point, its base confluent with cephalic margination, its form suggesting that of female *lethroides*, but in miniature.

Dimensions: This species averages the smallest of the genus (see Table I). Additional measurements of the type and allotype, in that order and in millimeters, are as follows: Breadth between anterior pronotal angles 4.8, 5.1; depth of emargination between these angles 1.25, 1.4; length pronotum between anterior and posterior angles 5.1, 5.4; caudal breadth of pronotum between angles 7.3, 7.6; length pronotal excavation from anterior margin (along slope) ± 2.8 , ± 2.2 ; width of excavation ± 2.8 , ± 2.0 ; maximum breadth across elytra 8.3, 9.1; length of elytra from line between humeri to apex 7.9, 8.6; breadth/length of exposed part of scutellum, both specimens 1.5/0.8; length of leg segments: fore tibia 5.0, 5.2; fore tarsus 2.6, 2.7; middle tibia 3.7, 3.9; middle tarsus 2.7, 3.1; hind tibia 4.5, 5.1; hind tarsus 3.0, 3.4; fore, middle, and hind tarsal claws, male 0.6, 0.8, 0.8, female 0.5, 0.7, 0.7; male, phallic theca, length 2.0, breadth 0.9.

Variation: In series collected at the same place and time there are great differences in size and marked heterogonic variation. The type and allotype are large and show close to the maximum development of the secondary sexual characteristics. Compared with small ones, such individuals are more robust, with relatively broader and more tumid pronotum, more expanded elytral humeri, and often broader fore tibiae with a wider dorsal setigerous groove. The dorsum also tends to be smoother, with the granules and rugulae less evident.

In the smallest males the secondary sexual modifications are very weakly developed. The clypeal horn is reduced to a low, slightly compressed, bluntly conical tubercle rising only about 0.25 mm. above the clypeal-occipital plane; the pronotum is much less tumid and less elevated than in "strong" males, and the mesocephalic excavation is no more than a small flattening, bordered caudad by a faint rim with a shallow mesal groove; the whole surface of the pronotum except the very rim of the depression is granulose, and the dorsal punctae, although present, are few and hard to see among the confluent rugulae and granulations. In females of comparably small size the clypeal tubercle is no more than a faintly raised elongate polished callus, and the pronotal excavation is very slight. The cephalomedian pronotal tubercle, on the other hand, remains quite large and prominent no matter how small the specimen and thus furnishes one of the more constant diagnostic characters of *M. gaigei*.

Variation has been observed in many other features, but seems worth recording in only three of them. The number of setae on the dorsal surface of the antennal scape averages distinctly greater than in any other species except *lethroides*, the range being three to nine with a mode of about five (the type is 7-8, the allotype 4-4); as in *lethroides* these setae are distributed bluntly irregularly along most of the enlarged distal part of the

scape, instead of being grouped mostly toward the base of the enlargement as in *cartwrighti*. The dorsal setigerous groove of the fore tibia varies considerably in width among specimens of the same size. In the large series from Columbia and Alachua counties it is occasionally interrupted, at the point where it normally jogs, just distad of the base of the median carina of the subdistal tooth, by a narrow shining obliquely transverse carina. Such individuals — about 7 per cent of the specimens examined — appear to violate one of the generic characters. The accessory carina is not, however, a direct continuation of the median carina of the subdistal tooth, such as occurs in *Thorectes* (Fig. 28), but results from increase in size of one of the interpunctal ridges. The transformation is evidenced in many individuals (about 8 per cent of the series) in which the accessory carina is partly formed or suggested. In some of the smaller individuals the setigerous groove is reduced to little more than a row of setigerous punctures, more or less irregularly spaced distad, and in one specimen with a gap opposite the base of the subdistal tooth.

The fossorial bristles on the margins of the transverse carinae of the middle and hind tibiae are more numerous and more uniformly spaced in *M. gaigei* than in the other species, but they show considerable variation. Those of the subdistal carina of the hind tibia range from 10 to 23, there being rarely fewer than 12; three or four are also usually present on the concave middle section of the carina while in the other species the bristles tend to be more crowded around the lobate carinal ends, with rarely more than two and often none in the central part.

Specimens examined: 341—205 males, 136 females (type, allotype, and paratypes), as follows:

FLORIDA: *Columbia County:* 3.9 miles north of Santa Fe River bridge on U.S. Highway 41, Oct. 26, 1929 (Hubbell) 27 ♂, 32 ♀ (including type, allotype) UMMZ; 4 miles north of High Springs on U.S. Highway 41 [very near last], March 19-25, 1953 (Howden and Dozier) 76 ♂, 44 ♀ HFH, UMMZ; *Dixie County:* Oldtown, April 1-5, 1929 (Hubbell) 1 ♂, 2 ♀ UMMZ; *Gilchrist County:* 0.6 mile south of Wilcox on State Highway 26, March 24, 1949 (Young) 1 ♀ UMMZ; R.16 E., T.10 S., secs. 9/10, March 30, 1949 (Young) 10 ♂, 7 ♀ UMMZ; *Alachua County:* High Springs, March 31, 1938, 1 ♂ HFH; Warren's Cave about 8 miles northwest of Gainesville, Nov. 6, 1924 (Hubbell, in pineland near entrance) 1 ♂, UMMZ; 4 miles west of Archer, March 22-23, 1949 (Young) 1 ♂, 1 ♀, and March 23-24, 1953 (Howden and Dozier) 75 ♂, 42 ♀ HFH, UMMZ; 2.1 miles southwest of Archer on State Highway 24, March 29, 1946 (Young) 8 ♂, 4 ♀ UMMZ; *Levy County:* 5 miles southwest of Archer on State Highway 13, March 29, 1946 (Young) 1 ♂, 1 ♀ UMMZ; *Marion County:* Dunnellon, Oct. 18-19, 1929 (Hubbell) 2 ♂, 2 ♀ UMMZ; *Citrus County:* 1 ♂, J. W. Green collection. Paratypes will be deposited in AMNH, BMNH, CAS, CM, CNC, CNHM, FAES, FSM, MCZ, MR, OLC, OUHM, USNM, and B. Dozier collection.

Distribution: This species is known only from the central part of the belt of rolling sandy uplands that extends unbroken from the Georgia line in eastern Madison and western Hamilton counties southward in western peninsular Florida to Pasco and Pinellas counties. This belt,

although continuous, is constricted at the Marion-Citrus County boundary, and is partly divided by a narrow tongue of flatwoods and swamp that runs north from Levy County into Gilchrist County. The region is bounded on all sides by other types of environment — hardwood hammocks, flatwoods, and swamps — in which *Mycotrupes* does not occur. Harper (1914) has described and mapped the area, which he calls the Peninsular Lime-sink Region; it is shown on the generalized vegetation map of Florida published by the Florida Agricultural Experiment Station (1938) as “rolling sandy pine land.” The uniformity and continuity of major habitat within this region and the distribution of records of *Mycotrupes gaigei* support the hypothesis that the range of that species may be approximately coextensive with the Peninsular Lime-sink Region, though it is certainly not everywhere present therein.

Habitat: The soils of the Peninsular Lime-sink Region are mostly deep, well-drained sands of the Norfolk and Blanton series, overlying porous limestone. The topography is level or rolling. Where the land has not been cleared for pasture or cultivation it is clothed with second growth and scattered remnants of the magnificent “high pine” forest that formerly occupied it. At present the most abundant trees over wide areas are turkey oak and bluejack oak, which occurred as understory in the original pine forest. They characterize a type of dry, sandy, open forest environment with much exposed soil, known locally as “turkey oak” or as “sand hills” (Plate VII). This is the principal habitat of *Mycotrupes gaigei*. The same or ecologically similar types of dry, open, sandy woodland are widespread in other parts of Florida, in Georgia, and in the Carolinas, and are the usual habitat of the other species of *Mycotrupes*. *M. gaigei* is not, however, confined to this single habitat. It also occurs in abundance in the “fossil dune” country around Archer in southwestern Alachua County, where the soil is deep, coarse, Lakewood sand, and the vegetation verges upon “sand scrub.” The sand hills and the sand scrub have been described by Hubbell and Goff (1940) and by Laessle (1942). Both are xeric situations subject to high insolation and extreme fluctuations in temperature and air humidity. Ground cover is usually scanty; there are clumps and patches of dwarf and seedling oaks and low shrubs that hold accumulations of dead leaves, and intervening areas that are bare except for a scattering of grasses and herbs and in which the soil is often bleached nearly white at the surface. In the sand hills, especially, a noticeable feature is the abundance of large and small mounds of sand thrown up by burrowing animals. Pocket-gophers (“salamanders”), gopher tortoises, lycosid spiders, ants, the cricket *Anurogryllus muticus*, and various species of scarab beetles — each on its own scale and in its own characteristic fashion marks the site of its burrows with these telltale sand heaps. *Mycotrupes gaigei*, like other species of its genus, makes distinctive little “push-ups,” scores of which, old and new, can sometimes be found within an area of a few hundred square feet.

Habits and life history: These are discussed in detail by Howden in Part III of this paper.

MYCOTRUPES CARTWRIGHTI, new species⁵

(Figs. 6, 13-15, 27, 29, 35, 44, 49, 55, 56)

Geotrupes lethroides Blatchley, 1928 (not of Westwood, 1837), *Florida Ent.*, 12:45 [St. Augustine and Enterprise, Florida].

Type: Male, Leon County, Florida, 6.5 miles east of Tallahassee, on north side of U.S. Highway 90, Sept. 10-12, 1929 (T. H. Hubbell, Field Cat. No. 80); *allotype* a female with the same data; both in UMMZ.

Diagnosis: Of moderate to large size for the genus, dorsum evenly granulose, elytra without evident striae, clypeus usually with gently and evenly arcuate anterior margin. Male with tall, relatively erect, straight-conical clypeal horn; pronotal excavation bordered caudad and laterad by an arcuate, almost semicircular rim interrupted only by a shallow and narrow mesal groove; ventrodextral thecal process simply spinose at tip, the spine curved dorsad and a little mesad. Female with cephalomedian pronotal tubercle a low rounded nodule or flattened callus, cephalad as broad as or broader than caudad, and confluent with cephalic margination. From *gaigei* this species is separable by the characters given in the key and in the diagnosis of *gaigei*. From *retusus* and *lethroides* it differs in the form of the thecal spine; from *retusus* also in the larger size, broader head, less convex clypeal margin, and taller and more erect male clypeal horn; from *lethroides* in its smaller size, mesally grooved instead of widely notched male pronotal crest, and small low cephalomedian pronotal tubercle in the female. *Mycotrupes cartwrighti* is very close to *M. pedester*, which may possibly be only subspecifically distinct; the two are compared in the key and in the diagnosis of *pedester*.

Description of male type: Moderately large for the species, body length ± 15 mm., pronotal breadth 10.9 mm.; surface unworn, specimen apparently newly matured. Dorsum dark reddish brown (usually black in older adults), venter and legs lighter reddish brown. *Head* (Figs. 6, 44, 49): Length from clypeal margin to occipital plica 3.15 mm., breadth across canthi 4.6 mm., distance from anterior angle of eye to outermost point of canthus 0.70 mm., to lateral angle of clypeus 0.85 mm. Clypeus 3.1 mm. broad, 1.95 mm. long, its anterior margin evenly and gently convex, distance from midpoint to line drawn between lateral angles 0.9 mm.; fronto-clypeal suture with its halves briefly curved near ends, thence straight, converging at an obtuse angle and meeting in a broad curve around caudal base of horn. Clypeal horn large, erect, rising abruptly from somewhat tumid central part of clypeus, a little compressed, conical with straight axis, caudal face subvertical, cephalic face sloping steeply to junction with base on a line with clypeal angles, the narrowly rounded tip rising 1.5 mm. above clypeal-occipital plane. Antennal scape rather abruptly swollen in distal three-fifths, the convex dorsal surface bearing near base of enlargement one large and one (left) or two (right) small setae,

⁵Named in honor of O. L. Cartwright, a leading student of the North American Scarabaeidae, who has given us valuable help in the present study.

beyond these bare except for marginal setae at apex. *Pronotum* (Figs. 6,55): Tumid and strongly convex, surface densely and discretely granulose except on marginations, polished rim of excavation, and cephalomedian tubercle; anterior angles bluntly rectangulate, very narrowly rounded, somewhat upbent and dorsally flattened ("explanate"), edge of pronotum deeply emarginate between them; side margins of pronotum coarsely marginate and somewhat explanate, increasingly so at caudal angles. Mesocephalic excavation well impressed, broader than long (± 4.6 by ± 3.3 mm.), its floor subplanate, its area slightly less than that of head; outline of excavation subcircular or broadly U-shaped, its margins low and indefinite cephalad, becoming abrupt and narrowly rounded at the crest in caudal portion, there forming an evenly arcuate, polished rim, subtending an angle of $\pm 130^\circ$ and broken only by a weak mesal groove; rim without evident punctae (though very minute ones are visible at a magnification of 60x); mesal groove continued down caudal face of pronotum, fading out just above hind margin. Cephalomedian tubercle a low but sharply elevated, compressed conical point, separated from cephalic margination and with apex 0.9 mm. from front edge of pronotum. *Legs*: Fore tibia (Fig. 27) rather broad, its distal breadth (inner margin to base of notch between the two distal teeth) 0.20 times its length; dorsal setigerous groove and impressed areas in angle between the two distal teeth broad, greatest width of groove (0.45 mm.) opposite base of subdistal tooth. Fossorial carinae on dorsal faces of hind (Fig. 35) and middle tibiae mesally emarginate, their ends strongly convex and that of mesal side lobate-produced, their margins armed with stiff bristles that are mostly grouped near the ends of the carina with few or none in middle; bristles of subdistal carina of left caudal tibia 8, of which 5 are on outer, 3 on inner end; of right caudal tibia 9, of which 5 are on outer end, 1 is in middle, and 3 are on inner end. Outer margins of intercarinal grooves without setae other than the bristles on marginal portions of carinae. Hind trochanter bluntly acuminate at tip. *Elytra*: Densely and almost evenly granulose, the granules discrete and almost wholly without alignment except for just discernible traces of the discal striae; elytral apices joining in an even curve without any notch. *Phallus* (Figs. 13-15): Very similar to that of *pedester*, differing as follows: mesal margin of ventrodextral thecal process concave, the terminal spine directed somewhat mesad as well as upward; left gonostylus with proximal margin convex, large basal portion deeper in relation to breadth than in *pedester*, and rather abruptly narrowed to base of the more parallel-sided distal prolongation by rounded excision of mesal margin.

Description of female allotype: Moderately large for the species, body length ± 15.2 mm., breadth of pronotum 10.3 mm. Like the male except as follows: Clypeus shallowly impressed and subplanate at sides and within narrowly reflexed anterior margin, slightly tumid in a central area that is longer than broad, clypeal tubercle rising from caudal portion of tumid region as a very low, narrowly compressed, subconical shining point; fronto-clypeal suture with sides nearly straight, convergent at an angle of about 115° to rounded angulate caudal apex. Pronotum (Fig. 56) much less inflated and lower than in male, its surface almost evenly convex, with mesocephalic excavation weakly indicated as a flattened, scarcely

impressed elongate cordiform area about 1 mm. wide and 1.5 mm. long, ill-defined, tapering caudad to a faint mesal groove that continues part way down the caudal slope of pronotum. Cephalomedian tubercle distinctive, developed as a triangular expansion of the unusually broad cephalic margination, the projecting point thus formed having a sharply angulate caudal apex and flattened surface no more elevated than the margination itself, the distance from edge of pronotum to tip of point 0.55 mm.

Dimensions: This species averages larger than *gaigei*, *pedester*, and *retusus*, but is distinctly smaller than *lethroides* (see Table I). Additional measurements of the type and allotype, in that order and in millimeters, are as follows: Breadth between anterior pronotal angles 5.2, 5.4; depth of emargination between these angles 1.7, 1.1; length of pronotum between anterior and posterior angles 6.4, 5.9; caudal breadth of pronotum between angles 9.6, 9.1; length of pronotal excavation from anterior margin (along slope) ± 3.3 , ± 1.6 ; width of this excavation ± 4.7 , ± 1.0 ; maximum breadth across elytra 10.5, 10.6; length of elytra from line between humeri to apex 9.4, 9.8; breadth/length of exposed part of scutellum, both specimens $\pm 2.1/\pm 1.0$; length of leg segments: fore tibia 5.7, 5.7; fore tarsus 2.8, 3.0; middle tibia 4.5, 4.5; middle tarsus 3.3, 3.2; hind tibia 6.1, 6.2; hind tarsus 3.8, 3.8; fore, middle, and hind tarsal claws, male 0.55, 0.73, 0.75; female 0.67, 0.78, 0.87; male, phallic theca, length 3.2, breadth 1.1.

Variation: The series available for study is small and probably does not include the full range of variability of the species. The differences between the smaller and larger specimens are, however, less than in comparable specimens of *gaigei*. In even the smallest males the clypeal horn is well developed though much smaller than in the type, and the pronotal excavation is well defined by a distinct U-shaped rim, though its area is smaller than that of the head instead of distinctly larger as in "strong" males. The cephalomedian pronotal tubercle of the male is almost always present, but shows the following variations: elongate or linear, connected with cephalic margination, 6; elongate or linear, separated from cephalic margination, 8; a small, circular callus or conical point, 4; a very small rounded callus or shining dot, 2; absent, 1 (Hinesville, Ga.). In the female the cephalomedian pronotal tubercle is confluent with the margin in all specimens examined, but varies as follows: triangular like that of type, 5; similar but with subcircular caudal outline, 5; similar to last but longer than broad, 2; linear, 1; subcircular and narrowly connected to margination, 1. Only in the last instance does its form approach that characteristic of *pedester*. The phallic spine varies somewhat in stoutness and curvature, but its tip is in all instances directed more or less mesad as well as dorsad, and the inner margin of the ventrodextral thecal process that bears it is more or less distinctly concave.

The antennal scape is usually bare on the dorsum between the apical fringe of setae and a group near the base of the swollen region, but in a few specimens there are scattered setae within this space. The number of dorsal setae on the scape varies as follows, with right and left scapes separately counted and the number of setae followed by number of scapes possessing them: Males, 1:4, 2:16; 3:8, 4:3, 5:3, 6:3, 8:1; females, 1:10, 2:10;

3:10; 4:1. The variation in number of bristles present on the subdistal carina of the caudal tibia is as follows: Male, 8-12, mode 9; female, 9-12, mode 10; 0, 1, or 2 commonly present on middle portion of carina.

The male from Hinesville, Georgia, although typical of *cartwrighti* in most respects including the phallic characters, is aberrant in lacking any trace of the cephalomedian pronotal tubercle and in having the clypeal horn much more inclined, with its anterior face sloping far forward. Since it is from a territory separated from the main body of the range of *cartwrighti* by the Altamaha River, it may prove representative of an atypical population or perhaps a distinct subspecies.

Specimens examined: 37--21 males, 16 females (type, allotype, and paratypes, except as noted) as follows:

GEORGIA: *Grady County*: May 2, 1935 (H. S. Peters) 1 ♂ OLC; *Thomas County*: Thomasville, August 24 and 28, 1938 (P. W. Fattig) 6 ♂, 6 ♀ OLC, HFH, UMMZ; April 11, 1940 (P. W. Fattig) 1 ♂ HFH; May 9, 1940 (P. W. Fattig) 1 ♂ HFH; April 22, 1940 (W. H. Thames, Jr.) 1 ♀ HFH; *Dooley County*: U.S. Highway 41 at Pennahatchee Creek, 2 miles north of Vienna, July 24, 1930 (H. Spieth, Field Cat. No. 32) 1 ♂ UMMZ; *Liberty County*: Hinesville, July 9, 1941 (J. G. Watts) 1 ♂ OLC.

FLORIDA: *Leon County*: North of U.S. Highway 90, 6.5 miles east of Tallahassee, Sept. 10-12, 1929 (T. H. Hubbell, Field Cat. No. 80) 5 ♂, 2 ♀ (including type, allotype) UMMZ; Tallahassee, June 10, 1922 (J. S. Alexander) 1 ♂ UMMZ; April 24, 1930, 1 ♀ UMMZ; *Duval County*: Jacksonville, May, 1900 (H. Klages Coll., C.M. Acc. 11414) 1 ♂ CM; Atlantic Beach, (Mrs. A. T. Slosson, Acc. 26226) 1 ♂ AMNH; *Dade County*: Miami, April 6, 1919 (H. M. Klages Coll., C.M. Acc. 11414) 1 ♂, 1 ♀ CM; May, 1919 (H. M. Klages Coll., C.M. Acc. 11414) 1 ♂ CM; "FLA.": (Coll. Chas. Schaeffer) 2 ♀ HFH; (F. H. Snow, December) 1 ♀ UK; (3356) 1 ♀ UK; (Carn. Mus. Acc. 349) 1 ♀ CM.

LOCALITY UNCERTAIN: "Comfort, Texas" (H. M. Klages Coll., C.M. Acc. 11414) 1 ♂ CM [probably mislabeled; not paratype].

Distribution: From the scattered records given above, it is evident that *cartwrighti* has the widest distribution of any of the species of *Mycotrupes*, extending from southwestern Georgia and Tallahassee, Florida, to the Atlantic Coast and southward to Miami. Considering the amount of trapping that has been done in this area, the small number of records probably indicates that colonies of the species are quite localized and perhaps rather sparsely distributed. The known localities for the species fall into two regional groups — southwestern Georgia and adjoining Florida, and along the Atlantic Coast from eastern Georgia to Miami. Blatchley's records of *lethroides* from St. Augustine, and from Enterprise in Volusia County, Florida, are almost surely attributable to *cartwrighti*. If the species does occur in interior peninsular Florida it is probably in the ridge section, where fairly widespread trapping has not brought it to light. The western part of the range of *cartwrighti* lies just north of the territory of *gaugei*, but the two have nowhere been found together. There is no reason to suppose that the species occurs much farther west than the limital

records of Grady County, Georgia, and Leon County, Florida, would indicate; it may well be that the Flint and Apalachicola rivers form the western boundary of its range. The record from "Comfort, Texas" is almost certainly an error.

Habitat: A series of five males and two females (including the type and allotype) was taken 6.5 miles east of Tallahassee, in eight molasses traps left for two nights in the margins of a mesophytic hardwood forest ("hammock") on a slope in the Tallahassee Red Hills district. The soil was a sandy loam of the Orangeburg series, with about 16 inches of loamy sand over bright red friable sandy clay. The forest was composed of black and white oak, hickory, sassafras, sweet gum, and scattered loblolly pines, with scanty undergrowth, and the ground surface was covered with a thin leaf litter, somewhat rooted about by hogs. No other habitat data on the species are available, but it seems likely that *cartwrighti* also occurs in more xeric environments with deep sandy soils.

MYCOTRUPES PEDESTER Howden, new species⁶

(Figs. 26, 32, 45, 50, 57, 58)

Type: Male, Punta Gorda, Charlotte County, Florida, Dec. 15-31, 1939 (H. Ramstadt); *allotype* a female from the same locality, April, 1951; both in UMMZ.

Diagnosis: Very similar to *M. cartwrighti*, from which it differs in the characters given in the key and as follows: male with clypeal horn less tall, more compressed and a little more inclined with caudal face slightly overhanging; halves of frontoclypeal suture distinctly more sinuate; area of pronotal excavation at maximum distinctly smaller than that of head; mesal margin of ventrodextral process of phallic theca nearly straight instead of concave, the apical spine directed dorsocaudad or slightly laterad instead of mesad; size in both sexes averaging less than in *cartwrighti*. From the remaining species *pedester* differs in much the same ways as does *cartwrighti*.

Description of male type: Size large and secondary sexual characters well developed for the species; body length \pm 15.0 mm., breadth of pronotum 9.6 mm. Dorsum bronze-black when dry, when wet distinctly metallic, bronzed with a suggestion of violaceous on tegmina and of green-bronze on anterior parts of pronotum; the legs and venter slightly paler than dorsum. *Head* (Figs. 45, 50): Length from clypeal margin to occipital plica 2.85 mm., breadth across canthi 4.3 mm., distance from anterior angle of eye to outermost point of canthus 0.7 mm., to lateral angle of clypeus 0.75 mm. Clypeus 2.8 mm. broad, 1.9 mm. long, its anterior margin weakly convex, becoming much more strongly so at sides, distance

⁶The description of this species, supplied by Howden, has been recast in the same form as the others.

from midpoint to line drawn between lateral angles 0.8 mm; frontoclypeal suture with its halves considerably sinuate, near caudal apex convergent at about a right angle and meeting in a narrow curve back of horn. Clypeal horn prominent but smaller and less erect than in *cartwrighti*, considerably compressed, bluntly rounded at tip, rising from a somewhat less extensive sloping base than does that of *cartwrighti*, the clypeal surface between base and rim more widely and deeply concave; tip of horn in side view rising 1.0 mm. above clypeal-occipital plane. Antennal scape more gradually and considerably less enlarged distad than in *cartwrighti*, that of each antenna with one large and two small setae on dorsal surface of distal half. *Pronotum* (Fig. 57): Tumid and strongly convex, like that of *cartwrighti* except as described in key and as follows: anterior angles more rounded and less explanate; mesocephalic impression shallower, its margins ill-defined cephalad, so that the excavate area appears widely open in front, its posterior margin delimited by a polished crest forming a very wide V and shallowly notched mesad by a faint groove that fades out about halfway down caudal slope of pronotum; the polished areas of crest briefly prolonged caudad on either side of groove, so that their outline suggests that of a butterfly's wings. Cephalomedian tubercle a very low, weakly defined callus, narrow, anteriorly acuminate and posteriorly bilobate, attingent to cephalic margin and its caudal end 0.7 mm. from edge of pronotum. *Legs*: As described for *cartwrighti*, except fore tibia and its setigerous groove slightly narrower; subdistal fossorial carina (Fig. 32) of both hind tibiae with four bristles on inner end and four (left) and five (right) on outer end, none in center. *Elytra*: As in *cartwrighti*, except apices minutely rounded, forming a tiny notch at junction. *Phallus*: Differing from that of *cartwrighti* as noted in key and diagnosis, and as follows: Left gonostylus with basal portion distinctly transverse, the proximal margin nearly straight, the distal portion more triangular and with more narrowly rounded tip, the inner margin concave-oblique.

Description of female allotype: Slightly smaller than male, of average size for the species; body length ± 12.2 mm., breadth of pronotum 8.2 mm. Like the male of *pedester* and the female of *cartwrighti* except as follows: *Clypeus* as in *cartwrighti*, except cephalic margin much more strongly convex at sides than mesad and a little more broadly reflexed; tubercle lower, less well defined, its surface less polished; frontoclypeal suture less sinuate than in male but more so than in female *cartwrighti*, curving distinctly inward from clypeal angles to about distal third, thence by a slight angulation becoming straight and convergent at an angle of 110° to the blunt-angulate apex. *Pronotum* (Fig. 58) with anterior angles as in male; cephalomedian tubercle as described in key, unlike that of *cartwrighti* females in being anteriorly narrowed and posteriorly weakly bilobate; cephalomesal impressed area very small and with indefinite margins, ± 1.2 mm. broad and long, otherwise resembling that of female *cartwrighti* and differing from male *pedester* as does that of female from that of male *cartwrighti*.

TABLE I
MEASUREMENTS AND RATIOS OF LARGEST AND SMALLEST SPECIMENS

	Male		Female	
	Largest	Smallest	Largest	Smallest
Length of pronotum, mm.				
<i>gaigei</i>	5.8	3.3	5.6	3.9
<i>cartwrighti</i>	7.1	5.4	6.6	5.0
<i>pedester</i>	6.1	4.7	5.7	4.3
<i>retusus</i>	6.2	4.1	6.4	4.4
<i>lethroides</i>	7.7	7.1	7.8	6.7
Breadth of pronotum, mm.				
<i>gaigei</i>	9.5	5.4	9.4	6.5
<i>cartwrighti</i>	11.9	9.1	11.3	8.7
<i>pedester</i>	9.6	7.9	9.3	7.3
<i>retusus</i>	10.5	7.0	10.8	7.5
<i>lethroides</i>	12.4	11.6	13.3	11.2
Length of elytra, mm.				
<i>gaigei</i>	8.4	5.3	8.9	6.4
<i>cartwrighti</i>	10.8	8.8	10.9	8.2
<i>pedester</i>	9.0	7.3	8.9	7.4
<i>retusus</i>	9.5	7.1	10.6	7.3
<i>lethroides</i>	11.1	10.0	11.9	10.0
Length of fore tibia, mm.				
<i>gaigei</i>	5.1	3.1	5.1	3.5
<i>cartwrighti</i>	5.8	4.9	5.9	4.8
<i>pedester</i>	5.5	4.3	5.2	4.3
<i>retusus</i>	5.2	3.9	6.0	4.1
<i>lethroides</i>	6.3	6.2	7.0	6.2
Length of clypeus, mm.				
<i>gaigei</i>	1.8	1.05	1.9	1.2
<i>cartwrighti</i>	2.1	1.8	2.1	1.7
<i>pedester</i>	1.9	1.5	1.6	1.4
<i>retusus</i>	2.1	1.6	2.4	1.6
<i>lethroides</i>	2.2	1.8	2.4	1.9

Breadth/length of pronotum - varying from 1.6 to 1.7 in all species.

Dimensions: Averaging smaller than *cartwrighti* but larger than *gaigei* (see Table I). Additional measurements of the type and allo-type, in that order and in millimeters, are as follows: Breadth between pronotal angles 4.9, 4.5; depth of emargination between these angles 1.5, 1.4; length of pronotum between anterior and posterior angles 6.1, 4.8; caudal breadth of pronotum between angles 8.3, 7.3; length of pronotal excavation from anterior margin (along slope) ± 3.0 , ± 1.2 ; width of this excavation ± 3.8 , ± 1.2 ; maximum breadth across elytra 9.6, 8.4; length of elytra from line between humeri to apex 9.0, 8.2; breadth/length of exposed part of scutellum, both specimens $\pm 1.4/\pm 0.7$; length of leg segments: fore tibia 5.5, 4.6; fore tarsus 2.4, 2.2; middle tibia 4.1, 3.8; middle tarsus 3.3, 2.6; hind tibia 5.7, 4.9; hind tarsus 3.4, 2.9; fore, middle, and hind tarsal claws, male 0.65, 0.85, 0.85; female 0.55, 0.70, 0.70; male, phallic theca, length 2.6, breadth 1.05.

TABLE I (Cont.)
MEASUREMENTS AND RATIOS OF LARGEST AND SMALLEST SPECIMENS

	Male		Female	
	Largest	Smallest	Largest	Smallest
Breadth of clypeus, mm.				
<i>gaigei</i>	2.7	1.5	2.8	1.9
<i>cartwrighti</i>	3.3	2.4	2.9	2.6
<i>pedester</i>	2.8	2.3	2.6	2.1
<i>retusus</i>	2.8	1.8	2.9	2.0
<i>lethroides</i>	3.4	3.1	3.5	3.0
Length pronotal excavation, mm., approx.				
<i>gaigei</i>	2.8	1.2	1.9	1.4
<i>cartwrighti</i>	4.3	2.2	2.7	1.3
<i>pedester</i>	3.0	2.0	2.1	1.1
<i>retusus</i>	3.1	1.2	1.3	---
<i>lethroides</i>	5.0	4.6	4.6	3.3
Breadth pronotal excavation, mm., approx.				
<i>gaigei</i>	3.3	1.4	1.9	1.3
<i>cartwrighti</i>	5.7	2.6	2.6	1.1
<i>pedester</i>	3.8	2.8	1.9	1.1
<i>retusus</i>	3.3	1.4	0.9	---
<i>lethroides</i>	6.0	5.5	4.6	3.3
Breadth/length of clypeus				
<i>gaigei</i>	1.50	1.43	1.47	1.58
<i>cartwrighti</i>	1.57	1.33	1.38	1.53
<i>pedester</i>	1.47	1.53	1.62	1.50
<i>retusus</i>	1.33	1.12	1.21	1.25
<i>lethroides</i>	1.55	1.72	1.45	1.58
Breadth/length of excavation				
<i>gaigei</i>	1.18	1.17	1.00	0.93
<i>cartwrighti</i>	1.33	1.18	0.96	0.85
<i>pedester</i>	1.27	1.40	0.90	1.00
<i>retusus</i>	1.06	1.17	0.69	----
<i>lethroides</i>	1.20	1.20	1.00	0.97

Variation: The small series studied is remarkably uniform in nearly all respects. Besides the type, only one other male shows any trace of the cephalomedian tubercle, which in this specimen is shorter but a little more elevated, separated from the cephalic margination, and only slightly broadened caudad. In the females this tubercle varies in outline from an exaggerated heart-shape to nearly circular, but is always constricted at its junction with the margination. The antennal scape is distinctly less tumid distad than in *cartwrighti*, and its dorsal setae are not so often disposed so as to leave a bare space between them and the apical fringe; the number of such setae varies as follows (notation as in *cartwrighti*): Males 1:2, 2:8; 3:8; 4:1; females 1:4, 2:4, 3:4. The variation in number of bristles on the subdistal fossorial carina of the hind tibia is as follows: Males, range 8-10, mode 9; females 8-11, mode 8.

Specimens examined: 16—11 males, 5 females (type, allotype, and paratypes), as follows:

FLORIDA: *De Soto County*: Arcadia, Oct., 1930 (T. H. Hubbell) 1 ♂ UMMZ; *Charlotte County*: Punta Gorda, Dec. 15-31, 1939 (H. Ramstadt) 1 ♂ (type), 1 ♀ HFH; March 15, 1940 (H. Ramstadt) 1 ♂ HFH; April 6, 1940 (H. Ramstadt) 1 ♀ UMMZ; April, 1951, 3 ♂, 1 ♀ MR, 1 ♂, 1 ♀ (allotype) UMMZ, 1 ♂, 1 ♀ HFH; *Lee County*: Fort Myers, Nov. 4, 1927 (H. E. Stevens) 2 ♂ FAES, UMMZ.

Distribution and habitat: None of the specimens is accompanied by field data; but from what is known of the occurrence of the other species, combined with personal knowledge of the localities from which *pedester* is recorded, we believe that the following prediction will prove correct. The species will probably be found to occur as localized colonies occupying the "scrub islands" that in this region stand isolated in the midst of the prevailing flatwoods, swamps, and marshes. It may also be present on the sandy coastal islands. The range of *Mycotrupes pedester* is separated from the nearest known occurrence of *cartwrighti* (at Miami) by the full breadth of the Everglades. The "scrub islands" of De Soto, Charlotte, and Lee counties, however, represent the "tail" of an archipelago of small and large scrub patches that stretches down the central ridge of the peninsula. Integradation between *pedester* and *cartwrighti* may someday be demonstrated along this chain, or *pedester* may be found to occupy much more of it than it is now known to do, or still other undescribed species may remain to be discovered in isolated segments of the chain.

Mycotrupes retusus (LeConte)

(Figs. 2, 3, 10-12, 24, 30, 33, 46, 51, 59, 60)

- Geotrupes (Mycotrupes) retusus* LeConte, 1866 (in part), *Proc. Acad. Nat. Sci. Philadelphia*, 1866:381 [original description; North Carolina to Louisiana (last certainly in error)]; Horn, 1868, *Trans. Amer. Ent. Soc.*, 1 (Jan., 1868): 314 [additional description]; Blanchard, 1888, *Psyche*, 6 (149-50): 106 [mention].
- Geotrupes retusus* LeConte: Horn, 1880, *Trans. Amer. Ent. Soc.*, 8 (May, 1880): 145 [Characters in key]; Henshaw, 1885, *List Coleoptera Amer. N. Mexico*, p. 89 [listed].
- Thorectes (Mycotrupes) retusus* (LeConte): Boucomont, 1902, *Genera Insectorum* (Wytzman), 7:16 [citation].
- ? *Geotrupes (Thorectes) aeneus* Felsche, 1909, *Deutsch. Ent. Zeitschr.*, 1909:765 [original description; Senegal (in error)]; Felsche, 1910, *Deutsch. Ent. Zeitschr.*, 1910:352 [synonym of *retusus*; not from Senegal].
- Geotrupes (Mycotrupes) lethroides* Boucomont, Feb. 1911 (in part not of Westwood, 1837), *Ann. Soc. ent. France*, 79(3)(1910):349 [*retusus* (erroneously) synonymized, with concurrence of Felsche].
- Geotrupes (Mycotrupes) lethroides* Boucomont, 1912 (in part not of Westwood, 1837), *Coleopterorum Catalogus* (Junk), 46:33 [including *retusus* and *aeneus* as synonyms]; Leng, 1920, *Cat. Coleopt. Amer. N. Mexico*, p. 252 [as last; "So. St., N.C., [not] La., Fla."]; Brimley, 1938, *Insects N. Car.*, p. 202 [N.C.]; Bradley, 1944 (in part), *Bull. Brooklyn Ent. Soc.*, 39:112 [in key; characters insufficiently diagnostic].

Lectotype, here selected: Male, bearing pinkish orange disk probably meaning "S. E. States," Type No. 3264-1 in LeConte Collection, MCZ; *lectallotype*, here selected, a female with similar disk and label "G. *retusus* McLeay," Type No. 3264-2 in same collection.

Although *Mycotrupes retusus*, the generitype, has stood as a synonym of *lethroides* since 1911, the two are actually widely distinct. The type series in the LeConte Collection consists of five specimens, numbered from one to five. Studied by Olson, and subsequently by Hubbell, it was found to contain three species. Specimens one and two are, respectively, a male and a female of *retusus* as here defined and are herewith made the lectotype and lectallotype of the species. Specimen three, a female from "Ga.," is *lethroides*; specimen four, a female labeled "Ga." (almost surely in error) is a worn specimen of *retusus* that can be matched by many of the females from South Carolina; and specimen five, a female from "Fla.," is typical of *cartwrighti*.

In his original description LeConte listed no material, and said of the species only that it occurs "from North Carolina to Louisiana." He was obviously confusing more than one species; aside from the male specimen of *cartwrighti* in the Carnegie Museum labeled "Comfort, Texas" (we think erroneously), there is nothing to suggest that *Mycotrupes* extends west as far as Louisiana, and *retusus* certainly occurs nowhere near that state. All of our own records of this species are from South Carolina, but inasmuch as LeConte specifically mentioned North Carolina in the original description we assume that he saw specimens from there. If so, they were undoubtedly *retusus* and may have been the two specimens without locality labels in the type series that we have selected as type and allotype of the species. LeConte's notebooks give no information concerning them. The known distribution of *retusus* would support the conjecture, but until there is actual evidence that the species occurs in North Carolina it would be premature to select that state as the type locality.

Diagnosis: Small to medium-sized for genus; dorsum evenly and densely granulose; elytra nonstriate but often with basal and lateral marginal corrugations; clypeus narrow, with strongly convex, evenly arcuate to paraboloid margin. Heterogony pronounced. "Strong" males have a rather large clypeal horn and distinctly excavate, tumid pronotum, the horn strongly inclined, the pronotal crest polished, "impunctate," arcuate with narrow and shallow mesal groove; "weak" males have the horn reduced to a small pyramidal tubercle and the pronotal excavation to a small, faintly impressed area without well-defined margins. Spine of ventrodextral apical process of phallic theca with a mesally directed tooth just before its tip, giving the whole spine the look of a long-necked, long-beaked, crested bird. Cephalomedian pronotal tubercle, when indicated at all, present as a small median projection of the cephalic margination, entirely absent in some males and many females. Female with clypeus gently tumid and tectate mesad, caudal part of tectation with a linear callus or faint crest most evident at its termination within caudal angle; pronotal impression very weakly developed as a shallow cephalomedian groove that is longer than wide, or absent.

Mycotrupes retusus differs from *gagei* by the characters given in the key and in the diagnosis of the latter, and from all other species of the genus by the narrower, more convex-margined clypeus, of which the mesal

tumid portion is subtectate, extending forward close to the margin, and the caudal apex is approximately rectangular. *M. lethroides* is the most closely allied species, scarcely separable from *retusus* on phallic characters, but markedly different in size, clypeal form, shape of horn and pronotal modifications of the male, and large conical cephalomedian pronotal tubercle of the female.

Description of male (specimen from Aiken, S. C., similar to but slightly larger than lectotype): Size large and heterogonic features maximally developed; body length ± 15.2 (lectotype ± 14.0) mm., pronotal breadth 9.9 (lectotype 8.0) mm. Entire surface black when dry; when wet the dorsum bronzy purplish black, shading to steely blue-black in places along margins, the venter and legs metallic greenish black to blue-black. *Head* (Figs. 2, 3, 46, 51): Length from clypeal margin to occipital plica 2.8 (lectotype 2.7) mm., breadth across canthi 4.3 (lectotype 4.2) mm., distance from anterior angle of eye to outermost point of canthus 0.75 mm., to lateral angle of clypeus 0.70 mm. Clypeus 2.75 mm. broad, 2.1 mm. long, its anterior margin an arc of approximately 90° of a circle, distance from midpoint to line drawn between lateral angles 0.85 mm., halves of frontoclypeal suture briefly incurved from ends, thence concave-convergent at about 90° to a point opposite horn axis, thence rounding base of horn in a paraboloid subangulate junction. Clypeal horn compressed-conical, axis straight and inclined caudad, back face vertical, tip rising 0.85 mm. above clypeal-occipital plane, front face strongly inclined, concave, merging at base with central tectate elevation that extends nearly to anterior margin; surface of clypeus narrowly impressed between this tumid central area and margin, more broadly so on either side of central elevation; front margin of clypeus narrowly reflexed throughout, a little depressed mesad and raised between center and lateral angles. Antennal scape gradually enlarged distad, in both antennae with 7 irregularly scattered dorsal setae. *Pronotum* (Figs. 2, 3, 59): As described for *cartwrighti*, except as follows: excavation shallow, broader than long (± 3.5 by ± 2.8 mm.), its area distinctly less than that of head, its floor concave with its halves forming a faint V along midline, its margins gently convex and indefinite anteriorly, posteriorly forming a tumid, polished arcuate crest, narrowly and shallowly grooved mesad where the halves of crest approach one another at a slight angle, polished areas "impunctate" (but minute punctae visible at 60x magnification); caudal slope of pronotum with very faint median impressed line; cephalomedian pronotal tubercle represented only by a minute rounded mesal projection from the cephalic margination, the latter more than usually broad along the occiput. *Legs*: Fore tibia (Fig. 24) narrow, its distal breadth (exclusive of teeth) 0.14 times its length; dorsal setigerous groove narrow, at broadest point (opposite base of subdistal tooth) 0.25 mm. wide; impressed areas at base of subdistal tooth narrow. Fossorial carinae on hind (Fig. 33) and middle tibiae as in *cartwrighti*; subdistal carina of hind tibia with 10 (left) and 11 (right) bristles of which 6 are on outer, 4 on inner lobes, and 1 (right tibia) in middle of carina. Hind trochanter narrowly rounded at tip. *Elytra*: Densely and evenly granulose, without evident striae, but with short wrinkles or rugulae along and at right angles to margins between scutellum and humeri and on

proximal half of side margins above lateral carinae; elytral apices meeting in a small but distinct notch, as in *pedester*. *Phallus* (Figs. 10-12): As described in key and diagnosis, differing from that of *lethroides* only slightly in form of gonostyli and less prolonged mesal tooth of thecal spine.

Description of female (specimen from Windsor, S. C., almost identical in size and form with lectallotype): Large for the species; body length ± 16.2 mm., pronotal breadth 10.0 mm. Like the male except as follows: Clypeus with central portion tumid and weakly tectate from within caudal angle nearly to front margin, a narrow linear callus extending along crest from weakly indicated subconical apex in caudal angle to a line drawn between the lateral clypeal angles; clypeal margin very narrowly reflexed; frontoclypeal suture as in male except caudal apex abruptly rectangulate. Pronotum (Fig. 60) lower, much less convex than in male; surface with a shallow median groove ± 1.0 mm. wide, extending from near fore margin nearly to summit and thence continued as a faint impressed line almost to hind margin; with two pairs of lateral impressions — the usual lateral foveolae, and an additional pair of small, shallow impressions situated at about the anterior third of pronotal length and about midway between center and sides; cephalomedian tubercle barely indicated as a small triangular projection from the heavy cephalic margination.

Dimensions: This species averages larger than *gaigei*, about the same size as *pedester*, and smaller than *cartwrighti* and *lethroides* (see Table I). Additional measurements of the described male and female are given here in that order and in millimeters, with those of the σ lectotype and ρ allotype added in parentheses when known: Breadth between anterior pronotal angles 5.0, (5.0), 5.2 (5.4); depth of emargination between these angles 1.4, 1.5; length of pronotum between anterior and posterior angles 6.0 (5.5), 6.0 (6.0); caudal breadth of pronotum between angles 7.5 (7.0), 8.8 (8.5); length of pronotal excavation from anterior margin (along slope) ± 2.8 , ± 2.4 ; width of this excavation ± 3.5 , ± 1.0 ; maximum breadth across elytra 9.6 (9.8), 10.3 (10.0); length of elytra from line between scutelli to apex 9.2 (9.5), 10.0 (10.0); breadth/length of exposed part of scutellum, both specimens $\pm 1.6/\pm 0.9$; length of leg segments: fore tibia 5.5, 5.3; fore tarsus 3.0, 2.5; middle tibia 4.4, 4.6; middle tarsus 3.5, 3.9; hind tibia 5.4, 5.9; hind tarsus 4.0, 4.2; fore, middle, and hind tarsal claws, male 0.65, 0.88, 0.88; female 0.68, 0.85, 0.90; male, phallic theca, length 2.8, breadth 1.1.

Variation: The series of *retusus* studied, though much smaller than that of *gaigei*, shows a comparably great range in size and in development of the male secondary sex characters. Most of the specimens are like those described above, of medium or large size for the species, but there is a complete gradation down to very small individuals (Fig. 2) of quite different appearance. The smallest male seen (from White Pond, S. C.) and the smallest female (from Aiken, S. C.) have the following measurements: length of body ± 10.2 , ± 10.4 ; of pronotum 3.7, 4.1; of elytra 6.0, 6.8; pronotal breadth 6.6, 7.1. The male closely resembles a small female. Its "horn" is a low compressed nodule like that on the clypeus of the average female; the pronotum is low, with evenly granulose surface, no trace of crests, and even less indication of the cephalomesal excavate area than

in most females. The smallest female differs much less from average females in clypeal and pronotal characters than does the smallest male from the larger members of its sex. Neither specimen shows any trace of the accessory foveolae present on the pronotum of an occasional large individual such as the lectallotype and described female.

The cephalomedian pronotal tubercle is very poorly developed in both sexes of *retusus*. In the males studied it is more or less indicated in 29 and absent in 7 (of which 4 are from Windsor, S. C.); in the females it is just appreciably present in 14 and absent in 19. When present it is invariably a median projection of the cephalic margination, not at all higher than the margination itself, and seldom projecting more, usually less, than the width of the margination. In the males it varies in outline from linear through rounded to triangular, or it has an irregular shape; in the female it is usually a tiny rounded or angulate excrescence of the edge of the margination.

The dorsal setae of the antennal scape range in number from 2 to 7, with a mode of 3; they are sometimes grouped near the middle and sometimes scattered along the distal half. The fossorial bristles of the subdistal carina of the hind tibia vary in number as follows: male, range 5-10, mode 8; female, range 7-11, mode 8; 0, 1, or 2 commonly present on middle part of carina.

Specimens examined: 71—38 males, 33 females (including lectotype and lectallotype), as follows:

? NORTH CAROLINA: As suggested above, the lectotype and lectallotype, although without locality labels, may have been from this state.

SOUTH CAROLINA (all OLC except as noted): *Kershaw County*: Blaney, Sept. 26, 1930 (Hubbell, Field Cat. No. 31) 1 ♂ UMMZ; Oct. 13, 1936 (Cartwright) 2 ♂, 1 ♀; *Richland County*: Columbia (all Cartwright) March 3, 1932, 2 ♂, 3 ♀; March 21, 1932, 3 ♂, 1 ♀; Oct. 25, 1932, 1 ♂, 2 ♀; Oct. 29, 1932, 3 ♂ [UMMZ, HFH each 1♂, 1♀]; *Lexington County*: Murray, Oct. 13, 1936 (Cartwright) 3 ♀; *Aiken County*: Windsor, Nov. 25, 1933 (Cartwright) 9 ♂, 6 ♀ [UMMZ, HFH each 1 ♂, 1 ♀]; White Pond (J. E. Webb), Nov. 4, 1932, 2 ♂, 1 ♀; Nov. 15, 1932, 1 ♂ (found dead); Dec. 14, 1932, 1 ♂; (J. G. Watts) Apr. 28, 1934, 1 ♀; (Cartwright) Jan. 1934, 3 ♂, 3 ♀ [UMMZ, HFH each 1 ♂, 1 ♀]; March 30, 1935 (Cartwright) 1 ♂ UMMZ; Sept. 7, 1951 (Howden) 1 ♂, 1 ♀ HFH; 2.3 miles north of Aiken, Mar. 26, 1953 (Howden and Dozier) 5 ♂, 9 ♀ HFH (except 1 ♀ UMMZ); (same date and collectors) 12.9 miles north of Aiken, 1 ♂ HFH; Picnic Area 17.5 miles north of Aiken, 1 ♀ UMMZ.

Synonymy: Although *Geotrupes (Thorectes) aeneus* Felsche, 1909, was placed as a synonym of *retusus* LeConte by its author in 1910, on the advice of G. Jacobsohn, this was solely on the basis of LeConte's description, and may not have been correct. The type of *aeneus*, erroneously labeled "Senegal," is from an unknown locality, and since neither LeConte's nor Felsche's descriptions are sufficiently diagnostic, only type examination can fix the status of this name. It may take precedence over one of those proposed in this paper.

Distribution: The known occurrences of *Mycotrupes retusus* all lie within the physiographic division of South Carolina designated by Cooke (1936) as the Congaree Sand Hills, except those from Aiken County, which are in the Aiken Plateau. Together these two regions stretch diagonally across the state along the inner edge of the Coastal Plain, where it abuts upon the Piedmont Plateau. They lie just inland from the highest of the coastal terraces, the Brandywine. The sand hills, though composed of residual materials from sandy Cretaceous and Eocene beds, are apparently ancient coastal dunes left stranded by withdrawal of the sea. The Congaree belt extends into North Carolina as far as More, Hoke, and Cumberland counties, and it is this continuity of environment that supports our conjecture that the types of *retusus* actually came from that state.

Habitat: The few field observations that have been recorded on the occurrence of *retusus* suggest that it is restricted to situations with deep sandy soils such as characterize the Congaree Sand Hills and parts of the Aiken Plateau. At Blaney, in the first-named region, Hubbell trapped a single male in an open stand of turkey, blackjack, and white oaks with scattered yellow pines, on the top of a sand hill 1.7 miles southwest of town on U.S. Highway No. 1. Here the soil was coarse yellow sand to a depth of several feet, the surface layer bleached white. At the Webb farm near White Pond on the Aiken Plateau, Cartwright found the species abundant in longleaf pine forests on deep sand, as Howden mentions below in his account of his own observations.

Habits and life history: See the notes by Howden in Part III.

Mycotrupes lethroides (Westwood)

(Figs. 1, 4, 16-18, 21-23, 31, 44, 47, 52, 64)

Geotrupes lethroides Westwood, 1837, *Mag. Zool. Bot.*, 1:256-57, Pl. VII, Fig. 5 [♂ - "Habitat in America Meridionali"].

Type: Male, as cited above; in Hope Museum, Oxford University.

It is surprising to find that this, the largest and most striking of the species of *Mycotrupes*, has gone unrecognized since its description one hundred and seventeen years ago. No author since Westwood has used the name correctly save in citing the original reference, and not until 1930 was the species again collected. We have already expressed our indebtedness to Dr. van Emden for comparing our specimens with Westwood's type and thus making the identification certain.

Type locality: Westwood's statement, "Habitat in America Meridionali" [South America], was evidently responsible for the failure of authors to recognize the affinities of *lethroides* and *retusus*, until in 1911 Boucomont was struck by their similarity and concluded that they must be the same. He wrote that the indication of locality given by Westwood was certainly false and should read "Southern States of North America." When our studies suggested that *lethroides* and *retusus* were probably not identical and this was verified by Dr. van Emden, we were still uncertain as to

which of the remaining species was that described by Westwood. We inclined toward *cartwrighti*, as having the widest range, occurring along the coast, and being most likely to have been collected by some early traveler or ship's officer. So much for guesswork; by a second comparison with the type Dr. van Emden fixed the name *lethroides* upon the present species, which is known only from the vicinity of Augusta, Georgia. Not until then did we remember John Abbot of Georgia. This famous but little known early naturalist, entomological artist, and collector⁷ spent most of his life in Burke, "Scriven" [Screven], and Bulloch counties, although he also lived at Savannah. About 1775 he spent some time on a plantation 30 miles south of Augusta, in Burke County; in 1814 he wrote to George Ord from his new residence at Jacksonburg in "Scriven" County, where he apparently stayed for some years.⁸ About this time he turned from ornithology almost exclusively to entomology and began to make the insect drawings from which he is best known and to send collections of insects to Europe, to be sold through dealers, in particular John Francillon of London.

Westwood described *Geotrupes lethroides* from the collection of Sir Patrick Walker in 1837; Abbot was sending insects from the part of Georgia where the species occurs in the years from 1814 on. The only conclusion possible seemed to be that the type was one of Abbot's specimens, probably purchased by Walker through Francillon. We wrote to Dr. van Emden expressing this opinion and asking whether any verification could be found. In reply he said: "I think your assumption that the type was collected by John Abbot is extremely probable, for the following reasons: The British Museum has two specimens of the same species with the following labels: (specimen a) 5506a, figured in Abbot's drawings of Georgian Insects. (no other label); (specimen b) 5506a. 'Lethroides Westw. Georgia, see Abbot's drawings, 5506.' The underlined words are a later addition in pencil. The British Museum accession number is missing, but as far as I can make out the number 5506a can only refer to an entry '*Geotrupes* ? 5506a,' the question mark standing for the unknown species. This material has the accession number (18) 39-18 and 39-19, and the specimens were 'bought at the sale of the late Mr. Milne.' According to Horn (*Ent. Beih.*, 3:177) a collection G. Milne was sold in 1839, and some of the Coleoptera went to the British Museum. Horn also states (l.c. 4:313) that Abbot's material was dispersed by dealers, e.g. Francillon, whose material went (l.c. 3:80) partly to the British Museum, partly to the Hope Museum, Oxford."

The type locality may therefore be given with some certainty as "east central Georgia," where Abbot's work was principally done, and the specimens here recorded from Augusta may be considered as topotypic.

⁷The most useful accounts we have found of Abbot's life and work are the following: S. H. Scudder, *The Butterflies of the Eastern United States and Canada* (Cambridge, 1889), Vol. I, Excursus XX, pp. 651-54; and Mrs. E. G. Allen, "History of American Ornithology before Audubon," *Trans. Amer. Phil. Soc.*, (n.s.) 41(3)(1951): 386-591. Chapter on "John Abbot of Georgia (1751-1840?)," pp. 543-49.

⁸Under the name Jacksonborough, "county seat of Scriven County, on Brier Creek," this town is still listed in a Gazetteer of 1853 as having 150 inhabitants; it had disappeared before 1880.

Diagnosis: This species, by far the largest and most robust of the genus, is unique in that the female pronotum is almost as strikingly modified as that of the male and equally diagnostic. Dorsum densely and evenly granulose; elytra without evident striae, but margins wrinkled as in *retusus*; clypeus broad, anterior margin much less strongly convex mesad than at sides, caudal apex obtuseangulate. Male with clypeal horn very tall, erect, almost circular in cross section; pronotal excavation very extensive, planate, far larger than head and reaching back of midlength of pronotum, bordered caudolaterad by a pair of polished crests, these somewhat gibbous and arcuate-convergent, but separated mesad by a broadly rounded trough; cephalomedian tubercle a short, compressed, longitudinal ridge with crest rising to a point at midlength; phallic characters like those of *retusus*. Female with somewhat reduced counterpart of the male pronotal excavation and bounding crests; cephalomedian tubercle distinctive, very large, rising from edge of pronotum as a heavy, conical, pointed tubercle that involves the whole of the margination; clypeus with central portion tumid, bearing a very low, broadly conical tubercle in caudal angle. *Lethroides* is closest to *retusus* in genital characters, though more like *cartwrighti* in appearance.

Description of male specimen (Augusta, Ga.): The specimen chosen for description is not that compared with Westwood's type by van Emden, but one which, according to van Emden's notes, is more nearly like the type in having maximal development of the heterogonic features. Size very large, form robust; body length ± 18.6 (of type ± 20.0), pronotal breadth 12.4 mm. Coloration distinctive; dorsum of head and thorax bronzy black and elytra, venter, and legs dark reddish brown when dry; when wet head, excavation and back slope of pronotum bronze-black, sides of pronotum more coppery, crests of pronotum black, elytra deep coppery red, or red-brown approximating but darker than Ridgway's Hematite Red. *Head* (Figs. 4, 47, 52): Length from clypeal margin to occipital plica 3.35 mm., breadth across canthi 5.2 mm., distance from anterior angle of eye to outermost point of canthus 0.9 mm., to lateral angle of clypeus 0.9 mm. Clypeus 3.35 mm. broad, 2.15 mm. long, its anterior margin very weakly convex except at sides, where it is strongly so, distance from midpoint of margin to line drawn between clypeal angles 1.0 mm., halves of frontoclypeal suture very weakly curved at ends and thence straight-convergent at an angle of 107° to the narrowly rounded caudal apex. Clypeal horn tall, cylindrical with bluntly rounded tip rising 1.5 mm. above clypeal-occipital plane, its axis curved slightly caudad, back face gently concave, front face a little convex, horn rising rather abruptly and subvertically from an almost circular low conical base which does not project far forward, so that clypeal surface is almost as broadly excavate in front of horn as at sides; clypeal margin a little depressed mesad, narrowly reflexed. Antennal scape gradually enlarged distad, that of each antenna with 4 dorsal setae in distal half. *Pronotum* (Figs. 4, 61): As described in diagnosis; excavation very large, slightly broader than long (± 6.0 by ± 5.0 mm.), floor planate rather than concave, side margins gently convex and indefinite anteriorly, bounded by a pair of tumid crests caudolaterad, these crests convergent caudad at an angle of 75° but separated mesad by a broad, deep,

rounded groove continuous with floor of excavation, crests highest caudad and their summits separated by ± 4.0 mm.; caudal slope of pronotum very abruptly convex-declivent, with a faintly indicated median impressed line; cephalomedian tubercle as described in diagnosis, much larger and more elevated than in any of the other species. *Legs*: Fore tibia (Figs. 21, 23) broad, its distal breadth exclusive of teeth 0.20 times its length; dorsal setigerous groove wide, maximum breadth 0.5 mm. at base of subdistal tooth, at that point with some setae scattered over the impressed area in addition to those along its mesal margin; impressed areas at base of subdistal tooth broad. Fossorial carinae on hind (Fig. 31) and middle tibiae as in *cartwrighti* and *retusus* but ends of carinae less lobate; subdistal carinae of both hind tibiae with four fossorial bristles on outer end, three on inner end, and two more widely spaced in center of carina. Hind trochanter (Fig. 64) bluntly acuteangulate at tip, its margin with numerous small setae in distal half. *Elytra*: As described for *retusus*. *Phallus* (Figs. 16-18): As described in key, differing from that of *retusus* only slightly, in form of gonostyli and longer mesal tooth of thecal spine.

Description of female specimen (plesiallotype, Augusta, Ga.): Large for the species, with maximum development of pronotal modifications; body length ± 19.8 mm., pronotal breadth 13.3 mm. Like the male except as follows: Clypeus with tumid mesal area extending farther forward than in male but not tectate, clypeal nodule a very low, broadly conical eminence in caudal angle, its tip polished. Pronotum showing a reduced counterpart of the male modifications, closely resembling in size and form of excavation and bounding crests well-developed males of *retusus* or *cartwrighti*; floor of excavation concave and weakly grooved mesad, in area about equal to that of head, margins broadly rounded cephalad but caudad forming an arcuate crest about as strongly grooved mesad as in *cartwrighti*, summit of crest smooth and polished as in male, with a few minute punctae along its sides. Cephalomedian tubercle (Fig. 62) uniquely developed, rising from cephalic margin as a tall, heavy conical point as prominent as the clypeal horn of moderately developed males of *retusus* and *gaugei*.

Dimensions: This is much the largest species of the genus, though individuals considerably smaller than those known probably exist (see Table I). Additional measurements of the described male and female, in that order and in millimeters, are as follows: Breadth between anterior pronotal angles 5.7, 6.5; depth of emargination between these angles 1.8, 1.9; length of pronotum between anterior and posterior angles 7.7, 7.8; caudal breadth of pronotum between angles 10.8, 11.6; length of pronotal excavation from anterior margin (along slope) ± 5.0 , ± 4.6 ; width of this excavation ± 6.0 , ± 4.6 ; maximum breadth across elytra 12.4, 13.6; length of elytra from line between humeri to apex 11.1, 11.9; breadth of exposed part of scutellum 2.1, 2.5; length of scutellum 1.0, 1.15; length of leg segments: fore tibia 6.3, 7.0; fore tarsus 3.85, 3.85; middle tibia 4.7, 5.5; middle tarsus 4.1, 4.4; hind tibia 6.5, 7.4; hind tarsus 4.3, 4.5; fore, middle, and hind tarsal claws, male 0.75, 1.0, 1.1; female 0.7, 1.0, 1.0; male, phallic theca, length 3.8, breadth 1.4.

Variation: The six males and five females which we have studied are all from the same locality and all but three from the same colony; they doubtless exhibit only a small part of the variability that occurs in the species. To judge from the development of the heterogonic characters, they represent the size range from medium to large, and smaller individuals with less striking pronotal and head modifications are to be expected. All but one are colored like the described male; the exception is a male taken by Cartwright in March, in which the elytra are bronze-black when dry and coppery instead of red-brown when wet. No two of the males have the pronotal excavation of exactly the same form and extent. In some it is broadly truncate-U-shaped, as in the described male; in others it is more narrowed caudad with the mesal trough dividing the crests narrower, though still broad and deep. It was one of these specimens that was sent to van Emden for comparison with the type, and his notes on the type specimen, given below, should be read with this in mind. Another specimen with the more V-shaped form of excavation has the floor of the excavation tumid where it enters the trough between the crests, leaving shallow grooves on each side that form a V at the foot of the bounding crests. The cephalomedian tubercle is an almost linearly compressed ridge in three specimens, merely compressed-conical in the others. The elytra of the three largest males have conspicuous marginal rugae at the base and sides which are faint in the other specimens, and also show three fairly large but shallow hollowings of the elytral surface just above the lateral carina in the proximal third of the margin. In the females the form and size of the cephalomedian tubercle (Fig. 62) are quite constant, but the excavation and its bounding crests are more strongly developed in the described female than in any of the others. The smallest female has an excavation that is smaller in area than the head, and crests which, though polished and mesally grooved, are only weakly defined.

The dorsal setae of the antennal scape vary from four to nine, with a mode of six, and are distributed along the distal half of the scape without any gap such as in common in *cartwrighti*. The fossorial bristles of the subdistal carina of the caudal tibia vary in number as follows: male, range 9-12, no marked mode; female 9-12, mode 11.

Notes on Westwood's type: Dr. van Emden has furnished the following comparisons between the type of *lethroides* and the specimen sent him, which was one of those with the narrower pronotal excavation. "Horn of head in the type like that of your specimen but somewhat longer and somewhat more compressed at base, *not* reaching as far forward as in *cartwrighti*. Clypeus fore margin more rounded than in your specimen, much as in *cartwrighti*. Tubercle at front margin of pronotum much as in your specimen, but even longer and more compressed, therefore more sharply defined. Prothoracic impression at least as large as in your specimen and reaching quite as far beyond middle, the pair of gibbosities [crests] on disc separated even more broadly and conspicuously, the saddle between them with a pair of very slight impressions, which diverge posteriorly, so that a slight median convexity is formed, which itself is divided by a shallow median furrow. Granules of elytra as in *cartwrighti*, much denser and more clearly defined than in your specimen. Pushing edges of

hind tibiae as in your specimen. The genitalia of the type have unfortunately not been dissected." Dr. van Emden concluded that the two specimens were of the same species, and in this we concur.

Specimens examined: 11—6 males, 5 females (including plesiallotype here described), as follows:

GEORGIA: *Richmond County*: Augusta, Sept. 27, 1930 (Hubbell, Field Cat. Nos. 38, 39) 4 ♂, 4 ♀ UMMZ (including plesiallotype), BMNH, HFH; March 2, 1944 (Cartwright 2 ♂, 1 ♀ OLC.

Distribution: Although as yet *lethroides* is known only from Augusta, it will probably be found to range southwestward in Georgia in the belt called the Fall Line Hills and in the adjoining Louisville Plateau, which respectively are physiographically equivalent to the Congaree Sand Hills and Aiken Plateau of South Carolina and include areas of similar environment. The valley of the Savannah River constitutes a barrier between the range of this species and that of *retusus*.

Habitat: The eight specimens collected by Hubbell were taken in 12 molasses traps left out for eight nights, on a sandy hilltop south of Rocky Creek, a short distance south of Augusta on U.S. Highway No. 1. The hill summit bore an open, scrubby forest of turkey oak and scattered longleaf pines, with openings where there was a sparse growth of grass and herbage and much bare sand, bleached white on top. Beneath the surface the soil was coarse yellow sand to a considerable depth. The environment was very similar to that in which *retusus* was taken in the Congaree Sand Hills at Blaney, South Carolina, and also to the xeric turkey oak habitat of northern Florida.

PART II. THE RELATIONSHIPS AND DISTRIBUTION OF *MYCOTRUPES*

By Theodore H. Hubbell

THE genus *Mycotrupes* is only one example among many of animal groups that are restricted to the southeastern Coastal Plain of North America and that within this region of low relief and widespread environments show striking endemism and localization of their species. Allopatric distribution of closely related but distinct species causes no surprise when it is encountered in archipelagoes or mountain areas, where the geographic or ecological isolation is apparent. In expanses of uniform environment like the Great Plains, on the other hand, most species have extensive ranges and show only clinal or subspecific differences within the area. To find a region where, in small space and relatively uniform environment, many animal groups are represented by a number of very distinct species with mutually exclusive ranges, is a phenomenon that calls for explanation, especially when in this region similar or complementary distributional patterns tend to occur in unrelated species groups.

I have long been interested in the problems posed by these peculiarities of the Coastal Plain fauna, especially as they are manifested in the Orthoptera. The basic cause is evidently to be sought in the history of the region and will be discussed below; but the detailed knowledge of the systematics and distribution of many diverse groups that will be required to work out a general solution is not yet available. The present study of *Mycotrupes* is a contribution to such knowledge, but only a beginning even with respect to this genus. Additional species of *Mycotrupes* may perhaps exist in the Carolinas, central Florida, or Alabama, though it seems unlikely; and we have only fragmentary distributional data on the five species at present known.

In treating of *Mycotrupes*, I shall first discuss its systematic position and relationships and then take up the relation of its species to one another and the significance of their distributional pattern.

SYSTEMATIC POSITION AND RELATIONSHIPS

Mycotrupes is a member of the family Scarabaeidae, subfamily Geotrupinae, tribe Geotrupini. Nearly all authors have followed LeConte in treating it as a subgenus of *Geotrupes* Latreille, 1796; only Boucomont (1902:15) gave it another status, placing it as a subgenus of *Thorectes* Mulsant, 1842, at the same time that he made the latter a full genus instead of a subgenus of *Geotrupes*. In subsequent publications Boucomont returned to the usual treatment. Horn (1868:314) considered *Mycotrupes* to be intermediate between the Old World groups *Chelotrupes* Jekel, 1865, and *Thorectes*. It is interesting to note that Westwood (1837:257), in describing

Geotrupes lethroides, wrote that its characters "seemed to be of higher value than those indicating a species," though he did not venture to make it the type of a new genus.

In the attempt to discover the relationships of *Mycotrupes* I have made detailed comparisons of its species with others representing most of the described genera and subgenera of the Geotrupini. These studies show that there is no close relationship to *Chelotrupes*, to *Thorectes*, or to any of the North American groups of *Geotrupes*, with one possible exception to be noted below. They have also convinced me that the classification of the Geotrupinae currently in use, which we owe to Jekel and to Boucomont, is largely artificial. Howden has expressed the same opinion in correspondence. This classification was originally based upon a few easily observed characters that could be seen without relaxing specimens, not to speak of dissecting them. Even my own studies, of necessity limited since I am not a specialist in this order of insects, have brought to light various apparently significant but unused taxonomic characters in nearly all parts of the body which were examined. Judged by such features, some of the so-called genera and subgenera are evidently heterogeneous, while other "subgenera" of *Geotrupes* are strongly differentiated groups worthy of generic rank, as is *Mycotrupes*. Before a more "natural" classification can be established comparative morphological studies will have to be made on many species, with attention given to the characteristics of both adults and larvae.

Boucomont (1912) listed the genera and subgenera of the Geotrupini as follows (those starred having North American representatives): *Enoplotrupes* Lucas, with subgenera *Enoplotrupes* and *Gynaecoplotrupes* Oberth.; *Ceratophyus* Fisch.; *Ceratotrupes* Jekel; *Typhoeus* Leach, with subgenera *Typhoeus* and *Chelotrupes* Jekel; *Geotrupes** Latreille, with subgenera *Stereopyge* Costa, *Geotrupes*, *Anoplotrupes** Jekel, *Trypocoprpris* Motsch., *Allotrupes* Francois, *Peltotrupes** Blanchard, *Cnemotrupes** Jekel, *Onychotrupes** Jekel, *Phelotrupes* Jekel, *Bootrupes* Bouc., *Thorectes* Mulsant, and *Mycotrupes** Lec. *Peltotrupes* is being raised to generic rank by Howden (in press), and *Mycotrupes* is here accorded the same status.

Mycotrupes has little in common with the first three of the genera listed above. It bears no resemblance to the type species of *Typhoeus*, *typhoeus* (L.), but is superficially somewhat like the generitype of subgenus *Chelotrupes*, which is *T. (C.) momus* (Ol.).¹ Among the groups listed above as subgenera of *Geotrupes*, the one closest in appearance to *Mycotrupes* is *Thorectes*, which today is commonly treated as a genus.

The characteristics shared by *Chelotrupes*, *Thorectes*, and *Mycotrupes* that have led some earlier workers to associate them are as follows: metathoracic wings absent; elytra short and fused; form compact, rotund;

¹*Chelotrupes* does not appear to me to be even subgenerically separable from *Typhoeus* Leach. I have compared specimens of both generitypic species and find that they are more closely allied than is *momus* to *hostius* Gené, the only other species currently placed in *Chelotrupes*. In pronotal modification, mandibular form, and sternal characters *momus* is very close to *typhoeus* (Fig. 36). Although *momus* and *hostius* both differ from *typhoeus* in lacking metathoracic wings and in having connate tegmina, these characteristics have been probably independently acquired by them.

dorsum dull black; middle segment of antennal club unspecialized, its margin uniformly thick and uniformly exposed all around when club is closed. The Old World genus *Lethrus* Scopoli, 1777, with many named subgenera, also has all these features save the last, but it possesses modifications of the antennal club and other characters² so distinctive that it has long been placed in a separate tribe, the Lethrini. The similarities of *Lethrus* to *Mycotrupes*, although striking, are certainly the result of parallel modifications, and so also, I believe, are those of *Mycotrupes* to the less distantly related *Chelotrupes* and *Thorectes*.

Mycotrupes differs from *Chelotrupes*, *Thorectes*, and all other Geotrupini in having a broad, deep notch between the tumid pronotum and the strongly convex elytral bases, as seen from the side. It is also unique in the granulose and almost impunctate dorsum, the aberrant mandibular form, the nature of the secondary sexual specializations of the head and pronotum, and the extent of the emargination of the distal tooth of the male fore tibia. The last feature is, however, foreshadowed in *Thorectes* and some species of *Geotrupes s.l.* *Mycotrupes* also differs markedly from both *Chelotrupes* and *Thorectes*, as well as from all species of *Geotrupes* with which it has been compared, in the structure of the mesosternum (cf. Figs. 37, 38). Bradley (1944) was apparently the first to note the modifications of the mesosternum in the Geotrupini, and he used them in his key to the North American species of *Geotrupes*.

Additional differences of *Mycotrupes* from *Chelotrupes* and *Thorectes* are found in the strongly sinuate caudal margin of the pronotum and in the armature of the middle and hind tibiae. The lack of margination along the hind edge of the pronotum separates *Mycotrupes* from *Chelotrupes* and from the generitype and most species of *Thorectes*; but *Thorectes hoppei* Hagenb. lacks such margination, which is also very weak mesad in some of the other species of the same genus. *Mycotrupes* is unlike *Chelotrupes* in head form and greater convexity of body and unlike *Thorectes* (and some *Geotrupes s.l.*) in that the dorsal setigerous groove of the fore tibia is undivided by the median carina of the subdistal tooth (cf. Figs. 21-28 and discussion of variation in *gaigei*).

With a single observed exception, *Mycotrupes* alone among the Geotrupinae has a ridge on the ventral surface of the caudolateral angle of the pronotum that forms, with the angle, a shallow groove into which fits the humeral carina of the elytron. This coaptation functions as an accessory hinge between the prothorax and the hind part of the body, related to the movements performed in burrowing, and mechanically more efficient than the central hinge between prothorax and mesothorax because the pivot points are far out at the sides.

²Among these are the following: A tendency to macrocephalism and extraordinary mandibular enlargement and modification in the males of some groups; legs slender; abdominal venter extremely reduced. A feature of the Lethrini I have not seen described elsewhere is the strongly granulate surface of the concealed dorsocaudal face of the narrow and unusually transverse hind coxa, and the complete absence from it of a stridulatory ridge. In the tribe Geotrupini this coxal surface is smooth or only weakly granulate, and it always bears an oblique stridulatory ridge somewhere in the second fourth of its length.

The exception just noted is *Geotrupes (Cnemotrupes) ulkei* Blanchard (1888:106), a small black species described from Virginia and recorded from Monte Sano, northern Alabama, by Loding (1935), who discusses its habits. This species also possesses the hinge-groove on the pronotum and has other points of resemblance to *Mycotrupes* along with marked differences. The metathoracic wings are reduced to small stubs (a fact not hitherto recorded); the form is short and rotund, and the antenna and dorsal setigerous groove of the fore tibia are as in *Mycotrupes*. The mesosternum is like that of *Mycotrupes* except that the intercoxal portion bears a strongly elevated compressed point that overhangs the caudal face of the mesofurcal pit. Among the numerous differences between *G. ulkei* and *Mycotrupes* are the following: in the former the dorsum is polished, punctate, and without granulations, the elytra have regular rows of deep punctae, the humeral angles of the elytra are but little expanded, the distal tooth of the fore tibia is undivided in both sexes, and the middle and hind tibiae have four instead of three complete dorsal carinae, the proximal one being only a little less perfectly formed than the others. Lastly, the mandibles of *Geotrupes ulkei* are distinctively specialized. The apex is tridentate, somewhat as in *Mycotrupes*, but with an asymmetric development of the mesoproximal flattened tooth. On the left mandible this tooth is narrow and deeply grooved, while on the right mandible it is broad and shallowly concave above.

Revisionary studies will probably show that *G. ulkei* requires subgeneric or even generic separation from *Geotrupes s.s.* Its points of difference from *Mycotrupes* are so numerous that the resemblances are probably the result of convergent evolution, although it is possible that *ulkei* and *Mycotrupes* are distantly allied. Their principal point of resemblance is the pronotal hinge; only in *Geotrupes egeriei* Germar have I seen even a suggestion of it elsewhere in the Geotrupini.

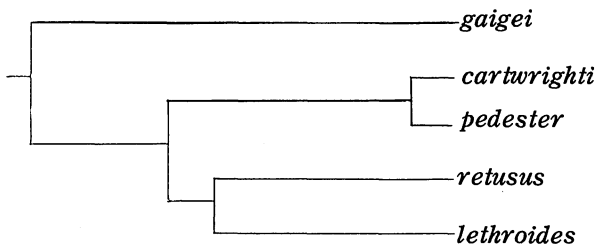
My conclusion from the survey summarized above is that *Mycotrupes* has no existing close relatives, though it was doubtless derived from some form which would today be placed in the genus *Geotrupes s.l.* Its resemblances to Old World groups are to be interpreted as parallelisms, evolved in stocks not closely allied but adapted to similar modes of life. The wide morphological divergence of *Mycotrupes* from other Geotrupini connotes a long independent evolutionary history, and this in connection with the distributional evidence given below leads me to conclude that the genus arose a long time ago in the region which it now occupies and that it was already differentiated and in residence by middle Pliocene times.

RELATIONSHIPS OF THE SPECIES

The five species of *Mycotrupes* are so related that four clear-cut dichotomies can be recognized. The first sets off *gaugei* from the other four species, which may be called the *lethroides* group; the second divides *cartwrighti* and *pedester* from *retusus* and *lethroides*; and the third and fourth separate the species of these two pairs.

In a number of respects *gaigei* seems closer to the hypothetical ancestral condition than do the others. The great majority of Geotrupini have a smooth, punctate dorsum and striate-punctate elytra. In *gaigei* there are distinct punctae on the pronotum and faint but evident striae on the elytra. The dorsum is distinctly nodulose only along the sides of the elytra and pronotum; the higher parts have a confused pattern of tiny rugulae that look as if the nodules had melted together, and a large central part of the pronotum is almost smooth. It is not easy to decide whether this represents a stage in the development of the densely and evenly nodulose surface characteristic of the other species or has been derived from such a surface, but the former seems the more likely. The simple phallic spine of *gaigei* is certainly more primitive than the bird-beaked spine of *retusus* and *lethroides*.

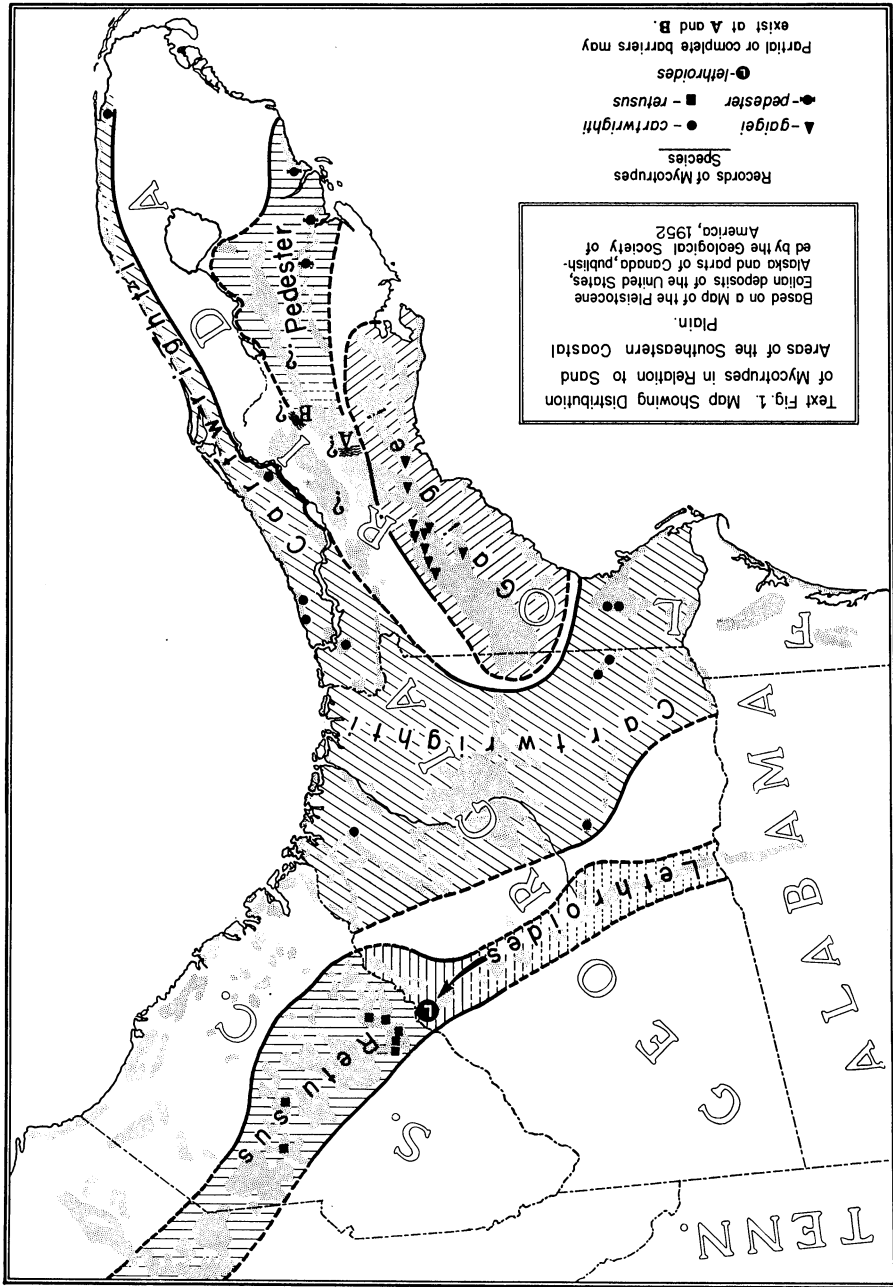
In the *lethroides* group, *cartwrighti* and *pedester* are the more generalized. They have a simple phallic spine not unlike that of *gaigei* and do not show the divergent extremes of modification of the secondary sex characters of head and pronotum found in *retusus* and *lethroides*. *Cartwrighti* and *pedester* are also much more closely related than are any other two members of the genus and are the only ones which may conceivably prove to be subspecies of a single species. *Retusus* and *lethroides* both have the bird-head phallic spine, but in all other respects they are widely different and have obviously been completely isolated for a long time in spite of the proximity of their ranges. In diagram, these conclusions as to relationships may be expressed as follows:



THE PRESENT DISTRIBUTION OF THE SPECIES

All of the species of *Mycotrupes* require deep, well-drained sandy soils in which to construct their five to eight foot vertical burrows. The distribution of such soils in the southeastern Coastal Plain is extensive but patchy, as may be seen on the accompanying map (text Fig. 1).³ All known occurrences of *Mycotrupes* are shown on this map and are seen to coincide

³Based on a map of the Pleistocene eolian deposits of the United States, Alaska, and parts of Canada, published in 1952 by the Geological Society of America. Minor changes and additions have been made from detailed local soil maps and personal observations.



with certain of the sand areas; but a large number of the localities where the beetles may perhaps occur have not yet been searched for them. Except for LeConte's unverified record of *retusus* from North Carolina, the genus seems to occur only in South Carolina, Georgia, and Florida. It would be remarkable if the veteran collector Loding had missed it in Alabama.

The geologists who made the map upon which ours is based classified the sand deposits under three heads: (1) coastal beaches and active dunes; (2) deposits of pure quartz sand, partly eolian, largely stabilized, with undulating surface and some dunes; and (3) deposits of sand in which other minerals are mingled with quartz, water-laid below but wind-worked in the upper part, stabilized, with undulating surface and dune forms. Apart from the beaches and active coastal dunes, all of the deposits of Florida and those of western Georgia and the Fall Line Sand Hills of that state are placed in the second class, while those of southeastern Georgia and all of the South Carolina Coastal Plain belong to the third. *Mycotrupes* respects this classification to the extent of avoiding the beaches and active dunes, but pays no attention to the distinction between the other sand deposits. All that it seems to require of its habitat is that the sand be deep and stabilized by a plant cover which is usually an open forest of pine or turkey oak, or sometimes sand scrub. The upper layers of the sand deposits have developed into a number of different soils, of which the Norfolk sand and Norfolk fine sand are by far the most extensive and widespread. *Mycotrupes* is commonly associated with these soils, but is also known from sands of the Orangeburg and Lakewood series and may perhaps occur in those of the Ruston, Blanton, and St. Lucie series. The soils named are well described by Henderson (1939).

In view of the restriction of *Mycotrupes* to the sand areas, the origin of these is of interest. Although they are spread all the way from the coast to the foot of the Piedmont, there can be no doubt that they are the sands accumulated along and inland from old strand lines of the sea — ancient beaches, dune belts blown up from the beaches by the wind, and offshore deposits laid down under water and later exposed to wind action. Nearly all of them are at least in part of eolian origin, which accounts for their undulating topography; the occasional hills are "fossil" sand dunes.

The highly localized occurrence of colonies of *Mycotrupes* is obviously the result of their ecological requirements and the discontinuous distribution of suitable environments. These factors, however, afford no explanation of the species distribution. Each of the five known species is restricted to a particular part of the Coastal Plain and has exclusive possession of the scattered sand areas within its territory. They also show a peculiar geographic pattern in terms of their relationships. Two allied but very different species, *lethroides* and *retusus*, occur along the innermost edge of the Coastal Plain, one in Georgia and the other in South Carolina, separated only by the Savannah river. Another two still more closely related species, *cartwrighti* and *pedester*, together are spread over most of southern Georgia and peninsular Florida; they almost surround but do not encroach upon the territory of the last species, *gaigei*, which is restricted to western peninsular Florida and is in some respects the most primitive as well as the most aberrant member of the genus.

This is a geographic pattern of the same type as is shown by a number of flightless groups of Orthoptera found in the same region (cf. Hubbell, 1932, 1952), although the distribution of each group differs from that of the others in detail. A common factor capable of explaining the existence of such patterns must be sought, and the nature of that factor seems evident — the changes in the relations of land and sea during the Pleistocene.

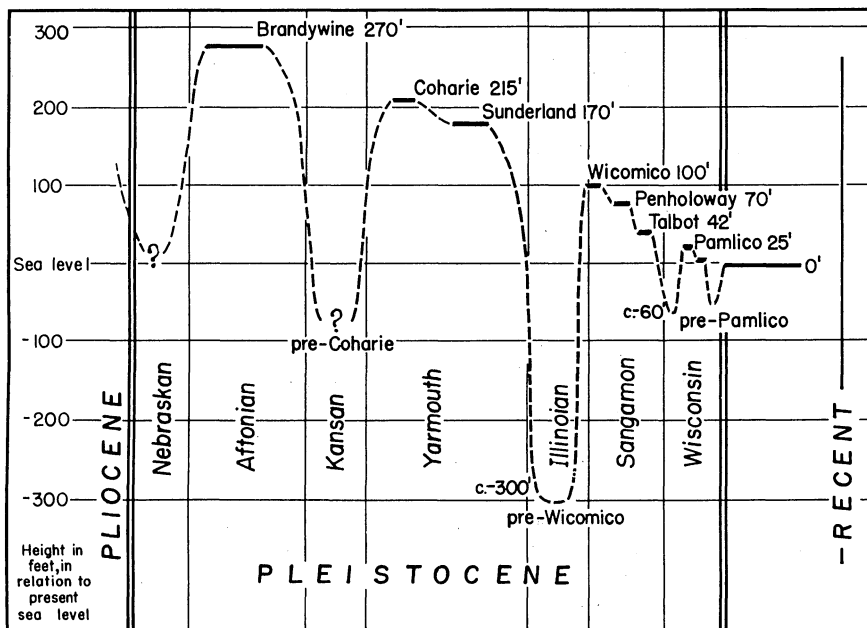
THE POST-PLIOCENE HISTORY OF THE SOUTHEASTERN COASTAL PLAIN

The following brief account is based largely upon the publications of C. Wythe Cooke (1925, 1936, 1945), the leading authority on the geology of the Coastal Plain. He has devoted many years to study of the marine terraces, and our current interpretation of the events which they record is largely owing to his work, though many others have contributed to it.

In middle Pliocene times the Gulf of Mexico extended farther to the north than now, and Florida was a short, stubby peninsula that ended at about the level of Tampa and had its east and west shores 50 or more miles west of their present location. Along the coast littoral sands and gravels were being laid down to make the Citronelle formation, and the land surface had for bedrock the sandy phosphatic Hawthorn formation of Miocene age. In what is now the Peninsular Lime Sink Region, the Hawthorn overlay the porous Ocala limestone, and here solution leached out the phosphates and other binding materials and left the residue of the Hawthorn as a deep, nearly pure, unconsolidated quartz sand known as the Alachua formation. The surface layers of this deposit must have been much like the modern Norfolk sands, and a "high pine-turkey oak" forest probably covered the region. The Alachua formation, still unconsolidated, lies today as it was formed, save for a thin overwash of Pleistocene marine sand; it is the home of *Mycotrupes gaigei*.

The Pliocene closed with a general warping of the crust that submerged the Coastal Plain north of Cape Cod and deepened the Gulf geosyncline. The Citronelle shore deposits were raised to a height of 300 feet in what is now north central Florida and submerged along the southwestern side of the Pliocene peninsula. Most of the area occupied by the Alachua formation was apparently somewhat raised. The end of this crustal warping is taken as the beginning of the Pleistocene.

Without any deformation of the crust, the margins of the Coastal Plain were repeatedly drowned and drained during the Pleistocene. The rises in sea level are thought to have coincided with the warm interglacials, when the water of the continental glaciers was returned to the sea; the recessions were caused by growth of the ice sheets. In addition, there seems to have been a progressive lowering of average sea level throughout the epoch, owing to causes not yet agreed upon. The stages of high water level are recorded by a series of marine terraces, of which seven are well developed. They fall into four groups, three of which apparently correspond to the three major interglacial stages, and the fourth to the recession of the Wisconsin ice. The first terrace of each group shows the features of



Text Fig. 2. A diagram showing the relations of the Pleistocene terraces of the southeastern Coastal Plain, the elevations and depressions of sea level, and their presumed chronology; based on Cooke (1945).

a shoreline of submergence, while the others are shorelines of emergence that mark halts in the withdrawal of the seas. The extent of recession of the sea level during the glacial stages is largely conjectural, though there is some basis for the estimates given. The succession of the terraces and low-water stages is presented diagrammatically in text Fig. 2, in which their presumed relations to the glacial chronology are also shown.

THE EVOLUTIONARY HISTORY OF *MYCOTRUPES*

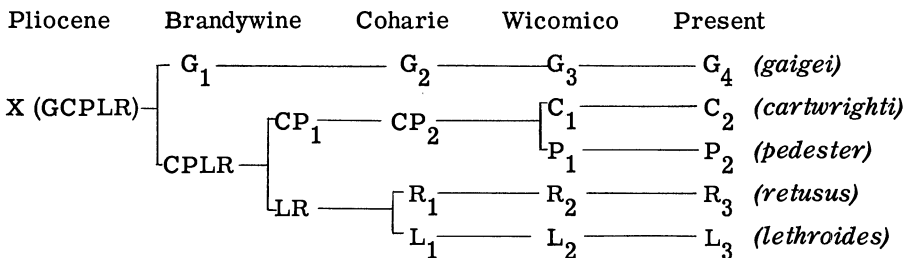
In the attempt to reconstruct the events in the evolutionary history of *Mycotrupes* I have made three assumptions, two concerning the beetles and one of a geological nature. The first is as to the antiquity of the genus and its long occupancy of the region where it now occurs; my reasons for making this assumption have already been given. The second is that *Mycotrupes* has always had as limited powers of dispersal as it does now. Let us consider this point further.

Today, wherever *Mycotrupes* goes it must walk. To judge from the marked reduction of the wing-bearing metathoracic region and related changes of the body, it seems probable that loss of wings was one of the first modifications that took place in the ancestral stock. *Mycotrupes* is restricted by its mode of life to areas of deep sand. For such an animal, swamps, marshes, flatwoods, and dense hammocks must be almost complete barriers, and a river as insurmountable an obstacle as the sea. One

can scarcely call upon hurricanes to fling them across barriers when they spend most of their lives six feet underground. So let us assume that wherever *Mycotrupes* has gone in the past, it arrived over sandy highways, on foot.

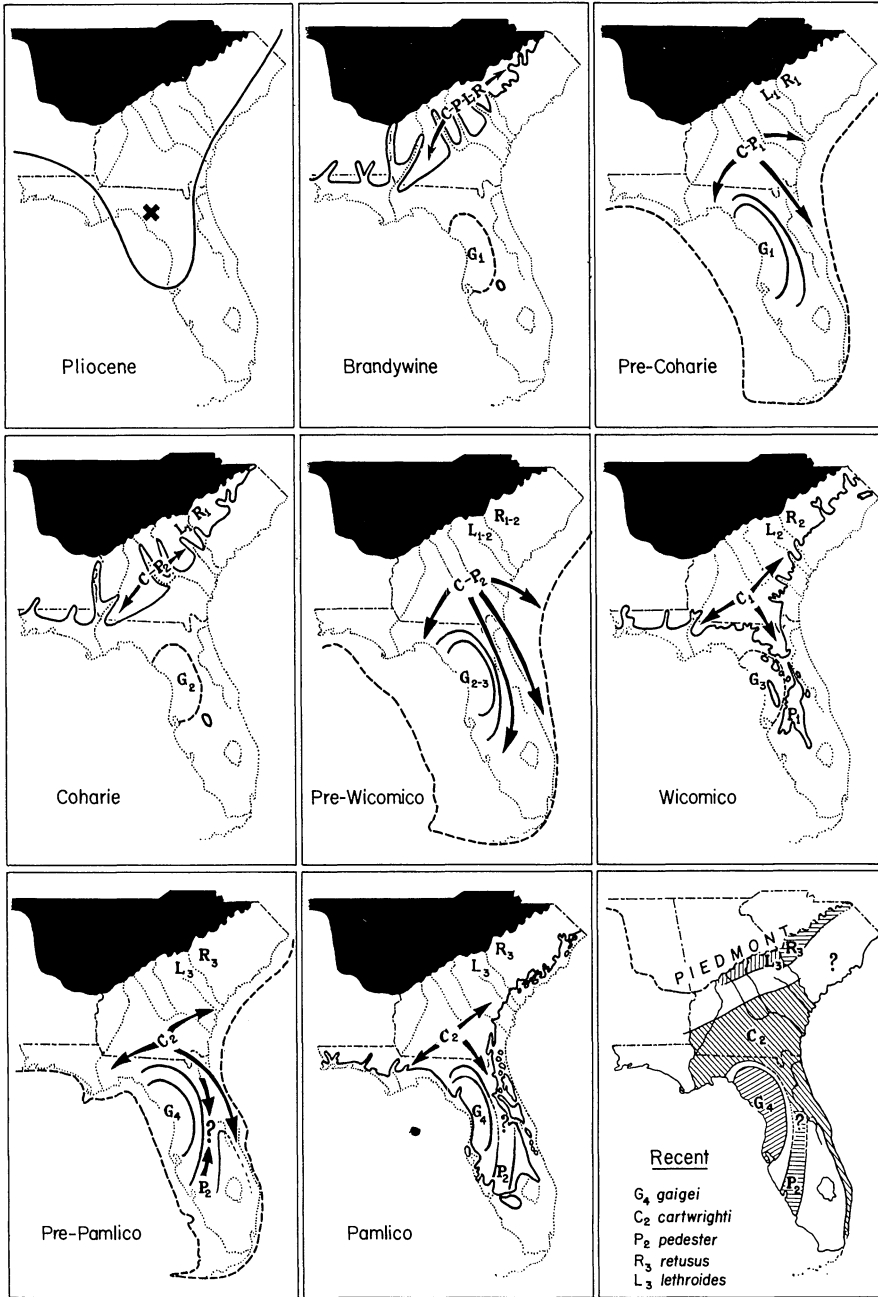
My third assumption is an act of faith, based on grounds that seem good to me and to most zoogeographers, but not to geologists. It is that there has been land in central Florida since the Pliocene, at least in the form of a few reasonable-sized islands. Not so long ago the geologists would have none of this, at least for the highest Pleistocene level of the sea, but in his latest maps Cooke has left a tiny island exposed just about where it is needed. If it were only a little larger! There exists in central Florida a group of endemics — ferns, wingless grasshoppers, blind subterranean crayfish and crickets, amphibians, and reptiles, to mention only some of them — that occur only in this region, and show every indication of prolonged isolation. Carr (1940:6) has discussed this problem, and although some of his conclusions are no longer tenable in the light of more complete geological knowledge, his arguments for the persistence of islands in central Florida on zoogeographical grounds are still valid. Perhaps the surface of the higher points has been lowered by weathering, solution, or wind action, or a very slight amount of warping may have occurred.

The hypothesis as to the evolutionary history of *Mycotrupes* here presented is not the only possible one, but it is the only one I have been able to make that takes into account both the degrees of relationship of the species and their geographic distribution. The species relationships were diagrammed above in the discussion of that topic. That diagram is here repeated in another form, using symbols to represent the species and grouped symbols to stand for common ancestral stocks, and placing the divergences between populations in relation to specific Pleistocene events.



The symbols used in the above diagram are given on the accompanying series of outlines (text Fig. 3) that show the changes in configuration of the southeastern Coastal Plain from middle Pliocene to the last Pleistocene submergence. The stages represented by the Sunderland, Penholoway, and Talbot terraces, which were temporary halts during recessions of the sea, are omitted.

Whether or not the events postulated in the following account actually took place, obviously something along these lines must have happened, not only to *Mycotrupes* but to all other animal groups of the region that were unable to move about freely. Admitting it to be guesswork, I shall tell the story as though it were fact and let it speak for itself.



Text Fig. 3. The configuration of the southeastern Coastal Plain in the middle Pliocene and at six successive stages of the Pleistocene, compared with that of the present; based on Cooke (1945). The Piedmont region is shaded. The letter symbols represent hypothetical ancestral populations of *Mycotrupes*, as discussed in the text, except that those of the last chart stand for the existing species.

In middle Pliocene times *Mycotrupes* is assumed to have been present somewhere within the southeastern Coastal Plain in the form of an ancestral stock X (GCPLR). Perhaps X lived in the broad expanse of deep sands provided by the Alachua formation, or perhaps on the areas of stabilized sands back of the coastal beaches. X had a somewhat punctate dorsum, weakly striate elytra, the beginnings of a granulose surface, and in the male a phallus with simple thecal spine. Early in the Aftonian interglacial the sea came creeping over the land. As it spread it first narrowed the peninsula and then broke it up into islands, which became smaller and smaller. At the same time the shoreline, accompanied by sandy beaches and preceded by dune belts, moved inland along the whole margin of the Coastal Plain. The population of X thus became divided into two — an insular population, G₁, and a mainland population, CPLR. The latter moved inland with the belt of advancing coastal sands. Perhaps as it went it encountered areas of residual sands where it could live, but if so it could have occupied them only until the sea caught up with it again. Eventually, the water ceased to rise and came to a halt at the level of the Brandywine terrace. There it stayed for a long time, furnishing eolian sands for the building of the Fall Line Sand Hills of Georgia and the Congaree Sand Hills of South Carolina as well as lesser deposits on the Aiken Plateau and elsewhere.

In these sand hills and along the coastal belt CPLR found a congenial and undisturbed home. It developed the evenly nodulose surface found in all its descendants and lost its remaining traces of dorsal punctae and elytral striae; but it still retained the simple thecal spine. There was no impassable barrier between the South Carolina and Georgia populations, for the Savannah River flowed into the sea amid the coastal sand hills and flats, and changes at its mouth would have permitted occasional transfers. Meanwhile, down on the Florida islands G₁ persisted without great change.

With the coming of the Kansan glacial stage the sea began to retreat. The part of the CPLR population living back in the sand hills stayed there, forming LR, while another part, CP₁, spread coastward in the wake of the retreating sea, doubtless leaving colonies behind in such areas of deep sand as the sea had provided. LR developed a new character, a bird-head thecal spine, while CP₁ held to the original form. As the sea level fell the Coastal Plain rivers were rejuvenated, and the Savannah began to re-excavate its former valley. In time the LR population was divided into two, L₁ in Georgia and R₁ in South Carolina. In Florida G₁, changing toward G₂, also expanded as the islands grew and coalesced, but was kept from contact with the spreading CP₁ population by gaps in the distribution of the deep sand areas.

The Yarmouth submergence that reached its high point at the level of the Coharie terrace saw much the same sequence of events repeated. This time the sea did not penetrate so far inland, and the CP population, now CP₂, was pushed back only to the middle belt of the Coastal Plain in Georgia; nothing is known of the CP group in South Carolina. R₁ and L₁ continued their differentiation to become R₂ and L₂, and G₂ changed only slightly to G₃ in its once more insular home.

With the coming of the Illinoian glacial stage the sea again retreated, and the ranges of CP₂ and G₃ expanded as before. This time, if not earlier, CP₂ succeeded in spreading down the central Florida ridge as well as along the east coast. When the sea returned in Sangamon time to the level of the Wicomico terrace, the southern end of the ridge section was cut off as an island, and much of the territory occupied by CP₂ was again submerged, so that the population was divided into C₁ in Georgia and north Florida and P₁ in the southern peninsular island. The post-Talbot emergence may or may not have reunited them as subspecies; their present geographic relations are not known. The later minor changes of sea level have had little effect upon the ranges of the various populations save that C₂ has apparently been able to spread south along the east coast of Florida as far as Miami in post-Pamlico (Recent) time. The end result is the species as they are now: R₃ and L₃ farthest inland, highly modified through their long isolation; G₄ in its expanded Florida island, primitive yet aberrant; and C₂ and P₂, the most recently segregated pair of species, the former wide-ranging and variable, the latter apparently isolated but perhaps still in contact with its parent form somewhere in central Florida.

Hypothetical as this explanation is, and much as it leaves unexplained, I think it is true in considerable part. There can be little doubt that *retusus* and *lethroides* arose in the way described, or that *pedester* was separated from *cartwrighti* by the means suggested. The case for *gaugei* is the weakest, in that it hypothecates a group of persistent central Florida islands that perhaps did not exist. I have, however, been unable to think of an alternative that would account for the requisite long-time isolation and the present distribution of the *gaugei* stock. It would be interesting to see the methods here used applied to other better known groups of Coastal Plain animals. Not until this has been done will it be possible to assess the validity of the conclusions presented.

PART III. HABITS AND LIFE HISTORY OF *MYCOTRUPES*,
WITH A DESCRIPTION OF THE LARVA OF *MYCOTRUPES GAIGEI*¹

By Henry F. Howden

Burrowing animals are notoriously difficult to study, and the species of *Mycotrupes* are more so than most because of the depth to which they dig. The following observations have been made at the cost of many hours of hard labor, in which I have been helped by the associates mentioned below. My notes relate only to *Mycotrupes retusus* and *M. gaigei*; the other species are presumably quite similar in habits and life history.

Mycotrupes retusus (LeConte)

In September, 1951, Dr. P. O. Ritcher and I made a trip to Aiken and White Pond, in Aiken County, South Carolina, to collect *Mycotrupes retusus*. We learned that for the preceding six weeks there had been no appreciable amount of rain in the vicinity, and the ground was extremely dry. During our two-day visit (September 6 and 7) we saw no signs of surface activity on the part of the beetles. We visited the Webb farm near White Pond, where O. L. Cartwright had previously found *retusus* to be abundant. There we were able to collect a few specimens by carefully scraping away the pine litter under thick stands of longleaf pines. Faint traces of old "push-ups" could be seen after the litter was removed, and these old burrows were then dug out, by means of a post-hole digger and sifter. The sand was extremely dry and powdery to a depth of six or seven feet.

In this way we collected the following specimens, all of which seemed inactive and almost in a state of aestivation. They were all old individuals, fully colored and with tibiae worn from digging. September 6, one female at a depth of 36 inches under a stand of longleaf pines at White Pond, and one male at a depth of 27 inches under an isolated longleaf pine tree three miles north of Aiken; September 7, one male at a depth of 17 inches and another at 33 inches, at White Pond, in the same area where the female was taken the previous day.

The female and one of the males were kept alive and taken to North Carolina State College at Raleigh, North Carolina, where I was working. They were placed in a screen wire cage, two feet in diameter and three feet deep, and the cage was sunk in the soil of a sandy pine woods 18 miles east of Raleigh, where conditions seemed similar to those in the Aiken

¹Contribution No. 99, Department of Zoology and Entomology, University of Tennessee, Knoxville, Tennessee.

area. The pair was kept supplied with cow dung, fungi, rotten bananas, and pine litter. The beetles appeared to feed on the rotting fungi and bananas, but they never constructed any brood cells, perhaps owing to the fact that the depth to which they could dig was limited to three feet. To judge from my later observations on *Mycotrupes gaigei* the brood cells would normally be five to six feet underground.

One interesting fact that came to light is that the adults, particularly the females, apparently have a long active life. Other North American Geotrupinae which I have studied have an adult life of usually only six to eight months, with a maximum duration of one year. These two individuals of *retusus* were certainly not newly emerged when collected and may well have been adult for some months. On April 24 and on June 18, 1952, their cage was dug up, and both were found alive and active in separate burrows each about two feet deep. No food material was evident in the burrows on either occasion. On August 4, 1952, when the cage was again dug up, the male was dead. The female remained active until the middle of October, 1952, when she was injured accidentally and killed. Up to this time she had survived in the cage for 13 months, and the span of her life as an adult may have been considerably longer. It is interesting in this connection to note that in another burrow-inhabiting insect, the blind camel-cricket *Typhloceuthophilus floridanus*, Hubbell has reported the length of adult life as well over a year.

Mycotrupes gaigei Olson and Hubbell

This species has been collected many times by Hubbell and Young, and their observations on its habitat preferences have been summarized in Part I of this paper. Most of their specimens were collected in traps baited with molasses or honey-water, though some were dug out by Young. Dead specimens were picked up on the surface of the ground by Young in late March, and Young's notes mention finding accumulations of the elytra of this species under logs, wherethe insects may have been carried by mice that had caught them in the open.

In March, 1953, Byrd K. Dozier accompanied me on a trip to Florida to secure life history material of *Mycotrupes gaigei*. We were able, through Hubbell's directions, to find two large aggregations. One of these, four miles north of High Springs on U.S. Routes 41 and 441, is about one-quarter mile south of the place where Hubbell collected the types in 1929. The other is about two miles west of Archer in southwestern Alachua County, on State Highway 24.

The High Springs area consists of a sand ridge with an open stand of turkey oak (*Quercus laevis*) and a few live oaks (*Q. virginiana*). At the time of our visit it showed evidences of having been recently burned over, so that there was little ground cover; cattle grazed there, and cow droppings were numerous. The Archer site was more open, with scattered turkey oaks and live oaks and with patches of bare sand showing between clumps of wire grass. A pasture lay on the other side of the road from the area where *Mycotrupes* was collected. "Push-ups" were numerous in

both localities, near some of which traps were set out. These were tin cans sunk into the ground and partly filled with fermenting malt, or a mixture of malt and propionic acid. Although both types of bait were effective, the latter was slightly more so.

At about 4:30 p.m. on March 19 we set out 30 traps in the area north of High Springs. At 8:30 p.m. the traps were examined and found to contain about 30 *Mycotrupes*. Only one specimen was taken during the following hour, and none during the night. On March 23 a dozen traps were set out two miles west of Archer, about noon. By 4:00 p.m. the traps held 15 specimens. Thus, it would appear that *Mycotrupes gaigei* is active on the surface during the day and in the evening, and not at night.

Many of the adults collected showed but little abrasion from burrowing. Several such unworn males and females were placed alive in a vial and shortly afterward were noted attempting to mate. The mating response, the unabraded appearance, and the ease with which many of the specimens were later pinned, all suggest that they had recently emerged and were somewhat teneral.

Not all of the specimens had this appearance, however; a few, mainly females, had the dorsal granulations and margins of the fore tibia considerably worn. One of these was dug from a vertical 60-inch burrow. These may have been survivors of the previous year's generation, to judge from my experiences with *M. retusus*.

In the High Springs area, where most of our observations were made, the burrows of *M. gaigei* were very numerous. Some of the "push-ups" were as much as five or six inches in diameter and three or four inches high. The burrow typically opened directly under the center of the "push-up," as with species of the genus *Geotrupes*. The hole descended vertically for some distance, often to a depth of more than six feet. Digging with a post-hole digger yielded 16 specimens, taken from 16 burrows with barely indicated fresh "push-ups." These burrows were often open at the entrance, without a plug of sand, and in almost every instance yielded a male.

On March 20, in the High Springs habitat, we excavated an area three feet wide by six feet long that contained three fairly fresh "push-ups" and six old ones (see Pl. VII). Each burrow was followed down, so far as possible, by thrusting a long straw into it. None of the burrows was traced with certainty, however, owing to disturbance during digging and to plugs of sand in the burrows. After a depth of three feet was reached several of the burrows reopened and from there down were fairly easy to follow. One unexcavated burrow continued downward at least a foot beyond the seven-foot level, as determined by thrusting a straw into it. A number of old larval cells were found, at depths of 55, 58, 60, 66, 70, 77, and 82 inches. In one cell where the larva had not developed, the food material appeared to be old cow dung, packed into a wad about 1.5 to 2 inches long by 0.75 inches in diameter. The other old cells were so filled with sand and the food had been so completely consumed that nothing could be ascertained about it.

Finally, after finding the old cells, a full-grown third instar *Mycotrupes gaigei* was discovered in its pupal cell, at a depth of 66 inches.

Further digging in the vicinity produced two other larvae, also in their pupal cells, at depths of 72 and 78 inches. From the position of the cells, it seemed quite probable that all originated from one vertical burrow, from which they branched at different depths.

The pupal chambers were small, measuring slightly under two inches in length by about 0.75 inches in diameter. All food material had been consumed, and the larva was in a cell composed merely of a thin coating of its own feces. The cell itself was very fragile. In this respect it differed from the usual cells of *Geotrupes blackburnii* or *G. splendidus*, which not only have a layer of the original food material on the outside, but are lined within by a thick hard coating of the fecal material of the larva. The pupal cells of *Geotrupes* have walls 3 or 4 mm. thick, while the walls of the pupal cells of *Mycotrupes gaigei* were scarcely 1 mm. thick.

The Larva of Mycotrupes gaigei

The three larvae obtained in the type locality near High Springs, Florida, on March 20, 1953, were immediately preserved. The following description is based upon them.

Maximum width of head capsule 3 to 3.2 mm. (smaller in comparison to body size than in larvae of *Geotrupes*).

Head capsule light yellowish tan, with surface finely wrinkled. On each side above the single posterior frontal seta is a large shallow circular indentation in the frons and epicranium. On each side above this indentation on the epicranium is a row of five or six long epicranial setae (Fig. 69). Frons on each side has one posterior frontal seta, two to four setae in each anterior angle, one exterior frontal seta, and across the frons a row of five or six anterior frontal setae (Fig. 69). Clypeo-frontal suture absent. *Labrum* trilobed and considerably wider than long. Both *clypeus* and *labrum* somewhat asymmetrical. *Antenna* (Fig. 70) cylindrical with the first or basal segment bearing three setae on its outer apical surface. Second segment only very slightly shorter than first, reduced in diameter by almost one-third, and bearing an inner apical conical sense organ. Last or third antennal segment greatly reduced in length and diameter; slightly less than one-third as long as second segment. *Mandibles* slightly asymmetrical, almost identical in configuration and setation with those of *Geotrupes blackburnii* (described and illustrated by Ritcher, 1947, p. 23, Figs. 22, 23). *Maxilla* with stridulatory area (Fig. 73) having five to seven small teeth in an irregular row on each stipes, and a shorter row of four teeth near the posterior margin of the palpifer. *Hypopharynx* with two strongly asymmetrical oncyli. *Glossa* not emarginate, bearing 20 or more fine setae. On each side, in front of the hypopharyngeal oncyli, is an irregular row of 20 or more sensilla at the midline; just anterior to this row are several small setae and a peculiar darkened area (Fig. 73) that is slightly elevated and apparently more sclerotized than the surrounding portions of the glossa. This small dumbbell-shaped sclerotized area in

front of the row of sensilla has not been observed in the larvae of other Geotrupini. *Epipharynx* (Fig. 72) with tormae vague laterally, united mesally, with anterior and posterior tormae present. Phobae surround the vaguely spiculate pedium, which anteriorly has an irregular row of about 20 sensilla. Each chaetoparia with 12 to 15 chaetae.

Abdomen swollen, with flattened anal lobes protruding on each side of last abdominal segment. Spiracles cribriform, with respiratory plates crescent-shaped. Spiracular plate of eighth abdominal segment smaller than the others. Dorsa of abdominal segments one to eight with two vaguely delimited dorsal annulets; all annulets of these segments, except the first, with patches of setae which become longer on segments six to eight. Last abdominal segment slantingly flattened caudad (Fig. 71). Definitive lines of endoskeletal figure not fused at any point. Endoskeletal figure adjacent and ventral to anal opening lacking abrupt angles (Fig. 71), gradually rounded, becoming constricted to a narrow stalk. *Legs* three-segmented, with pro- and mesothoracic legs long and metathoracic legs reduced, in same manner as in species of *Geotrupes* (see Ritcher, 1947, p. 25, Fig. 24) and *Peltotrupes* (see Howden, 1952, p. 44, Fig. 2). Stridulating area of mesothoracic legs consisting of a ridged area on the outer portion of each coxa. Opposite this, the stridulatory area of the metathoracic legs consists of a series of small teeth, 9 to 12 on the inner surface of the fused trochanter-femur, and sometimes one on the tibio-tarsus. Tip of each leg with a minute colorless tubercle surrounded by long setae (Fig. 74), but lacking the small brownish claw present in some species of *Geotrupes*.

The larva of *Mycotrupes gagei* differs in several respects from those of other Geotrupini. The configuration of the endoskeletal figure below the anal opening (Fig. 71) will readily separate it from the known larvae of species of other genera. Also, the characteristics of the tormae of the epipharynx (Fig. 72) and the glossa with the small sclerotized area anterior to the row of sensilla (Fig. 73) will readily separate *Mycotrupes gagei* from other Geotrupini.

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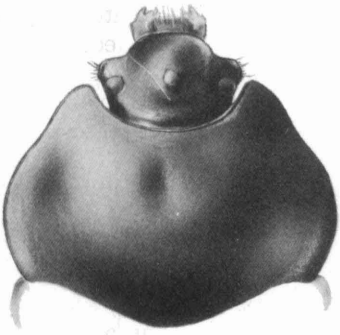
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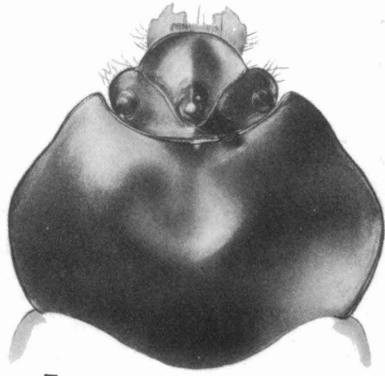
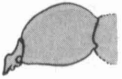
PLATE II. DORSAL AND LATERAL VIEWS OF HEAD AND PRONOTUM

- Fig. 2. *Mycotrupes retusus* (LeConte). "Weak" male, Windsor, S. C.
Fig. 3. *Mycotrupes retusus* (LeConte). "Strong" male, Windsor, S. C.
Fig. 4. *Mycotrupes lethroides* (Westwood). Described male, Augusta, Ga.
Fig. 5. *Mycotrupes gaigei*, new species. Male type, Columbia County, Fla.
Fig. 6. *Mycotrupes cartwrighti*, new species. Male type, Tallahassee, Fla.

PLATE II



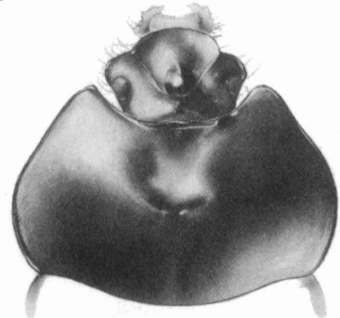
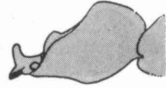
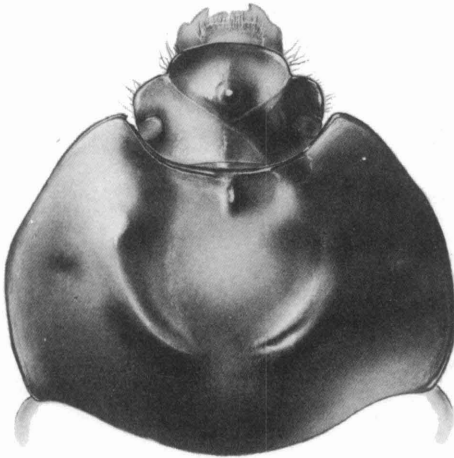
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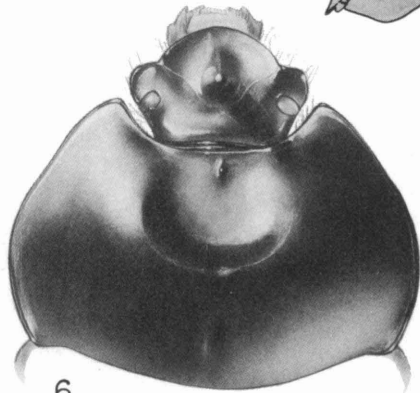
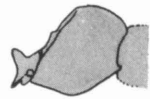
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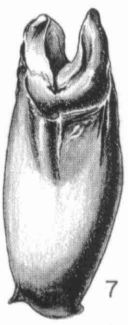


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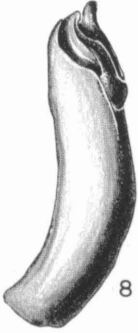
PLATE III. PHALLIC STRUCTURES AND ELYTRA

- Figs. 7-9. *Mycotrupes gagei*, new species. Dorsal, dextral, and ventral views of phallus, male type, Columbia County, Fla.
- Figs. 10-12. *Mycotrupes retusus* (LeConte). Dorsal, dextral, and ventral views of phallus, male, Windsor, S. C.
- Figs. 13-15. *Mycotrupes cartwrighti*, new species. Dorsal, dextral, and ventral views of phallus, male type, Tallahassee, Fla.
- Figs. 16-18. *Mycotrupes lethroides* (Westwood). Dorsal, dextral, and ventral views of phallus, male, Augusta, Ga.
- Fig. 19. *Mycotrupes gagei*, new species. Inner surface of left elytron, female, Columbia County, Fla.
- Fig. 20. *Thorectes laevigatus* (Fabr.). Inner surface of left elytron, male, Bandol, Dept. Var, France.

PLATE III



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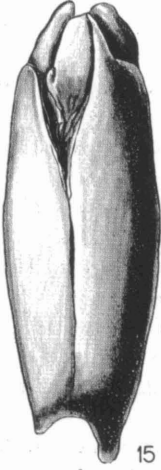
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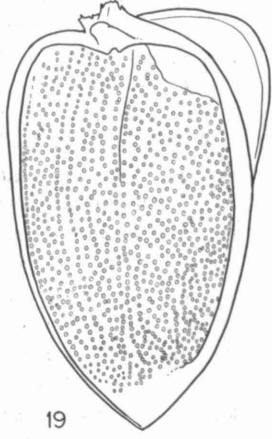
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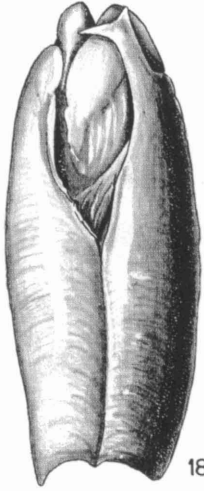
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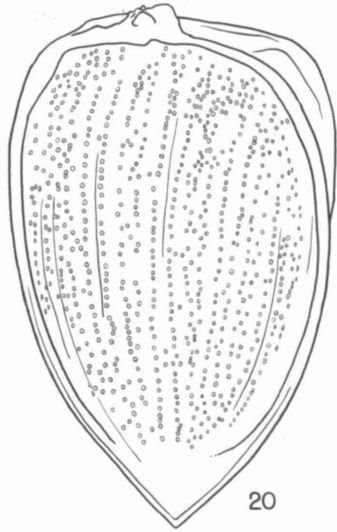
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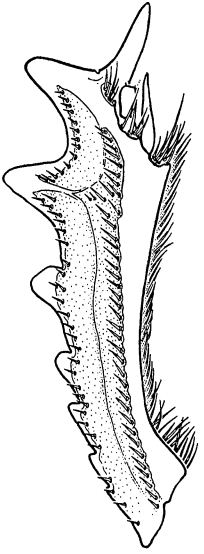


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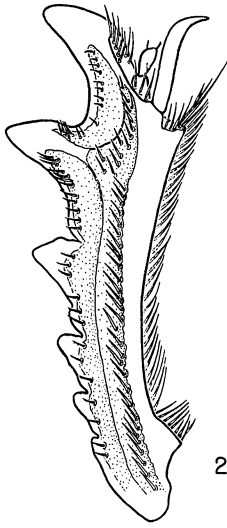
PLATE IV. STRUCTURE OF FORE TIBIA AND HIND TARSAL CLAWS

- Fig. 21. *Mycotrupes lethroides* (Westwood). Dorsal view of fore tibia, male, Augusta, Ga.
- Fig. 22. *Mycotrupes lethroides* (Westwood). Dorsal view of fore tibia, female, plesiallo-type, Augusta, Ga.
- Fig. 23. *Mycotrupes lethroides* (Westwood). Distal end of left fore tibia, described male, Augusta, Ga.
- Fig. 24. *Mycotrupes retusus* (LeConte). Distal end of left fore tibia, male, Columbia, S. C.
- Fig. 25. *Mycotrupes gagei*, new species. Distal end of left fore tibia, male type, Columbia County, Fla.
- Fig. 26. *Mycotrupes pedester* Howden, new species. Distal end of left fore tibia, male type, Punta Gorda, Fla.
- Fig. 27. *Mycotrupes cartwrighti*, new species. Distal end of left fore tibia, male type, Tallahassee, Fla.
- Fig. 28. *Thorectes laevigatus* (Fabr.). Distal end of left fore tibia, male, Bandol, Dept. Var, France.
- Fig. 29. *Mycotrupes cartwrighti*, new species. Distal segment and claws of hind tarsus, male type, Tallahassee, Fla.
- Fig. 30. *Mycotrupes retusus* (LeConte). Distal segment and claws of hind tarsus, male, Columbia, S. C.

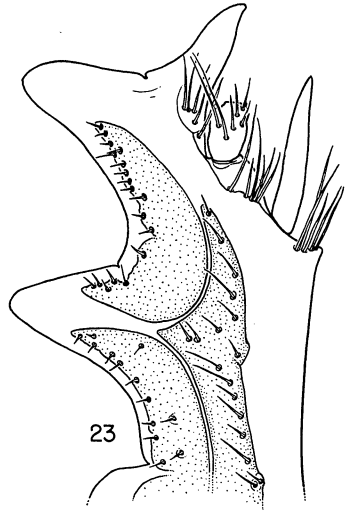
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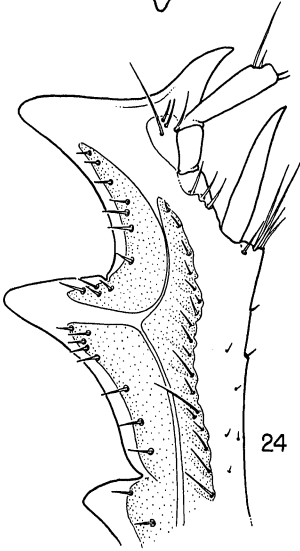
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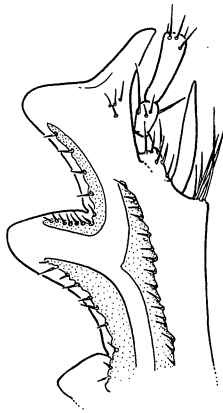
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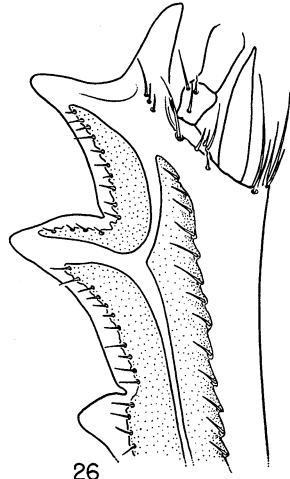
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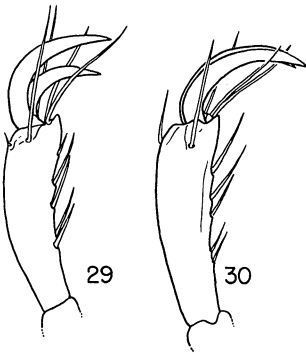
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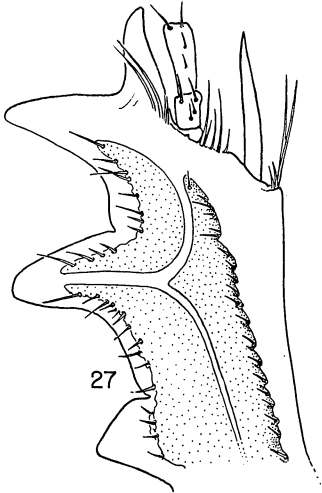
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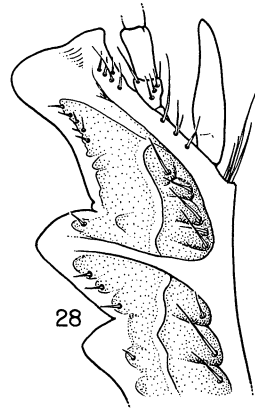
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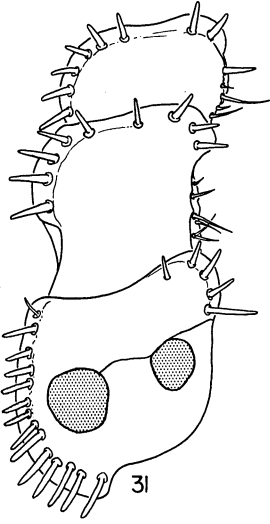


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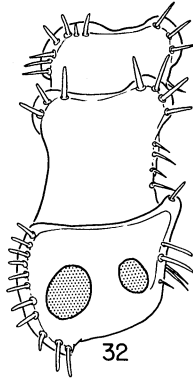
PLATE V. STRUCTURES OF HIND TIBIA, MESOSTERNUM, AND MANDIBLE

- Fig. 31. *Mycotrupes lethroides* (Westwood). Distal aspect of left hind tibia, described male, Augusta, Ga.
- Fig. 32. *Mycotrupes pedester* Howden, new species. Distal aspect of left hind tibia, male type, Punta Gorda, Fla.
- Fig. 33. *Mycotrupes retusus* (LeConte). Distal aspect of left hind tibia, male, Columbia, S. C.
- Fig. 34. *Mycotrupes gaigei*, new species. Distal aspect of left hind tibia, male type, Columbia County, Fla.
- Fig. 35. *Mycotrupes cartwrighti*, new species. Distal aspect of left hind tibia, male type, Tallahassee, Fla.
- Fig. 36. *Typhoeus typhoeus* (L.). Mesosternum seen obliquely from left, male, France.
- Fig. 37. *Thorectes laevigatus* (F.). Mesosternum seen obliquely from left, male, Bandol, Dept. Var, France.
- Fig. 38. *Mycotrupes gaigei*, new species. Mesosternum seen obliquely from left, female, Columbia County, Fla.
- Figs. 39, 40. *Thorectes laevigatus* (F.). Dorsal and ventral views of left mandible, male, Bandol, Dept. Var, France.
- Figs. 41, 42. *Mycotrupes gaigei*, new species. Dorsal and ventral views of left mandible, female, Columbia County, Fla.

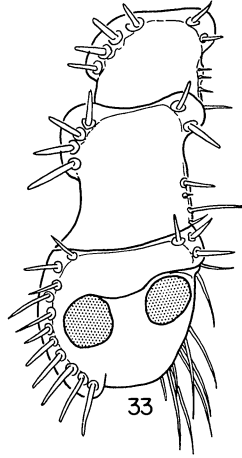
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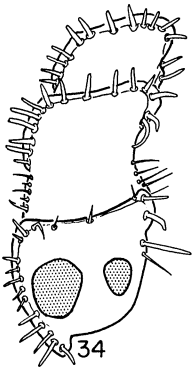
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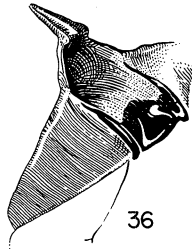
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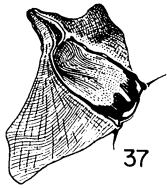
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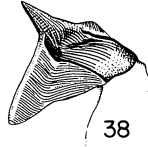
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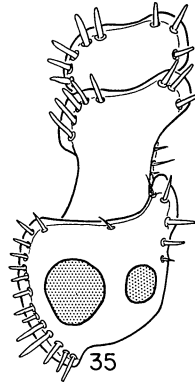
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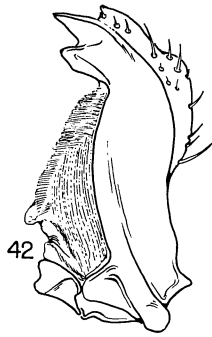
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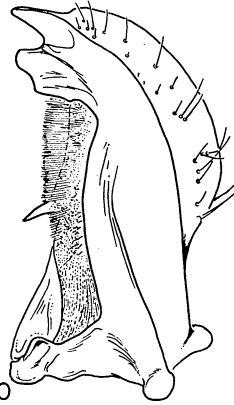
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PLATE VI. STRUCTURES OF HEAD, PRONOTUM, AND HIND TROCHANTER

- Fig. 43. *Mycotrupes gaigei*, new species. Dorsal outline of head, male type, Columbia County, Fla.
- Fig. 44. *Mycotrupes cartwrighti*, new species. Dorsal outline of head, male type, Tallahassee, Fla.
- Fig. 45. *Mycotrupes pedester* Howden, new species. Dorsal outline of head, male type, Punta Gorda, Fla.
- Fig. 46. *Mycotrupes retusus* (LeConte). Dorsal outline of head, male, Columbia, S. C.
- Fig. 47. *Mycotrupes lethroides* (Westwood). Dorsal outline of head, described male, Augusta, Ga.
- Fig. 48. *Mycotrupes gaigei*, new species. Profile of head from left, male type, Columbia County, Fla.
- Fig. 49. *Mycotrupes cartwrighti*, new species. Profile of head from left, male type, Tallahassee, Fla.
- Fig. 50. *Mycotrupes pedester*, new species. Profile of head from left, male type, Punta Gorda, Fla.
- Fig. 51. *Mycotrupes retusus* (LeConte). Profile of head from left, male, Columbia, S. C.
- Fig. 52. *Mycotrupes lethroides* (Westwood). Profile of head from left, described male, Augusta, Ga.
- Figs. 53, 54. *Mycotrupes gaigei*, new species. Front margin of pronotum, male type, (53), female allotype (54), Columbia County, Fla.
- Figs. 55, 56. *Mycotrupes cartwrighti*, new species. Front margin of pronotum, male type (55), female allotype (56), Tallahassee, Fla.
- Figs. 57, 58. *Mycotrupes pedester* Howden, new species. Front margin of pronotum, male type (57), female allotype (58), Punta Gorda, Fla.
- Figs. 59, 60. *Mycotrupes retusus* (LeConte). Front margin of pronotum, male (59), female (60), Columbia, S. C.
- Figs. 61, 62. *Mycotrupes lethroides* (Westwood). Front margin of pronotum, described male (61), female plesiallotype (62), Augusta, Ga.
- Fig. 63. *Mycotrupes gaigei*, new species. Ventral view of right hind trochanter, male, Columbia County, Fla.
- Fig. 64. *Mycotrupes lethroides* (Westwood). Ventral view of right hind trochanter, described male, Augusta, Ga.

PLATE VI

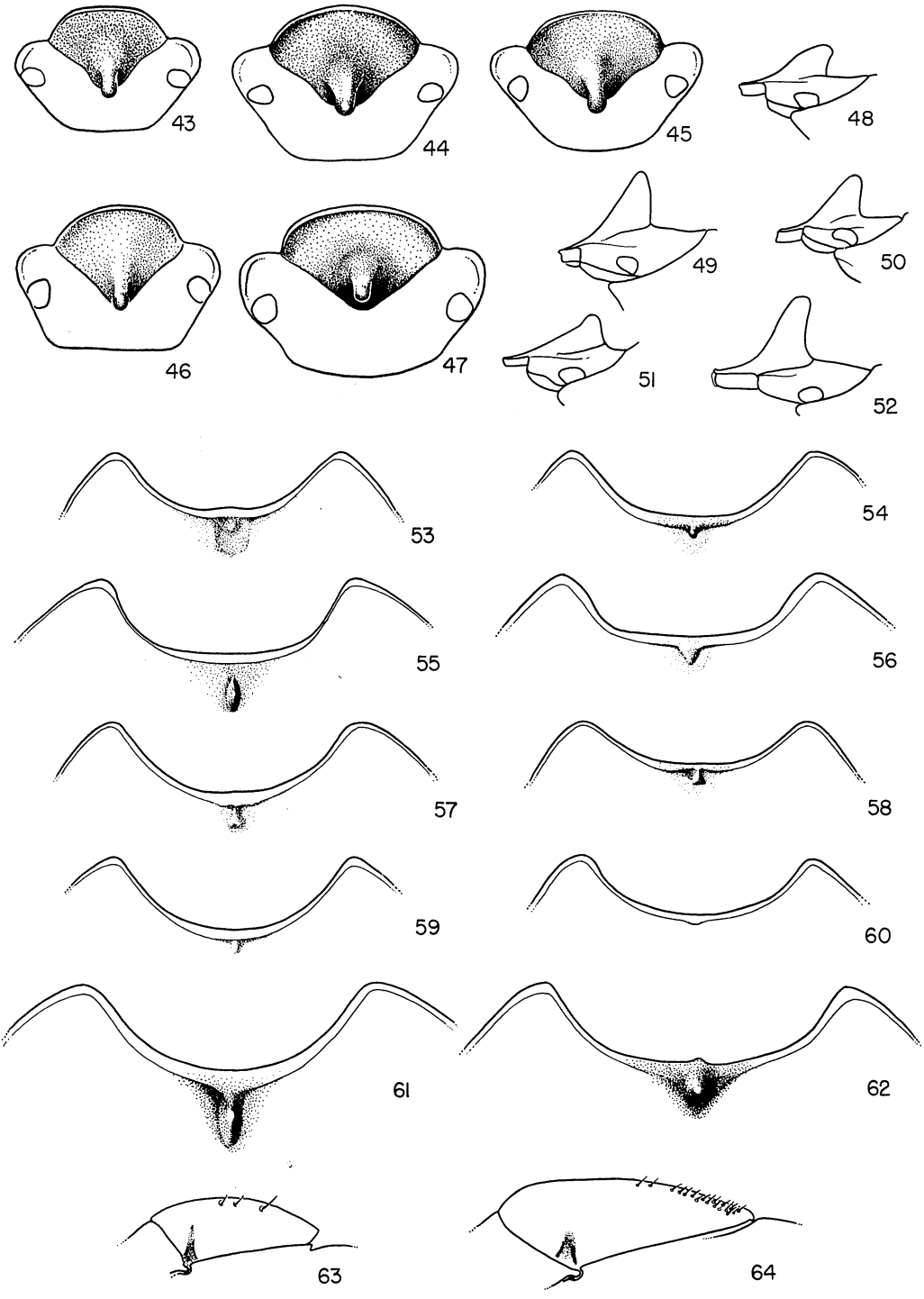


PLATE VII. THE HABITAT OF MYCOTRUPES GAIGEI

Photographs taken by Henry F. Howden at the type locality in Columbia County, Fla., about four miles north of High Springs.

- Fig. 65. General view of the environment. This is typical, open "high pine-turkey oak" or "sand hills" country, with deep coarse sandy soil of the Norfolk series. The small piles of sand in the foreground are "push-ups" of *Mycotrupes gaigei*; the larger heaps farther off are pocket-gopher ("salamander") mounds.
- Fig. 66. A closer view of the "push-ups" made by *Mycotrupes gaigei*, with Dozier pointing to one of them.
- Fig. 67. Another view of the habitat, showing the sand thrown up from the excavation in which were found the larvae of *Mycotrupes gaigei* described in this paper.
- Fig. 68. Dozier in the excavation shown in Fig. 67. The total catch from this digging was one female *Mycotrupes gaigei*, taken at a depth of five feet, and three third instar larvae of the species, found in pupal cells at depths between 5.5 and 6.5 feet.

PLATE VII

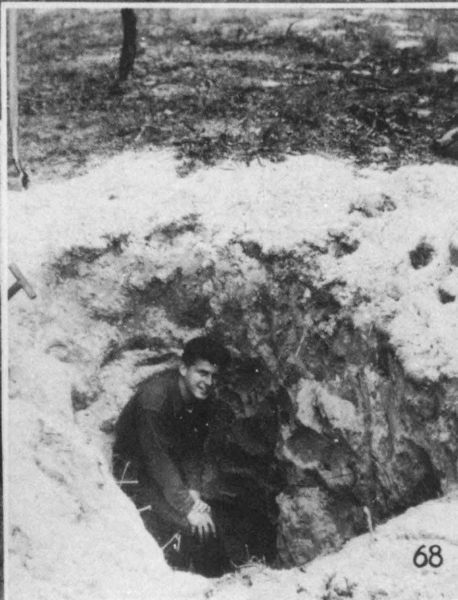


PLATE VIII. THIRD INSTAR LARVA OF *MYCOTRUPES GAIGEI*

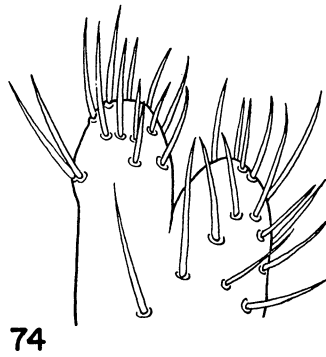
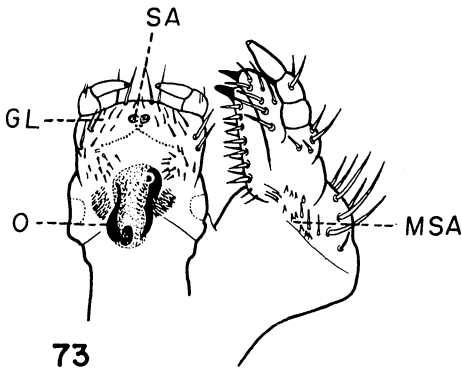
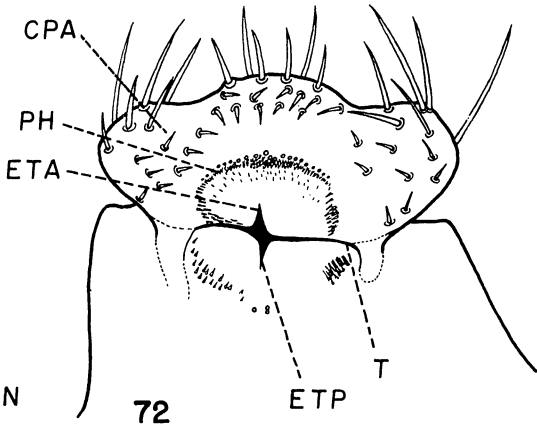
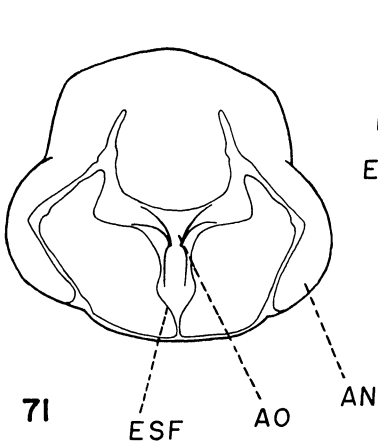
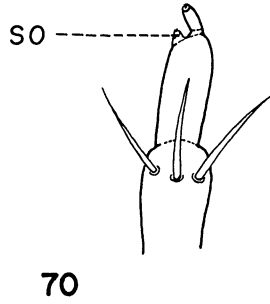
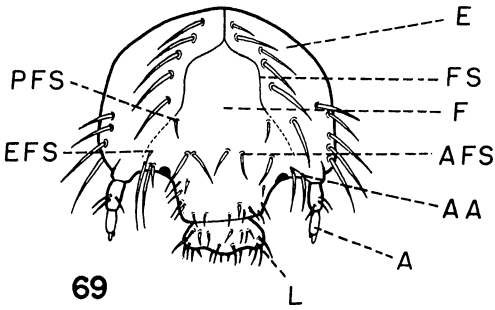
- Fig. 69. Head capsule, cephalic view.
Fig. 70. Right antenna, dorsal view.
Fig. 71. Last abdominal segment, caudal view.
Fig. 72. Epipharynx.
Fig. 73. Maxilla and hypopharynx.
Fig. 74. Tip of tibiotarsus of right mesothoracic leg.

Explanation of lettering

A--Antenna	F--Frons
AA--Setae of anterior angle of frons	FS--Frontal suture
AFS--Anterior frontal setae	GL--Glossa
AN--Anal lobes	L--Labrum
AO--Anal opening	MSA--Maxillary stridulatory area
CPA--Chaetoparia	O--Oncylus
E--Epicranium	PFS--Posterior frontal setae
EFS--Exterior frontal setae	PH--Phoba
ESF--Endoskeletal figure	SA--Sclerotized area
ETA--Anterior epitormae	SO--Conical sense organ
ETP--Posterior epitormae	T--Torma

All figures greatly enlarged

PLATE VIII



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