Speculations on Some Beetles, Barriers, and Climates During the Pleistocene and Pre-Pleistocene Periods in Some Non-glaciated Portions of North America

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Introduction

Climatic factors often strongly influence insect distributional patterns. Not only present but some past climatic influence may be reflected in existing distributional patterns, particularly if the insect is sedentary and limited in its ability to disperse. If the evolutionary history of sedentary groups of insects can be deduced and correlated with past habitats, it may provide valuable evidence concerning the sequence of past climates. This paper attempts to make such deductions, using as a basis the speciation and distributional patterns of certain genera of scarabaeid beetles.

Much of our information on Pleistocene climates and past barriers to dispersal has been based on pollen studies (Dillon, 1956; Heusser, 1960; Wendorf, 1961) and on distributional patterns of vertebrates (Darlington, 1957). A number of papers on the subject have appeared in recent years, several of them obviously in disagreement. Comprehensive reviews on some aspects discussed here have been published by Deevey (1949), Dillon (1956), Dorf (1959), Flint (1957), Hubbs (1958), Durham and Allison (1960), Martin and Harrell (1957), and Martin (1958). These papers give summaries of a number of aspects of Pleistocene climates and barriers that I mention briefly or omit entirely.

Initially, there are two assumptions that have to be made concerning the antiquity of the genera under consideration, particularly as there is no fossil evidence. In the seven genera of Scarabaeidae considered, which are *Mycotrupes, Peltotrupes, Gronocarus, Fossocarus, Acoma, Podolasia,* and *Pleocoma,* all species are seemingly flightless, or at least the females are flightless, with the possible exception of *Peltotrupes.* Flightlessness itself is no indication of antiquity and may often be a recent adaptation since many large genera have some flightless species. However, when all the species in a genus are flightless, I believe it fair to assume that, in most cases, the flightless condition[1] developed early in their evolution. My first and most important assumption is that I am dealing with enough genera and species so that rapid evolutionary change in all of them seems unlikely, and therefore at least some of the species have a long evolutionary history. Supporting this important argument for antiquity is the fact that none of the genera considered appears to have closely related genera living today, at least in the New World. The early development of flightlessness on the generic level is also important to my second assumption: that flightless groups of allopatric species, existing in similar, restricted habitats and separated by seemingly minor barriers, are indicative of relict populations that have survived and evolved in the same general areas in which they occur today.

[1] The wingless condition may perhaps be due to insular development (Darlington, 1943), particularly in the case of *Mycotrupes.*

These assumptions are not unprecedented. T. H. Hubbell (*in* Olson, Hubbell, and Howden, 1954) gives a detailed account of the possible evolutionary history of *Mycotrupes* and hypothesizes (p. 42) 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 no later than the middle Pliocene time." E. G. Linsley (1938) in his discussion of the evolutionary history of *Pleocoma* suggests that the genus was already well established during the Miocene. Both Hubbell and Linsley have discussed the reasons for making their assumptions, and I hope to support their arguments by including data on additional genera that have similar habits and habitats. A synthesis of this information then serves as a basis for making additional assumptions and speculations.

For convenience, I have divided the genera considered into three groups: (1) those occurring in the coastal plain area of the southeastern United States, from South Carolina to Florida and to eastern Texas; (2) those occurring in the arid "Southwest," which includes all of the area from the lower Rio Grande region in Texas through southern New Mexico, southern Arizona, Baja California, Sonora, and the western plateau region of Mexico from northern Chihuahua south to eastern Durango; and (3) those occurring in the western coastal states of California, Oregon, and Washington.

It should be emphasized that the beetles discussed in each of these groups are not closely related and that the speculations on the barriers and climates of each area are developed to a large extent independently. Barriers for one group may be pathways of distribution for another. Except for the reasoning concerning the antiquity of the various groups, the discussion and development of ideas may differ radically.

The Southeastern Genera: Mycotrupes, Peltotrupes, Gronocarus, Fossocarus

These four genera occur in similar habitats along the inland sand ridges which extend along the Gulf Coast and into parts of Florida, Georgia, and South Carolina. The sand ridges, commonly called "sand hills," are composed of deep, well-drained sands of varied origin. The gently rolling "hills" are sparsely covered by live oak, turkey oak, and blue jack oak and by several species of pines. Ground cover is sparse and consists of scattered clumps of grass and accumulations of leaf litter in the depressions. There are often expanses of bare, bleached sand, where great fluctuations of surface temperature and moisture occur. The fauna of this xeric habitat contains many species of burrowing animals, and a distinct characteristic of these areas are the piles of sand, large and small, that mark the entrances to various types of burrows.

The fairly uniform sand-hill habitats are dissected by numerous rivers, streams, and swamps and were subjected to various degrees of inundation by the sea during the Pleistocene. These prehistoric seas are, at least in part, responsible for sand-hill habitats, having formed various terraces of differing elevations, as described in detail by Cooke (1945:245). Cooke, MacNeill (1951), and others have proposed names for the various terraces, the highest being the Brandywine, approximately 270 feet above the present sea level. According to Cooke, most of peninsular Florida and the adjacent coastal sand hills were inundated during the Pleistocene. While this theory has been widely accepted, doubt has been expressed on geological grounds[2] by Doering (1958) and Altschuler and Young (1960) concerning the upper levels attained by the sea during the Pleistocene. Also Clench and Turner (1956:104) state that "There appears to be some good evidence among the freshwater mollusks for the existence of an island in what is now central Florida during the period of fluctuation of the epicontinental

[2] In a recent paper, R. Q. Oaks, Jr., and N. K. Coch (1963, Science, 140:979–983) postulate six cycles of the Pleistocene seas, with maximum heights above present levels of 45 feet, and disagree with the theory of "terrace-stratigraphy."

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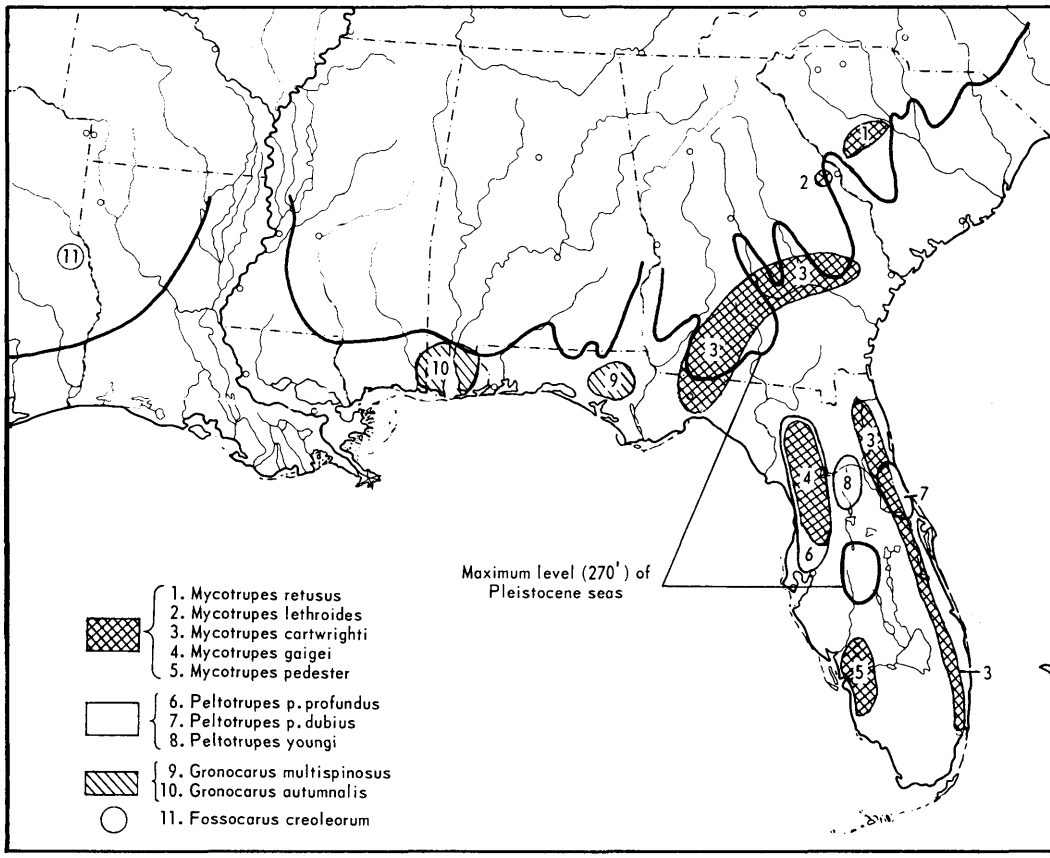

MAP 1. Distribution of the genera *Mycotrupes, Peltotrupes, Gronocarus,* and *Fossocarus.*

Pliocene and Pleistocene seas. Though the differences between many of the species of central and southern Florida and the regions to the north are not great, they exist in sufficient numbers to warrant an explanation." Proper interpretation of the extent of flooding of the sand hills and of the development of islands is very important in any analysis of the speciation of groups occurring in the southeastern sand-hill habitats. Conversely, the presence of certain groups may be of assistance in determining whether the habitat in which they occur was inundated during the Pleistocene.

Before making any effort to correlate extant species with past geological events, some understanding of the habits of the insects is necessary. *Mycotrupes* and *Peltotrupes,* both in the tribe Geotrupini, have essentially similar habits. Both occur only in areas of deep sand and dig extremely deep burrows. At the ends of the burrows, which have a depth of from five to nine feet, the larval brood chambers are constructed and provisioned by the adults. The few brood cells of *Mycotrupes* that have been found were composed of old horse or cow dung (Howden, *in* Olson et al., 1954). *Peltotrupes* forms a large, loosely packed cell of surface litter composed of oak leaves, pine needles, male pine cones, bits of bark, etc. (Howden, 1952). In both genera the larvae complete their entire development without ever leaving the cells. Therefore, any dispersal or migration of the species must take place during the adult stage. In *Mycotrupes* the metathoracic wings are reduced to small "buds," while

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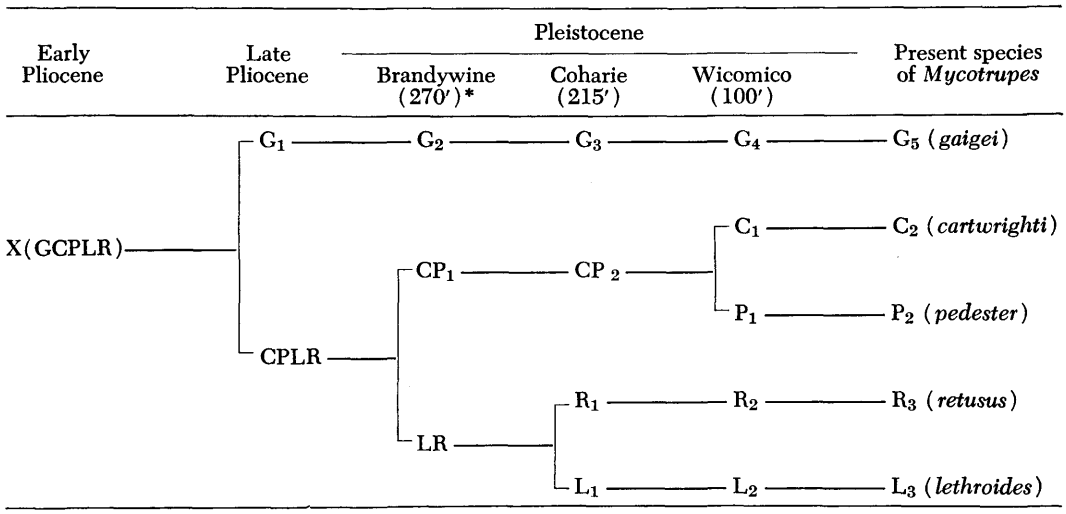
TABLE 1—POSSIBLE EVOLUTION OF THE SPECIES OF *MYCOTRUPES*, BASED ON PRESENT DISTRIBUTION, MORPHOLOGY, AND FLUCTUATIONS OF SEA LEVEL (AFTER HUBBELL, *IN* OLSON ET AL., 1954).



* Supposed maximum height of sea.

Peltotrupes has apparently functional wings which are somewhat smaller than in other Geotrupinae. However, as far as is known, *Peltotrupes* is flightless; I have never been successful in making specimens fly nor found evidence of flight. I believe it has been a resident in sandy habitats for a long period, a belief based partly on a unique larval habit which prevents the sand from caving in when the larva consumes its loosely packed food. As the food is eaten, the larva uses its own fecal material to construct a tube around itself. The larva never leaves the tube but merely extends the head and thorax to pull food into the tube, lengthening the tube and increasing its diameter as necessary. This adaptation, when considered in conjunction with adult and larval morphology, makes me believe that *Peltotrupes* has been long confined to its present habitat.

Gronocarus and *Fossocarus*, both in the Melolonthinae, occur in sand-hill habitats along the Gulf Coast west of the Appalachicola River. The few specimens I have taken occurred in areas where turkey oaks and wire grass predominated. The habits of these beetles are unknown, but I assume that, like most Melolonthinae, the larvae are root feeders and the adults leaf feeders. The females in both genera have the metathoracic wings reduced to small buds.

The distribution of the four genera (Map 1) presents an interesting picture. *Mycotrupes* is composed of five allopatric species. *Mycotrupes retusus* (LeC.) occurs in a line along the inland sand hills in South Carolina, north of the Savannah River. Immediately across the river in Georgia *Mycotrupes lethroides* (Westwood) occurs. South of this, *Mycotrupes cartwrighti* Olson and Hubbell occurs in a wide band from the Appalachicola River through southern Georgia and down the east coast of Florida. The range of the most distinctive species, *Mycotrupes gaigei* Olson and Hubbell, is in western peninsular Florida north of Tampa. *Mycotrupes pedester* Howden has the most restricted range, occurring only in Charlotte County, Florida.

The hypothetical ancestral history of *Mycotrupes* was depicted by Hubbell (*in* Olson et al., 1954:47–51), who postulated that the genus was differentiated in the Pliocene. I concur with Hubbell on the

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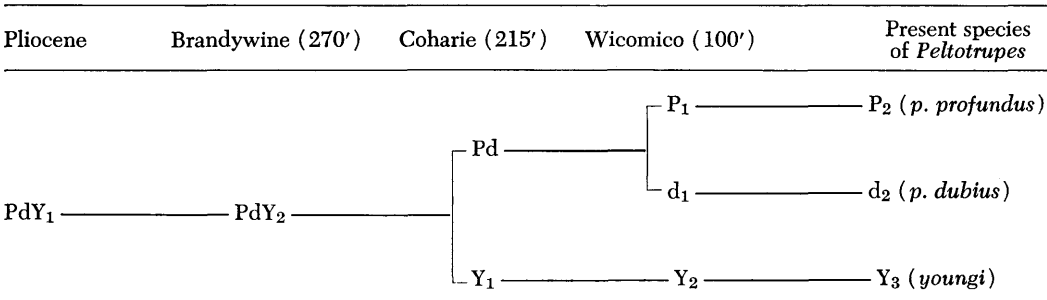
TABLE 2—POSSIBLE EVOLUTION OF THE SPECIES OF *PELTOTRUPES*, BASED ON PRESENT DISTRIBUTION, MORPHOLOGY, AND FLUCTUATIONS OF SEA LEVEL.



relationships and method of isolation of the species, i.e., between rivers and on islands formed by successive flooding of parts of the sand hill areas. He was perhaps too conservative in the estimation of the time needed for speciation. I believe the parental stock of *gaigei* differentiated from that of the others (CPLR) during the Pliocene and consider the *retusus–lethroides* group as having separated no later than the Brandywine (Table 1). My reasons are based on somewhat indirect evidence. Compared subsequently to the evolutionary picture of *Pleocoma* in California and *Acoma* and *Podolasia* in Baja California, the pattern of speciation in *Mycotrupes* appears to have been developing in the Pliocene. Since *Mycotrupes* appears to be at least as primitive morphologically as these genera, I conclude that the development of the species of *Mycotrupes* may date back to similar times. This means that some area in west-central Florida was never completely inundated during the Pleistocene, as was suggested by Hubbell (*in* Olson et al., 1954). It also means that during the entire Pleistocene *M. gaigei* probably occupied its present range and that the *lethroides–retusus* group occurred fairly close to the Aiken–Augusta areas occupied by those species today.

The distribution of the species of *Peltotrupes* shows a close correlation in many respects with the species of *Mycotrupes*. I consider that the genus *Peltotrupes* (Howden, 1955) consists of two closely related species, one including two subspecies. *Peltotrupes profundus profundus* Howden occurs on the west coast of Florida and has a distribution almost identical to that of *Mycotrupes gaigei*. On the east coast of Florida, *Peltotrupes profundus dubius* Howden occupies areas also occupied by *Mycotrupes cartwrighti*. I consider *dubius* a subspecies, not only because it is extremely close morphologically to typical *profundus*, but because I suspect that the two populations merge somewhere in central Florida. The second species, *Peltotrupes youngi* Howden, occupies a rather restricted range of sand hills in the vicinity of Interlachen, Florida. This area is of interest for two reasons: first because it is apparently devoid of *Mycotrupes*, and secondly because it has approximately a 2°F higher annual mean temperature than the neighboring areas occupied by both genera. While the genus *Peltotrupes* is not closely related to other Geotrupini, its present-day species are closely related and seemingly are of rather recent origin. My assumptions on their possible speciation are presented in Table 2.

The genera *Gronocarus* and *Fossocarus* (Howden, 1960) have a linear distribution in suitable habitats along the Gulf of Mexico west of the Appalachicola River. *Gronocarus multispinosus* Howden occurs in western Florida from De Funiak Springs to Panama City. *Gronocarus autumnalis* Schaeffer is found in Mobile and Baldwin counties of Alabama. *Fossocarus creoleorum* Howden is known only from a

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female taken at Weirgate, Texas. The two genera are quite distinct but are more closely related to each other than to any other North American genus. They apparently have been distinct for a long period of time, but the speciation of *Gronocarus* probably occurred during the middle Pleistocene, in a manner similar to that surmised for *Peltotrupes*.

Having discussed the relationships within the four southeastern genera, I shall now consider the mechanism of isolation. If the genera have had a long evolutionary history, some of the barriers affecting them today must also have influenced their distribution in the past. It has already been mentioned that the dispersal of all of the genera must occur in the adult stage and that all the adults, or at least the females, are flightless (with the possible exception of *Peltotrupes*). Map 1 shows that a number of species are separated by major river systems. *Mycotrupes lethroides* and *retusus* are isolated by the Savannah River. The genus *Mycotrupes* stops abruptly east of the Appalachicola River, and *Peltotrupes* does not occur north of the Suwannee River. The eastward range of *Gronocarus* stops at the Appalachicola, and the genus is separated from *Fossocarus* by the Mississippi River.

Apparently suitable habitats for all of these genera occur on both sides of these river systems. It has long been argued that rivers are not effective barriers, for even flightless insects may be washed from one side to the other, or the river may change its course. If the rivers do not act as barriers (there are no major rivers between some species of *Mycotrupes* and *Peltotrupes*), what isolating factor is responsible? None of the species are found in the poorly drained pine–palmetto flatlands. The deep burrowing habit of the beetles, in conjunction with their need for well-drained soils, apparently limits all the species to the sand hills. Since the species are flightless, a few miles of flatland may represent an insurmountable barrier. All the rivers mentioned, when they reach the sand hill areas, are accompanied by extensive swamps and flat, poorly drained bottomlands. These particular systems have long been established and, with their associated lowlands, have apparently limited the spread of some of the species. During the Pleistocene the factors affecting isolation were altered by flooding of the lowland areas. Successive flooding not only isolated elevated areas, but the water might occasionally have acted as a dispersal agent, carrying adults from one island to the next over distances that, when the lowlands were exposed, were effective barriers. The relationships and distributions of the species at present, lack of species in low, coastal sand hills, or even in other suitable areas, can most reasonably be explained by the changes in sea level known to have occurred during the Pleistocene. Accordingly, the occurrence of various species in peninsular Florida and in the high inland sand hills indicates that at least some of these areas were exposed during the highest levels of the Pleistocene seas.

So far, I have mentioned the possible antiquity of the four genera, their survival over a long period in restricted habitats, and the barriers that apparently limit their distribution. There is one other interesting feature common to all the species in all four genera: they all are reproductively active during the winter or early spring months.

Table 3 shows that the genus *Mycotrupes* has a longer period of adult surface activity than do the other groups. I have previously discussed adult longevity for *retusus* (Part III *in* Olson, Hubbell, and Howden, 1954), and I expect a similar longevity of adults among the other species. If the adults often survive for more than a year, it is not surprising that occasional individuals may be collected at odd times, particularly under unusually cool climatic conditions occurring early or late in the summer. The peaks of adult activity, however, as indicated in Table 3, fall in October and November and again in February, March, and April. The 30-year average mean tem-

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TABLE 3—PERIODS OF SURFACE ACTIVITY BASED ON COLLECTIONS OF ADULTS.*

	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	April	May	June	July
Peltotrupes profundus				1		11	57	52	1	1		
p. dubius							1	15	5			
youngi							40	310	24			
Mycotrupes gaigei			64	1				298	21			
pedester			1	2	1		2	1	15	3		
cartwrighti (Ga.)	12**							15	2	2		2**
cartwrighti (Fla.)		7			1				3	1	1**	
retusus		3	12	18	1	6		25	4			
lethroides		8						3				
Gronocarus autumnalis				6								
multispinosus				4	4		1	4				
Fossocarus creoleorum								1				
Total	12**	18	77	32	7	17	101	724	75	7	1**	2**

* The figures indicate numbers of individuals. Records were compiled from many collections and represent many years of collecting; in some cases by residents of the areas; therefore, any bias due to intensive periods of collecting should be relatively small.

** Single collections, all of one species, *M. cartwrighti.*

peratures in these months for various counties in which the species occur is given in Table 4.

Generally, the peaks of adult surface activity fall between the first frost date (November) in the fall and the last frost date (March) in the spring. The average mean temperature for these months is about 62°F (± 8° depending on locality). During this period none of the beetles are active above ground at temperatures below 40°F. Apparently all the species are active mainly from midafternoon to about 10 PM and are particularly active when the late afternoon temperatures reach about 65° to 75°F. I have not found the beetles active on the ground when the temperature was much above 80°.

What explanations are there for the activity of these genera during the cool months of the year? This is certainly not typical for most North American insects or even for most of the sand-hill species. I have so far made four assumptions: (1) all the genera are of considerable antiquity, (2) they are long-time residents in the Southeast or migrated there early in the Pleistocene, (3) the species were for the most part differentiated during the Pleistocene due to isolation caused by successive flooding and exposure of lowland areas, and (4) the unusual distributional patterns remain today because of restricted habitat requirements and the inability of the species to traverse what are, for most other insects, minor barriers. If valid, these assumptions can be used as a basis for speculation on the unusual winter activity of the four genera. If a sedentary species with an optimum temperature for adult activity of 60° to 65°F is restricted to an environment that is rapidly becoming too hot for its survival during summer, there are not many alternatives for survival. It can either (1) adapt to the warmer climate or (2) change its period of adult activity to a cooler season. While other sand-hill insects may and do become active in early spring, few show the October to April pattern of *Mycotrupes, Peltotrupes, Gronocarus,* and *Fossocarus.* Also, while the deep burrowing of *Peltotrupes* and *Mycotrupes* may be related to moisture, it also may be related to temperature.

Other genera of Geotrupinae survive in the sand hills in much shallower burrows,

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TABLE 4—WINTER TEMPERATURES IN THE SOUTHEASTERN UNITED STATES: 30-YEAR NORMALS (°F)—1931–1960.

Station, county, and state	Oct.	Nov.	Feb.	Mar.	April	Avg. for station
Gainesville 3WSW Alachua Co., Fla.	72.1	63.7	59.6	63.6	69.5	65.7
Plant City	74.0	66.6	62.9	66.1	70.8	68.1
Hillsborough Co., Fla. Tampa WB. APT.	74.7	66.8	62.7	66.0	71.4	68.3
De Funiak Springs Walton Co., Fla.	70.1	59.5	56.5	61.4	68.6	63.2
Citronelle	69.0	58.5	55.0	59.9	67.1	61.9
Mobile Co., Alabama Mobile WB. APT.	68.9	57.9	54.7	59.3	66.6	61.5
Richmond Co., Ga. Augusta WB. APT.	65.2	54.1	49.3	54.9	63.2	57.3
Thomasville	68.8	58.9	55.4	60.3	67.1	62.1
Thomas Co., Ga. Thomasville WB City	69.7	59.4	55.3	60.4	67.8	62.5
Aiken Aiken Co., S.C.	65.7	55.6	50.5	56.1	64.5	58.5
Kirbyville Forest Ser. Newton Co., Tex.	68.3	57.5	54.9	59.7	66.9	61.5
Average °F by month	69.7	59.9	56.1	60.7	67.6	62.8
Approx. °C equivalent	21	15.5	13	16	19.5	17

WB.—Weather Bureau
APT.—Airport

and many have a typical spring–summer period of activity. Table 5 gives a comparison of collection dates for a few species in the related genus *Geotrupes* in various states. Adults of both *G. splendida* and *G. blackburnii* are active in the cooler months in the more southern states. In the more northern states there is a distinct shift toward a typical summer activity pattern. I believe there was a similar shift in the pattern of the four genera under discussion. This type of optimum temperature shift is not usual, even in North American *Geotrupes*. As shown in Table 5, *G. egeriei* is active in the Florida sand hills in almost every month of the year, with no indication of greater activity during a particular season. In more northern states its activity is merely restricted to the warmer months. This type of pattern is, in general, typical of most of the North American Geotrupinae and certainly differs from that of *Mycotrupes* and *Peltotrupes*.

All the evidence indicates that the four genera under consideration have changed their period of adult activity. Deep burrowing may indicate a temperature adaptation which could be of considerable antiquity since it has been an important factor in limiting dispersal. The sequence of these habits may have been as follows. The parent species lived in sandy habitats. During the first interglacial period, the sand areas were fragmented by the sea, dispersal was restricted, causing inbreeding and perhaps fostering the development of the flightless condition. During warmer periods the deep burrowing habit was developed and also the change in surface activity to cooler months. While adult activity probably varied with climatic changes, the other changes apparently were not reversible and played an im-

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TABLE 5—ADULT ACTIVITY OF SOME NORTH AMERICAN *GEOTRUPES*, BASED ON COLLECTION DATES. (FIGURES INDICATE NUMBERS OF INDIVIDUALS.)

Geotrupes	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
splendida												
Georgia	–	1	2	1	2	2	–	–	1	–	–	1
Raleigh, N.C.*	3	2	6	54	14	1	–	–	1	36	11	17
Penn.	–	–	1	2	–	8	24	16	7	5	2	–
Mich.	–	–	–	2	2	6	17	115	5	2	–	–
blackburnii												
Georgia	1	1	5	5	1	–	–	–	–	4	22	–
Raleigh, N.C.*	29	18	25	10	8	–	–	–	4	82	114	40
Penn.	–	–	1	10	3	5	1	2	2	22	4	1
egeriei												
Fla.	5	–	10	3	–	3	1	5	7	2	11	1
N.C.	–	–	–	–	8	7	26	7	4	6	1	–

* Data from traps (see Howden, 1955:241, 267).

portant role in the development of the genera as they exist today.

If the assumption that 60°–65°F has been the approximate optimum temperature of development through much of the evolutionary history of the four genera is correct, then for a considerable time during the glacial period of the Pleistocene, summer temperatuers in Georgia, northern Florida, and across the Gulf States may have had a mean summer or spring temperature not greatly in excess of 60° or 65°F. This would indicate that the summer climate for these areas during the glacial advances was approximately similar to that of Marquette, Michigan, which has a July mean of 65.3°F. This reasoning substantiates or is partly substantiated by pollen studies that have been made in the Southeast. Deevey (1949: 1375) discussed the occurrence of white spruce, larch, and arbor vitae near the Gulf Coast in Louisiana, and Dillon (1956:170–171) reviewed some of the pollen studies made in the Southeast. I have said that the "summer" temperature was equivalent to that of Marquette, Michigan. While the present study indicates a somewhat cooler summer climate than was suggested by Dillon (who believed there was at most a 5° to 10° difference from present temperature), it does not furnish any facts pertinent to the possible winter climate. However, if the winters had a January mean as warm at 35°F, as postulated by Dillon (1956:170), it would help to explain the survival of many sedentary endemic species of insects (as well as plants) in the southeastern United States, which today do not extend their range northward much beyond Maryland. Deevey (1949) has presented this idea of a narrow temperature range in discussing the odd mixture of northern conifers with the tulip tree, sweet gum, tupelo, and magnolia in the Pleistocene deposits of Louisiana. He states (p. 1375), "Such a mixture implies a lessening of seasonal climatic differences, the summers in Louisiana being cool enough for spruces, while the winters were still warm enough for magnolias." Also Darlington (1956:6) has pointed out the fact that "temperate" climates near the equator that have a low mean temperature may nevertheless show a narrow range between extremes. The data presented here on the habits of the flightless genera of Scarabaeidae in the Southeast seem to be in accord with this idea of a cool climate with a rather narrow temperature range.

The Southwestern Genera: Acoma, Podolasia

These genera, residents of the Sonoran and Chihuahuan deserts, while not closely

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related taxonomically, have apparently evolved along parallel lines in similar habitats. Taxonomically, *Acoma* (26 species) has been reviewed by Cazier (1953) and by Howden (1958, 1962) and *Podolasia* (8 species, one undescribed) by Howden (1954, 1958). In these papers there is little information on the habits of either genus.

During May 1959, I observed a number of populations of *Podolasia* (2 species) and *Acoma* (1 species) in the Big Bend region of Texas and found the female of *Podolasia bottimeri* Howden.[3] Both genera were found to have very similar habitat preferences, *Acoma* being, however, more restricted in distribution.

Generally, the habitats in which the species were found were within a few hundred yards of the Rio Grande but not in areas regularly flooded by the river. All populations occurred in rather flat, alluvial, dry-wash areas—not in the washes themselves but in the sand–clay banks which, in most cases, were covered with a good growth of mesquite (*Prosopis juliflora* [Swartz] DC.). The soil, when dry, cracked into a network of fissures one to three inches deep; in areas where the cracking was deeper, no *Podolasia* or *Acoma* were found. Also, no specimens were taken more than half a mile from the Rio Grande, even in areas where the habitat appeared ideal. Usually the beetles became active at dusk. A large number were collected at lanterns; however, the lights did not appear to attract them from any great distance. In one case, the lanterns were placed 50 yards from the typical mesquite habitat, and during half an hour not a single specimen was collected. The lantern was then moved to the edge of the wash area, and a dozen specimens were collected in ten minutes. After a month's work in the area, the evidence had become strong that the species have an extremely limited habitat preference and are restricted to a narrow band along the Rio Grande.

[3] I was extensively aided in this work by my colleague Dr. E. C. Becker and by Mr. L. J. Bottimer, Kerrville, Texas, who earlier had found the colony of *P. bottimeri*.

The distributions of the species were by no means uniform. Just beyond the western boundary of the Big Bend National Park, 2 miles west of Lajitas, two species of *Podolasia* were taken; at Lajitas only one species; at Castolon, 10 miles east of Lajitas in the Park, both species occurred; on the eastern side of the Park, approximately 40 miles downstream (east) from Lajitas, at Hot Springs, one species of *Podolasia* was taken; while at Boquillas, three miles east of Hot Springs, the other species of *Podolasia* and a species of *Acoma* occurred.

Of the approximately 500 specimens collected by searching and at light, all were males. No females of *Acoma* were found, and of *Podolasia* only females of *bottimeri* were collected. These were found at Hot Springs at depths of 8 to 12 inches in the sandy soil at the base of an old building, after males had been noted running on the ground. There was no indication of well-established burrows or food material. The females were heavy-bodied and flightless, lacking metathoracic wings and in general appearance resembling diminutive *Pleocoma* females. Intensive searching and digging in other areas did not disclose additional females, either of *P. bottimeri* or of other species. I can only conclude that the females rarely if ever appear on the surface of the ground and that new colonies are probably established only when females are washed out of their burrows to a new location by a severe flood. This means of dispersal appears to explain most satisfactorily the present distributional pattern and speciation in both *Acoma* and *Podolasia*.

During the summer of 1961, I studied other populations of *Acoma* in Sonora, Arizona, and Baja California. In all cases the beetles occurred in the mesquite–alluvial soil habitats, not far from a major drainage system.

In general, my field observations indicate that these two genera are not closely related but have very similar and unusual habitat requirements. Both occur near large drainage systems, or where these systems occurred in the past. Many of the species groups are distributed in a linear pattern

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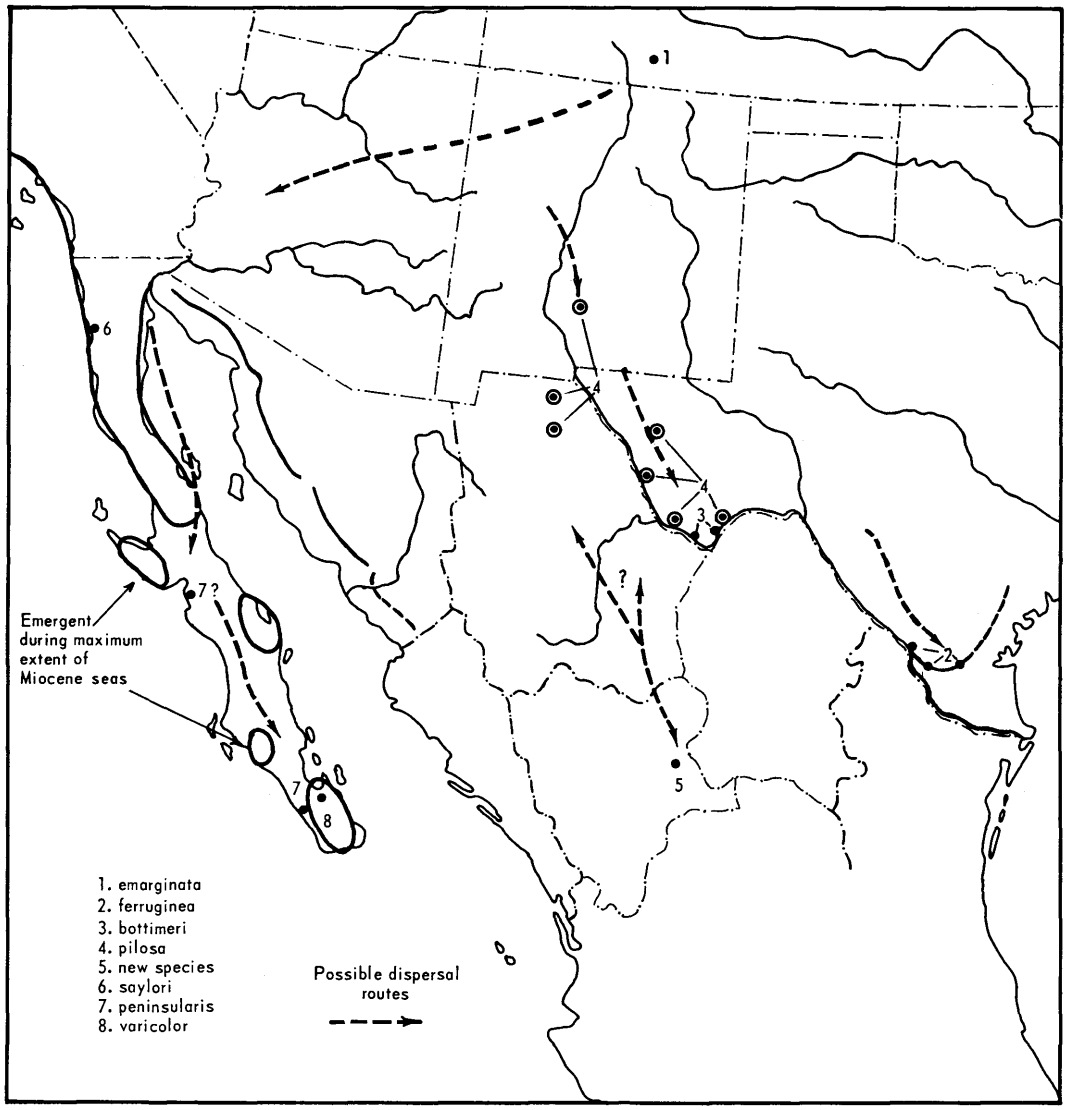

MAP 2. Distribution of the species of *Podolasia*.

related to these major drainage systems. Several species groups may occur either together or separately along one drainage system; this can produce a very unusual pattern of two species being sympatric, then allopatric, then one of them sympatric with either the same or another species. While the ancestral forms were probably winged and widely dispersed, today the various species are found in areas where flooding has deposited a thick layer of sandy clay soil but where heavy annual flooding does not now occur. In addition, dispersal of the present species is apparently extremely limited, owing to the flightless condition of the females.

Morphological studies show that specimens from a single colony are relatively uniform, and that the farther apart the colonies, the more often they are morphologically separable.

The morphological and distributional

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data combine to suggest that dispersal is very limited and occurs mainly by fertile females being washed from their burrows and surviving until deposited in a favorable downstream location. This mechanism would help to explain the distributional and speciation picture of these beetles, which roughly approximates distributional patterns of some fish in various river systems. If this is the method of dispersal of these two genera, a number of interpretations can be made from present distributional patterns.

Speculation on Barriers and Distributional Patterns

Several species, such as *Podolasia pilosa* Howden and *Acoma arizonica* Brown, are found in areas not connected by a linear drainage. Their present distribution rather suggests dispersal around the margin of a lake, with the central area being invaded as the lake dried. Many of the localities where *Podolasia pilosa* has been collected lie within the formation known as "La Mesa," which extends from the vicinity of Las Cruces, New Mexico, southward into Mexico. W. T. Lee (1907:11) states that "It is probable that La Mesa is the northern extremity of the broad interior basin of northern Mexico, the lowest parts of which, containing undrained lakes, occur 25 to 50 miles south of the international boundary. At some former time this basin was probably occupied by a large lake, the northern extremity of which covered La Mesa."

If *Podolasia pilosa* and possibly others, such as *Acoma arizonica*, were distributed around Pleistocene lakes, it would indicate that at least some of the speciation of both genera was pre-Pleistocene, for if differentiation was occurring rapidly, populations from the widely scattered colonies that are apparently unassociated with well-defined drainage systems should show considerable morphological diveregnce.

At this point, a brief discussion of the general distributional patterns of the two genera seems pertinent (Maps 2, 3). The eight species of *Podolasia* are easily divided into two main groups. One group, characterized by having a distinct carina across the vertex of the head, is composed of three species, all occurring in Baja California. The other, consisting of five species, lacks the carina on the vertex and occurs in southern Utah, in eastern Durango, and along the Rio Grande drainage area. This group can further be subdivided as indicated in Table 6.

The twenty-seven species of *Acoma* present a much more complex picture, but generally the species in Baja California and along the west coast of Sonora have characters or combinations of characters not found in the groups inhabiting the Gila, Colorado, or Rio Grande drainage systems (Map 3). The relationships and the major morphological differences are indicated in Table 7; further elaboration seems unnecessary.

The separation of both genera into distinct groups possibly occurred as early as the Miocene. The distributional patterns and occurrence of relict populations in widely scattered areas both indicate this and are discussed subsequently.

This development of species in the pre-Pleistocene periods is most evident in Baja California. Maps 2 and 3 show the maximum extent of the seas in Baja California during the Miocene as depicted by Durham and Allison (1960:60). Superimposed on these maps are the distributions of the species of *Podolasia* and *Acoma*. Five emergent areas are indicated for Baja California during this period; the resemblance of the present distributional pattern of groups of species with these emergent areas is difficult to explain by geological phenomena in later epochs. Also, the occurrence of related species on each side of the Gulf (keeping in mind the flightless condition of the female) indicates that, in at least one period, the Gulf was scarcely more than the width of a large river (probably in the vicinity of Tiburon Island), as was the case at certain times in the Oligocene and perhaps during several parts of the Pleistocene.

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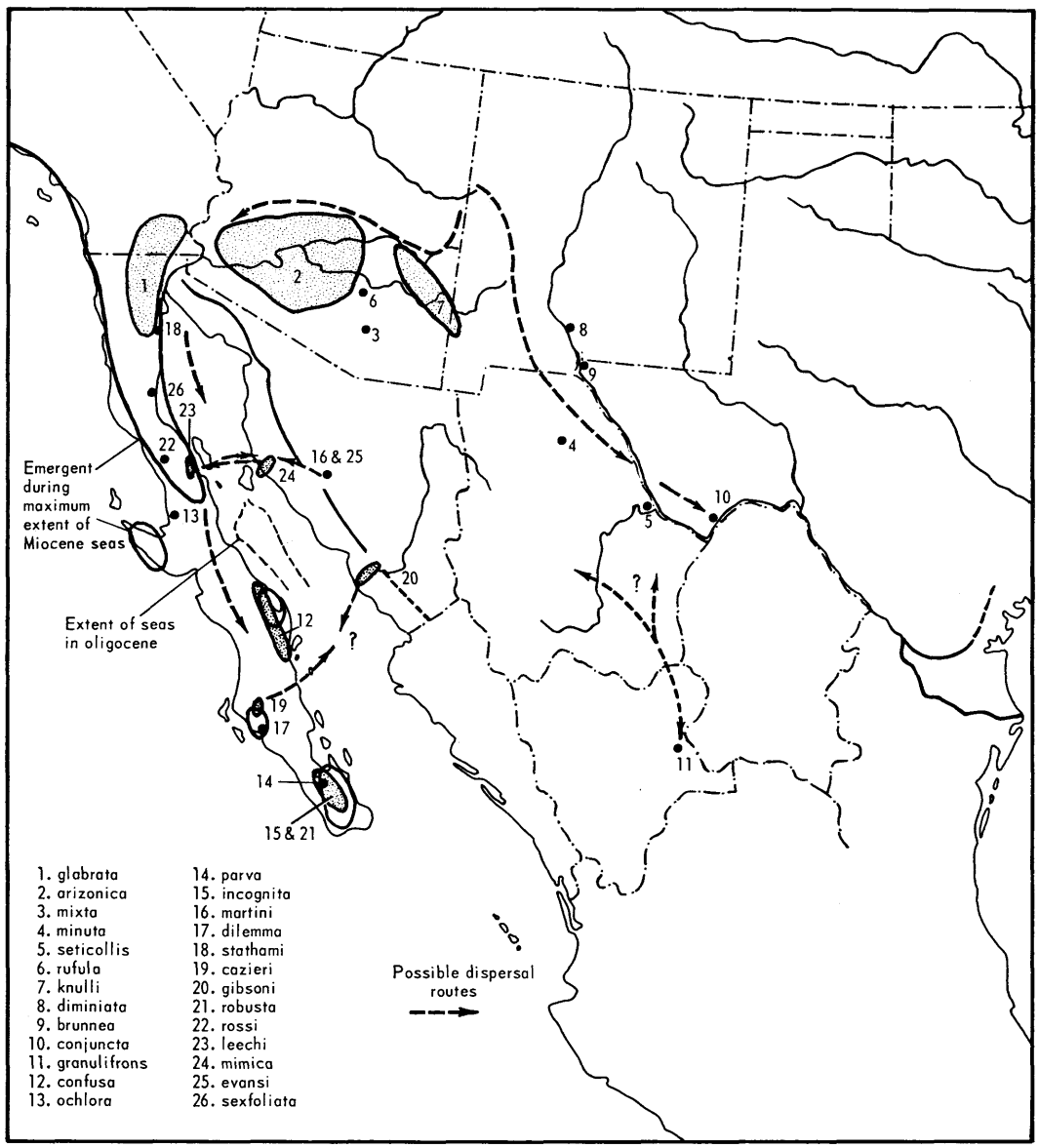

MAP 3. Distribution of the species of *Acoma*.

Another explantation would be that the precursors of present-day species were derived in the lower Colorado River system and were washed down both sides of the Gulf. However, the similar species occurring approximately opposite each other on either side of the Gulf and nowhere else makes the first theory more plausible.

There are other factors affecting this distribution, such as the apparent absence of *Acoma* (or *Podolasia*) in areas of volcanic ash. Also some species now occur in areas not long emergent, and I can only conclude that the species moved into these areas by being washed down recent drainage systems.

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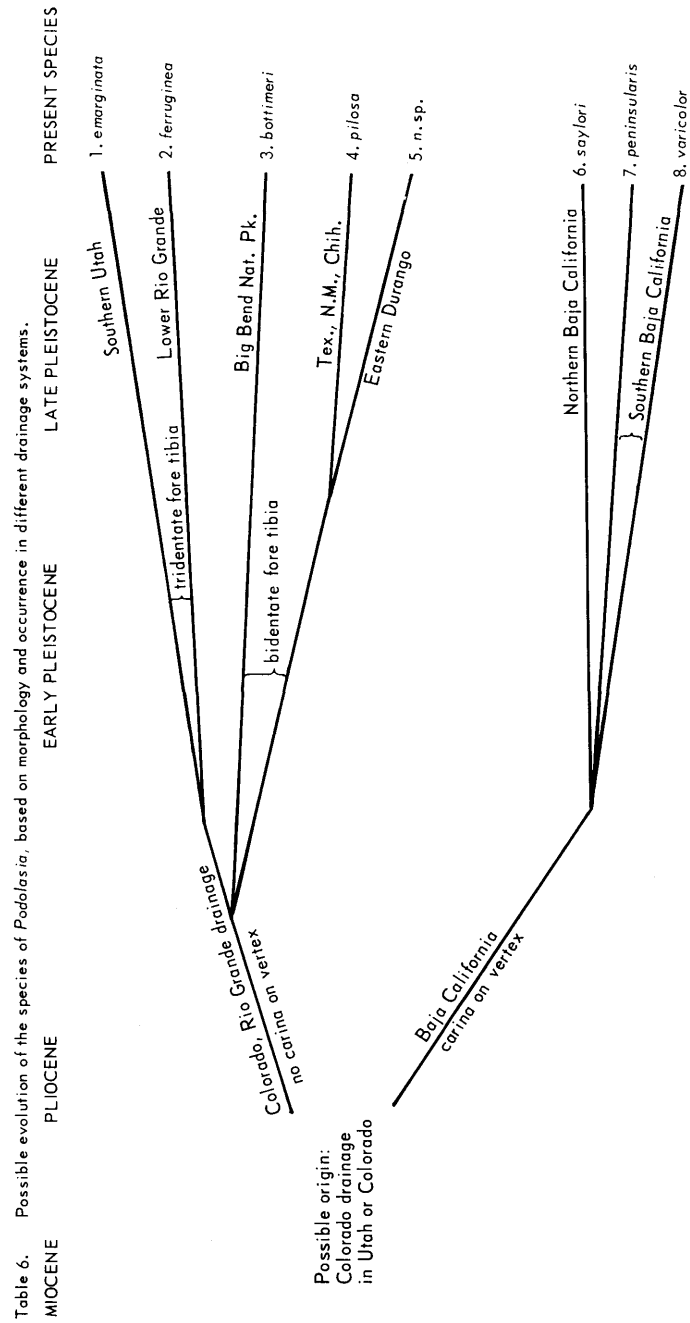

Table 6. Possible evolution of the species of *Podolasia*, based on morphology and occurrence in different drainage systems.

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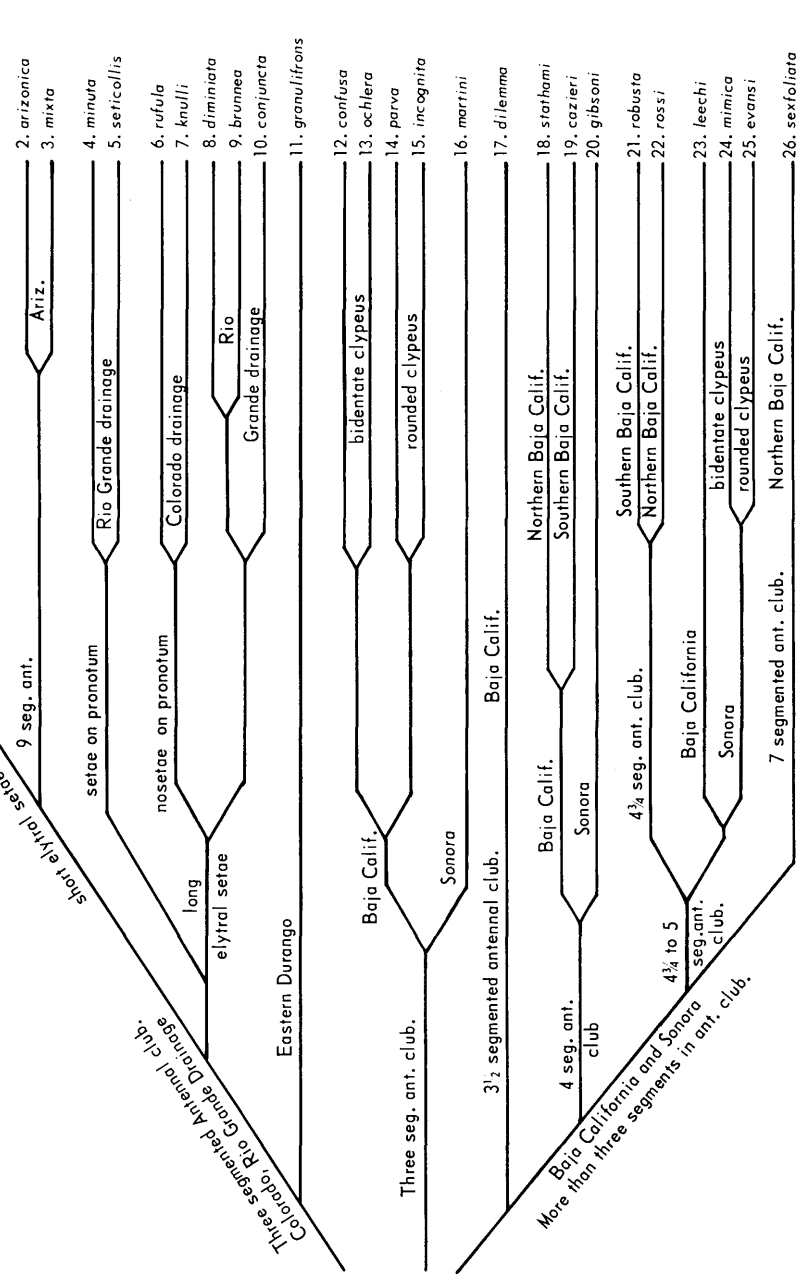
Table 7. Possible evolution of the species of *Acoma*, based on morphology and occurence in different drainage systems.



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In general the distribution of *Acoma* and *Podolasia* around the Gulf of California does not differ greatly from distributional patterns of other Scarabaeidae endemic to this area. Actually, many of these patterns are still rather obscure, partly due to lack of collecting along the coast of Sonora and Sinaloa. In his discussion of the entomofauna of Baja California, Truxal (1960:165) perhaps should have cited more specific examples of known distributions and should have stressed factors that might explain some of the distributional patterns. The higher elevations of the La Paz region have been isolated in several geological periods, and the area at present is isolated from other forested regions by the extremely arid central portion of Baja California. Isolation by high water and periods of increased precipitation undoubtedly have allowed both survival of relict species and also development of endemic forms. During the Eocene and again in the Miocene, isolated emergent areas were present not only at La Paz but near Magdalena Bay, Santa Rosalia, and the Vizcaino Peninsula. Today, in these areas endemic species of *Acoma* occur, but the number of endemics is not as pronounced as in the Cape Region, and north of Santa Rosalia the same or very closely related species may occur on either side of the Gulf, as is the case with *A. mimica* Howden and *A. leechi* Cazier. The strong Sonoran similarities in the peninsular fauna have been noted by Truxal (1960) and others, but the fact that in *Acoma* related species occur on opposite sides of the Gulf seems to indicate that at some time the species have crossed the Gulf and that the Sonoran fauna did not necessarily invade Baja California from the north. Even in extreme northern Baja California, endemic species such as *A. stathami* Cazier and *P. saylori* Howden occur, indicating a certain amount of isolation even in this region. In general, the scarabs show these patterns more strongly than many other groups of insects, being rather sedentary and often very restricted in their habitat requirements.

This pattern of relict populations prevails also in some areas outside of Baja California. *Acoma granulifrons* Howden, endemic to extreme eastern Durango, shows affinities to both the Sonora and Rio Grande groups. Today the Gomez Palacio–Torreon area, in which this species is found, is apparently a basin, and the inference from the morphology of *granulifrons* and the associated, undescribed species of *Podolasia* is that the area has not been connected by a drainage system with any of the more northern systems for a long time. There is little need to go into detail about the distributional patterns of other species, many of which show close interrelationships. Their speciation probably occurred in dry periods during the Pleistocene. Usually, related forms are on related drainage systems, with several species such as *P. pilosa* apparently having been distributed around the margins of ancient lakes. However, the most eastern species, *Podolasia ferruginea* LeConte, has been apparently distributed in a manner similar to that of some of the coastal forms in Baja California, i.e., along an old shoreline. While almost certainly distributed along the Rio Grande at one time, this species now occurs only near the Rio Grande in the vicinity of Laredo, Texas, at the edge of the escarpment above the lowland regions north of Rio Grande City and along a wash near Falfurrias. These areas generally coincide with the high levels attained by the ocean during the Pleistocene. This pattern of distribution seems to indicate that *P. ferruginea* was differentiated before the Pleistocene since the populations, while now isolated from each other, are still morphologically alike.

Speculation on Southwestern Pleistocene Climate

So far, I have avoided mention of the seasons in which adults of *Acoma* and *Podolasia* are active, stressing their limited habitat preference and methods of dispersal. The two genera occupy areas representing the Sonoran and Chihuahuan deserts, or at least the major drainage sys-

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tems of these deserts. There is no apparent season of peak activity of adults of either genus or for a group of species. Often desert forms have their flight periods associated with seasonal rains, but this does not appear to be true of *Acoma* or *Podolasia*. In May and June of 1961, I collected in Arizona, Sonora, and in the San Felipe region of Baja California. According to residents, drought conditions at this time were extremely severe, yet *Acoma* was collected in some numbers at Yuma, Arizona, Hermosillo, Sonora, and near San Felipe, Baja California. Some of the same species were taken by other collectors in the same months in different years. Also the same species have been taken from two to four months later in the season in the same localities. Generally, *Podolasia* occurs in May and June and *Acoma* from May through August. All the species avoid extreme daytime heat, becoming active in the evening, often not flying until after 10 PM. Apparently these genera have long been associated with and are well adapted to the mesquite habitats in which they live.

According to botanical evidence presented by Axelrod (1958) and Dillon (1956), the desert floras were well established prior to, and were not greatly reduced during, the Pleistocene. Dillon (1956:173–174) deduced that the temperature during the Pleistocene in the southern United States and northern Mexico did not vary greatly from that of today, with a mean temperature perhaps at most 5°–10°F lower. He also concluded (pp. 168–169) that rainfall was then somewhat greater in the Southwest (10 to 20 inches), seemingly arguing against the theory that lakes could form with only slightly more rainfall than at present and slightly lower temperatures, which would produce a lower rate of evaporation.

In general, the distributional patterns of *Acoma* and *Podolasia* seem to indicate the presence of an extensive area of the "mesquite thicket" type of vegetation along the southwestern drainage systems during the Pleistocene, with conditions at lower elevations in the desert not drastically different from those of today. The Sonoran and Chihuahuan deserts were almost certainly smaller but apparently extended across the continent during the Pleistocene and restricted north–south movement of many invertebrates and plants. Martin and Harrell (1957) present a number of arguments supporting this view. In their summary, they state (p. 478), "The eastern North American element in the humid montane fauna of Mexico is much smaller than that evident in the flora. At one station in northeastern Mexico, this element comprised 29 percent of the arboreal flora and two percent of the vertebrate fauna. . . . Present evidence thus suggests that few temperate-forest animals were able to cross the arid Texan barrier in the Pleistocene." Dorf (1959:195–196) presents a different viewpoint, but from the present studies and scarab distribution in general, I believe that the "arid barrier" existed throughout the Pleistocene.

In the Scarabaeidae such widely distributed genera as *Onthophagus* and *Geotrupes* show a distinct separation of species between the faunas of the United States and Mexico. *Geotrupes blackburnii* Fabr. and *Onthophagus hecate* Panz. occur commonly over the eastern half of the United States, where they have differentiated into subspecies; however, neither has extended its range into Mexico, even though both are strong fliers. Of approximately 30 species in these two genera endemic to eastern forested regions, none have extended into Mexico, and none of the 20 or so species occurring on the humid eastern escarpments of Mexico occur in the eastern United States. The similarity of the Mexican amber fossils (Hurd, Smith, and Durham, 1962) to present Mexican species indicates that many present species groups or genera were already there in the Miocene and that the insect faunas of the United States and Mexico had already started to diverge.

The inferences drawn from the distributions of *Acoma* and *Podolasia* in the desert regions seem to agree with the opinions

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presented by Martin and Harrell (1957), Dillon (1956), and others. The idea of the antiquity of the desert insect fauna was discussed in some detail by Van Dyke (1939:264), who believed that in general the modern assemblage of desert insects evolved "in its present territory or very close to it." He believed that at least some elements of the fauna may have evolved as early as the Tertiary. Blair (in Hubbs, 1958:422) states, "The specific question is one of how permanent has been the grassland barrier." It seems that it has existed for a long time, with little pronounced climatic variation.

The Western Genus Pleocoma

Almost all of the information presented here has been furnished by Dr. E. G. Linsley and Dr. P. O. Ritcher. Their help has been invaluable, and I am particularly indebted to Dr. Linsley for his notes and an excellent set of distributional maps which, with little modification, are reproduced here (Maps 5, 6).

The habits and distribution of the genus have been discussed by Davis (1935), Linsley (1938, 1946, 1956a, b), Ritcher and Beer (1956), and a number of other authors. The females of all species are flightless, live in burrows, and are found in quite restricted habitats. The males fly during the fall rains and in rare instances have been known to fly in snowstorms. All the general arguments concerning the antiquity (lack of close relatives, etc.) of *Mycotrupes* can be applied to *Pleocoma*, plus perhaps a few others. Linsley in his 1938 paper gives the following excellent summary of the distribution of the genus as then known (pp. 98–99):

> The large extent of the known territory occupied by *Pleocoma* today, even if one excepts the Alaska record, when considered in the light of the limited means of dispersal, indicates a relatively ancient distribution. The genus was, in all probability, already widespread in the Miocene and its distribution was undoubtedly affected by the climatic and topographic changes which have taken place since that period. During the Pliocene much of California was occupied by inland seas. An arm of the sea extended inward through Humboldt County, another just north of the present San Francisco Bay, a third near Monterey Bay, etc. As a result much of the San Joaquin Valley was under water, and the coastal region south from the Sonoma area was represented by a chain of islands. When the known present distribution of *Pleocoma* is superimposed upon a palaeogeographic map of Pliocene California a striking correlation is observable between its present occurrence and the distribution of Pliocene land masses. No known localities are far from these former land areas. This may possibly account for the absence of the genus from many parts of California, and also suggests additional regions where species may yet be found (i.e., coastal region in Monterey, San Luis Obispo, Mendocino, and Del Norte Counties; Santa Inez and Santa Lucia Mts., etc.). If the Alaskan record is correct, a large region, including British Columbia, Alberta, Montana, Idaho, etc., must be considered as possibly having once contained, or even still contains *Pleocoma*. The chains of mountains in this region (Rocky Mts., Bitter Root Mts., etc.) may well have offered the migration lanes by which the present representatives of the genus reached Utah. The widespread Pleistocene glaciation may account for the absence of the genus from these areas today, if indeed it is entirely absent, although, in view of the tolerance of many existing species for cold and wet conditions, one would expect the survival of some species on nunataks or along the margin of the glaciated area. We must wait, therefore, for more complete distributional information before any general conclusions may be drawn on the basis of geological evidence.

With little modification, Linsley's comments apply today. A considerable amount of information on the habits and ranges of the Oregon species has been added by Linsley (1956a, b) and Ritcher and Beer (1956), and further work is in progress. A new species has recently been discovered in Kern Co., California, but none of the new records change the overall picture as described by Linsley. There is some doubt about the Alaskan record of *P. trifoliata* Linsley, near Seward, but considering the time of year most species are active it cannot be ignored. Heusser (1960) discusses the possible survival of plants in unglaciated areas near Seward during the Pleistocene.

The distribution of the genus is indicated on Map 4, and the California distributions of the major groups are shown on Maps 5

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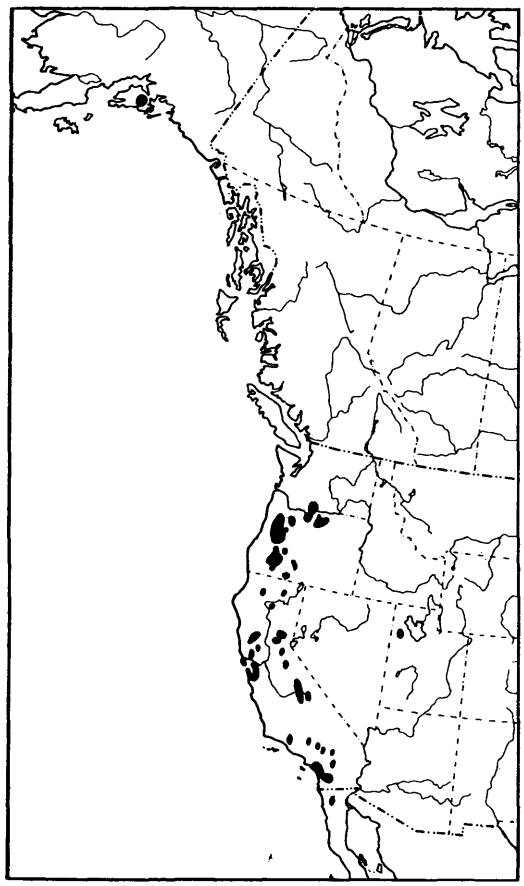

MAP 4. Distribution of the genus *Pleocoma*.

and 6 (after Linsley). While the present distribution of *Pleocoma* is not, as far as known, associated with existing drainage systems, the inference, based on present distributional patterns and lack of mobility, is that the genus was distributed along shorelines during the Pliocene or before. The general pattern of speciation, flightless females, relict populations, etc., roughly parallels that of *Acoma*, and while the overall distributional picture is still poorly known and probably cannot be explained by any one hypothesis, transportation of the flightless females by washing along shorelines seems to be one of the better possibilities. The genus can be divided into two major groups, those with four or five lamellae in the antennal club and those with six or seven. Usually the species with six or seven lamellae are found at higher elevations than the others, and possibly the two groups dispersed in different geological periods.

The collection dates for males of *Pleocoma* indicate that peak activity for most species occurs in the months of October, November, and December. Because of the extremely varied topography, county weather records are of little use, but the emergence coincides with the advent of the fall rains. While moisture is an important factor, *Pleocoma* shows a decided tolerance for low temperatures. Ritcher and Beer (1956:181) reported the following observation on *Pleocoma d. dubitalis* Davis in Oregon: "In 1954, flight began October 16 (Forest Grove) and continued, when conditions were favorable, through the second week in November. The largest flight observed took place on November 5 when 75 males were taken between 6:53 and 7:40 AM in MacDonald Forest, five miles northwest of Corvallis. During this time a gentle rain was falling and the temperature was 51°F." Tolerance to cool weather is not limited to the adults; Ritcher and Beer also reported (p. 183) that eggs held at a temperature of 56° to 58°F hatched in 13 days.

Speculation on Speciation and Climate

Ritcher (in litt.) has pointed out that the larger flights often occur during the cooler times of the day. If moisture alone were the major environmental factor influencing time of activity, a peak flight period during rains in the afternoon or evening (normally the time of maximum daily temperature) might be expected. Though information on the activity of *Pleocoma* above ground is admittedly sketchy, it is strikingly similar to that of the southeastern genera *Mycotrupes*, *Peltotrupes*, *Gronocarus*, and *Fossocarus*. In *Pleocoma* we have a large, supposedly ancient genus, all species of which have flightless females. None of the species occur in areas glaciated during the Pleistocene, so I assume that they have been and are quite sedentary. Distributionally, there

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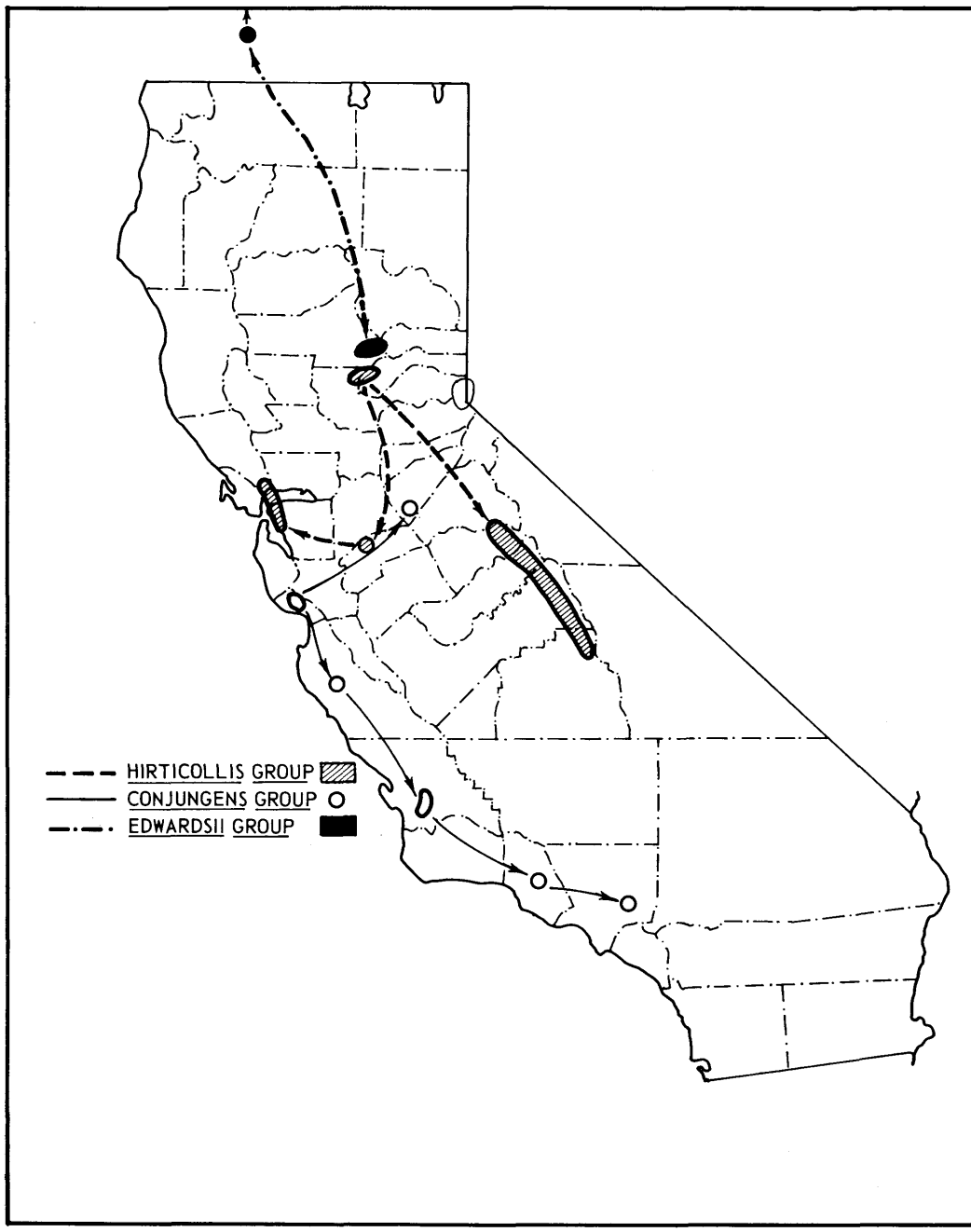

MAP 5. Species groups of Californian *Pleocoma* with antennal club of six or seven long lamellae. Higher elevations.

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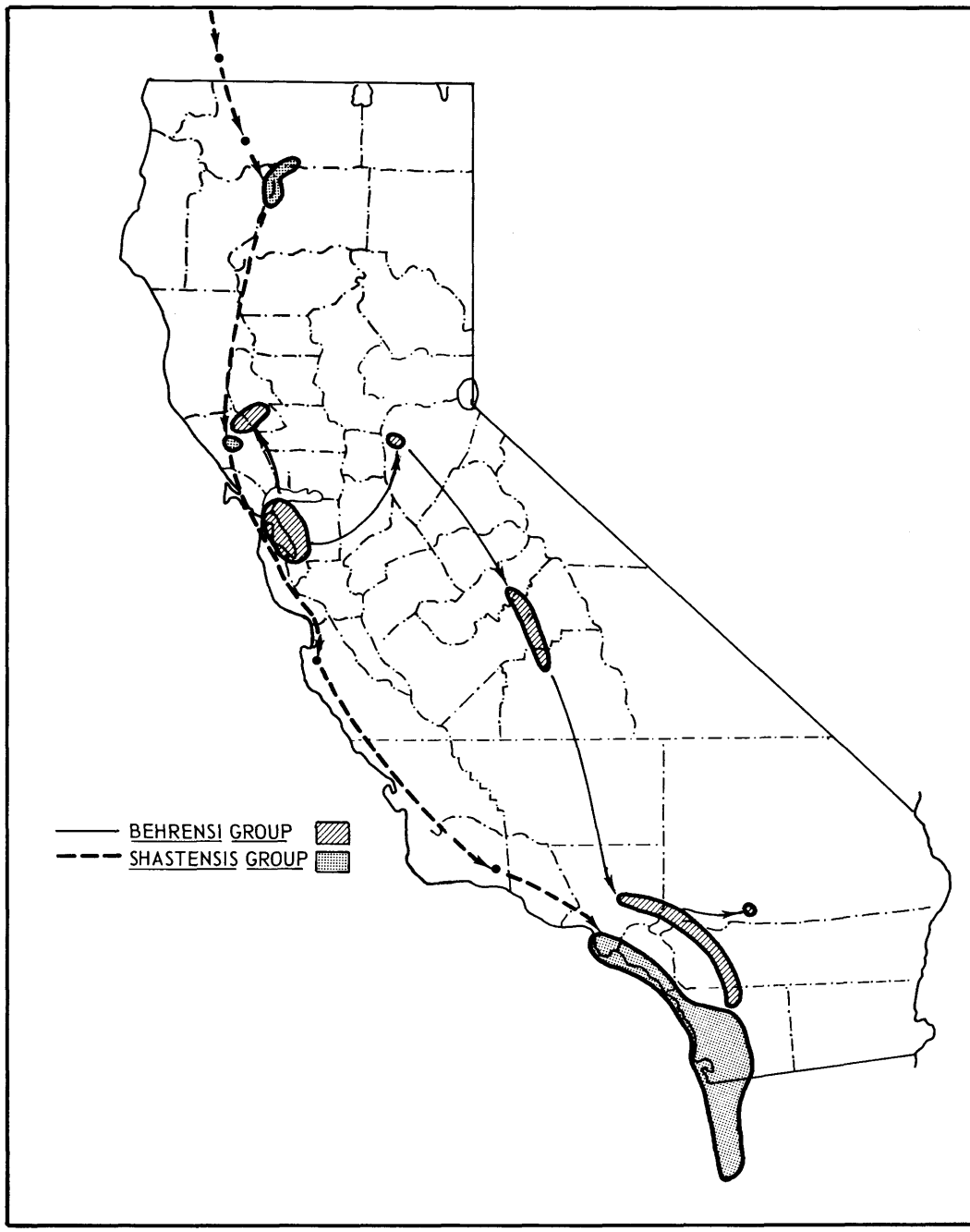

MAP 6. Species groups of Californian *Pleocoma* with antennal club of four or five long lamellae. Lower elevations.

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are chains of related species, the closely related ones probably having differentiated during the Pleistocene. All are cold-tolerant and active at an unusual time of year for scarab beetles. As in the case of the southeastern genera, it seems possible that they changed their period of activity, rather than adapting to hotter, drier weather. If this is true, then in the area near Corvallis, Oregon, in which Ritcher reported the flight of *Pleocoma d. dubitalis*, portions of the summer climate during the glaciated periods of the Pleistocene must have been both cooler, 50° to 60°F, and wetter than at present.

General Climatic Conditions

Two major theories have been advanced concerning the general climatic conditions that probably occurred in the southern, nonglaciated areas in North America during the major periods of glaciation in the Pleistocene. Flint (1947:452–456) considers that temperatures everywhere fell synchronously 4° to 8°C below present levels. Dillon (1956:168) believes there was a clinal depression of temperature ranging from perhaps 5°F in average temperature near the equator to perhaps a 25°F depression from present temperatures along the margins of the ice sheet.

A good deal of supporting evidence and speculation has been presented on each side. In a recent group of papers (assembled by Wendorf, 1961) on studies of pollen, invertebrates, and vertebrates of the Llano Estacado in eastern New Mexico and western Texas, Wendorf (p. 130) concludes (mostly because of the pollen studies, I believe) that July and January temperatures averaged 15° to 20°F cooler than today in the area studied. This depression in temperature he dated as occurring from 15,000 to 22,500 years ago. Dorf (1959) presents considerable evidence supporting this severe climatic change, but Hibbard (1960) concludes that, while summer temperatures were cooler, winter temperatures were not unlike those found today.

The temperatures suggested by Wendorf for an area only two hundred miles north of the Rio Grande appear extreme and, if insect distributions and their apparent centers of endemism mean anything, such depressions of temperatures in that area or in coastal areas appear very unlikely. My own conclusions are that summers both in the Southeast and along the Pacific Coast of the United States were considerably cooler (and perhaps wetter) during the major glacial periods of the Pleistocene. I am not completely in accord with Dillon (1956) on this but agree with his idea of moderate winter climates in these areas. If there was a temperature gradient and not a synchronous depression, the sea probably moderated the winter temperatures in both the Southeast and on the Pacific Coast, much as it does today. I agree with Dillon's general conclusions that the hot, arid areas of the Southwest may have been reduced in size during the Pleistocene but almost certainly were not eliminated. The many desert species of insects, including numerous flightless ones such as *Acoma* and *Podolasia*, probably could not have survived any great climatic fluctuations such as suggested by Dorf (1959) or Wendorf (1961). The same argument holds true for Baja California and coastal Sonora and Sinaloa. I doubt if the complex endemic desert fauna of Baja California would have survived any great climatic change; moreover, the fauna had no convenient refuge to which to migrate during the Pleistocene.

These ideas need considerable reinforcement before they can be called anything but speculation. However, none of the flightless genera mentioned occur in any area that was glaciated. For that matter, few species of flightless scarabs occur in the areas that were largely covered by glaciers. Other groups can be fitted into the overall picture. The flightless cicindelid genus *Omus* shows a distributional pattern roughly similar to that of *Pleocoma*. Some other species of insects, now either living in the subarctic or arctic or at high elevations, or having an early or late seasonal period of activity, are flightless or have reduced wings. Whether

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any of these species will add to the type of information presented here is an interesting question. As more information is accumulated on flightless species, other interpretations or explanations may become apparent, and we may well find a number of contemporary flightless species useful tools for the interpretation of past events. At present I can only say that in most respects, Dillon's theories on the Wisconsin Climate of the Pleistocene and his theoretical life zones (1957:174, Fig. 10) appear reasonable to me in the light of the present study.

Acknowledgments

A number of people have provided information, suggestions, and data that have been useful in the preparation of this paper.

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Dr. G. B. Leech, Department of Mines and Technical Surveys, Ottawa, made a number of helpful suggestions, particularly with some of the geological aspects of the paper. I am also indebted to Dr. P. J. Darlington, Jr., Museum of Comparative Zoology, Cambridge; Dr. E. G. Munroe, Entomology Research Institute, Ottawa; Dr. T. H. Hubbell, University of Michigan, Ann Arbor; and Dr. J. D. Lattin, Oregon State College, Corvallis, for constructive comments on many aspects of the paper.

Lastly, I am indebted to the Office of Climatology, Weather Bureau, United States Department of Commerce, for the climatological information used in Table 4.

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