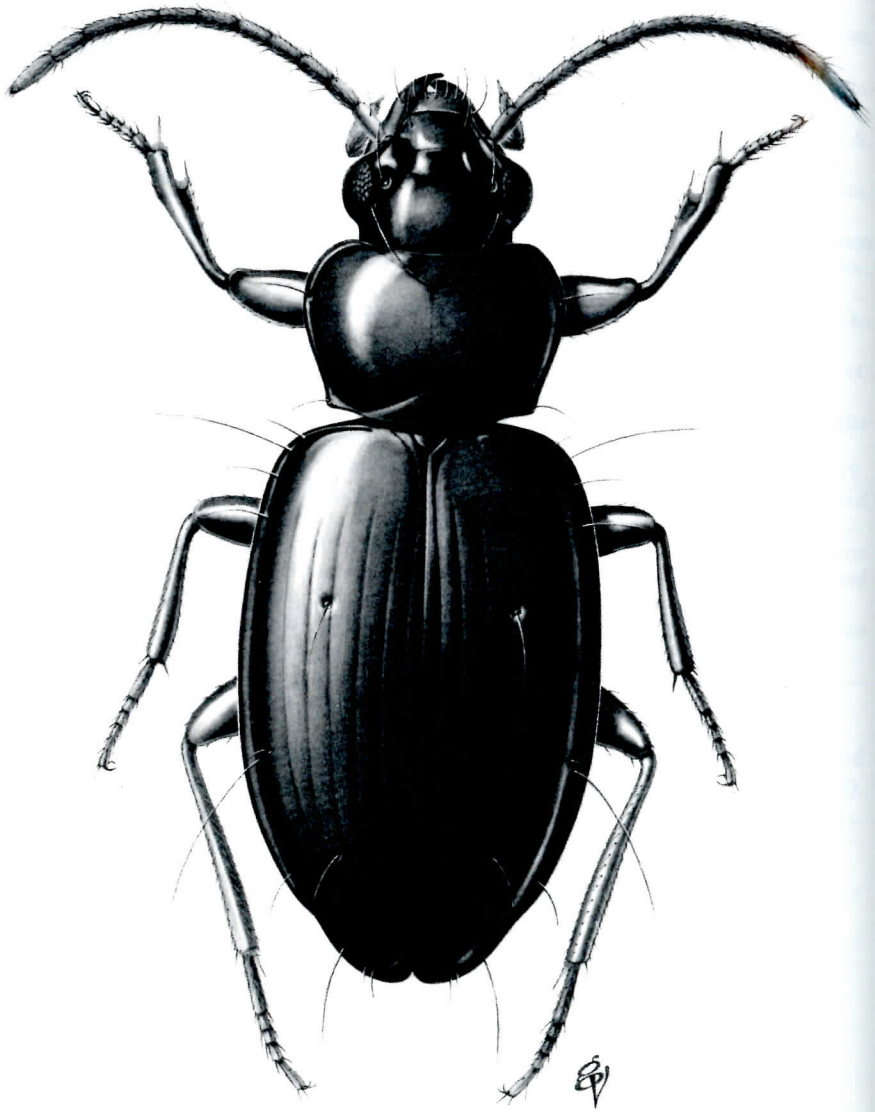


Frontispiece: Habitus of *Paratachys potomaca*, n. sp., Plummers Island, Maryland.

NATURAL HISTORY OF PLUMMERS ISLAND, MARYLAND

XXVI. The Ground Beetles of a Temperate Forest Site (Coleoptera: Carabidae): An Analysis of Fauna in Relation to Size, Habitat Selection, Vagility, Seasonality, and Extinction

Terry L. Erwin

Abstract.—Plummers Island, Maryland, USA, a collectors' focal point for over 75 years in the Washington, D.C. area, was sampled for ground beetles extensively between 1901 and 1915, 1970 and 1978, and intermittently between 1915 and 1970. Specimens collected were stored at the National Museum of Natural History, Washington. Data from these specimens and their accompanying labels, as well as associated cardfiles and literature, were synthesized to provide species profiles and a faunal history between 1901 and 1978. During this period, 214 species, at one time or another, were represented in the fauna. These species are arrayed in 24 Tribes, 69 genera. There were 160 species in the first decade and 101 in the last, thus as the island's flora changed from open Juniper-Grassland to the submature Oak-Hickory-Maple of today, the number of carabid species dropped considerably. This drop in number was accompanied by a change in species composition from open-habitat species to forest dwellers, from wingless species to winged species, from species with larger-sized individuals to species with smaller-sized individuals. Other concurrent shifts occurred in color, as somber species replaced brighter, metallic species, and species with isodiametric microsculpture were replaced by those with transverse microsculpture which produces iridescence. These and other changes reflect, in part, the successional development of the vegetation; they also reflect more subtle environmental changes not yet fully understood. Size distribution of the fauna follows that of a bimodal curve. The suggestion by Darlington that ants depress the curve is explored with the conclusion that it is possible but still untested. During the period 1901 to 1978, all the larger species (over 20 mm) became locally extinct, those new to the fauna were all small to medium-sized (2 to 11 mm). Members of the fauna collectively show diverse ecological range; nearly all habitats are occupied by carabid beetles. Most species overwinter in the adult stage; the number of larval hibernators has been decreasing during the last 75 years. Most species are nocturnally active; 15.8% of the fauna is diurnal only and these members are on average smaller in size than nocturnal forms. The fauna is composed of widespread species, middle latitude species, a large northern element, a small southern element, and a very small introduced element. Most species at the site are fully winged and vagile dispersants; those brachypterous species in the fau-

na early in the century have mostly become locally extinct; all species new to the site after 1959 are fully winged and mostly highly vagile dispersants. The kind of smaller species new to the floodplains suggests that a high quantity of organic debris was added to the substrate. During the Pleistocene, the Plummers Island fauna was a species reservoir and was not much disrupted as a fauna like that at the edge of the ice. At present, the relatively rich fauna of Plummers Island is in a modern refugium as development and environmental destruction proceeds in an accelerated fashion on all sides.

Contents

Introduction

The family of ground beetles, Carabidae, lends itself particularly well to comparative faunal analyses because it is geographically widespread, numerous in species, especially diverse ecologically, and increasingly becoming better known taxonomically (Ball, 1979; Darlington, 1943; Erwin, 1981). Current estimates place the size of the family at ca. 40,000 described species and many, many more are in the process of being described at present. Latitudinally, the family ranges from well above the Arctic Circle (78°56′N on West Spitsbergen; Bengston et al., 1975) to southernmost South America (ca. 55°S at Puerto Williams, Tierra del Fuego; Darlington, 1965). They are present on all large islands and all continents except Antarctica (presently); they are on most small islands including such isolated Pacific ones as those of the Hawaiian archipelago, Bonin Islands, Gilbert Islands, Easter Island, and even Rodrigues in the Indian Ocean. In terms of life style, carabid habits range from blind troglobites to terricoles and arboricoles, from subaquatic to semidesertic forms, from vicious carnivorous predators to seed eaters. They range in size from 0.7 mm (Anillina) to 66.0 mm (Scaritini) and they are diverse structurally, chromatically, and chemically (defense secretions, see Moore and Wallbank, 1968; Moore, 1979; Aneshansley et al., 1969; Eisner et al., 1977).

With such diversity inherent in this single family of beetles, a well-planned faunal analysis based on sound current and historical knowledge of ecologic ranges and occurrence should be indicative of changing diversity in the environment. Reading environmental diversity through ground beetle faunal analysis may prove to be a baseline for a much finer-tuned monitoring system than heretofore available because of the ground beetles' stenotopic nature, their numbers, and their ecologic ranges. Perturbations in the environment (e.g. Freitag, 1979), whether "natural" or man-made, could be more readily detected.

Goals.—Lindroth's (1945–1949) ecological analyses of Fennoskandischen Carabidae and Darlington's (1952–1971) ecological and zoogeographical analyses of New Guinea Carabidae were milestones as detailed studies of a large group of closely related insects in a specific place (Erwin, 1972). As with the direction and methods of these monumental achievements in mind that I embarked on the present study and subsequently planned expansion of it for future comparisons with faunas at other sites. It is the goal of this series of comparative faunal analyses, of which this paper constitutes the first, to provide a composite carabid natural history of lowland forest sites around the world both in and out of the tropics, and to analyze the faunas with respect to several parameters including size, composition, ecologic ranges, seasonality, vagility, extinction patterns, and historical zoogeographic aspects. The compilation of baseline data for each site will allow students and workers at each area to begin monitoring their respective faunas and will allow me to begin interfaunal comparisons. I believe that these

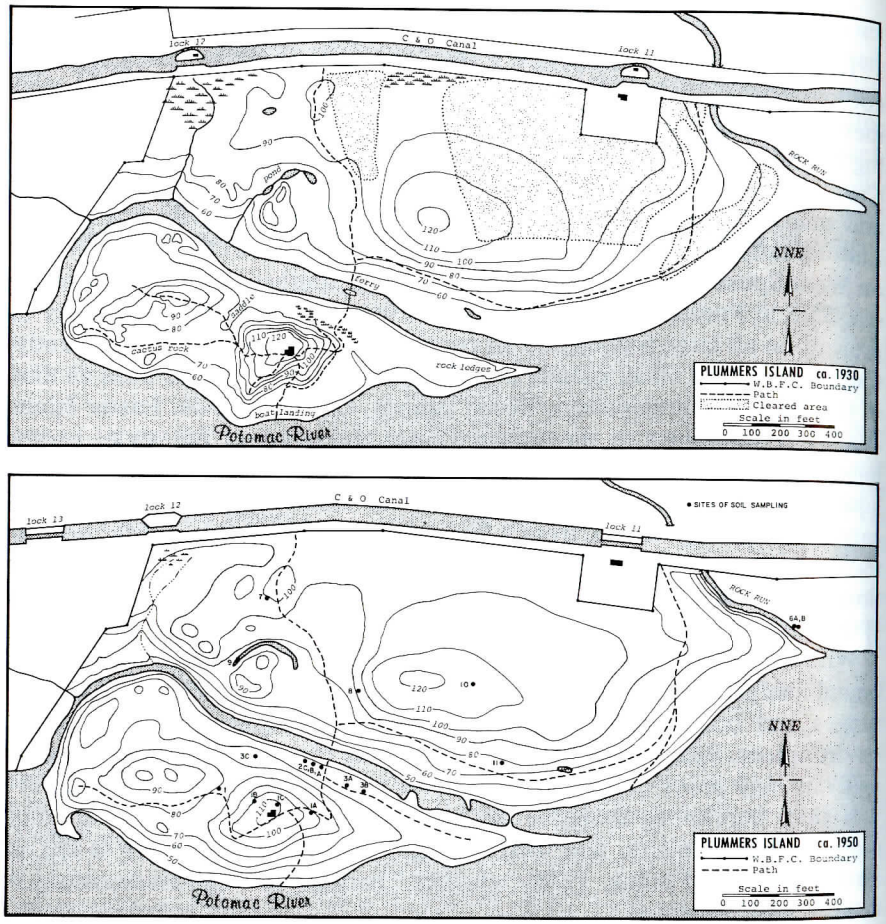


Fig. 1. Topographic maps of study site (exclusive of Virginia shore) with landmarks referred to in text; la) ca. 1930, lb) ca. 1950 with locations of soil samples of Table 1.

faunal comparisons will provide information pertinent to the elucidation of the ecologic and zoogeographic evolution of Carabidae and will provide data to address the concept of taxon pulses (Erwin, 1979, 1981; Erwin and Adis, 1981). This is my ultimate goal.

Site Description and History.—Plummers Island, the study site of present interest, has been a semi-protected environment since 1901 as a result of lease occupation and subsequent purchase by the Washington Biologists' Field Club. The Plummers Island site is located 14.5 kilometers northwest of The Mall, Washington, D.C., on the Potomac River in Montgomery County, Maryland. For the purposes of this study, the adjacent Virginia shore is included. The "mainland" Maryland property, 15.58 hectares, belonged to the Club for a number of years and was frequently collected by Barber and Schwartz, and others. I have also collected extensively the land between Rock Run (old sense, see map) and the Beltway (Fig. 1) during 1971 to 1978. Barber collected extensively on the Virginia shore, probably reaching the area by boat. Due to this shore's near inaccessibility, I have done very little extensive work there although I sampled it on a few occasions with long walks up the Potomac River from Turkey Run Park. The part of Virginia shore sampled constitutes about 3.6 hectares, the same amount of land as the Island itself. Thus, the total study site is about 23 hectares of land, in the form of a northeast-southwest transect 957 m wide, 643 m long; an area which includes also the Potomac River and northside Channel (Fig. 1).

The topography of the site has changed very little since 1901 with the exception of Rock Run which was dammed at its mouth in 1922 by a squatter. The flooded area caused some alluvium to be added to the easternmost edge of the study site but that is all. The squatter was evicted in 1927 and the dam subsequently destroyed; the remains of the cement work and pillars can still be found today. After the building of the beltway and various diversions built on Rock Run, this stream now empties into the Potomac both at the north end of the Island under the Beltway interchange and where it is shown to empty on Fig. 1. The substrate of the island's western and eastern perimeter has fluctuated over the years as floods deposit and carry away sand, cover sand with layers of silt, and remove or deposit drift materials. Old maps of the site show a marsh on the island's secondary floodplain between the cabin's knoll and the ferry slip. This area is now sandy and no different than the adjacent floodplain. Low marshy areas still exist near the towpath (Fig. 1). Large tracts of cleared area (Fig. 1) were left to revert to forest after the Club purchased mainland property. These areas now are mostly stands of *Pinus virginiana* with an understory of trailing vines. Much of the vegetation of the island's upland was apparently cut in the 1800's, as early photographs (Fig. 2) show no or little tree cover except *Juniperus virginiana*. This species is noted in the area as a pioneer species in abandoned fields and dry habitats.

The only other major change at the site during the past 79 years was the building of the circumferential highway (Beltway 495) and Cabin John Bridge just west of the Island. Although the road and bridge have little affect on the flora and fauna of the site, except perhaps the grassy median strip being used as avenues of dispersal for open habitat species (Krombein, 1964), the gas combustion engines of the heavy traffic using the roads have increased noise levels and heavy metal "fallout" (Hale, pers. comm., 1976). The effects of noise have not been studied; the affects on lichens by heavy metal fallout are presently under long-term study by Hale (pers. comm.).

Activities of human existence up river have certainly resulted in changes in silt carried and deposited by the river. Unfortunately, measurements of

Fig. 2. Plummers Island from the Virginia shore, January 1905; photograph by A. A. Doolittle.

the changing silt levels were not recorded at Plummers Island. Other kinds of water pollution coming down river also must have affected the shore lines, particularly heavy deposits of organic debris. These changes were not recorded at the Island either, although changes in the shoreline carabid fauna during the last 79 years indicate considerable environmental perturbation.

Geology.—Geomorphologic aspects at the study site and in surrounding areas are well known (Carr, 1950). Plummers Island lies about 8 kilometers to the west of the Fall Line (where the Coastal Plain interfaces with the Piedmont Plateau) on the Piedmont Plateau. The island is formed on a hard outcropping of granite gneiss which rises 23 meters above the water line. This same rock formation is exposed on both the "mainland" and Virginia shore as well. At some places on the "mainland" there are exposed schists as well, which have broken down and become small stone slabs on, or loose pieces in, the top soil. The clay overburden varies in depth depending upon location. Sands are deposited on the floodplains to varying depths and are mixed with clay in some places. Sands of the primary floodplain are recurrently overlain with varying thicknesses of silt. During dry periods, the exposed silts cake polygonally exposing the underlying sands along the bottom of the cracks. Loams are formed in upland forests where the trees are oldest. Large granite gneiss talus slopes occur on the Virginia shore and

Table 1.—Partial soil chemistry at Plummers Island (see Fig. 1b for sample locations) where H = high, VH = very high, L = low, VL = very low, and M = moderate.

Sample location	pH	Mg^{+2}	P_2O_5	K_2O	Ca^{+}
1A	4.5	18VL	20L	105M	20
1B	4.5	14VL	125M	150M	40
1C	5.1	250VH	30L	231H	3000+
2A	7.6	148H	45L	60L	3000+
2B	7.3	162H	55M	84M	3000+
2C	7.4	242VH	40L	111M	3000+
3A	7.6	282VH	40L	114M	3000+
3B	7.6	170H	60M	87M	3000+
3C	7.7	300+VH	25L	132M	3000+
4	6.2	206H	30L	129M	2200
6A	7.1	160H	30L	63L	540
6B	7.2	298VH	35L	156M	3000+
7	4.5	18VL	15VL	90M	20
8	5.6	110H	50L	201H	1160
9	4.9	90M	25L	114M	240
10	4.4	16VL	20L	108M	20
11	5.2	46M	15VL	150M	280

on the northeast side of the Island below the cabin; a small talus slope occurs on the mainland near the Ferry-Towpath Trail.

Soil chemistry was tested at sites 1 through 10 (Fig. 1b). In general, floodplains have slightly basic pH, while uplands have highly acidic soils (Table 1). Tests for several chemical components were made for amounts in soils at the 10 sites. Mg^{+2} is correlated negatively with elevation, that is it is highest in the floodplains, lowest in the upland forests. P_2O_5 is relatively constant throughout, except at site 1B, which had twice the value of all other sites. This area is the traditional dumping grounds for oyster shells after the WBFC Fall Field Day and this may account for altered soils on that particular slope. K_2O appears to have no correlation with elevation or site, although the two high values are both in mixed mid-elevation forest, and the lowest values are on the floodplain. Ca^{+2} is correlated negatively with elevation, that is the highest concentrations are in the floodplains, lowest at sites in the upland forest.

Topography.—The study site is quite diverse topographically (Fig. 1). The Virginia shore is a steep northeast-facing slope with very little flat floodplain. The Island consists of two uplands or knolls, one with the cabin standing at 38 m elevation (23 m above the river) and the other at 30.5 m. The Island is elongate, oriented with its long axis east-west. Upstream the blunt end of the Island is mostly solid rock with overburden only in low depressions. Downstream much sand and silt is recurrently deposited. At

one time a small pond occurred near the shore at the southern edge of the west end, and often small temporary ponds would be left on the southwest floodplain (P. J. Spangler, pers. comm.). In the early years a marsh occurred below the cabin on the Ferry Trail; this marsh has long since disappeared, filled in during river flooding; this suggests that flood patterns may have changed in recent years. The "mainland" is the most diverse area topographically. Two knolls are dominant and their relief provides drainage enough to form two small rivulets and to feed Rock Run. One rivulet forms in a forest swamp near Lock 12 and enters the Channel; it does not have permanent water flow. Three connected woodland ponds supply the second rivulet; it is not permanent either and the ponds are intermittently dry. Rock Run, at the eastern boundary of the site, is a fairly deep ravine with permanent water flow along its base. It empties into the Potomac at a relatively wide delta. Rock Run was dammed in 1922 and alluvium was added to the study site on its eastern boundary. The dam was removed later when the Club acquired land east of Rock Run. In the early part of the century a marsh also occurred near the tow path, midway between Lock 11 and Lock 12; this has since filled in and is now pine-broadleaf subclimax. Extensive areas near Lock 11 and the Ferry Trail were at one time plowed and cultivated but have since reverted to pine-broadleaf subclimax; these areas have a gently rolling contour.

For the most part, the "mainland" primary floodplain banks are quite steep, sloping to the Channel at 30° or more while the Island banks are 15° or less (except at the rocky west end). The Virginia primary floodplain banks are also quite shallowly pitched.

Flora.—Over the years, various authors (Killip and Blake, 1935, 1953; Leonard and Pierce, 1939; Leonard and Killip, 1939; Leonard, 1935) dealt with plants of the Plummers Island site. Unfortunately, Killip and Blake's (1935) list is the last botanic contribution and is in need of updating. This list does cover 720 species however, and is useful for our purposes. Aldrich and Duval (1943) provided a classification of forest habitats while undertaking a census of breeding bird populations. I adapted this classification to present needs by splitting and elaborating it as follows for the purpose of describing the site and its dominant flora (see also Figs. 22 to 29).

I. Floodplain Forest: climax stands of mature cottonwood (*Populus virginiana*), sycamore (*Platanus occidentalis*), boxelder (*Acer negundo*), ash (*Fraxinus americanus*), and elm (*Ulmus americana*) standing on secondary and tertiary floodplains, mixed with smaller trees and shrubs, substrate of sand and sandy clay; in existence in its present state since 1901 and before.

II. Upland Forest: subclimax stands of young oaks (*Quercus* spp.), hickories (*Carya* spp.), maples (*Acer* spp.), hackberry (*Celtis* spp.), beech (*Fagus grandifolia*), American hornbeam (*Carpinus caroliniana*), and butternut

(*Juglans cinerea*) standing on rolling and sloping well-drained uplands, mixed with smaller trees and shrubs, with scattered or clumped conifers (*Pinus virginiana, Juniperus virginiana*) at higher elevations, substrate of loamy clay on the surface and clay beneath; in existence, as a unit, from mid-1920's.

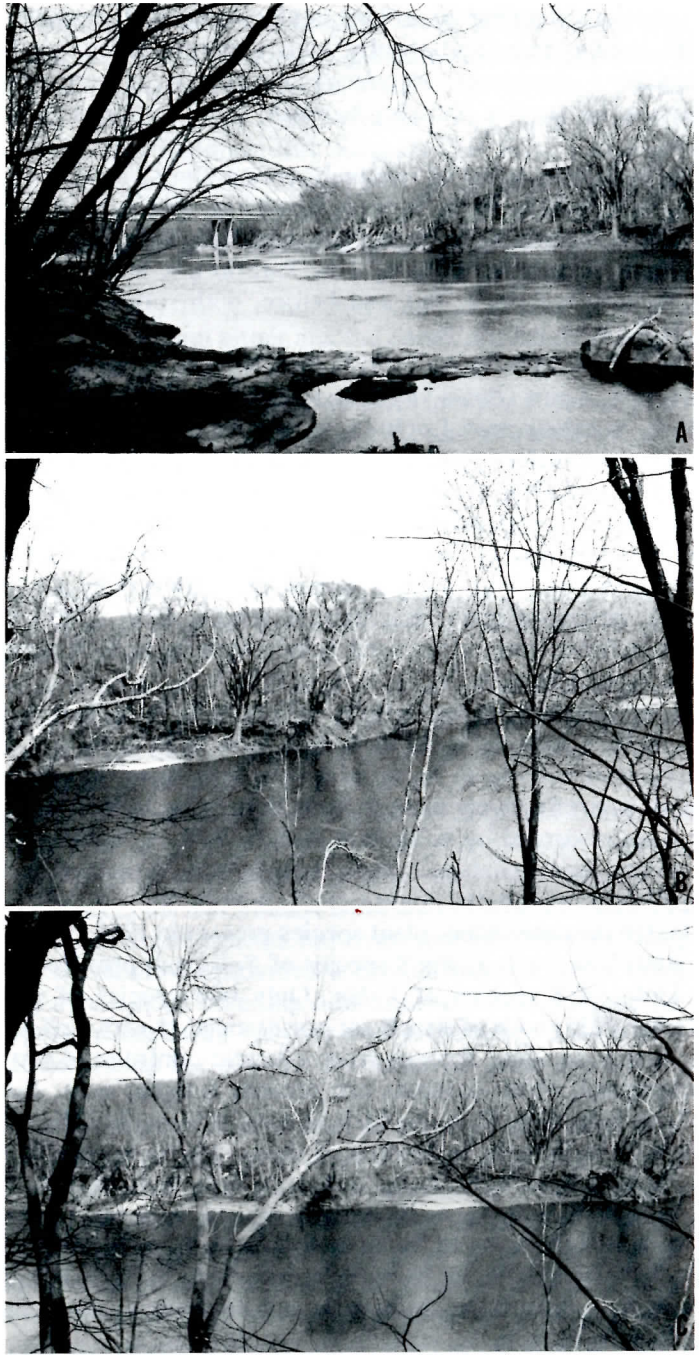
III. Swamp Forest: stand of relatively young elm (*Ulmus fulva*), maple (*Acer* sp.), butternut (*Juglans cinerea*), Black haw (*Viburnum prunifolium*), "Ironwood" or American Hornbeam (*Carpinus caroliniana*), and scattered smaller species standing at edge of Tow Path in low poorly drained area, probably in existence since 1901 and before, with substrate of rich peaty and organic debris lying on loam.

IV. Open Field: cultivated to 1918, then with many grasses, presently transition forest of pine (*Pinus virginiana*) and young Upland Forest species noted above, standing near Lock 11 adjacent to Tow Path, substrate of loamy clay on the surface and clay beneath.

A comparison of Figs. 2 and 3 shows that in 1905 much of the upland western portion of the Island was treeless. Whether this was due to logging or agriculture is unknown. Protection of the Island through Club purchase allowed the forest to return to near climax conditions (Fig. 3). The *Open Field* (Fig. 1) described above has also returned to forest. Thus Club protection of the forest trees decreased floral richness and eliminated open habitats for ground beetles.

Other minor habitats present before 1933 included a *Typha* marsh (Fig. 1) where certain species of carabids would have been found. At one time, chestnut (*Castanea dentata*) occurred on the Island and mainland and, of course, now it is effectively absent from the region. Other species, nondominant ones, recorded by Killip and Blake (1935) as "extinct" or absent from the Island and mainland were probably not significant in terms of ground beetle microhabitats because most carabids are not tied to specific host plants. On the other hand, plant species present in 1935, but now absent from the study site, such as the 8 species of *Solidago,* provided microhabitats for adults of 6 species of *Lebia*. Only two species of *Lebia* were collected after 1935, both of which are not associated with *Solidago*.

Plant cover in an area, through microclimatic control and providing of cover, determines which carabids are present for that area. Since most species of carabids at the Plummers Island site are terricoles, the plant cover affects them in such ways as amount of shade, log (cover and hibernation sites) producing rates (average age of trees), type and amount of leaf fall (controlling near-ground microclimate, cover, soil structure, and soil pH). Minor portions of the carabid fauna such as the arboricoles would be affected by kind and number of trees which provide under bark, heartwood, and leaf surface habitats, and by having certain species of leaf beetles for ectoparasitoid *Lebia* spp.



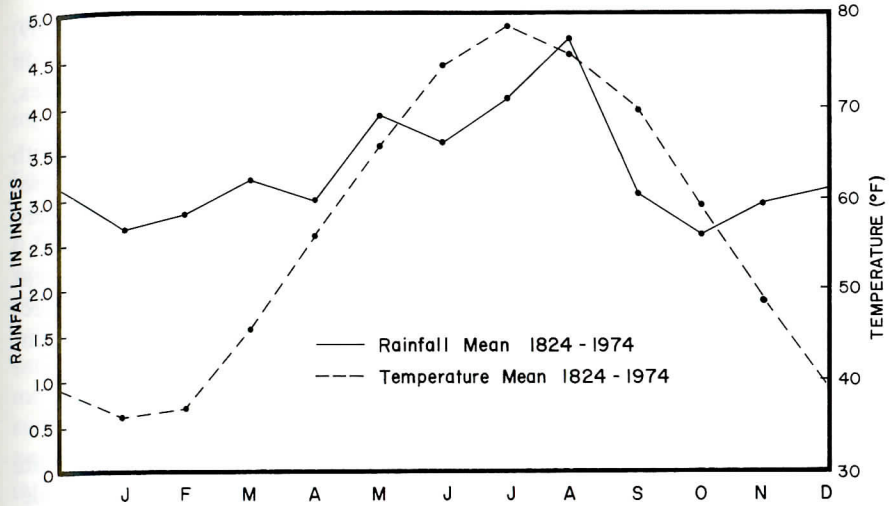


Fig. 4. Precipitation and temperature monthly means between 1824 and 1976 for the Washington area.

Climate.—The general climate, as represented by rainfall and temperature, is illustrated in Fig. 4. The recording stations are within 25 kilometers of Plummers Island and reasonably useful for our purposes. Records have been kept since 1824, thus the graph is based on 150 years of mean monthly rainfall and temperature. In 1960, the recording station in downtown Washington was closed and the station at National Airport, about 6 kilometers south, became the area's weather center. Both stations recorded data between 1941 and 1960 and the readings were almost duplicates, the largest discrepancy occurring in 1953 with a 7 inch differential; most other years showed 2 to 5 inch differential. The Plummers Island site is about 18 kilometers northwest of downtown and 25 kilometers northwest of National Airport.

Although annual rainfall and temperature must affect populations over long periods of time, years of maxima and minima too affect local populations, especially those in a geographic transition zone such as the middle Atlantic states of Maryland and Virginia. Irregular fluctuations in rainfall are certainly not as important as in drier areas, but they do exert some influence in our area. The mean annual rainfall between 1824 and 1974 was 40.92 inches. During 1826, 1848, and 1930, the mean annual rainfall was less

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Fig. 3. Plummers Island from the Virginia shore, March 1976; 3a) Cabin John Bridge and west end of Island, 3b) middle of Island, 3c) east end of Island; photographs by the author.

than 23 inches; the period 1824 to 1828 had less than 29 inches. During 1889, 1936, 1948, and 1972 the average was 51 inches or more. Such fluctuation must surely have great impact on populations of primary floodplain species, and quite probably other species as well.

Generally, the annual cycle of rainfall (Fig. 4) in the area is bimodal with a minor peak in May, a trough in June, and a major peak in August. Temperature (Fig. 4) is unimodal, peaking in July. No data on microclimate are available, except that springtime carabid activity begins when the soil, 25.0 mm below the surface, reaches 4.5°C. It is likely that near-ground ambient humidity, soil humidity, and soil temperature affect carabid habitat selection. These measurements should be undertaken if monitoring of local environment is to be done.

Methods

Descriptions.—Every species of carabid beetle known to occur at the site during the time period 1901 through 1978 is annotated below. These descriptions are composites of data taken from various literature sources, but mainly Lindroth (1961b–1969), and from my own field work. These data were coded and computerized for analysis by selected listings or Pearson Correlation methods.

Collecting.—Barber, Schwartz, and other early collectors left no records of their carabid collecting methods nor did they label their specimens as to microhabitat. I, and other contemporary collectors mentioned in acknowledgments, use standard hand-collecting techniques in general and most of these were employed at the study site, which may be designated by the following terms:

a. Digging/sifting—removal of upper soil layers and sifting for beetles therein.

b. Netting—aerial netting of flying individuals.

c. Quaking—stomping riverbanks (elsewhere lakeshores or alkali flats) where the soil is dried and cracked forcing the carabids to run across the surface from one crack to another.

d. Raking—removing leaf-litter from the soil surface, on which carabids might hunt, or hide during quiescent periods.

e. Removing cover—turning stones, logs, and bark under which carabids hide during their quiescent periods.

f. Splashing—hand or bucket splashing water onto shore forcing beetles to evacuate small hiding places.

g. Sweeping/beating—using a sweep net or beating sheet on foliage and twigs of live and dead trees and shrubs or other vegetation such as grass.

h. Treading—systematically depressing mud and other wet soil, emergent vegetation, or decaying leaf litter at water's edge with both feet effectively removing air pockets from upper centimeters of substrate forcing carabids to the surface.

i. Washing—raking leaves and other debris into water, then stirring, forcing beetles to the surface where they try to swim to shore.

In addition, some past collectors such as Barber used baited pitfalls and light traps to catch specimens. Since I am primarily interested in microhabitats, I did not use such trapping techniques for this study.

Measurements.—For the purpose of this study only total length (TL) was used as an indicator of size. For each species, measurements were taken of the largest and smallest individuals in the collections at the USNM. These were then compared with size ranges given by Lindroth (1961b–1969) for the same species. Where USNM material differed considerably from Lindroth's measurements, the entire sample from Plummers Island (USNM) was measured and averaged. In these cases (very few), the latter measures are given and used herein, on the assumption that the difference is an anomaly present in the Potomac populations on or about the study site. For each species, following range measures the average length is given in parentheses. The methods of measuring are given in Erwin and Kavanaugh (1980) and Erwin (1978).

Computer.—Data from specimens and their accompanying labels were stored and retrieved using SELGEM (L. Erwin, 1976). Meristic qualities of the environment and specimens were key-punched on cards and processed by IBM hardware using standard software for use in simple statistics. Graphs were generated from the data base by Honeywell hardware and an accompanying plotter.

Habitat Classification

With experience gained in several years of field work, L. Erwin (1976) outlined habitats and microhabitats from the perspective of ground beetles. Her paper deals with the handling of natural history data with computers and the resulting needs for strict formatting both at the field and laboratory levels. I have used her system for the Plummers Island discussions and found the system to be useful because carabid beetles throughout the world have similar limits to their ecologic ranges.

Ecologists have defined *communities* on the basis of floral composition and in part these are useful for carabid studies. However, some of these communities are either too complex, on one hand, or simplified when discussing carabid communities. Rather than introducing a new term for "carabid community" L. Erwin (1976) narrowed the old term "community" and gave examples. Her community types are useful for purposes here, namely, "Cultivated Land," "Fallow Field," "Marsh," "Pond," "Forest," "Riparian," and "Seepage." These terms are simply broad expressions of environ-

ments in which carabid microhabitats are found. Most carabids are restricted to one of these communities; those living in two or more are of special interest because of their broader ecologic latitude (Erwin, 1979).

"Pond" refers to the edges of small, natural water impoundments of both the permanent and intermittent type. Carabids live both at the soil/water interface and on emergent vegetation near the shore (e.g. Oodini). "Riparian" refers to the edge of rivers, streams, creeks, runs, or brooks (rills) whether they be permanent or intermittent. Some old Barber and Schwarz labels use the term "freshet" for water runoff pathways made during storms or heavy rains. Litter (leaves and small twigs) is piled up along these pathways and carabids are frequently in and among this debris. The remaining community terms are self-explanatory. Those represented at the Plummers Island site are depicted in Figs. 21 to 34.

Carabids are zoned vertically in most communities. L. Erwin (1976) devised terminology for indicating carabid zones under the general heading of "Macrohabitat." Five such zones are useful for purposes here, namely "Canopy," "Undercanopy," "Supra-epigean," "Epigean," and "Hypogean." These are self-explanatory except "Supra-epigean" which refers to elevated substrata in open land, for example on or in an old log in a fallow field. Within each macrohabitat there are one or more microhabitats. L. Erwin (1976) defines this as a "single word description of the micro-environment with which the specimen is associated" and provides numerous examples.

Morphology

General.—Very little has been published on carabid beetle form and function in relation to habitats and habits, although such connections are absolutely necessary in order to understand evolutionary processes and their causes in a group of organisms (Erwin, 1979). One of the aims of the present study is to determine if there are any general rules that apply to carabid structure in relation to habitat preference. Some of those discovered as part of this study were discussed elsewhere already (Erwin, 1979). Evans (1977), Hlavac (1971), Lindroth (1974) and Valentine (1973) analyzed and discussed others.

Through analysis of the carabid fauna at Plummers Island, I noted certain trends in habitat preference for species of certain colors and color patterns, with certain microsculpture configurations, and with certain types of protarsal vestiture. A search for these and similar trends in other geographical areas may allow some hypotheses to be erected which allow predictions about carabid evolutionary trends.

Color.—Although the relationship between color of members of a species and their biotope has never been adequately studied for ground beetles, it is apparent to any collector of these beetles that somber-colored species occur in higher latitudes and more shaded environments and brighter-colored species occur closer to the equator and in the canopy or sunny areas, at least. Data gathered at Plummers Island indicate several trends in color/biotope relationships. Thiele (1977) summarizes what little has been done on this subject and cites Kirchner (1960), Krogerus (1948), and Lindroth (1974). Thiele's comments and these other studies are based, unfortunately, on certain narrow habitats or few species.

Table 2.—Leg-color distribution among ground beetles at Plummers Island by period of occurrence in the fauna.

	Total fauna 1901–1978		Early fauna 1901–1933		Continuous fauna 1901–1978		Late fauna 1959–1978	
Leg-color	n	%	n	%	n	%	n	%
Pale	123	57.5	63	58.9	47	57.3	13	52.0
Dark	82	38.3	42	39.2	31	37.8	9	36.0
Bicolored	9	4.2	2	1.9	4	4.9	3	12.0
Total	214		107		82		25	

Color, in the strict sense, is not part of "Morphology" however, in most revisionary studies "color" has been regarded in the broad sense, and it is integumental structure that determines some aspects of color s.l. (e.g. iridescence). I therefore discuss "color" as part of this section. Kavanaugh (pers. comm.) separated and described 3 different elements of "color." True color, i.e. pigment, or lack of pigment, is basic to all insects. "Reflection" in the sense of metallic sheen is a result of light's defraction through the cuticle, wax layers, and air spaces in the cuticle. "Luster" is the effect of mechanical break-up of incident light caused by surface microsculpture. It is highly likely these three elements have different selective pressures (Erwin, 1979), hence here I shall consider them separately.

Leg-color.—Among ground beetles color of legs generally appears in one of three modes: Unicolorous dark, unicolorous pale, or bicolored. Table 2 and Fig. 5a provide data on the distribution of these color-types in the 4 major biotopes at Plummers Island. Several significant aspects are as follows:

1. No bicolor-legged species lives in the forest;
2. Dark-legged species predominate the forest and pond biotopes while pale-legged species predominate the riparian and open biotopes;
3. Bicolor-legged species are rare at this latitude, as compared with tropical biotopes;
4. Bicolor-legged species are late arrivals at the site;
5. Loss of both dark and pale-legged species in Forested and Open biotopes was dramatic while these groups increased in the riparian habitat.

These aspects are examined below (see Evolutionary Considerations).

LEG COLOR DISTRIBUTION AMONG BIOTYPES AND DECADES

	Forest	Riparian	Pond	Open	Tn
dark legs	n = 38 61.29%	n = 23 23.46%	n = 3 42.85%	n = 18 38.29%	82
	I II III IV	I II III IV	I II III IV	I II III IV	
	52.63 5.26 2.63 39.47	21.73 0 21.73 56.52	33.33 0 33.33 33.33	77.77 5.55 11.11 5.55	
pale legs	n = 24 38.70	n = 70 71.42	n = 2 28.57	n = 27 57.44	123
	50.00 16.66 4.16 29.16	35.71 2.85 17.14 44.28	0 0 0 100.00	70.37 14.81 0 14.81	
bicolored legs	n = 0	n = 5 5.10%	n = 2 28.57%	n = 2 4.25%	9
	– – – –	0 0 20.00 80.00	0 0 100 0	50 50 0 0	
Total n	62	98	7	47	214

Fig. 5a. Leg color distribution among biotopes and decades (I = 1901–1920, II = 1921–1960, III = 1961–1978, IV = 1901–1978).

Metallic reflection.—This character occurs throughout the family Carabidae in varied states; it is more common in some tribes than others (Lebiini and Callistini have many metallic members while Anthiini (see Erwin, 1979) and Patrobini have none).

Although metallic and partially metallic species are a small component of the carabid fauna at Plummers Island (43 of 214 species), I have analyzed and discussed them for future comparative purposes. Metallic reflection is an important element of tropical carabid faunas and I will compare and contrast temperate-tropical faunas in a subsequent paper (Erwin, in prep.).

Metallic body and/or head reflections may sometimes be vivid metallic, other times rather dull metallic. For purposes here, degree of metallic reflection was recorded as follows: metallic, non-metallic, partially metallic. The latter category includes species with metallic spots, margins, or head only; the subtle grade of difference between metallic and non-metallic was arbitrarily and subjectively categorized in a few cases, for example the "bronze" *Amara* species were not considered to be metallic.

Distribution of these character states in time and space is presented in Fig. 5b. Several significant aspects are as follows:

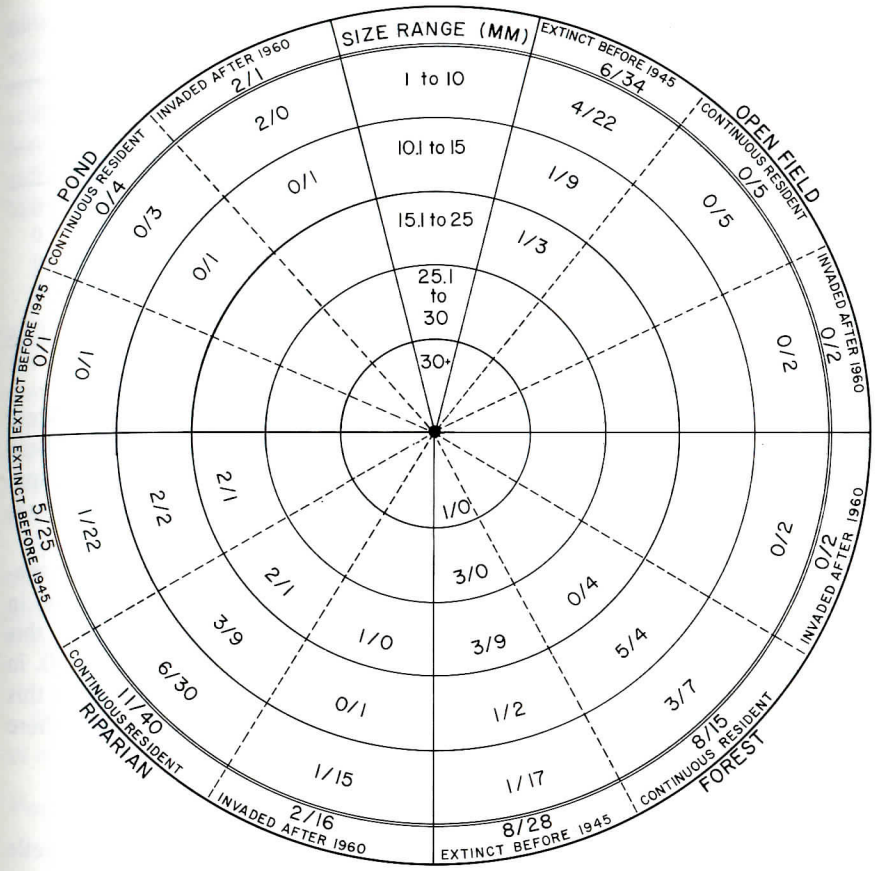

Fig. 5b. Numbers of metallic/non-metallic species of carabids arranged by size classes from small (outer ring) to large (inner circle) with habitat community (large wedges) and period of residence at site (small wedges).

1. The greatest number of species with metallic coloration (35.6%) live in the forest, the least in the open (14.6%);
2. Species with partially metallic coloration became locally extinct before 1936;
3. Species with metallic coloration dropped dramatically in number during the time period 1901–1935 with 13 species becoming locally extinct; only 3 species with metallic coloration invaded the area subsequent to 1935; 17 species remained stable throughout the period;
4. Although the extent and maturity of the forest at the site increased, the number of metallic forest species decreased and 5 of the 7 species lost were over 12 mm in length, 3 of them over 15 mm.

Table 3.—Protarsal vestiture distribution among ground beetles at Plummers Island by period by occurrence in the fauna.

Protarsal vestiture	Total fauna 1901–1978		Early fauna 1901–1933		Continuous fauna 1901–1978		Late fauna 1959–1978	
	n	%	n	%	n	%	n	%
Absent	20	9.3	8	7.5	9	11.0	3	12.0
1 Linear Row	18	8.4	7	6.5	9	11.0	2	8.0
2 Linear Rows	105	49.1	59	55.1	33	40.2	13	52.0
Pads	71	33.2	33	30.8	31	37.8	7	28.0
Total	214		107		82		25	

A detailed profile of the species shows that all of the "open" species were *Lebia* and were commonly collected on *Solidago* spp. (goldenrod). These plants no longer grow within the study area, thus the absence of *Lebia* spp. is undoubtedly due to the absence of *Solidago*. The climax forest eliminates the goldenrod by eliminating open habitats where the plants grow.

One recently discovered pond edge carabid species is found only by special collecting techniques (washing litter) and may not have been found in the early days; since the pond has not changed in 75 years, I suspect this to be the case. The second pond species was found only once, in 1960, in a special temporary pond at the west end of the island. The removal of this pond by subsequent flooding also eliminated the carabid species and there is no evidence that it has returned.

Microsculpture

The fine lines seemingly etched into the outer layers of ground beetle cuticle have long been noticed and used as taxonomic features (Andrewes, 1929). Lindroth (1974) dealt with carabid microsculpture with the aim of determining function of transverse lines set so close that they cause iridescence. Erwin (1979) also dealt with this problem and suggested correlations of microsculpture types with specific habitats. The latter paper was based in part on data taken from the present study. Almost invariably, members

Table 4.—Elytral vestiture distribution among ground beetles at Plummers Island by period of occurrence in the fauna.

Vestiture	Total fauna 1901–1978		Early fauna 1901–1933		Continuous fauna 1901–1978		Late fauna 1959–1978	
	n	%	n	%	n	%	n	%
Present	21	9.8	11	10.3	9	11.0	1	4.0
Absent	193	90.2	96	89.7	73	89.0	24	96.0
Total	214		107		82		25	

of canopy species have flat isodiametric meshes, sea beach and alkali slough species have granulate isodiametric meshes, species of rich organic bogs or swamps have transverse lines, tree bark species have posteriorly elevated scales, riparian species have isodiametric or slightly transverse meshes, and forest species are highly variable. It is probable that this surface texture aids the beetle mechanically in its substrate and is not for the purposes of light reflection to deceive predators (Hinton, 1969, 1970).

Vestiture

Among the species at Plummers Island site (n = 214), there is a direct correlation between large size and increased male protarsal vestiture (Pearson Correlation Coefficient = −0.3964, s = 0.001). Small beetles tend to have one row of modified setae, or no setae whatever. Larger beetles tend to have spongy pads or two linear rows of modified setae. Data in Table 3 indicate that species with two linear rows of setae dominate the fauna and species with pads are nearly as dominant. The species with no special protarsal vestiture are predominantly Scaritini.

Elytral vestiture (Table 4) occurs in only 10.0% of the fauna, and only one additional species with vestiture has been added since 1959. The majority of these species belong to the genera *Brachinus, Chlaenius,* and *Galerita*.

Checklist of Species

Taxonomic Arrangement.—Taxonomic sequence follows that of Erwin et al. (in prep.), A Checklist of the Ground Beetles of the New World.

Family Carabidae

A. Subfamily Omophroninae

1. Omophronini

1.01 *Omophron americanum* Dejean (1831:583)

B. Subfamily Paussinae

2. Brachinini

2.01 *Brachinus cyanipennis* Say (1823a:143)

2.02 *Brachinus fumans* Fabricius (1781:307)

2.03 *Brachinus cordicollis* Dejean (1826:466)

3. Nebriini

3.01 *Nebria lacustris* Casey (1913:56)

3.02 *Nebria pallipes* Say (1823b:78)

4. Notiophilini

4.01 *Notiophilus aeneus* Herbst (1806:235)

4.02 *Notiophilus semistriatus* Say (1823b:81)

4.03 *Notiophilus novemstriatus* LeConte (1848:450)

5. Elaphrini

5.01 *Elaphrus californicus* Mannerheim (1843:190)

5.02 *Elaphrus ruscarius* Say (1834:417)

6. Carabini
   - 6.01 *Carabus limbatus* Say (1823b:77)
   - 6.02 *Carabus vinctus* Weber (1801:42)
   - 6.03 *Carabus serratus* Say (1823b:77)
   - 6.04 *Carabus sylvosus* Say (1823b:75)
   - 6.05 *Calosoma scrutator* Fabricius (1775:239)
   - 6.06 *Calosoma calidum* Fabricius (1775:237)
7. Cychrini
   - 7.01 *Scaphinotus unicolor* Fabricius (1787:198)
   - 7.02 *Scaphinotus ridingsi* Bland (1863:354)
   - 7.03 *Sphaeoderus stenostomus* Weber (1801:43)
8. Megacephalini
   - 8.01 *Megacephala virginica* Linné (1766:657)
9. Cicindelini
   - 9.01 *Cicindela repanda* Dejean (1825:74)
   - 9.02 *Cicindela sexguttata* Fabricius (1775:226)
   - 9.03 *Cicindela punctulata* Olivier (1790:27)
   - 9.04 *Cicindela rufiventris* Dejean (1825:102)
10. Scaritini
   - 10.01 *Scarites subterraneus* Fabricius (1775:249)
   - 10.02 *Pasimachus depressus* Fabricius (1775:94)
   - 10.03 *Dyschirius sphaericollis* Say (1823b:23)
   - 10.04 *Dyschirius globulosus* Say (1823b:23)
   - 10.05 *Dyschirius pilosus* LeConte (1857a:80)
   - 10.06 *Dyschirius affinis* Fall (1901:209)
   - 10.07 *Dyschirius haemorrhoidalis* Dejean (1831:511)
   - 10.08 *Ardistomis viridis* Say (1823b:21)
   - 10.09 *Clivina bipustulata* Fabricius (1801:125)
   - 10.10 *Clivina americana* Dejean (1831:503)
   - 10.11 *Clivina impressifrons* LeConte (1844:50)
   - 10.12 *Clivina dentipes* Dejean (1825:415)
   - 10.13 *Clivina ferrea* LeConte (1857a:81)
   - 10.14 *Schizogenius ferrugineus* Putzeys (1846:653)
   - 10.15 *Schizogenius lineolatus* Say (1823b:22)
11. Rhysodini
   - 11.01 *Omoglymmius americanus* Laporte (1836:58)
   - 11.02 *Clinidium sculptile* Newman (1838a:666)
12. Bembidiini
   - 12.01 *Bembidion inaequale* Say (1823a:151)
   - 12.02 *Bembidion confusum* Hayward (1897:52)
   - 12.03 *Bembidion honestum* Say (1823b:82)
   - 12.04 *Bembidion americanum* Dejean (1831:87)
   - 12.05 *Bembidion levigatum* Say (1823b:84)

   - 12.06 *Bembidion fugax* LeConte (1848:467)
   - 12.07 *Bembidion nigrum* Say (1823b:85)
   - 12.08 *Bembidion semistriatum* Haldeman (1843:303)
   - 12.09 *Bembidion lacunarium* Zimmermann (1869:248)
   - 12.10 *Bembidion variegatum* Say (1823b:89)
   - 12.11 *Bembidion rapidum* LeConte (1848:460)
   - 12.12 *Bembidion castor* Lindroth (1963:366)
   - 12.13 *Bembidion affine* Say (1823b:86)
   - 12.14 *Bembidion impotens* Casey (1918a:129)
   - 12.15 *Bembidion pedicellatum* LeConte (1857b:6)
   - 12.16 *Bembidion quadrimaculatum* Linné (1761:211)
   - 12.17 *Anillinus barberi* Jeannel (1963:150)
   - 12.18 *Mioptachys flavicauda* Say (1823b:87)
   - 12.19 *Tachyta nana inornata* Say (1823b:87)
   - 12.20 *Elaphropus granarius* Dejean (1831:61)
   - 12.21 *Elaphropus levipes* Casey (1918a:186)
   - 12.22 *Elaphropus saturatus* Casey (1918a:187)
   - 12.23 *Elaphropus incurvus* Say (1834:440)
   - 12.24 *Elaphropus vivax* LeConte (1848:468)
   - 12.25 *Elaphropus tripunctatus* Say (1834:439)
   - 12.26 *Elaphropus vernicatus* Casey (1918a:181)
   - 12.27 *Elaphropus ferrugineus* Dejean (1831:59)
   - 12.28 *Pericompsus ephippiatus* Say (1834:439)
   - 12.29 *Paratachys proximus* Say (1823b:88)
   - 12.30 *Paratachys scitulus* LeConte (1848:471)
   - 12.31 *Paratachys potomaca*, new species
   - 12.32 *Paratachys obliquus* Casey (1918a:201)
   - 12.33 *Paratachys corruscus* LeConte (1848:472)
   - 12.34 *Polyderis laevis* Say (1823b:88)
13. Patrobini
   - 13.01 *Patrobus longicornis* Say (1823b:40)
14. Pterostichini
   - 14.01 *Europhilus sordens* Kirby (1837:25)
   - 14.02 *Agonum octopunctatum* Fabricius (1798:55)
   - 14.03 *Agonum fidele* Casey (1920:116)
   - 14.04 *Agonum tenue* LeConte (1854:48)
   - 14.05 *Agonum placidum* Say (1823b:43)
   - 14.06 *Agonum striatopunctatum* Dejean (1828:167)
   - 14.07 *Agonum rigidulum* Casey (1920:75)
   - 14.08 *Agonum aeruginosum* Dejean (1828:168)
   - 14.09 *Agonum excavatum* Dejean (1828:169)
   - 14.10 *Agonum ferreum* Haldeman (1843:299)
   - 14.11 *Agonum extensicolle* Say (1823b:54)

14.12 *Platynus decentis* Say (1823b:53)
14.13 *Platynus cincticolle* Say (1823b:52)
14.14 *Platynus parmarginatum* Hamilton (1893:306)
14.15 *Platynus tenuicolle* LeConte (1848:222)
14.16 *Platynus caudatus* LeConte (1863a:7)
14.17 *Calathus gregarius* Say (1823b:47)
14.18 *Synuchus impunctatus* Say (1823b:45)
14.19 *Olisthopus parmatus* Say (1823b:49)
14.20 *Olisthopus micans* LeConte (1848:230)
14.21 *Atranus pubescens* Dejean (1828:122)
14.22 *Loxandrus velocipes* Casey (1918b:390)
14.23 *Loxandrus circulus* Allen (1972:157)
14.24 *Myas coracinus* Say (1823b:59)
14.25 *Pterostichus tristis* Dejean (1828:324)
14.26 *Pterostichus honestus* Say (1823b:51)
14.27 *Pterostichus chalcites* Say (1823b:56)
14.28 *Pterostichus lucublandus* Say (1823b:55)
14.29 *Pterostichus ohionis* Csiki (1930:638)
14.30 *Pterostichus stygicus* Say (1823b:41)
14.31 *Pterostichus coracinus* Newman (1838b:386)
14.32 *Pterostichus novus* Straneo (1944:127)
14.33 *Pterostichus lachrymosus* Newman (1838b:387)
14.34 *Pterostichus moestus* Say (1823b:42)
14.35 *Pterostichus corvinus* Dejean (1828:281)
14.36 *Pterostichus caudicalis* Say (1823b:56)
14.37 *Evarthrus sigillatus* Say (1823b:42)
14.38 *Evarthrus approximatus* LeConte (1848:354)

15. Zabrini
15.01 *Amara exarata* Dejean (1828:509)
15.02 *Amara avida* Say (1823a:148)
15.03 *Amara musculis* Say (1823b:35)
15.04 *Amara impuncticollis* Say (1823b:36)
15.05 *Amara anthobia* Villa (1833:33)
15.06 *Amara familiaris* Duftschmidt (1812:119)
15.07 *Amara aenea* De Geer (1774:98)
15.08 *Amara angustata* Say (1823b:36)

16. Callistini
16.01 *Chlaenius tomentosus* Say (1823b:60)
16.02 *Chlaenius emarginatus* Say (1823b:63)
16.03 *Chlaenius prasinus* Dejean (1826:345)
16.04 *Chlaenius cordicollis* Kirby (1837:22)
16.05 *Chlaenius aestivus* Say (1823b:62)
16.06 *Chlaenius laticollis* Say (1823b:64)

16.07 *Chlaenius sericeus* Forster (1771:58)
16.08 *Chlaenius impunctifrons* Say (1823b:64)
16.09 *Chlaenius nemoralis* Say (1823b:65)
16.10 *Chlaenius tricolor* Dejean (1826:334)
16.11 *Chlaenius pensylvanicus* Say (1823b:66)

17. Oodini
17.01 *Oodes amaroides* Dejean (1831:674)
17.02 *Stenocrepis cupreus* Chaudoir (1843:761)

18. Licinini
18.01 *Dicaelus elongatus* Bonelli (1813:448)
18.02 *Dicaelus politus* Dejean (1826:391)
18.03 *Dicaelus ambiguus* Laferté (1841:44)
18.04 *Dicaelus teter* Bonelli (1813:449)
18.05 *Dicaelus furvus* Dejean (1826:388)
18.06 *Dicaelus dilatatus* Say (1823b:68)
18.07 *Dicaelus sculptilis* Say (1823b:68)
18.08 *Dicaelus purpuratus* Bonelli (1813:447)
18.09 *Badister notatus* Haldeman (1843:299)
18.10 *Badister flavipes* LeConte (1853:388)
18.11 *Badister reflexus* LeConte (1880:166)

19. Harpalini
19.01 *Cratacanthus dubius* Beauvois (1805:108)
19.02 *Harpalus faunus* Say (1823b:28)
19.03 *Harpalus pensylvanicus* De Geer (1774:108)
19.04 *Harpalus longicollis* LeConte (1848:396)
19.05 *Harpalus erythropus* Dejean (1829:258)
19.06 *Harpalus caliginosus* Fabricius (1775:240)
19.07 *Harpalus viduus* LeConte (1865:103)
19.08 *Harpalus spadiceus* Dejean (1829:336)
19.09 *Harpalus herbivagus* Say (1823b:29)
19.10 *Harpalus fulgens* Csiki (1932:1182)
19.11 *Harpalus opacipennis* Haldeman (1843:301)
19.12 *Episcopellus autumnalis* Say (1823b:48)
19.13 *Trichotichnus vulpeculus* Say (1823b:30)
19.14 *Trichotichnus dichrous* Dejean (1829:258)
19.15 *Selenophorus opalinus* LeConte (1863b:13)
19.16 *Selenophorus gagatinus* Dejean (1829:112)
19.17 *Selenophorus pedicularius* Dejean (1829:100)
19.18 *Selenophorus ellipticus* Dejean (1829:108)
19.19 *Geopinus incrassatus* Dejean (1829:21)
19.20 *Notiobia nitidipennis* LeConte (1848:388)
19.21 *Notiobia terminata* Say (1823b:48)
19.22 *Anisodactylus discoideus* Dejean (1831:831)

19.23 *Anisodactylus carbonarius* Say (1823b:32)
19.24 *Anisodactylus nigerrimus* Dejean (1831:842)
19.25 *Anisodactylus melanopus* Haldeman (1843:302)
19.26 *Anisodactylus agricola* Say (1823b:33)
19.27 *Anisodactylus rusticus* Say (1823b:32)
19.28 *Anisodactylus verticalis* LeConte (1848:378)
19.29 *Amphasia interstitialis* Say (1823b:57)
19.30 *Bradycellus rupestris* Say (1823b:91)
19.31 *Bradycellus badipennis* Haldeman (1843:202)
19.32 *Bradycellus atrimedeus* Say (1823b:39)
19.33 *Stenolophus ochropezus* Say (1823b:54)
19.34 *Stenolophus* "alpha"
19.35 *Stenolophus plebejus* Dejean (1829:424)
19.36 *Stenolophus humidus* Hamilton (1893:305)
19.37 *Stenolophus comma* Fabricius (1775:248)
19.38 *Stenolophus lecontei* Chaudoir (1868:164)
19.39 *Stenolophus rotundicollis* Haldeman (1843:302)
19.40 *Stenolophus conjunctus* Say (1823b:90)
19.41 *Acupalpus* "alpha"
19.42 *Acupalpus* "beta"
19.43 *Acupalpus hydropicus* LeConte (1863a:17)
19.44 *Acupalpus testaceus* Dejean (1829:460)
19.45 *Acupalpus pauperculus* Dejean (1829:463)
20. Masoreini
20.01 *Tetragonoderus fasciatus* Haldeman (1843:298)
21. Odacanthini
21.01 *Colliuris pensylvanica* Linné (1767:620)
22. Lebiini
22.01 *Lebia atriventris* Say (1823b:13)
22.02 *Lebia tricolor* Say (1823b:11)
22.03 *Lebia grandis* Hentz (1830:255)
22.04 *Lebia viridipennis* Dejean (1826:452)
22.05 *Lebia viridis* Say (1823b:14)
22.06 *Lebia analis* Dejean (1825:265)
22.07 *Lebia solea* Hentz (1830:256)
22.08 *Lebia pectita* Horn (1885:133)
22.09 *Lebia lobulata* LeConte (1863a:5)
22.10 *Lebia ornata* Say (1823b:13)
22.11 *Lebia pumila* Dejean (1831:388)
22.12 *Coptodera aerata* Dejean (1825:277)
22.13 *Dromius piceus* Dejean (1831:353)
22.14 *Apristus subsulcatus* Dejean (1826:451)
22.15 *Calleida viridipennis* Say (1823b:9)
22.16 *Plochionus timidus* Haldeman (1843:298)

22.17 *Pinacodera limbata* Dejean (1831:320)
22.18 *Apenes lucidula* Dejean (1831:320)
23. Zuphiini
23.01 *Zuphium americanum* Dejean (1831:298)
24. Galeritini
24.01 *Galerita janus* Fabricius (1792:136)
24.02 *Galerita bicolor* Drury (1770:94)

Annotated List of Species

OMOPHRONINI. The "round sand-beetles" are a minor group of small or medium-sized beetles which inhabit edges of water bodies in sandy locations. The adults spend the day in burrows in the littoral zone and the nights running along the same area in search of food or mates, or for the purpose of oviposition. These beetles eat dead or dying arthropods; they are vagile dispersants and fly at night. Larvae inhabit burrows in the sand and are probably predatory. These beetles ooze a chemical defense (higher saturated acids; Moore, 1979) which is mildly musty; even so at least one species falls prey to *Bufo americanus*, the American Toad (Larochelle, 1974d). The tribe is distributed throughout the Holarctic and Ethiopian Regions and along the northern edges of both the Neotropical and Oriental Regions. One species is known from the Plummers Island site.

1.01 *Omophron americanum* Dejean (1831:583)

Commonly found along both sides of the Channel on the primary and secondary floodplain which consists of sand and silt; often found in great numbers. In our area, these beetles are not restricted to bare sites, but may be found up in the floodplain forest where the adults hibernate under leaves, logs, and even under bark. During the day both the larvae and adults hide in burrows in the sand; they come out to forage at night. These beetles are fully winged and according to Larochelle (1972b, 1975a) they fly on humid and sunny days. Many examples were collected on the Island and adjacent shores between 1905 and the present (HSB & EAS, WLM, RCS, JLW, PJS, GGP, TLE & DRW). No teneral specimens seen. Adults were collected in March, April, May, July, August, September, and October. According to Lindroth (1961b) adults hibernate. Larochelle (1974b) found these beetles hibernating on "mounds" in November, in Quebec. Total length, 5.1 to 7.0 mm (6.0).

BRACHININI. The "bombardier beetles" constitute a major group of small to very large colorful beetles with a well-developed chemical defense system; these beetles crepitate a noxious, almond-odored, hot spray at their adversaries (quinones; Moore, 1979). These beetles occur in a variety of habitats, but most live near water where their larvae are ectoparasitoid on water beetle pupae (Brachinina) or mole cricket egg clutches (Pheropso-

phina). Adults feed on dead or dying arthropods or scavenge other such materials. Most members are highly vagile dispersants, although a few groups are flightless. These beetles are nocturnal in habits and hide under stones, logs, etc. during the day. The tribe is distributed throughout the globe, although most species are approximate to the equator. Three species were found in the past at the Plummers Island site, but have not been seen recently.

2.01 *Brachinus cyanipennis* Say (1823a:143)

Usually found under stones or debris on sandy clay on the primary or secondary floodplain of fairly large rivers. Adults are scavengers on dead or dying arthropods and forage at night. Larvae are probably ectoparasitoid on water beetle pupae. These beetles are fully winged and fly (Erwin, 1970); they are attracted to lights. Only six examples were collected on the Island and adjacent Virginia shore between 1907 and 1924 (HSB, WLM). There are no recent records. Teneral specimens were collected in August. Adults were collected in April, May, June, and August. Hibernation takes place in the adult stage and larvae are in the fauna in mid-summer. Total length, 8.0 to 12.1 mm (10.0).

2.02 *Brachinus fumans* Fabricius (1781:307)

This is the most ubiquitous bombardier beetle species in the Nearctic Region and is found near all sorts of water bodies, alkaline or fresh, in gravel and stoney places. During the day they hide under stones, logs, debris, and so forth and come out to forage at night. The adults are general scavengers on dead and dying arthropods; the larvae are probably ectoparasitoid on water beetle pupae. These beetles are fully winged and good fliers; they are attracted to lights. Only one example was collected on the Island, in 1908 (AKF). There are no recent records. No teneral specimens seen. The single adult was collected in April. Elsewhere adults overwinter and are active between March and October; larvae are present in the fauna in summer (Erwin, 1970). Total length, 9.0 to 14.0 mm (11.5).

2.03 *Brachinus cordicollis* Dejean (1826:466)

Usually found in the same habitat as *B. cyanipennis*. Adults and larvae with the same habits as the preceding two species. These beetles are fully winged and good fliers; they are attracted to light. Only two examples were collected, one on the Virginia shore in 1902, and one on the Island in 1905 (HSB). There are no recent records. No teneral specimens seen. Adults were collected in June and September. Elsewhere adults overwinter and are active between April and October; larvae are present in the fauna in summer (Erwin, 1970). Total length, 7.0 to 10.2 mm (8.6).

NEBRIINI. The nebriine beetles are a medium-sized group of cool or cold-adapted beetles of moderate size. Many species are found at high altitudes and high altitudes near snow or water. They are predators or scavengers, nocturnal in habits, and for the most part, flightless. Larvae occur in the same habitat as the adult and are active predators. The tribe is distributed throughout the Holarctic Region. Two species are known from the Plummers Island site.

3.01 *Nebria lacustris* Casey (1913:56)

Found commonly in the shade on gravel bars at the mouth of Rock Run on sand mixed with clay, under stones; at the southeast corner of Island on coarse sand mixed with silt, by splashing. These beetles hide during the day and forage at night on dead and dying insects along the stream margin. They are fully winged, but flight has not been recorded. Many examples were collected on the Island and adjacent shores between 1903 and the present (HSB, JLW, AKF, WLM, WVW, TLE & HF). Teneral specimens were found in April and May. HSB found a white adult, freshly emerged, in its pupal cell on a sandbar near the ferry in May. Adults were collected in March, April, May, October, November. Hibernation takes place probably both as an adult and larva. Total length, 9.5 to 11.7 mm (10.6).

3.02 *Nebria pallipes* Say (1823b:78)

Found with the preceding species under stones on gravel bars at mouth of Rock Run. These beetles are fully winged, but flight has not been recorded. Many examples were collected on the Maryland shore in 1974 (TLE & HF). No teneral specimens seen. Adults were collected in October. Lindroth (1961b) indicates larval hibernation, however, I suspect both larvae and adults do so. Total length, 10.0 to 11.5 mm (10.8).

NOTIOPHILINI. The "wrinkled-forehead carabids" are a minor group of rather homogeneous small beetles. Most species are found in drier parts of forested habitats, even dry places near water. They are predators, diurnal in habit, vagile, and feed on small arthropods such as Collembola and mites. Larvae occur in the same habitat and are predaceous. The tribe is strictly Holarctic in distribution. Three species are known from the Plummers Island site; one of them has not been seen recently.

4.01 *Notiophilus aeneus* Herbst (1806:235)

Found in moss and leaf litter near damp places in the deciduous woods, especially near the Pond. Adults are probably predaceous on small arthropods (Lindroth, 1961b). These beetles are fully winged and probably fly. They are diurnal (Larochelle, 1975a). Several specimens were collected on

the Island and adjacent Maryland shore between 1921 and the present (HSB, PJS, TLE & DRW). No teneral specimens seen. Adults were collected in April and May. According to Lindroth (1961b) adults hibernate. Total length, 5.0 to 5.7 mm (5.4).

4.02 *Notiophilus semistriatus* Say (1823b:81)

According to Lindroth (1961b), they are found on "open gravelly, rather dry ground, often moraine, with low thin vegetation." Adults are probably predaceous on small arthropods (Lindroth, 1961b). The species is wing-dimorphic. Only one example was collected on the Island in 1918 (JLW). It is a wingless male. There are no recent records. No teneral specimens seen. The single specimen was collected in July. Adults probably hibernate. Total length, 4.7 to 5.4 mm (5.0).

4.03 *Notiophilus novemstriatus* LeConte (1848:450)

Commonly found in the Virginia-Maryland area since the turn of the century, but not discovered on the Island until 1962 (PJS) even though Barber and Schwarz collected many examples in other areas (Michigan) and must have known how to find them. Usually associated with pine needles on dry forest floors. Adults are probably predaceous on small arthropods (Lindroth, 1961b). The species is wing-dimorphic and according to Lindroth (1961b) winged individuals are rare. Several specimens were found on the Island in 1962 (PJS), 1971 (GFH), and 1972 (GFH). It is likely the species is now established on the pine area near the cabin. No teneral specimens seen. Adults were collected in June and July. In our general area specimens were also collected in October. Hibernation is probably as an adult. Total length, 3.4 to 4.7 mm (4.0).

ELAPHRINI. The "marsh and bog beetles" are a minor group of homogeneous small to medium-sized beetles. All species are more or less hygrophilous, and as their common name implies they live in marshes and bogs or these kind of places along streams and rivers. Some species are riverine strand dwellers. They are predators, diurnal in habit, vagile dispersants, and rapid, but clumsy runners. They capture and eat small arthropods in much the same fashion that tiger beetles do. Larvae occur in the same habitat, are nocturnal, and are predacous. The tribe is strictly Holarctic in distribution. Two species are known from the Plummers Island site.

5.01 *Elaphrus californicus* Mannerheim (1843:190)

Found commonly on wet silt near the water on both sides of the Channel and along the river. Although cryptic in color and behavior these beetles are made active (and visible) by splashing water over the silt. They are

active in the daytime, fully winged, and probably fly quite well, although they mostly run to escape capture. They are attracted to white lights (Larochelle, 1973). Several examples were collected on the Island and adjacent shores between 1905 and the present (HSB, PJS, GFH, TLE & DRW, TLE). No teneral specimens seen. Adults were collected in April, May, and July. Larochelle (1974b) found these beetles hibernating on "mounds" and two inches deep in mounds in November and December in Quebec. Total length, 6.3 to 8.0 mm (7.2).

5.02 *Elaphrus ruscarius* Say (1834:417)

Found with *E. californicus* on the silt on both sides of the Channel; with the same habits. They are active in the daytime, fully winged, and probably fly quite well, although they mostly run to escape capture. Many examples collected on the Island and adjacent Maryland shore between 1905 and the present (DHC, WSF, GFH, TLE, DRW). No teneral specimens seen. Adults were collected in March, April, and July. According to Lindroth (1961b) adults probably hibernate. Total length, 6.7 to 7.2 mm (7.0).

CARABINI. The "firey hunters" (*Calosoma*) and "pupae and worm eaters" (*Carabus*) constitute a major group of very large beetles. These beetles live in a variety of habitats; the former are, in part, tree climbers. All species are highly predaceous on various types of invertebrates, and have been used experimentally for biological control purposes. Larvae are also highly predaceous and nocturnal in habit. These beetles spray a chemical defense (unsaturated acids, aromatic aldehydes; Moore, 1979) which is sourly musty; even so at least two species fall prey to *Bufo americanus,* the American Toad (Larochelle, 1974d). The tribe is cosmopolitan (*Calosoma*), but *Carabus* spp. are restricted to the Holarctic Region. Six species in two genera are known from the Plummers Island site; none of these have been seen recently.

6.01 *Carabus limbatus* Say (1823b:77)

According to Lindroth (1961b) found in "wet deciduous woods . . . beech-maple forest, often near water." The beetles are apparently attracted to sugar. They are wingless and not capable of flight. HSB and WMM collected these beetles in pitfall traps. Many examples were collected on the island and adjacent shores between 1905 and 1920 (HSB, HSB & WMM, HSB & EAS, LOJ, WLM, DHC). There are no recent records. Teneral specimens were found in April, July, and September. Adults were collected in March, July, September, and October. The beetles overwinter in the adult stage; larvae are present in the fauna in spring and early summer. Total length, 20.0 to 25.0 mm (22.5).

6.02 *Carabus vinctus* Weber (1801:42)

According to Lindroth (1961b) found in "wet deciduous woods . . . beach-maple forest, often near water" and more dependent upon it than the previous species. The beetles are wingless and not capable of flight. Several examples were collected on the Island and adjacent Virginia shore between 1905 and 1914 (HSB, HSB & EAS, RCS). There are no recent records. No teneral specimens seen. Adults were collected in May, July, August, and September. The life cycle is probably the same as the previous species. Total length, 20.0 to 25.0 mm (22.5).

6.03 *Carabus serratus* Say (1823b:77)

According to Lindroth (1961b) found on "open, gravelly ground, usually moraine, with sparse vegetation: at the foot of rock-falls, on railway embankments, in gravel pits, on sun-exposed wood-glades, with *Chamaenerium angustifolium*." The specimen collected on the Island by HSB was found at the cabin. These beetles are wing-dimorphic and apparently the long-winged forms fly. All our specimens are short-winged. They are both nocturnal and diurnal (Larochelle, 1975a). Only two specimens were found, on the Virginia shore, in 1912 (HSB) and on the Island in 1923 (HSB). There are no recent records. No teneral specimens seen. Mating occurs in June in Quebec (Larochelle, 1972e). Adults were collected in May and September. Lindroth (1961b) states that adults hibernate in Newfoundland. Total length, 16.0 to 24.0 mm (20.0).

6.04 *Carabus sylvosus* Say (1823b:75)

Found in the same habitat as *C. limbatus* and *C. vinctus* (Lindroth, 1961b). These beetles are short-winged and incapable of flight. Only one specimen was collected on the Island, in 1922 (HSB). Several other examples were "trapped" on the opposite side of the river in Virginia in 1905, 1920, 1921 (HSB). There are no recent records. No teneral specimens seen. Adults were collected in September, October, and November. Hibernation is undoubtedly in the adult stage. Total length, 24.0 to 28.0 mm (26.0).

6.05 *Calosoma scrutator* Fabricius (1775:239)

According to Lindroth (1961b) found in open hardwood forests. Adults range widely and climb trees quite well; the larvae do not climb at all (Burgess and Collins, 1917). Adults prey upon Cankerworms, tent caterpillars, and army worms; larvae also eat these caterpillars plus pupae of the same species. These beetles are fully winged and fly very well; they are attracted to lights. Only three specimens were collected on the Island between 1902 and 1907 (HSB). A single dead specimen was collected on the Maryland shore in March of 1912 (HSB). There are no recent records. No teneral

specimens seen. Adults are active through the summer, seen from June and July, and enter hibernation in the fall; larvae are in the fauna in the summer. A long and detailed report on the bionomics of this species is given by Burgess and Collins (1917). Total length, 25.0 to 36.0 mm (30.5).

6.06 *Calosoma calidum* Fabricius (1775:237)

According to Lindroth (1961b) "terricolous and inhabits open rather dry fields with low vegetation." These are poor climbers, but will go up the trunk of trees for caterpillars occasionally. Both adults and larvae are predaceous on cutworms, and they will also eat tent caterpillars and army worms (Burgess and Collins, 1917). They can be collected by tying burlap sacks around the lower trunks of trees, a device which congregates their prey; they will also come to sugar used for "sugaring" for moths. They are fully winged and probably fly quite well; they are attracted to lights. They are both nocturnal, and according to Larochelle (1975a), diurnal as well. Only one specimen was collected on the Island, in 1913 "at light." There are no recent records. No teneral specimens seen. Adults overwinter and are found in the late spring and throughout the summer (seen from May). Larvae are present in the fauna in summer. A long and detailed report on their bionomics is given by Burgess and Collins (1917). Total length, 19.0 to 25.0 mm (22.0).

CYCHRINI. The "snail-eaters" are a moderate-sized group of medium to very large, robust beetles. These beetles are terricolous and nocturnal; they frequent rocky talus slopes or the burrows of rodents or other soil burrowers during the day and for winter hibernation. Although their mouthparts appear to be highly adapted to eating mollusks and they are known to do just that, they have been observed eating a great variety of dead or dying arthropods, and even fruit (Greene, 1975; Noonan, 1967). The majority of species are forest dwellers, some at very high altitudes in the American southwest and in the European Alps. They are rapid runners for such large beetles and all species in the tribe are flightless with fused elytra. These beetles spray a chemical defense (aromatic aldehydes; Moore, 1979) which is sourly musty. The tribe is Holarctic in distribution. Three species in two genera have been found at the Plummers Island site; two of these have not been seen recently.

7.01 *Scaphinotus unicolor* Fabricius (1787:198)

Found in and around rocky outcroppings in the eastern deciduous forest, usually under logs or at night foraging in the leaf litter. Adults and larvae eat snails, at least in part, but probably also take other kinds of food (Greene, 1975) and Larochelle (1972f) indicates they eat "white grubs of May Beetle." The beetles are wingless and not capable of flight. Many

examples were collected on the Island and adjacent Virginia shore between 1902 and 1943 (HSB, EAS, WMM, EAC). There are no recent records. Teneral specimens were collected in June. Adults were found in June and September. Adults and larvae probably hibernate in logs, in deep fissures in rock outcroppings, or in rodent burrows. Total length, 27.0 to 30.0 mm (28.5).

7.02 *Scaphinotus ridingsi* Bland (1863:354)

Found in rocky, moist sites in the shade along streams and in and around steep rocky outcroppings near the river. They are most easily found at night when they are out foraging for snails (Larochelle, 1972f) and other prey (Greene, 1975), and they are attracted to "black molasses" pit fall traps (Valentine, 1935). The beetles are wingless and not capable of flight. Many examples were collected on the Virginia side of the river, opposite the Island, between 1902 and 1933 (HSB, WMM, JMV). No teneral specimens seen. Adults were collected in June, August, September, and October. Adults probably hibernate and the life cycle is most likely similar to the preceding species. Mating was observed in September (HSB), therefore it is possible eggs or larvae also overwinter. The adult life span is probably more than one year. Total length, 17.7 to 18.2 mm (18.0).

7.03 *Sphaeoderus stenostomus* Weber (1801:43)

Commonly found in a variety of habitats, on the island, from upper dry primary floodplain to the dry pine groove near the cabin. They can be found in leaf litter, under stones and logs, and occasionally on the surface in the day; they forage at night for snails, slugs, and perhaps other prey (Greene, 1975). I have kept them alive in lab by feeding them small snails and flank steak. The beetles are wingless and not capable of flight. Many examples were collected on the Island and adjacent shores between 1903 and the present (HSB, WMM, AKF, FK, TES, GFH, TJS, PJS, GGP, TLE). No teneral specimens seen. Adults occur in March through October. I have collected mating pairs in late fall, although Lindroth (1961b) indicates adults overwinter, so it is possible that either eggs are laid in the fall and they too overwinter or females retain a spermatophore for use in the springtime. Total length, 12.0 to 14.0 mm (13.0).

MEGACEPHALINI. The "large-headed tiger beetles" are a minor group of medium to very large beetles. They are terricolous, rapid runners, with nocturnal habits and live in the vicinity of water. They eat small arthropods or other invertebrates which they actively capture. Their larvae are found in burrows in the soil, the head capsule sealing the entrance, awaiting small arthropods to come near enough to pop out and make the capture. These beetles ooze a chemical defense (aromatic aldehydes; Moore, 1979). The

tribe is distributed throughout the globe, although most species are approximate to the equator. Only one species is known from the Plummers Island site; this species has not been seen recently.

8.01 *Megacephala virginica* Linné (1766:657)

Found under cover during the day or out running at night on wet silt flats or in stream cuts where there are wet sandy banks. These beetles are fully winged and fly; they are attracted to lights. According to Larochelle (1974c) their diet is quite varied and consists of moths, beetles, other insects, and worms. Only two examples were collected along the Maryland shore adjacent to the Island, in 1914 (EAS) and 1921 (HSB). There are no recent records. No teneral specimens were seen. Adults were collected in September. The stage in which hibernation occurs is not recorded. Total length, 17.0 to 20.0 mm (18.5).

CICINDELINI. The "tiger beetles" are a major group of small to large beetles. They are mostly terricolous, although some species frequent the leaves of low vegetation, and others are true arbicoles. They eat small arthropods or other invertebrates which they actively capture. These beetles are very rapid and agile runners, many species quickly take to flight, a few are flightless. Their larvae are found in burrows in the soil, the head capsule sealing the entrance, awaiting small arthropods to come near enough to pop out and make the capture. The tribe is distributed throughout the globe, although most species are approximate to the equator. Four species are known to occur on the Plummers Island site; two of these have not been seen recently.

9.01 *Cicindela repanda* Dejean (1825:74)

Commonly found (during the right season) below Cactus Rock on sand bars and silt flats where there is little or no vegetation, and on sunny exposed strand along the Maryland shore. Adults and larvae prey on a variety of small arthropods, and adults have been recorded eating worms. These beetles are excellent fliers and on warmer days must be caught with a net. I have seen virtual swarms of these insects on the Potomac sand bars. Larvae inhabit shallow burrows on the warm dry sandy banks at the upper edge of the secondary floodplain. Many examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, AKF, DHC, FK, WP, WLM, WVW, GGP, GNP, ABG, TLE). Adults were collected in March, April, June, July, September, October, and November. According to Shelford (1908) eggs are laid in May and June in sloping ground, usually sand; apparently both larvae and adults overwinter. Mating was observed on the Island in June (HSB); in May in Quebec (Larochelle, 1972e). Total length, 10.0 to 12.0 mm (11.0).

9.02 *Cicindela sexguttata* Fabricius (1775:226)

Unlike most *Cicindela,* these beetles live in the forest, in particularly rich deciduous woods, in shady areas; they are commonly seen running along shady trails and will run under things or into leaf litter to escape rather than fly; they are often found under bark or stones. Adults prey on small spiders, lepidopterous larvae, gnats, beetles, and ants. Larvae live in burrows in sand or clay-bearing humus and eat small arthropods that wander past. These beetles are fully winged and probably fly on occasion. Many examples were collected on the Island and adjacent shores between 1902 and the present (HSB, WLM, AHP, WVM, LLB, KK & PDH, TLE). According to Shelford (1908) eggs are laid in June or early July, larvae feed and reach third instar and overwinter in this stage; adults emerge the following spring. Adults were collected from the Island in March, April, and May. Total length, 12.0 to 14.0 mm (13.0).

9.03 *Cicindela punctulata* Olivier (1790:27)

According to Willis (1967) found in disturbed habitats such as dirt roads, paths, road cuts, eroded gullies, vacant lots, field edges, and so forth. Both larvae and adults prey on small arthropods. The beetles are fully winged and are good fliers. Several examples were collected on the Island and along the Maryland shore between 1905 and 1918 (DHC, AKF, LOJ, FK, WLM). There are no recent records. According to Shelford (1908) eggs are laid in relatively dry hard soil, usually humus, in July. Mating occurs in August in Quebec (Larochelle, 1972e). The larvae hibernate and again feed between April and June, pupate, and emerge as adults. The adults do not hibernate. Adults were collected in July and September. Total length, 11.0 to 13.0 mm (12.0).

9.04 *Cicindela rufiventris* Dejean (1825:102)

Found in the same habitats as the preceding species and also in open places in the woods where there are sandy spots. Adults have been recorded feeding on click beetles (Larochelle, 1974c). These tiger beetles are fully winged and are good fliers. Several specimens were collected on the Island and adjacent Maryland shore between 1901 and 1916 (HSB, WLM, ADA). There are no recent records. Adults occur in July and August on the Island. The life history is not recorded. Total length, 10.0 to 11.5 mm (10.8).

SCARITINI. The "pedunculate ground beetles" are numerous and diverse; this group has minute members and also the largest of the family. The entire tribe is adapted, more or less, to a fossorial way of life. They are known to eat such foods as corn seed, cutworms, and dead and dying arthropods. Some groups possess the powers of highly vagile dispersants, while others

are flightless, some even blind and living in caves. They are mostly nocturnal in habit. The few species which are active diurnal runners run clumsily. Larvae are highly predatory and usually active in the soil. The tribe is cosmopolitan. Fifteen species in five genera are known from the Plummers Island site; six of these have not been seen recently.

10.01 *Scarites subterraneus* Fabricius (1775:249)

Found on sandy dry soil, often near water, in burrows beneath large stones or logs and occasionally under debris or drifts; also found in gardens (clay soil). These beetles are fully winged and can fly quite well; they are often found coming to lights at night. They are known to eat cutworms and other fleshy lepidopterous larvae. Larvae are found in the same habitat as the adults. Several specimens were collected on the Island and adjacent Maryland shore between 1902 (HSB) and 1962 (PJS). No teneral specimens seen. Adults were found in April, June, and October. A single larva was found in August. Adults probably overwinter. Total length, 16.0 to 20.0 mm (18.0).

10.02 *Pasimachus depressus* Fabricius (1775:94)

Found occasionally in pine barrens under oak logs (D. R. Whitehead, pers. comm.) in New Jersey. None of the specimens found on the Island have ecology labels attached. The species is flightless. Many examples were collected on the Island and adjacent Maryland shore between 1902 (HSB) and 1919 (LLB), but none have been discovered since then. Since the beetles are so large it is likely that they no longer occur on the island or in the surrounding area covered by this study. Subteneral and teneral specimens were collected in June; mating also occurs in June. Adults, at least, overwinter. Adults were collected from May through September. Total length, 24.0 to 29.0 (26.5).

10.03 *Dyschirius sphaericollis* Say (1823b:23)

Found on silty sand along the Channel and on the river edge; best obtained by splashing the surface with water and waiting for the beetles to rise. Usually these beetles are found with *Bledius* (Staphylinidae) or *Heterocera* (Heteroceridae) and feed on their larvae. Members of this species are fully winged and probably fly. Several examples were collected on the Island and adjacent Virginia shore between 1902 and the present (EAS, HSB & EAS, WLM, PH, JLW, TLE & DRW). Tenerals have been found elsewhere in the latter part of the summer, through October. Adults have been collected in April, May, July, August, and September. Adults, most likely, hibernate (Lindroth, 1961b). Total length, 4.2 to 5.2 mm (4.7).

10.04 *Dyschirius globulosus* Say (1823b:23)

According to Lindroth (1961b), "Not strictly riparian, though often occurring in the uppermost zone of river banks. On moderately moist sand or sand-mixed clay with thin depressed vegetation, often tiniest moss, bare in spots. Not dependent on *Bledius*." They are often found in drift material as well. The species is wing-dimorphic. Only two specimens collected, one from the Island and one from the adjacent Maryland shore in 1903 and 1918 (HSB, EAS) respectively. Teneral adults are recorded elsewhere in late summer. Adults were collected in April, May and July. Hibernation takes place in the adult stage. Larochelle (1974b) found the beetles hibernating on "mounds," "along edges of wooden [sic] areas" and "in a hedge of hawthorn" between January and March in Quebec. Total length, 2.6 to 3.2 mm (2.9).

10.05 *Dyschirius pilosus* LeConte (1857a:80)

Found in low damp places in the forest on the secondary floodplain and on the steeper clayish banks of the Channel and river. The low damp places in the forest are sandy with low sparse prostrate vegetation and bare spots. The beetles are made active by treading on the soil and vegetation. The wings are fully developed and probably functional. Many examples were collected on the Island and adjacent shores between 1905 and the present (EAS, HSB, JLW, GFH, TLE). The beetles are numerous when located and there appears to be no connection with *Bledius*. Teneral adults are found in late summer. Adults were collected in March, April, May, August, and September. Hibernation takes place, most likely, in the adult stage. Total length, 2.7 to 3.2 mm (3.0).

10.06 *Dyschirius affinis* Fall (1901:209)

According to Lindroth (1961b) "strictly riparian and found on steep sandy-clayish banks of rivers in company of *Bledius*." The beetles are fully winged and fly; they are attracted to lights. Only one example was collected on the Island, in 1905 (HSB). Teneral adults are found elsewhere in the late summer. The single adult was collected in August. Hibernation takes place, most likely, in the adult stage. Total length, 2.7 to 3.0 mm (2.9).

10.07 *Dyschirius haemorrhoidalis* Dejean (1831:511)

Found on bare wet silt along the Channel near the ferry landing by quaking. These beetles are fully winged and probably fly. Several examples were collected on the Island between 1904 and the present (JLB & HSB, HSB & EAS, TLE). No teneral specimens seen. Adults were collected in April, May, July, and August. It is probable that adults hibernate. Total length, 2.7 to 3.0 mm (2.9).

10.08 *Ardistomis viridis* Say (1823b:21)

Commonly found on wet silt on both sides of the Channel, below Cactus Rock, and other similar sites on the Island's southeast margin. These beetles can be flushed out by quaking and spashing water over the mud. They run rather awkwardly and can be easily captured. They are fully winged and fly commonly; they are attracted to lights. Many examples were collected on the Island and adjacent Maryland shore between 1960 and the present (PJS, TLE & DRW). These beetles are very commonly in high numbers in the right situation and it is peculiar that they were not collected earlier. Teneral specimens were collected in August. Adults were collected in April, June, and August. Hibernation takes place, undoubtedly, in the adult stage. Total length, 5.0 to 6.5 mm (5.8).

10.09 *Clivina bipustulata* Fabricius (1801:125)

Found in buried layers of leaf litter mixed with silt on the primary floodplain of the river at the southwest corner of the Island, among the roots of shore grasses, and in highly organic and decaying vegetation at the edge of the Pond and Trail Pond. These beetles are best obtained by treading and splashing the vegetation and mud. The wings are fully developed and the beetles fly; they are attracted to light. Several examples were collected on the Island and adjacent shores between 1902 and the present (HSB, EAS, WLM, TLE & DRW). No teneral specimens seen. Adults were collected in April, May, June, and August. Teneral specimens from nearby areas (e.g. Beltsville, Maryland) are dated August and September. Adults hibernate. Total length, 5.8 to 7.5 mm (6.7).

10.10 *Clivina americana* Dejean (1831:503)

Found in damp or wet leaf litter which has partially decomposed at the edge of forest ponds in shady sites. The beetles are best obtained by raking the litter into the water and washing it; the beetles float to the surface and can be skimmed off by hand. The beetles are fully winged and probably fly. Many examples were collected at the Pond, on the Island, and on the Virginia shore between 1903 and the present (EAS, HSB, PJS, TLE & DRW). No teneral specimens seen. Adults were collected March, April, June, July, August. Teneral specimens from nearby areas (e.g. Fairfax, Virginia) were found in August, September, and October, therefore hibernation takes place as an adult. Total length, 4.7 to 6.0 mm (5.4).

10.11 *Clivina impressifrons* LeConte (1844:50)

According to Lindroth (1961b) found on river banks some distance from the water on sandy clay. The adults are partly carnivorous and also eat germinating seed corn (Phillips, 1909). The beetles are fully winged and fly

quite well; they are attracted to light. Only one example was collected on the Island, in 1908 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in May. According to Phillips (1909) adults hibernate. Total length, 5.9 to 7.0 mm (6.5).

10.12 *Clivina dentipes* Dejean (1825:415)

Found in a variety of habitats: under stones in the shade at the mouth of Rock Run, on the silt near the water of the Channel, in partially decaying leaf litter at the margin of Trail Pond. Adults are fully winged and fly. Several examples were collected on the Island and adjacent shores between 1902 and the present (HSB, JLW, LLB, PJS, TLE & DRW, GGP, TLE & HF). No teneral specimens seen. Adults were collected in April through October. Teneral specimens from nearby areas (e.g. Nelson County, Virginia) are dated August, therefore hibernation takes place as an adult. Total length, 7.0 to 9.0 mm (8.0).

10.13 *Clivina ferrea* LeConte (1857a:81)

Found on the primary floodplain of large rivers in fine sand or silt (TLE, in Kansas) and in soil of cotton fields and peach orchards. Adults are fully winged and fly; they are attracted to lights. Only one specimen was collected on the Maryland shore, in 1903 (WVW). There are no recent records. No teneral specimens seen. The single adult was collected in April. Elsewhere (e.g. Mississippi) teneral adults were collected in July and August. Hibernation takes place in the adult stage. Total length, 4.5 to 6.1 mm (5.3).

10.14 *Schizogenius ferrugineus* Putzeys (1846:653)

Found in moist sand on beaches of rivers, lakes, and the ocean (DRW, pers. comm.). Adults are fully winged and fly; they are attracted to lights. Three specimens were collected on the Island, in 1903, 1908, and 1912 (HSB, HSB & EAS). There are no recent records. No teneral specimens seen. Adults were collected in April, May, and June. Teneral specimens from nearby areas (e.g. Chesapeake Beach) are dated August and September, therefore hibernation takes place as an adult. Total length, 3.1 to 3.8 mm (3.5).

10.15 *Schizogenius lineolatus* Say (1823b:22)

According to Whitehead (1972) these beetles are found in gravel bars along streams. On the Island they occur in coarse sand mixed with clay along the river; we obtained the specimens by splashing water over the sand. The adults are fully winged and probably fly. Three specimens were recently collected on the Island, in 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April. According to Whitehead (1972) adults

are found between April and October; it is probable that adults hibernate. Total length, 3.8 to 4.4 mm (4.1).

RHYSODINI. The "wrinkled bark beetles" are a minor group of small, slender, and somewhat cylindrical animals which live in wood (living or dead), roots, or under bark. These beetles eat fungal mycelia, at least in part, but their natural history is very poorly understood at present. Bell (1979) suggests that these beetles are excellent "rafters" and have dispersed this way to remote islands, as most groups are wingless and do not fly. If this is so, their food source of fungal mycelia in wood would travel with them making them excellent "founders." Their daily activity is unknown; they leave the wooden substrate only during dispersion and are infrequently found out of the substrate. They occur in most parts of the world at medium to low elevations; there are a great many species on oceanic islands. Only one species of this tribe is known to occur at the Plummers Island site; however, it is probable that a second species in a different genus also occurs there (see below).

11.01 *Omoglymmius americanus* Laporte (1836:58)

Members of this species have been found at Great Falls, Virginia. They occur in a "wide range of host trees" (Bell, 1970) including maple, oak, and elm. Since these trees are common on the Island, it is likely that this common species of beetle will turn up there, especially since they are capable of flight.

11.02 *Clinidium sculptile* Newman (1838a:666)

Found under the bark and in the wood of pitch pine (*Pinus rigida*) and tulip-tree (*Liriodendron tulipifera*), but according the Bell (1970) only in logs, dead roots, or lower stumps of these trees, and the wood must be partially decayed and somewhat moist, although firm. These beetles have strongly reduced flight wings and are not capable of flight. Many examples were collected on the island and adjacent shores between 1902 and 1917 (HSB, EAS, WLM, WMM). There are no recent records. According to Bell (1970) "several true teneral specimens from Washington, D.C., are dated Sept. 6." Adults were found in April, May, June, and September. Hibernation undoubtedly takes place in the adult stage in the wood. Total length, 6.5 to 7.6 mm (7.0).

BEMBIDIINI. The "minute carabids" are a major group of very small to small beetles. They are mostly terricoles, but a few are arboricoles and some are cavernicoles. These beetles eat dead and dying arthropods and some are specialized predators of insect eggs, others are highly predaceous.

Most species are highly vagile dispersants, some are wing-dimorphic, and some others are flightless. Many species are diurnal, many other nocturnal; many are confined to water edges, others to very dry situations. The defense chemical system of these small beetles houses aliphadic ketones, higher saturated acids, and aromatic aldehydes (Moore, 1979) and oozes these against predators; however, at least one species was found in the gut of an American Toad, *Bufo americanus* (Larochelle, 1974d). These beetles occur in most habitats in most parts of the globe, at high and low elevations. Thirty-six species in 8 genera are known to occur at the Plummers Island site; 13 species have not been seen recently.

12.01 *Bembidion inaequale* Say (1823a:151)

Found at the margin of running water on clay or clay mixed with sand where there is very sparse or no vegetation. Adults are active during the day, mating, running, and flying in the sunshine; they feed on dead and dying arthropods washed up on the shore. They are made active by splashing water on the sand and are then captured (with great difficulty) before they fly. Many examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, WLM, AKF, JCC, RPC, RCS, WSF, JLW, TLE & DRW). One teneral specimen was collected in July. Adults were collected March through August. Hibernation takes place in the adult stage. Total length, 4.6 to 5.6 mm (5.1).

12.02 *Bembidion confusum* Hayward (1897:52)

According to Lindroth (1963) found on "bare, clay-mixed sand near water, both rivers and lakes." The adults feed on dead and dying arthropods that are washed up on shore. They are fully winged and fly rapidly. Only one example was collected on the Island, in 1918 (JLW). There are no recent records. No teneral specimens seen. The single adult was collected in July. Teneral specimens from elsewhere (e.g. Kansas) were collected in August and September, therefore hibernation takes place probably as an adult. Total length, 4.5 to 6.7 mm (5.6).

12.03 *Bembidion honestum* Say (1823b:82)

According to Lindroth (1963) found on barren gravel banks of rivers and brooks, however in our area also found on silt close to the water on the Maryland side of the Channel; taken by splashing the silt with water. These beetles are fully winged and probably fly. Two examples were found on the Maryland shore, in 1973 (TLE). No teneral specimens seen. Adults were collected in April. Closely related species hibernate as adults and it is probable these do also. Total length, 5.6 to 6.8 mm (6.2).

12.04 *Bembidion americanum* Dejean (1831:87)

According to Lindroth (1963) found on "gravelly soil near water where there is sparse vegetation of *Eleocharis* and *Carex*." I have collected it also on sandy silt along a river in Texas. One adult in USNM was found eating a mosquito larva. The beetles are fully winged and fly quite well; often taken in light traps. Only two examples were collected on the Island, in 1905 and 1906 (HSB). No teneral specimens seen. The adults were collected in April and August. Hibernation takes place in the adult stage. Total length, 5.0 to 6.0 mm (5.5).

12.05 *Bembidion levigatum* Say (1823b:84)

Commonly found in coarse sand and gravel mixed with silt on the south side of the Island east of Cactus Rock. They are made active by splashing water over the substrate; often they run in the sunshine. The beetles are fully winged and no doubt fly. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (WLM, HSB, JLW, WVW, GFH, TLE & DRW). Specimens collected in July and August were subteneral; adults were collected in April, May, June, July, and August. Hibernation takes place in the adult stage. Total length, 5.5 to 7.2 mm (6.4).

12.06 *Bembidion fugax* LeConte (1848:467)

Commonly found in a variety of situations; on coarse gravel and sand mixed with silt, in leaf litter on the secondary floodplain, under small branches on the secondary floodplain, and under bark of a downed tree after high water. On the river bank it can be taken by splashing water over the substrate. The beetles are fully winged and no doubt fly. Many examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, RCS, JLW, PJS, GFH, TLE & DRW, DRW). Subtenerals were collected in July and August. Adults were found in April, May, June, July, August, and September. Hibernation takes place in the adult stage. Total length, 5.0 to 6.0 (5.5).

12.07 *Bembidion nigrum* Say (1823b:85)

According to Lindroth (1963) found in gravel and sand mixed with clay along the margin of small rivers and quiet small brooks. According to Larochelle (1974a) found "on barren soil, usually gravel mixed with sand and clay, on river banks . . . in crevices of steep banks . . . under stones . . . often associated with *Schizogenius lineolatus* Say and [*Paratachys*] *tripunctatus* Say." The beetles are fully winged and probably fly. According to HSB card file two specimens were collected on the Island in 1903 and 1906 (HSB) and one on the Virginia shore in 1905. I have not been able to

locate any of these specimens in USNM. There are no recent records. No teneral specimens seen. Adults were collected in June, August, and September. According to Lindroth (1963) hibernation takes place in the adult stage. Total length, 3.7 to 4.4 mm (4.0).

12.08 *Bembidion semistriatum* Haldeman (1843:303)

According to Lindroth (1963) found on gravel and sand banks along running water, usually in shady places. The beetles are fully winged and probably fly. Only one example was found on the Virginia shore, in 1912 (PRM). No teneral specimens seen. The single adult was collected in July. According to Lindroth (1963) hibernation takes place in the adult stage. Total length, 3.5 to 4.2 mm (3.9)

12.09 *Bembidion lacunarium* Zimmerman (1869:248)

Found in damp sand under stones in cool shady places and not dependent on water; also according to Lindroth (1963) in damp moss and leaves in the same situation. The beetles are wingless. Only two examples were collected on the Island, in 1905 (DHC) and another unlabeled as to year and collector. No teneral specimens seen. The adults were collected in June and August. Hibernation takes place, most likely, as an adult. Total length, 4.7 to 6.0 mm (5.4).

12.10 *Bembidion variegatum* Say (1823b:89)

Common on the secondary floodplain in low damp places with sandy clay substrate and short prostrate vegetation; also under bark of dead stumps (e.g. *Platanus*). These beetles are fully winged and fly. Many examples were collected on the Island and adjacent shores between 1903 and the present (HSB & JLW, WLM, DHC, EAS, GFH, GGP, TLE). No teneral specimens seen. The adults were collected in January and February hibernating under sycamore bark; they were also taken in March through August, and October, November. Hibernation takes place in the adult stage. Total length, 4.6 to 5.7 mm (5.2).

12.11 *Bembidion rapidum* LeConte (1848:460)

Found on coarse sand mixed with gravel which occurs along the southeast margin of the Island. They were taken by splashing water on the substrate. These beetles are fully winged and probably fly. Only two specimens were collected on the Island, both recently in 1974 (TLE). No teneral specimens seen. Adults were collected in June; elsewhere they have been collected in May and July (Larochelle, 1975b). Hibernation takes place probably in the adult stage as in the nearest relatives. Total length, 3.8 to 4.4 mm (4.1).

12.12 *Bembidion castor* Lindroth (1963:366)

Very common in a variety of substrates on the Island and adjacent Maryland shore; under drift material on upper primary floodplain in sand, on wet silt in shade or sun on both sides of the Channel and along the river, under stones in the shade at mouth of Rock Run. The beetles are very active in the day flying and running in the sunshine. They are fully winged and fly; they are attracted to lights (Larochelle, 1973). Numerous examples were collected on the Island and adjacent shores between 1903 and the present (HSB, EAS, WSF, AKF, RCS, WLM, PJS, GFH, TLE & DRW, TLE & HF, TLE). Teneral specimens were collected in June and July. Adults were collected in March through September. Hibernation is in the adult stage. Larochelle (1972d) collected these beetles under snow in leaf litter at the edge of a eutrophic marsh in January, in Quebec, and (1947b) in and on "mounds" between November and March, in Quebec. Total length, 3.4 to 4.3 mm (3.9).

12.13 *Bembidion affine* Say (1823b:86)

Commonly found in a variety of habitats and substrates on the Island and adjacent Maryland shore; on wet, bare silt flats along river, in and under drift material on the upper primary floodplain on the southwest shore of the Island, in coarse sand mixed with clay on the southeast shore, on sandy clay on secondary floodplain in low damp places with prostrate vegetation. They are taken by splashing or treading and are often active in the sunshine. The adults are fully winged and fly. Numerous examples were collected on the Island and adjacent Maryland between 1902 and the present (HSB, HSB & EAS, OH, JLW, WSF, WLM, PJS, GFH, TLE & DRW, TLE). Teneral specimens were collected in July and August. Adults were collected March through August and October. Hibernation takes place in the adult stage. Total length, 2.9 to 3.5 mm (3.2).

12.14 *Bembidion impotens* Casey (1918a:129)

Found in drift material in sand on upper primary floodplain at the southwest corner of the Island below the Cactus Rock and in cracks of moist silt on the primary floodplain along the Maryland shore adjacent to the Island. The beetles are fully winged and fly. Only two specimens were found on the Island and adjacent Maryland shore recently, in 1972 and 1973 (TLE). No teneral specimens seen. The adults were collected in April and October; the April specimen is not fully pigmented and may be subteneral. However, Lindroth (1963) indicated adult hibernation. Total length, 2.4 to 3.2 mm (2.8).

12.15 *Bembidion pedicellatum* LeConte (1857b:6)

Found on dry sand at the uppermost part of the secondary floodplain on the northwest end of the Island (elsewhere, e.g. Oakton, Virginia, I have found these beetles running on ant mounds in the sunshine). The beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Virginia shore between 1912 and 1916 (HSB & EAS, WLM, GMG). No teneral specimens were collected. Adults were found in March, April, August, and October. Hibernation takes place probably as an adult. Total length 2.7 to 3.4 mm (3.0).

12.16 *Bembidion quadrimaculatum* Linné (1761:211)

According to Lindroth (1963) found on relatively moist fine sand or clay at the upper edge of the primary floodplain of rivers and upper parts of lake shores, and often in cultivated fields. These beetles have been observed feeding on the eggs of the mantid *Hylemyia*. The beetles are fully winged or with somewhat reduced apex, thus flight powers are not possessed by all individuals. They are both nocturnal and diurnal (Larochelle, 1975a). According to HSB card file one individual was collected on the Island in 1907; I have not been able to locate this specimen in USNM. Two additional specimens were collected, one on the Island and one on the adjacent Maryland shore in 1973 (TLE). No teneral specimens seen. Specimens were collected in April. According to Lindroth (1963) hibernation takes place as an adult. Larochelle (1972d) collected these beetles under snow in leaf litter at the edge of the eutrophic marsh in January, in Quebec, and (1974b) on and in mounds six inches deep between November and March, in Quebec. Total length, 2.8 to 3.7 mm (3.3).

12.17 *Anillinus barberi* Jeannel (1963:150)

Type-locality: Plummers Island, Maryland. Found under large stones in cool shaded areas in the forest (Barr, pers. comm.). These beetles are both blind and wingless and are true hypogean carabids. Several specimens were collected on the Island and adjacent shores between 1905 and 1931 (HSB, WMM). No recent specimens have been found. No teneral specimens seen. Adults were collected in March, April, May, and October. Nothing is known about their life cycle, but is seems likely that adults hibernate. Total length, 1.8 to 2.0 mm (Jeannel's measurements are too high for the same specimens) (1.9).

12.18 *Mioptachys flavicauda* Say (1823b:87)

Found commonly under bark of dead and dying hardwood trees (*Acer, Juglans, Populus,* and in California *Pinus ponderosa,* TLE). They prey upon small arthropods (and probably their eggs) in the wood and under bark. They are fully winged and fly. Several examples were collected on the Island and Virginia shore between 1905 and the present (HSB, GFH). No teneral specimens seen. The adults were collected March, May, June, July, August, and September. Hibernation takes place probably as an adult. Total length, 1.5 to 1.8 (1.7).

12.19 *Tachyta nana inornata* Say (1823b:87)

Found under the bark of a variety of host trees (*Pinus, Quercus, Abies, Ulmus,* and *Celtis*) where they prey on small arthropods. The beetles are fully winged and fly during the day. One specimen was collected on the Virginia shore in 1905 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in April. Other records (Erwin, 1975) indicate that adults hibernate. Total length, 2.3 to 3.2 mm (2.8).

12.20 *Elaphropus granarius* Dejean (1831:61)

Found on dry sand and gravel in open areas. These beetles are wing dimorphic and it is probable that the long wing form flies (found in drift on lake shores). HSB card file records specimens collected on the Island and adjacent shores between 1902 and 1907. I have not been able to locate any of the 8 specimens HSB recorded in the USNM. There are no recent records. No teneral specimens seen. The adults were collected in March through June, September, and October. Hibernation probably takes place as an adult. Total length, 1.9 to 2.3 mm (2.1).

12.21 *Elaphropus levipes* Casey (1918a:186)

Found in coarse sand mixed with silt on the southeast corner of the Island; the 1974 specimen was collected by splashing. These beetles are fully winged and fly. WHT found a specimen under bark. Only three examples were collected on the Island, in 1902 (HSB card file, not located in USNM), 1970 (WHT), and in 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April, August, and September. Hibernation probably takes place as an adult. Total length, 2.0 to 2.4 mm (2.2).

12.22 *Elaphropus saturatus* Casey (1918a:187)

Found with the preceding species on coarse mixed sand and according to Lindroth (1966) also found "along brooks in the transitional zone between sterile gravel and the carpet of vegetation." These beetles are fully winged and no doubt fly. Several specimens were collected on the Island or adjacent Maryland shore between 1902 and the present (HSB & EAS, GFH, TLE & DRW, TLE). A teneral specimen was collected in August. Adults were collected in March, April, and August. Hibernation takes place in the adult stage. Total length, 2.3 to 2.9 mm (2.6).

12.23 *Elaphropus incurvus* Say (1834:440)

Found in a variety of habitats on different substrates; with the two preceding species on coarse sand mixed with silt, on clay mixed with sand at low damp places on the secondary floodplain usually with low prostrate vegetation, and on baked silt along both sides of the Channel on the primary floodplain. These beetles are collected by splashing or by turning over caked silt slabs. They are fully winged and fly; they are attracted to light. They are diurnal. Numerous examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, WLM, PRM, WVW, GFH, TLE & DRW, TLE). Teneral specimens were found in June and July. Adults were collected in February through August. Hibernation takes place in the adult stage. Total length, 2.0 to 2.5 mm (2.3).

12.24 *Elaphropus vivax* LeConte (1848:468)

Found in the same places as the preceding species and according to Lindroth (1966) in the same place as *E. saturatus*. These beetles are fully winged and fly. Numerous examples were collected on the Island between 1902 and the present (HSB, EAS, WLM, WSF, RPC, TLE & DRW). Teneral specimens were collected in July and August. Adults were collected in March through August, October, and November. Hibernation takes place as an adult. Total length, 2.4 to 2.9 mm (2.7).

12.25 *Elaphropus tripunctatus* Say (1834:439)

Found on sand and gravel along running water where there is no vegetation. These beetles are fully winged and fly. HSB card file records specimens collected between 1902 and 1907 from the Island. I have not been able to find these specimens in the USNM. There are no recent records. No teneral specimens seen. Adults were collected in April, and July through October. Hibernation probably takes place as an adult. Total length, 2.6 to 3.2 mm (2.9).

12.26 *Elaphropus vernicatus* Casey (1918a:181)

Found in low damp places on the secondary floodplain in sand mixed with clay and covered in part by prostrate vegetation; also one specimen from coarse sand mixed with silt at the southeast corner of the Island. The former were taken by treading, the latter by splashing. The adults are fully winged and no doubt fly. Many examples were collected recently from the Island and adjacent Maryland shore, in 1973 and 1974 (TLE, TLE & DRW). No teneral specimens seen. Adults were collected in April and May. Hibernation probably takes place as an adult. Total length, 2.0 to 2.2 mm (2.1).

12.27 *Elaphropus ferrugineus* Dejean (1831:59)

Found on the Island and elsewhere in the nests of ants (*Lasius*) and probably an obligatory myrmecophile; however, I recently collected one example running on dry sand in the shade on the east end of the Island, at the upper edge of the secondary floodplain. Wings absent. Only two examples were found on the Island, in 1905 (EAS) and 1975 (TLE). Another from the Maryland shore was collected in 1903 (HSB). No teneral specimens seen. The adults were collected in April, July, and October. Nothing is known about the life cycle of these beetles. Total length, 2.5 to 3.1 mm (2.8).

12.28 *Pericompsus ephippiatus* Say (1834:439)

Found on wet sand mixed with clay along large rivers in the primary floodplain. The adults are fully winged and fly; they are attracted to lights (Erwin, 1974). Several specimens were collected on the Island between 1902 and 1924 (HSB & EAS, WSF). There are no recent records. One teneral specimen was collected in July. Adults were collected in May, June, July, and August. Hibernation takes place in the adult stage. Total length, 2.3 to 3.0 mm (2.7).

12.29 *Paratachys proximus* Say (1823b:88)

Found on coarse sand mixed with silt along the primary floodplain at the southeast corner of the Island, and on sand mixed with clay at low damp places on the secondary floodplain where there is low prostrate vegetation. The beetles are fully winged and fly; they are attracted to lights. Several specimens were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, RCS, EAS, TLE & DRW, TLE). One teneral specimen was collected in July. Adults were collected in April, May, July, and November. Hibernation takes place in the adult stage. Total length, 2.6 to 3.1 mm (2.9).

12.30 *Paratachys scitulus* LeConte (1848:471)

Found in a variety of habitats along the primary floodplain and in leaf litter at the edge of the Pond, usually close to the water on wet silt or sand mixed with silt, also under slabs of caked silt where there was still moisture, and among the roots of vegetation at the transition from sterile silt to secondary floodplain. These beetles are fully winged and fly readily in the sunshine. Many examples were collected on the Island and adjacent shores between 1905 and the present (EAS, HSB & EAS, DHC, GFH, TLE & DRW, TLE). No teneral specimens seen. Adults were collected in March, April, May, July, August, September, and October. Hibernation probably takes place as an adult. Total length, 2.6 to 3.0 mm (2.8).

12.31 *Paratachys potomaca*, new species (Frontispiece, Fig. 6)

Type-locality.—Plummers Island, Montgomery County, Maryland.

Type-specimens.—Holotype male in USNM (type number 76906), collected by D. H. Clemons in 1907; allotype in USNM, collected by D. R. Whitehead and T. L. Erwin in 1974; 9 paratypes in USNM, collected by DRW & TLE, and TLE.

Description.—Color rufopiceous, forebody slightly paler, elytra strongly iridescent; mouthparts, legs, and antennal scape testaceous; antennal flagellum infuscated. Head normal for genus, eyes small and almost flat. Pronotum narrow, slightly wider than head and elytron, narrowed basally, sides not at all sinuate, hind angles obtuse. Elytra oblong-oviform; sutural stria well impressed, second stria barely visible from oblique angle; recurrent groove hooked immediately around Ed 6. Microsculpture of head almost isodiametric and slightly granulate; pronotum with well impressed transverse meshes; elytron with finely impressed strongly transverse lines. Male with basitarsus of anterior leg spiniform. Male genitalia illustrated in Fig. 6. Total length, 2.0 to 2.3 mm (2.2).

Natural History.—Found in low damp places on the secondary floodplain on sand mixed with clay where there is prostrate vegetation and at the margins of the Pond in leaf litter; taken by treading or splashing. The wings are reduced to half the length of the elytron, thus the beetles are incapable of flight. The type series was collected in March, April, and May. None of these were teneral. Adults probably hibernate.

Distribution.—The range of this species extends from Massachusetts to North Carolina on the east side of the Appalachians, never far from the coast, but not restricted to the Coastal Plain.

Discussion.—This species has been referred to and confused with *P. corruscus* LeConte both in the literature and in collections. Members of *P. corruscus* are fully winged, broader across the humeri, and have large and rounded eyes.

12.32 *Paratachys obliquus* Casey (1918a:201)

According to Larochelle (1971) "Found at the edges of small, standing waters and rivers, in open or moderately shaded areas where the soil is clayish, often mixed with organic matters, and where the vegetation is scarce." These beetles are fully winged and probably fly. One example was collected along the towpath near the Island in 1960 (PJS). There are no recent records. No teneral specimens seen. The single adult was collected in June. Adults hibernate. Larochelle (1974b) found these beetles hibernating on a "mound" in November, in Quebec. Total length, 2.4 to 2.6 mm (2.5).

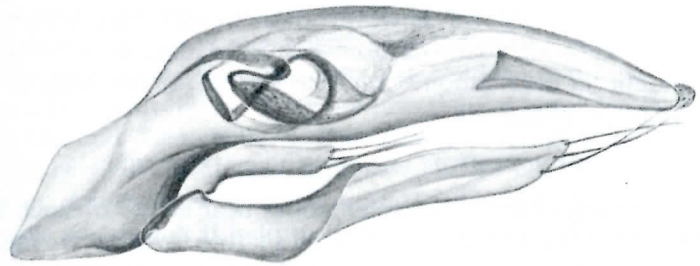

Fig. 6. Male genitalia, left lateral aspect, of *Paratachys potomaca*, n. sp., Plummers Island, Maryland.

12.33 *Paratachys corruscus* LeConte (1848:472)

Found in drift on the shores of lakes and rivers. These beetles are wing-dimorphic and the fully winged individuals fly; they are attracted to lights. Four examples were collected on the Maryland shore, in 1920 (HSB). There are no recent records. No teneral specimens seen. The adults were collected in May. Hibernation probably takes place in the adult stages as in other related species. Total length, 2.2 to 2.3 mm (2.3).

12.34 *Polyderis laevis* Say (1823b:88)

Found under stones in rich soil and at the borders of marshes (Lindroth, 1966) and I have found these beetles in Vermont on the refuse pile of ant nests in an open field with mixed herbs and grasses. The wings are fully developed and have fringe hairs; they no doubt fly. Only two examples were collected on the Maryland shore, in 1920 and 1923 (HSB). There are no recent records. No teneral specimens were seen. The adults were collected in April and May. Adults hibernate, Larochelle (1974b) found these beetles hibernating "in a hedge of hawthorn" and "in swampy areas, in clumps of moss and grass" in November to January, in Quebec. Total length, 1.3 to 1.5 mm (1.4).

PATROBINI. The "cross-groove carabids" are a very minor group of small to medium-sized beetles. They eat dead and dying arthropods and other invertebrates and are nocturnal in habit. Many species live by water, others in drier parts of forests. Most species are truly hygrophilous. These beetles are vagile dispersants; some are flightless. The chemicals of the defense secretion system are unknown, however, these beetles have been found in the gut of the American Toad, *Bufo americanus* (Larochelle, 1974d). The tribe is Holarctic in distribution. Only one species of this tribe is known from the Plummers Island site.

13.01 *Patrobus longicornis* Say (1823b:40)

Found in a variety of habitats; under stones near mouth of Rock Run, in leaf litter at edge of Pond, and according to Lindroth (1961b) "On meadows, in light deciduous forest, and on cultivated ground with rich vegetation. Usually on clayish soil. Often near margin of lakes and rivers but not really hygrophilous." Both short-winged and fully-winged specimens are found on the Island; the long-winged ones probably fly. These beetles were observed running during the day (Larochelle, 1975a) in Quebec. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (HSB, WLM, WVW, TLE & DRW, GGP, TLE & HF). Teneral specimens were found in June on the Island and in May in the District of Columbia. Mating occurs in June in Quebec (Larochelle, 1972e). Adults were collected in April, May, June, October, and November. Hibernation probably takes place both in the larval and adult stages. Total length, 9.2 to 14.8 mm (12.0).

PTEROSTICHINI. The "woodland or lined-winged beetles" are a very major group of small to very large beetles. This group contains a tremendous variety of adaptive kinds of species including scavengers, predators, and herbivores. Some species are known to have subsocial activities between adults and larvae. Species vary from nocturnal to diurnal, hygrophilous to xerophilous, and highly vagile dispersants to flightless. The tribe is cosmopolitan. Thirty-eight species in 11 genera are known from the Plummers Island site; 17 species have not been seen recently.

14.01 *Europhilus sordens* Kirby (1837:25)

Found on secondary floodplain in leaf litter on sand mixed with clay where it is damp. These beetles are fully winged and probably fly. Two examples were found on the Maryland shore, in 1974 and 1975 (TLE, DRW). No teneral specimens seen. The adults were collected in March and April. According to Lindroth (1966) the adults probably hibernate. Larochelle (1972a) has collected these beetles hibernating in rotten tree stumps in mid-November, in Quebec; and (1972d) from under snow in leaf litter at the edge of a eutrophic marsh in January, in Quebec; and (1974b) on and in "mounds" between November and February, in Quebec. Total length, 5.3 to 6.5 mm (5.9).

14.02 *Agonum octopunctatum* Fabricius (1798:55)

Found on the primary and secondary floodplain, on sand or sand mixed with silt where the soil is moist especially under deep piles of drift material below the permanent vegetation line. The beetles are fully winged and fly; they are attracted to lights. They are also diurnal and have been observed flying in the rain (Larochelle, 1975a). Several examples were collected on the Island between 1905 and the present (WLM, TLE). No teneral specimens seen. Adults were collected in May, June, and October. Hibernation takes place as an adult (Lindroth, 1966). Total length, 7.5 to 8.5 mm (8.0).

14.03 *Agonum fidele* Casey (1920:116)

According to Lindroth (1966) found at the margin of eutrophic ponds and in *Typha latifolia* marshes on sandy ground. According to Larochelle (1974a) found "at the borders of ponds, marshes, and brooks, in more or less shady places, where the soil is wet, under willows and alders." The wings are fully developed and the beetles probably fly. Only one specimen was collected on the Island, in 1917 (GMG Collection). There are no recent records. No teneral specimens seen. The single adult was collected in June. The stage in which hibernation takes place is unknown. Total length, 7.3 to 9.0 mm (8.2)

14.04 *Agonum tenue* LeConte (1854:48)

Found in low wet areas near Trail Pond and at its margins on sand mixed with much decaying leaf litter and wet humus; taken by treading. These beetles are fully winged and fly; they are attracted to light. Several specimens were collected on the Maryland shore in 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April. Hibernation probably takes place as an adult. Total length, 8.0 to 9.5 mm (8.8).

14.05 *Agonum placidum* Say (1823b:43)

According to Lindroth (1966) found in open sandy country, often in fallow or cultivated fields among marginal weeds, in sand pits; a definite xerophilous species. These beetles are fully winged and fly; they are attracted to lights. They are both nocturnal and diurnal and have been observed mating in the day (Larochelle, 1975a). Two examples were collected on the Island early, in 1905 (WLM). There are no recent records. No teneral specimens seen. Mating occurs in July in Quebec (Larochelle, 1972e). The adults were collected in May and June. According to Lindroth (1966) adults hibernate.

Larochelle (1972) collected these beetles hibernating in rotten tree stumps in mid-November, in Quebec. Total length, 6.8 to 8.8 mm (7.8).

14.06 *Agonum striatopunctatum* Dejean (1828:167)

According to Lindroth (1966) found in open country, not necessarily near water. The single specimen from the Island was probably collected in drift at the southwest corner of the Island, but unfortunately was not labelled as such along with the rest of the series. These beetles are fully winged and fly. One example was collected on the Island, in 1975 (TLE). No teneral specimens seen. The adult was collected in March. Hibernation undoubtedly takes place as an adult. Total length, 6.5 to 8.0 mm (7.3).

14.07 *Agonum rigidulum* Casey (1920:75)

Found in a variety of habitats; under drift on primary and secondary floodplain of the river, on sand mixed with clay in low damp places on the secondary floodplain where there is low prostrate vegetation, under stones along and at mouth of Rock Run about 1 to 2 meters from the water. These beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Maryland shore in 1972, 1973, and 1974 (GFH, TLE, TLE & HF). No teneral specimens seen. The adults were collected in April, May, and October. Hibernation probably takes place as an adult. Total length, 6.2 to 8.2 mm (7.2).

14.08 *Agonum aeruginosum* Dejean (1828:168)

According to Lindroth (1966) found very close to the water on soft, muddy soil with rich vegetation (*Carex, Scirpus, Solanum,* etc.) and in the shade of willows. These beetles are fully winged and fly. Only one specimen was collected on the Island, in 1919 (EAS & HSB). There are no recent records. No teneral specimens seen. The adult was collected in June. According to Lindroth (1966) adults hibernate. Total length, 5.2 to 6.5 mm (5.9).

14.09 *Agonum excavatum* Dejean (1828:169)

Found on coarse sand mixed with silt on the primary floodplain at the southeast corner of the Island along the river. Specimens were collected by splashing. One specimen was taken at very low water level running on bare drying silt along the Channel. According to Lindroth (1966) also found on bare spots near sphagnum bogs. These beetles are fully winged and probably fly. They were seen mating during the day (Larochelle, 1975a). Four examples were collected on the Island and adjacent Maryland shore recently, in 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April and May. Hibernation probably takes place as an adult. Total length, 6.0 to 7.5 mm (6.8).

14.10 *Agonum ferreum* Haldeman (1843:299)

Found commonly at the edge of the Pond in wet, partially decaying leaf litter on rather organic soil; collected by washing the leaf litter in the water. These beetles are fully winged and probably fly. Many examples were collected on the Maryland shore recently, in 1974 (TLE & DRW), 1975 (TLE). No teneral specimens seen. The adults were collected in April and July. Hibernation takes place as an adult. Total length, 6.5 to 7.5 mm (7.0).

14.11 *Agonum extensicolle* Say (1823b:54)

The most common beetle found on the Island or adjacent shores. They are found in a variety of habitats but usually on the primary and secondary floodplains on sand or sand mixed with silt or clay, under stones, in drift, under bark of logs and stumps, and right next to the water in coarse sand mixed with silt. These beetles are fully winged or short-winged; the macropterous ones fly. They are active during the day and were seen mating in the sunshine (Larochelle, 1975a). Numerous examples were collected on the Island and adjacent shores between 1902 and the present (EAS, HSB, AKF, DHC, RCS, PJS, GFH, TLE, GGP, TLE & HF). One teneral specimen was collected in June. Mating occurs in June in Quebec (Larochelle, 1972e). The adults were collected in March through October. Hibernation takes place as an adult. Total length, 6.8 to 10.4 mm (8.6).

14.12 *Platynus decentis* Say (1823b:53)

Commonly found in the forest under bark, and under logs and stones; also in leaf litter near the Pond where they were collected by raking the litter. The wings are apparently full, but according to Lindroth (1966) not functional. These beetles were seen running during the day (Larochelle, 1975a), but must primarily be nocturnal. Many examples were collected on the adjacent shores between 1905 and the present (HSB, TLE, GGP, TLE & DRW). No teneral specimens seen. Adults were collected in March, April, June, July, and October. Hibernation is as an adult. Larochelle (1972a) collected these beetles gregariously hibernating in rotten tree stumps in mid-November in Quebec; and (1972c) observed mating in captivity, in June; and (1974b) found them on "mounds" in November through February, in Quebec. Total length, 9.0 to 14.0 mm (11.5).

14.13 *Platynus cincticolle* Say (1823b:52)

According to Lindroth (1966) found in damp mixed woods under stones, under bark of fallen logs, and under the logs. The wings are fully developed and the beetles fly. Several specimens were collected on the Island between 1902 and 1919 (HSB, EAS). There are no recent records. No teneral spec-

imens seen. The adults were collected in July, August, and September. Adults hibernate. Total length, 10.0 to 11.5 mm (10.7).

14.14 *Platynus parmarginatum* Hamilton (1893:306)

Exact habitat unknown, but probably similar to preceding two species. These beetles are fully winged and fly; they are attracted to light. Many examples were collected on the Island and adjacent Virginia shore between 1909 and 1922 (HSB, WLM, EAS). There are no recent records. Three subteneral specimens were collected in August. Adults were collected in April, June, and August. Hibernation takes place as an adult. Total length, 8.5 to 10.3 mm (9.4).

14.15 *Platynus tenuicolle* LeConte (1848:222)

According to Lindroth (1966) found beneath stones along streams and on "steep, sterile, sandy-gravelly bank of river." According to Larochelle (1974a) found "along strongly, shady margins of streams and lakes, mostly in mountainous areas . . . with *Nebria lacustris* Casey." These beetles are fully winged and fly; they are attracted to light. Several specimens were found on the Island and adjacent Virginia shores between 1902 and 1912 (HSB). There are no recent records. No teneral specimens seen. Adults were collected in April, May, June, July, and September. According to Lindroth (1966) adults hibernate. Total length, 9.5 to 13.0 mm (11.3).

14.16 *Platynus caudatus* LeConte (1863a:7)

Found under stones on rich loamy soil beneath Oak and Hickory trees in the forest near the Pond. These beetles have no wings and are flightless. Several examples were collected on the Island and adjacent shores between 1905 and the present (HSB, HSB & WMM, TLE). Teneral specimens were collected in July and September. Adults were collected in March, July, and September. Hibernation takes place in the adult stage. Total length, 12.5 to 14.5 mm (13.5).

14.17 *Calathus gregarius* Say (1823b:47)

Found under logs and stones above the secondary floodplain in more open forest, usually in drier areas, and according to Lindroth (1966) often on sand. These beetles are wing-dimorphic, but usually short-winged as are all the available specimens from our area. They eat grass, pollen, and insect larvae (Lindroth, 1966). They were seen mating and running in the sunshine (Larochelle, 1975a). Beetles of the genus *Calathus* are known to house hydrocarbons and formic acid in their defense mechanism (Moore, 1979), however they have been found in the gut of *Bufo americanus,* the American Toad. Numerous examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, HSB, RPC, WLM, RCS, TLE).

No teneral specimens seen. Mating occurs in July in Quebec (Larochelle, 1972e). The adults were collected in January, March, April, July, August, September, and October. According to Lindroth (1966) hibernation may be in more than one stage; but certainly as an adult as indicated by the January capture; Larochelle (1972a) collected one specimen in a rotten tree stump in mid-November, in Quebec, and (1974b) found hibernating adults on and in "mounds" 14 inches deep and "along edges of wooden areas" in November and December, in Quebec. Total length, 8.2 to 10.8 mm (9.5).

14.18 *Synuchus impunctatus* Say (1823b:45)

According to Lindroth (1966) found "in open country and light forests, rather on dry ground (usually moraine), e.g. among leaves under *Rubus* and other bushes." These beetles are wing-dimorphic; the specimen from the Island is fully winged. Fully winged individuals fly; they are also attracted to light. They were seen running on the surface during a cloudy day (Larochelle, 1975a). Only one specimen was collected on the Virginia shore, in 1905 (HSB). There are no recent records. No teneral specimens seen. The adult was collected in September. According to Lindroth (1966) hibernation takes place exclusively in the larval stage. Total length, 8.7 to 11.2 mm (10.0).

14.19 *Olisthopus parmatus* Say (1823b:49)

According to Lindroth (1966) found at the edge of mixed woods on sandy moist soil in the shade, and to Larochelle (1974a) "in light deciduous and mixed forest, on gravelly or sandy soil, under dead leaves and stones . . . thick litter." These beetles are fully winged but flight is not yet known to occur. Only one specimen was collected on the Maryland shore, in 1918 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in October. According to Lindroth (1966) hibernation takes place as an adult. Larochelle (1972a) has collected a specimen of this species in a rotten tree stump in mid-November in Quebec. Total length, 6.5 to 7.5 mm (7.0).

14.20 *Olisthopus micans* LeConte (1848:230)

Found in wet leaves and twigs at the margin of Trail Pond; the underlying substrate was highly organic humus and the site was partially shaded. According to Lindroth (1966) also found in dense deciduous forest, predominately *Acer,* among wet leaves at the edges of a small rill where there were a few ferns, but little other vegetation. Wings fully developed and no doubt functional. Several examples were collected on the Maryland side of the Channel, in 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April. Hibernation probably takes place as an adult since

this is the case in the related *O. parmatus,* our other eastern species. Total length, 4.0 to 4.7 mm (4.4).

14.21 *Atranus pubescens* Dejean (1828:122)

Found in leaf litter and under logs and branches on the secondary floodplain where the soil is sandy. The wings are fully developed and probably functional. Several examples were collected between 1903 and 1974 (HSB, TLE, GGP). I have not been able to locate the HSB specimens; the data presented herein are from his card file. No teneral specimens seen. Adults were collected in April, October, and November. Hibernation takes place in the adult stage. Total length, 5.0 to 7.0 mm (6.0).

14.22 *Loxandrus velocipes* Casey (1918b:390)

According to Allen (1972) found in very wet leaf litter in swampy or Bayou situations. The beetles are fully winged and can fly; they are attracted to blacklights. Only one example was collected on the Island, in 1912 (HSB). There are no recent records. No teneral specimens seen. The adult was collected in July, and according to Allen (1972) they can be expected also in January, March, April, May, June, and October. Hibernation takes place in the adult stage. Total length, 9.0 to 10.1 mm (9.6).

14.23 *Loxandrus circulus* Allen (1972:157)

Found at the edge of the Pond in leaf litter; as the pond dries in the summer the beetles follow the receding water line and finally bury themselves in the mud, thus they are very hydrophilic. They can be found by splashing and by washing the leaf litter in the water. The adults are fully winged and can probably fly. Several specimens were found at the Pond in 1974 and 1975 (TLE & DRW, RTA). No teneral specimens seen. Adults were collected in April, July, and August. Hibernation probably takes place as an adult. Total length, 10.5 to 11.3 mm (10.9).

14.24 *Myas coracinus* Say (1823b:59)

According to Lindroth (1966) an inhabitant of the eastern forest. I have collected these beetles in Vermont where they were only found on small well-drained hummocks of soil in deep leaf litter on the forest floor. The wings are absent. Numerous examples were found on the Island and adjacent Virginia shore between 1906 and 1923 (HSB, EAS, AKF, RCS, WLM, WMM). There are no recent records. No teneral specimens seen. The adults were collected in April, September and October. Hibernation probably takes place in the adult stage. Total length, 14.0 to 20.0 mm (17.0).

14.25 *Pterostichus tristis* Dejean (1828:324)

Found under logs and branches in the forest. The beetles are wingless and cannot fly. According to Perrault (1973) these beetles are also found

under bark of fallen hardwood trees. WMM & HSB collected them in pitfall traps. Several examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, WLM, JLW, WMM, GGP). Teneral specimens were collected in June and July. Adults were collected in June, August, September, October. Hibernation probably takes place in the adult stage. Total length, 10.5 to 13.5 mm (12.0).

14.26 *Pterostichus honestus* Say (1823b:51)

Found under logs and branches in the forest in shady places. The wings are reduced to tiny scales. Several specimens were collected on the Virginia shore between 1903 and 1922 (HSB, HSB & EAS, JLW, FK, WP, WLM). There are no recent records. No teneral specimens seen. Adults were collected in April, September, and October. Hibernation probably takes place in the adult stage. Total length, 7.0 to 8.5 mm (7.8).

14.27 *Pterostichus chalcites* Say (1823b:56)

According to Lindroth (1966) found in open fields and in open woods on damp soil, usually near water. These beetles are fully winged and flight is common; they are attracted to lights. Only three examples were collected on the Island, in 1902 (HSB & EAS) and 1905 (HSB). There are no recent records. No teneral specimens seen. The adults were collected in May, June, and July. Adults hibernate. Larochelle (1974b) found these beetles hibernating "along" edges of wooden [sic] areas in late October, in Quebec. Total length, 10.5 to 13.0 mm (11.8).

14.28 *Pterostichus lucublandus* Say (1823b:55)

Found in a variety of habitats on the Island and adjacent Maryland shore; on sand mixed with clay in low damp places on the secondary floodplain where there is prostrate vegetation, under stones on the primary floodplain at the mouth of Rock Run, under caked silt slabs on primary floodplain of river at southwest corner of Island below Cactus Rock, and in forest under branches on sandy soil at the bottom of the Saddle. The beetles are fully winged although Lindroth (1966) doubts the ability of the wings to function. They are both nocturnal and diurnal (Larochelle, 1975a). Several specimens were collected on the Island and adjacent shores between 1902 and the present (HSB, TLE & DRW, WMM, GGP, TLE). No teneral specimens seen. Mating occurs in May, June, and July in Quebec (Larochelle, 1972e). Adults were collected in March, April, May, September and October. According to Lindroth (1966) adults hibernate, and larvae are present in the fauna in September. Larochelle (1972a) collected an adult specimen in a rotten tree stump in mid-November, in Quebec; and (1972d) under snow in leaf litter at the edge of a eutrophic marsh in January in Quebec; and (1974b) on "mounds" and in "mounds" 6 inches deep, in October to December, in Quebec. Total length, 9.0 to 14.0 mm (11.5).

14.29 *Pterostichus ohionis* Csiki (1930:638)

Found in the forest in leaf litter at edge of Pond and other stoney places along the Maryland shore. The wings are reduced and the beetles are flightless. Numerous examples were collected on the Island and adjacent shores between 1904 and the present (HSB, JLW, WMM, WLM, PJS, TLE & DRW, GGP, DRW). No teneral specimens seen. The adults were collected in March, April, May, June, July, and September. Hibernation probably takes place as an adult. Total length, 11.5 to 14.5 mm (13.0).

14.30 *Pterostichus stygicus* Say (1823b:41)

Under bark, in logs, and under logs and branches in hardwood forests and in "adjoining meadows with high vegetation" (Lindroth, 1966). These beetles are wingless. WMM & HSB collected these beetles in pitfall traps. Several examples were collected on the Island and adjacent Virginia shore between 1905 and the present (HSB, EAS, WMM, AKF, WLM, GGP). No teneral specimens seen. Adults were collected April, June, July, September, and October. Hibernation takes place as an adult. Total length, 12.5 to 18.0 mm (15.3).

14.31 *Pterostichus coracinus* Newman (1838b:386)

According to Lindroth (1966) found in forests, fields, and meadows. These beetles are wingless. Many examples were collected on the Island and adjacent Virginia shore between 1906 and 1919 (HSB, EAS & HSB). There are no recent records. No teneral specimens seen. The adults were collected in June, September, and October. According to Lindroth (1966) hibernation takes place in the adult stage. Total length, 12.5 to 18.0 mm (15.3).

14.32 *Pterostichus novus* Straneo (1944:127)

According to Lindroth (1966) found in dense, moist hardwood forests in leaf litter ("near a small brook"). The wings are absent. Only one example was collected on the Virginia shore, in 1918 (no collector label). No teneral specimens seen. The single adult was collected in September. According to Lindroth (1966) teneral specimens were collected in July; hibernation probably takes place as an adult. Total length, 16.0 to 19.5 mm (17.8).

14.33 *Pterostichus lachrymosus* Newman (1838b:387)

According to Lindroth (1966) found under stones or logs in deciduous or mixed wood. These beetles are wingless. WMM and HSB collected these beetles in pitfall traps. Several examples were collected along the Virginia shore, between 1905 and 1918 (HSB, WMM, FK, unlabeled). There are no recent records. No teneral specimens were seen. The adults were collected in September and November. Adults probably hibernate. Total length, 14.5 to 17.0 mm (15.8).

14.34 *Pterostichus moestus* Say (1823b:42)

According to Lindroth (1966) found in open woods or deciduous mixed forests in rotten logs. These beetles are wingless. Only three specimens were collected on the Island and adjacent shores between 1905 and 1932 (DHC, HSB, FK). There are no recent records. One subteneral specimen was collected in July. The adults were collected in July and September. Hibernation probably takes place as an adult. Total length, 15.0 to 17.0 mm (16.0).

14.35 *Pterostichus corvinus* Dejean (1828:281)

Found at the margin of the Pond in wet leaf litter; it was collected by washing the litter in the water and the beetle floated to the surface. These beetles are fully winged and probably fly. According to Lindroth (1966) they are very hydrophilous and occur where the pond edges are soft and highly organic, usually with rich vegetation such as *Carex* and grasses. They have been observed mating during the day (Larochelle, 1975a). Two specimens were collected on the Maryland shore between 1906 and the present (DHC, TLE & DRW). No teneral specimens seen. Mating occurs in May and June in Quebec (Larochelle, 1972e). The adults were collected in March, April, and September. According to Lindroth (1966) adults hibernate, and larvae are full grown by June. Larochelle (1974b) found these beetles hibernating in "mounds" 10 inches deep in November and December, in Quebec. Total length, 11.5 to 15.0 mm (13.3).

14.36 *Pterostichus caudicalis* Say (1823b:56)

Found under stones on primary floodplain at mouth of Rock Run where there is no vegetation, but according to Lindroth (1966) also found at the borders of eutrophic pools and ponds where the soil is soft and contains highly organic material, usually in shady spots. These beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Maryland shore between 1908 and the present (JLW, HSB & EAS, WP, TLE, TLE & HF, GGP). No teneral specimens seen. Adults were collected in March, April, July, and October. Hibernation takes place as an adult; larvae are found in early summer. Total length, 10.0 to 13.0 mm (11.5).

14.37 *Evarthrus sigillatus* Say (1823b:42)

According to Freitag (1969) found in leaf litter in the deciduous forest and under cover in pastures. These beetles are wingless. Only one example was collected on the Island in 1909 (EAS). There are no recent records. No teneral specimens seen. The single adult was collected in July. Adults from nearby areas (e.g. Great Falls, Virginia) were collected in October; it is probable that hibernation takes place in the adult stage. Total length, 13.4 to 18.3 mm (15.9).

14.38 *Evarthrus approximatus* LeConte (1848:354)

These beetles are found on the secondary floodplain of the Island (northeast side) under chips of wood (Kavanaugh, pers. comm.); one specimen from Rosslyn, Virginia, was collected in drift along the Potomac. These beetles are wingless. Four specimens were collected on the adjacent shores between 1905 and 1924 (EAS & HSB, HSB); Kavanaugh collected many individuals in 1976. One teneral specimen was collected in July. Adults were collected in June, July, and September. Hibernation probably takes place as an adult. Total length, 8.4 to 10.9 mm (9.7).

ZABRINI. The "seed-eating carabids" are a moderate-sized group of small to medium-sized beetles. They eat seeds of various grasses, Cruciferae, and other plants, but also are known to eat insect eggs and they scavenge on dead or dying arthropods (Frank, 1971a, b). Most species are nocturnal in habits, but many of the more metallic *Amara* s.str. species run in the sunshine near sidewalks, thus are synanthropic. Many species are highly vagile dispersants, others are wing-dimorphic. They live in a variety of habitats but most species are rather xerophilous. Many species are known to be preyed upon by *Bufo americanus,* the American Toad. The tribe is Holarctic in distribution. Eight species are known from the Plummers Island site; 4 of these have not been seen recently.

15.01 *Amara exarata* Dejean (1828:509)

Found in dry, sandy places in forests. These beetles are nocturnal; they are fully winged and fly; they are attracted to light. Many examples were collected on the Island and adjacent Virginia shore between 1902 and 1919 (HSB, EAS, JLW, WLM). There are no recent records. One teneral specimen was collected in May. Adults were collected in April, May, June, and October. Larvae hibernate, but according to Lindroth (1968) so do adults. Total length, 7.3 to 10.0 mm (8.7).

15.02 *Amara avida* Say (1823a:148)

According to Lindroth (1968) on open, moderately dry, often sandy ground, especially disturbed areas with grasses and herbs next to cultivation or in fallow fields. These beetles are fully winged and probably fly. Only one example was collected on the Island, in 1905 (HSB & EAS). There are no recent records. The single specimen is teneral and it was collected in May. Hibernation takes place in the larval stage. Total length, 7.4 to 9.8 mm (8.6).

15.03 *Amara musculis* Say (1823b:35)

Found on dry, usually sandy soil with sparse vegetation. These beetles are fully winged and fly; they are attracted to light. Only one specimen was collected along the Maryland shore, in 1903 (WVW). There are no recent records. No teneral specimens seen. The single adult was collected in June. According to Lindroth (1968) hibernation takes place in the larval stage. Total length, 3.9 to 6.5 mm (5.2).

15.04 *Amara impuncticollis* Say (1823b:36)

Found under drift along the southeast corner of the Island and according to Lindroth (1968) in moderately dry country with rich mixed vegetation usually of a weedy character, and especially around human habitation. These beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (HSB, EAS, WVW, WLM, TLE). No teneral specimens seen. The adults were collected in March, April, June, July, and August. Lindroth (1968) suggests both larval and adult hibernation. Total length, 6.7 to 8.5 mm (7.6).

15.05 *Amara anthobia* Villa (1833:33)

Found commonly in drift along the river at the upper edge of the primary floodplain on sand and sand mixed with silt. DRW found one specimen raking leaf litter on the Maryland side of the Channel. These beetles are winged and probably fly. This is the first record of these beetles occurring in eastern North America. They were introduced into the Pacific Northwest before 1945 where they were discovered by M. Hatch; Lindroth found them in Golden Gate Park, San Francisco in 1958. They come from Europe. Numerous examples were collected on the Island and adjacent Maryland shore in 1974 and 1975 (TLE, DRW). Teneral specimens were collected in June and July. Adults were collected in March, April, June, and July. Hibernation takes place as an adult. Total length, 6.0 to 7.0 mm (6.5).

15.06 *Amara familiaris* Duftschmidt (1812:119)

Found in drift with the preceding species. These beetles are winged and fly; they have been collected in rotary trap (Lindroth, 1968). They were observed flying during the day (Larochelle, 1975a). This is another European introduction, but has been recorded in both the east and west for a long time (since 1919 in the west, 1924 in the east). Many examples were collected on the Island between 1924 and the present (HSB, PJS, TLE). No teneral specimens seen. Adults were collected in March and June. Hibernation takes place as an adult. Larochelle (1974b) found a specimen in a field during a thaw, in January, in Quebec. Total length, 5.6 to 7.2 mm (6.4).

15.07 *Amara aenea* De Geer (1774:98)

Found in drift with the preceding two species and according to Lindroth (1968) usually on dry, open grassland, usually on sand; often on lawns in

parks and gardens. These beetles are fully winged and fly; they are attracted to lights. They have been observed mating, flying, and running during the day (Larochelle, 1975a). This species is another European introduction, and is still restricted to northeastern United States even though it was here earlier than the previous two species. Only three examples were collected on the Island, in 1974 and 1975 (TLE). No teneral specimens seen. The adults were collected in March and June. Hibernation takes place in the adult stage. Larochelle (1974b) found these beetles hibernating in or on "mounds" between November and January, in Quebec. Total length, 6.2 to 8.8 mm (7.5).

15.08 *Amara angustata* Say (1823b:36)

According to Lindroth (1968) found on open ground with meadow type vegetation, with grasses. These beetles have been observed feeding on unripe grass seeds (*Poa pratensis*). They are fully winged and probably fly. Only three examples were collected on the Island between 1907 and 1920 (EAS, WLM, RCS). There are no recent records. No teneral specimens seen. The adults were collected in May and August. Adults hibernate. Larochelle (1974b) found an adult on a "mound" "November 20–December 31" in Quebec. Total length, 5.3 to 8.0 mm (6.7).

CALLISTINI. The "beautiful carabid beetles" are a major group of small to large beetles. They are scavengers for the most part, but a few species have mouthparts highly adapted to prey-capture. Most species are nocturnal in habit, but some are active in the sunshine near water. Both hygrophilous and mesophilous species occur in this tribe. These beetles are highly vagile dispersants; very few are wingless. Adults spray a defense chemical (hydrocarbons, phenols, and quinones; Moore, 1979) from their pygidial glands which is strong and musty; even so two species are commonly eaten by *Bufo americanus*, the American Toad (Larochelle, 1974d). The tribe is cosmopolitan with most species approximate to the equator. Eleven species are known from the Plummers Island site; 5 of these have not been seen recently.

16.01 *Chlaenius tomentosus* Say (1823b:60)

Found in dry disturbed areas, e.g. gravel pits (Lindroth, 1969). According to Larochelle (1974a) found "in open, dry country with sandy or gravelly soil, in hilly fields, with more or less low vegetation . . . under stones." These beetles are fully winged and fly; they are attracted to lights. Only two examples were collected on the Island, in 1903 (WVW) and 1919 (HSB). There are no recent records. No teneral specimens seen. The adults were collected in May and August. Hibernation probably takes place in the adult stage (Lindroth, 1969). Total length, 12.5 to 18.0 mm (15.3).

16.02 *Chlaenius emarginatus* Say (1823b:63)

Found under stones and logs in moist areas in the forest above the secondary floodplain. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent shores between 1905 and the present (EAS, HSB, WMM, RCS, TLE). No teneral specimens seen. Mating occurs in May in Quebec (Larochelle, 1972e). Adults were collected in March, May and June. Hibernation takes place in the adult stage. Larochelle (1974b) found these beetles hibernating "in woods, under stones or vegetal debris" in late October, in Quebec. Total length, 12.1 to 18.1 mm (15.1).

16.03 *Chlaenius prasinus* Dejean (1826:345)

Found beneath driftwood on sandy shores of large rivers (Bell, 1960). These beetles are fully winged and probably fly. They feed on dead and dying insects washed up on shore. Only two examples were collected on the Island, in 1905 (DHC) and 1907 (HSB). There are no recent records. No teneral specimens seen. The adults were collected in June and July. According to Bell (1960) teneral specimens were found in September, therefore adult hibernation is likely. Total length, 15.6 to 17.8 mm (16.7).

16.04 *Chlaenius cordicollis* Kirby (1837:22)

According to Bell (1960) found on the shores of lakes and large rivers where there is clay and gravel with stones and sparse low vegetation. These beetles are fully winged and fly. Only two examples were collected on the Virginia shore, in 1902 (HSB) and 1918 (JLW). There are no recent records. No teneral specimens seen. The adults were collected in June and September. According to Lindroth (1969), hibernation takes place in the adult stage. Total length, 12.4 to 15.3 mm (13.9).

16.05 *Chlaenius aestivus* Say (1823b:62)

Found under wood and stones from near water's edge to moist forest floor, most commonly on secondary floodplain on sand and sand mixed with silt; often found under bark of large logs. These beetles are wing-dimorphic; only the short wing form seen from our area. Many examples were collected on the Island and adjacent shores between 1902 and the present present (HSB, HSB & JLW, WMM, WLM, TLE & DRW, TLE, GGP). No teneral specimens seen. The adults were collected in March through June, and August and September. According to Bell (1960) adults hibernate. Total length, 14.5 to 16.05 mm (15.5).

16.06 *Chlaenius laticollis* Say (1823b:64)

Found beneath stones and drift in the primary and secondary floodplain on sandy soil mixed with decaying leaf litter. These beetles are fully winged

and probably fly. Three examples were collected on the Island and adjacent Maryland shore in 1972 and 1974 (TLE, TLE & DRW, GFH). No teneral specimens seen. The adults were collected March, May and June. Hibernation takes place in the adult stage. Total length, 13.9 to 17.1 mm (15.5).

16.07 *Chlaenius sericeus* Forster (1771:58)

Found at the margin of the river on wet silt and sand where there is sparse vegetation; made active by splashing. These beetles are fully winged and fly; they are attracted to lights. They were also observed running in the sunshine (Larochelle, 1975a). Many examples were collected on the Island and adjacent shores between 1901 and the present (HSB, EAS, TLE & DRW). One teneral specimen was collected in July. Mating occurs in May in Quebec (Larochelle, 1972e). The adults were collected in April through August, and November. Adults hibernate. Larochelle (1974b) found these beetles hibernating on "mounds" and six inches deep in "mounds" in November and December, in Quebec. Total length, 11.4 to 16.1 mm (13.8).

16.08 *Chlaenius impunctifrons* Say (1823b:64)

Found under stones on primary floodplain along the mouth of Rock Run. These beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Maryland shore between 1918 and the present (JLW, GFH, TLE & HF). One teneral specimen was collected in July. Adults were collected in April, May, July, and October. Hibernation takes place in the adult stage. Larochelle (1972d) collected a specimen under snow in leaf litter at the edge of a eutrophic marsh in January, in Quebec, and (1974b) in "mounds" six inches deep in November and December, in Quebec. Total length, 13.0 to 16.0 mm (14.5).

16.09 *Chlaenius nemoralis* Say (1823b:65)

According to Lindroth (1969) found under cover near river banks; according to Bell (1960) also synanthropic in yards and gardens. These beetles are fully winged and fly; they are attracted to lights. Only two specimens were collected: on the Virginia shore, in 1907 (WLM) and at light on the Island, in 1932 (HSB). There are no recent records. No teneral specimens seen. Adults were collected in April and October. Hibernation probably takes place in the adult stage, but this needs to be confirmed. Total length, 10.7 to 13.0 mm (11.9).

16.10 *Chlaenius tricolor* Dejean (1826:334)

Found beneath stones on primary floodplain at mouth of Rock Run and under stones or leaf litter on secondary floodplain adjacent to Channel. These beetles are fully winged and fly; they are attracted to lights. They were also observed running in the sunshine (Larochelle, 1975a). Many examples were collected on the Island and adjacent Maryland shore between 1902 and the present (HSB, HSB & EAS, GMG, LLB, WLM, TLE, TLE & DRW, TLE & HF, GGP). No teneral specimens seen. Adults were collected in March through October. Hibernation takes place in the adult stage. Larochelle (1974b) found these beetles hibernating gregariously on "mounds," in "mounds" 20 inches deep and "along edges of wood [sic] areas" in October and December, in Quebec. Total length, 10.1 to 13.5 mm (11.8).

16.11 *Chlaenius pensylvanicus* Say (1823b:66)

According to Lindroth (1969) found at the borders of small ponds or standing streams with rich vegetation and bare patches of soil. These beetles are winged and fly; they are attracted to lights. Only one example was collected on the Island, in 1905 (DHC). There are no recent records. No teneral specimens seen. The single adult was collected in April. Hibernation takes place as an adult (Lindroth, 1969). Larochelle (1974b) found one specimen hibernating on a "mound" in November, in Quebec. Total length, 10.4 to 11.9 mm (11.2).

OODINI. The "jelly-bean beetles" are a minor group of small to large beetles. Most species are extremely hygrophilous, so much so that they are to found in ankle-deep water among emergent vegetation. They are structured more like water beetles than the "typical carabid" and have characteristics of beetles which mate in the water (tarsomeres). It is not known what they eat, but they are probably scavengers. They are nocturnal in habits, and highly vagile dispersants. The tribe is cosmopolitan in distribution. Two species representing two genera are known from the Plummers Island site; one of these was collected only once in 1960 (see below).

17.01 *Oodes amaroides* Dejean (1831:674)

Found in the mud of the Pond when there was no surface water; leaves wet on under sides, decaying; soil moisture high in lowest parts of Pond, less so toward borders. Also found in drift on pure sand at the southwest corner of the Island. These beetles are fully winged and probably fly. Three examples were collected on the Island and adjacent Maryland shore between 1903 and the present (WVW, TLE, DRW). No teneral specimens seen. The adults were collected in May, July, and August. Hibernation probably takes place as an adult but this remains to be confirmed. Total length, 7.5 to 9.0 mm (8.3).

17.02 *Stenocrepis cupreus* Chaudoir (1843:761)

Exact habitat unknown, but probably near water in rich vegetation where there are emergent plants. These beetles are fully winged and probably

fly. Three examples were collected on the Island in 1960 (PJS). There are no recent records. No teneral specimens seen. The adults were collected in August. The stage in which hibernation occurs is unknown. Total length, 9.5 to 10.0 mm (9.8).

LICININI. The "notched-mouth carabids" are a moderate-sized group of small to large beetles. Many species are hygrophilous, many others mesophilous living on the forest floor among leaf litter or under logs. They probably have special food requirements due to their peculiar mandibular structure, and it has been supposed they eat snails. They are nocturnal in habits; some groups are totally wingless, others are highly vagile dispersants. Adults spray a defense chemical (hydrocarbons and formic acid; Moore, 1979) from their pygidial glands which is pungent; even so two species are commonly eaten by *Bufo americanus*, the American Toad (Larochelle, 1974d). The tribe is cosmopolitan in distribution with most species approximate to the equator. Eleven species in two genera are known from the Plummers Island site; 6 of these have not been seen recently.

18.01 *Dicaelus elongatus* Bonelli (1813:448)

According to Ball (1959) found on dry hillsides and in moist leaf litter in swampy places. These beetles are wingless and cannot fly. Only one example of this species was collected on the Island, in 1901 (HSB). No teneral specimens seen. The single adult was collected in November. According to Lindroth (1969) hibernation takes place in the adult stage. Total length, 14.9 to 19.0 mm (17.0).

18.02 *Dicaelus politus* Dejean (1826:391)

Commonly found under stones in mixed forest above the secondary floodplain on loamy soil where there is much ground cover of prostrate vegetation, not restricted to damp places; and found in more exposed sites at base of rock outcroppings under stones. These beetles are wingless and cannot fly. Numerous examples were collected on the Island and adjacent shores between 1902 and the present (HSB, WMM, FK, TLE, GGP). Teneral specimens were collected in September. Adults were collected in March, April, May, June, September, and October. Hibernation takes place in the adult stage. Total length, 10.7 to 15.0 mm (12.9).

18.03 *Dicaelus ambiguus* Laferté (1841:44)

Found beneath stones in the same habitat as the preceding species. These beetles are also wingless and cannot fly. Numerous examples were collected on the Island and adjacent shores between 1902 and the present (HSB, EAS, GMG, JLW, TLE). One subteneral specimen was collected in September. Adults were collected in March through September. Hibernation takes place in the adult stage. Total length, 18.0 to 21.5 mm (19.8).

18.04 *Dicaelus teter* Bonelli (1813:449)

According to Ball (1959) found under cover in moist forests. I found a specimen in litter and short grass beneath a tree above the secondary floodplain at the southwest corner of the Island. These beetles are wingless and cannot fly. WMM & HSB collected these beetles with pitfall traps. Numerous examples were collected on the Virginia shore between 1905 and 1921 (HSB & EAS, HSB, RCS, WMM) and one was observed on the Island in 1974 (TLE). One subteneral specimen was collected in September. The adults were collected in April, May, June, September, and October. Hibernation takes place in the adult stage. Total length, 14.9 to 21.4 mm (18.2).

18.05 *Dicaelus furvus* Dejean (1826:388)

According to Ball (1959) found in open, river bottom woods. These beetles are wingless and cannot fly. According to HSB card file, specimens were collected from both the Island and adjacent Virginia shore in 1905, 1907, and 1918 (HSB). I have not been able to locate these specimens in USNM. There are no recent records. No teneral specimens seen. The adults were collected in July and September. It is probable that hibernation takes place in the adult stage. Total length, 13.8 to 18.8 mm (16.3).

18.06 *Dicaelus dilatatus* Say (1823b:68)

According to Ball (1959) found under cover in open fields and along stream margins. These beetles are wingless and cannot fly. Numerous examples were collected on the Island and adjacent Virginia shore between 1902 and 1925 (HSB, JLW & HSB, HSB & EAS, WLM, JZ, WMM, GMG). There are no recent records. One teneral specimen was collected in September. Adults were collected in March through June, and August through October. Hibernation takes place in the adult stage. Total length, 21.5 to 23.5 mm (22.5).

18.07 *Dicaelus sculptilis* Say (1823b:68)

Exact habitat unknown. These beetles are wingless and cannot fly. Only one example was collected on the Island, in 1905 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in March. It is probable that hibernation takes place in the adult stage. Total length, 14.3 to 26.0 mm (20.2).

18.08 *Dicaelus purpuratus* Bonelli (1813:447)

Exact habitat unknown. These beetles are wingless and cannot fly. According to Lindroth (1969) they have been observed feeding on snails. Numerous examples were collected on the Island and adjacent shores between 1902 and 1919 (HSB, HSB & EAS, PRM, RCS, AKF, WLM, WMM, JLW, GMG). There are no recent records. No teneral specimens seen. Adults

were collected in March through October. It is probable that adults hibernate. Total length, 20.6 to 25.0 mm (22.8).

18.09 *Badister notatus* Haldeman (1843:299)

Found in low damp places in wet and decaying leaf litter on the secondary floodplain near Trail Pond. According to Lindroth (1969) also on clay-sand on the steep banks of a stream, and to Larochelle (1974a) "on open dry gravelly country, with sparse or moderate vegetation, often in gravel-pits, but also in waste places and gardens . . . under stones, on slopes." These beetles are wing-dimorphic with most specimens having reduced wings; all specimens seen from the Island and adjacent area are short winged. Several examples were collected on the Island and adjacent Maryland shore between 1905 and the present (EAS, HSB & EAS, OLC, DRW). No teneral specimens seen. Adults were collected in April, May, and October. Adults hibernate. Larochelle (1972d) collected these beetles under snow in leaf litter at the edge of a eutrophic marsh in January, in Quebec, and (1974b) in and on "mounds" in November and December in Quebec. Total length, 3.8 to 4.7 mm (4.3).

18.10 *Badister flavipes* LeConte (1853:388)

Found in low damp sandy place on the secondary floodplain where there was much shade and low prostrate vegetation. These beetles are fully winged and probably fly. Only one example was collected on the Maryland shore adjacent to the Island, in 1974 (TLE). No teneral specimens seen. The single adult was collected in May. The stage in which hibernation takes place is unknown. Total length, 5.1 to 6.2 mm (5.7).

18.11 *Badister reflexus* LeConte (1880:166)

Exact habitat unknown. These beetles are fully winged and probably fly. Only two examples were collected on the Island, in 1905 (HSB). There are no recent records. No teneral specimens were seen. The adults were collected in April and October. Hibernation probably takes place as an adult. Total length, 3.8 to 4.4 mm (4.1).

HARPALINI. The "dingy carabids" are a major group, probably the largest of the carabids, of small to large beetles. Most species eat vegetable matter, usually seeds, but they are also known to scavenge on dead or dying invertebrates of various kinds. They live in almost all kinds of habitats, and range from hygrophily to xerophily. Most species are nocturnal and highly vagile dispersants; others however, are wingless. Adults spray a defense chemical (hydrocarbons and formic acid; Moore, 1979) from their pygidial glands which is mildly musty; even so several species are commonly eaten

by *Bufo americanus,* the American Toad (Larochelle, 1974d). The tribe is cosmopolitan in distribution. Forty-five species in 12 genera are known from the Plummers Island site; 27 of these have not been seen recently.

19.01 *Cratacanthus dubius* Beauvois (1805:108)

Found in open, dry, often cultivated fields and prairie under "cow pies," etc. The species is wing-dimorphic; the single specimen collected on the Island is fully winged. Only one example was collected on the Island, in 1902 (HSB & EAS). There are no recent records. No teneral specimens seen. The single adult was collected in July. Teneral specimens from nearby areas (e.g. Fairfax, Virginia) were collected in June and August. It is probable that hibernation takes place in the adult stage. Total length, 7.5 to 11.5 mm (9.5).

19.02 *Harpalus faunus* Say (1823b:28)

Found under drift on primary floodplain where the soil consists of sand and a small amount of silt. According to Lindroth (1968) also found in disturbed places such as gravel pits, and to Larochelle (1974a) "in open country, in sandy dry fields with scarce vegetation, under bark and boards; in waste places, sand-pits and roadsides . . . repeatedly found with *Calosoma calidum* . . . ." This and the following four species probably eat grass seeds as part of their diet. These beetles are fully winged and fly. They are attracted to light. Several examples were collected on the Island between 1902 and the present (EAS, HSB, AKF, TLE). No teneral specimens seen. The adults were collected in July through October. Hibernation takes place in the larval stage (Larochelle, 1975b). Total length, 8.4 to 13.0 mm (10.7).

19.03 *Harpalus pensylvanicus* De Geer (1774:108)

According to Lindroth (1968) found in open dry country with grassy and weedy vegetation, often quite high, especially cultivated land, gravel pits, and road sides. These beetles feed on seeds, roots, etc. of grasses and *Ambrosia,* etc. (Lindroth, 1968). They are fully winged and fly; they are attracted to lights. They were also observed running and mating during the day (Larochelle, 1975a). According to HSB card file, many examples were collected on the Island and adjacent Virginia shore between 1902 and 1907 (HSB). I saw only one specimen in USNM that was collected on the Island in 1932 (HSB), at light. There are no recent records. No teneral specimens seen. The adults were collected in June, July, August, and September. Hibernation takes place in the larval stage (Lindroth, 1968), and adult stage as Larochelle (1974b) found a specimen on a "mound" in November in Quebec. Total length, 10.1 to 15.2 mm (12.7).

19.04 *Harpalus longicollis* LeConte (1848:396)

Found under stones on primary floodplain along Rock Run in the shade and where the soil was sand mixed with clay. According to Lindroth (1968) also found in damp grassy places or gravel pits. These beetles are fully winged and fly; they are attracted to light. Examples were collected on the Island and adjacent shores in 1905 (HSB, WLM) and 1974 (GGP, TLE). No teneral specimens seen. Adults were collected in August, September, and October. Hibernation probably takes place in the larval stage (Larochelle, 1975b). Total length, 10.3 to 15.0 mm (12.6).

19.05 *Harpalus erythropus* Dejean (1829:258)

According to Lindroth (1968) found in fields and open woods on dry, sandy or clayish soil. These beetles are winged and fly; they are attracted to lights. Many examples were collected on the Island and adjacent Maryland shore between 1902 and 1932 (HSB, EAS, JLW, WLM, RPC, AKF). There are no recent records. Several examples collected in June seem to be subteneral. Adults were collected in March, June, July, August, and September. Hibernation takes place probably both as larvae and adults. Total length, 9.7 to 11.4 mm (10.6).

19.06 *Harpalus caliginosus* Fabricius (1775:240)

According to Lindroth (1968) found on open, usually sandy ground with sparse vegetation. The adults feed on *Ambrosia* seeds, pollen, and other insects. These beetles are fully winged and fly; they are attracted to light. They were also observed running on the surface during the day (Larochelle, 1975a), and climbing vegetation to mate (Grunwald, pers. comm.). Only one example was collected on the Island, in 1905 (HSB & EAS). There are no recent records. No teneral specimens seen. The single adult was collected in June. According to Lindroth (1968) adults hibernate. Total length, 17.5 to 25.5 mm (21.5).

19.07 *Harpalus viduus* LeConte (1865:103)

According to Lindroth (1968) found under stones in dry open places, and to Larochelle (1974a) "always at the borders of woods (preferably maple woods), on rather dry sandy soil. It prefers hills and uplands . . . it buries into the soil or hides under dead leaves . . . [in] clearings and [on] woody roads." These beetles are fully winged and are probably capable of flight. Many examples were collected on the Island between 1908 and 1923 (HSB & EAS). There are no recent records. Teneral specimens were collected in April, July, and August. Adults were collected in March, May, July, and August. Hibernation takes place as an adult. Total length, 12.0 to 13.5 mm (12.8).

19.08 *Harpalus spadiceus* Dejean (1829:336)

Exact habitat unknown. The wings are reduced and the beetles are not capable of flight. Only one specimen was collected on the Virginia shore, in 1923 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in April. Teneral specimens from New York (September) and New Jersey (April) indicate larval and possible adult hibernation. Total length, 8.8 to 10.5 mm (9.7).

19.09 *Harpalus herbivagus* Say (1823b:29)

According to Lindroth (1968) found in open country often on moraine with sparse vegetation. Adults have been observed eating grass shoots. These beetles are fully winged and fly. They were observed mating, running, flying, and feeding during the day (Larochelle, 1975a). According to HSB card file examples were collected from both the Island and adjacent Maryland shore in 1903 and 1905 (HSB). I have not been able to locate these specimens in USNM. There are no recent records. No teneral specimens seen. According to Lindroth (1968) teneral specimens were discovered elsewhere in late summer. HSB collected adults in April. Hibernation takes place as an adult. Larochelle (1974b) found these beetles hibernating on and in "mounds" and "in a field, in thawing time" in November and December, in Quebec. Total length, 7.5 to 11.0 mm (9.3).

19.10 *Harpalus fulgens* Csiki (1932:1182)

Found in drift on upper edge of primary floodplain on sand at the southwest corner of the Island. These beetles are fully winged and probably fly. Several specimens were collected on the Island and adjacent Maryland shore between 1903 and the present (EAS, HSB & EAS, TLE). A teneral adult was collected in October. Adults were collected in March, April, June, and October. Hibernation takes place as an adult. Total length, 5.8 to 7.2 mm (6.5).

19.11 *Harpalus opacipennis* Haldeman (1843:301)

According to Lindroth (1968) found in open, dry country with sand or gravelly soil. These are fully winged and probably fly. Three examples were collected on the Island between 1908 and 1919 (DHC, HSB). There are no recent records. No teneral specimens seen. Adults were collected in April, May, and June. It is likely that adults hibernate. Total length, 8.8 to 9.0 mm (8.9).

19.12 *Episcopellus autumnalis* Say (1823b:48)

Found in leaf litter in open woods above the secondary floodplain where the soil is loamy; found under silt cakes at upper edge of primary floodplain

on pure sand, at the southwest corner of the Island. These beetles are fully winged and probably fly. Four examples were collected on the Island and adjacent Maryland shore in 1974 (TLE & DRW). No teneral specimens seen. Adults were collected in April and May. Hibernation takes place in the adult stage. Total length, 6.5 to 8.0 mm (7.3).

19.13 *Trichotichnus vulpeculus* Say (1823b:30)

Found under stones on primary floodplain at mouth of Rock Run in the shade where the substrate consists of sand and gravel. According to Larochelle (1974a) this is "a deciduous forest species, found under the barks of logs . . . [on] hills . . . with *Pterostichus honestus* Say and *P. tristis* Dejean." These beetles are fully winged and fly; they are attracted to lights. Many examples were collected from the Island and adjacent shores between 1903 and the present (HSB, EAS, RCS, JLW & HSB, WLM, AB, AKF, GGP, TLE & HF). One teneral specimen was collected in September. Adults were collected in March, June, July, August, September, October. Hibernation takes place in the adult stage. Total length, 9.0 to 10.0 (9.5).

19.14 *Trichotichnus dichrous* Dejean (1829:258)

According to Lindroth (1968) found in open dry woods under logs. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected from the Island and adjacent Virginia shore between 1902 and 1932 (HSB, EAS & HSB, HSB & JLW, LLB, RCS). There are no recent records. No teneral specimens seen. Adults were collected in June, July, August and September. The stage in which hibernation occurs is unknown. Total length, 9.0 to 11.0 mm (10.0).

19.15 *Selenophorus opalinus* LeConte (1863b:13)

According to Lindroth (1968) found on dry ground and in drift, and to Larochelle (1974a) "on open dry hills, on sandy soil, with scarce vegetation, under stones . . . with . . . *Chlaenius tomentosus* Say." These beetles are winged and fly; they are attracted to light. Only one specimen was collected on the Island, in 1907 (WLM). There are no recent records. No teneral specimens seen. The single adult was collected in July. Hibernation takes place in the adult stage (Larochelle, 1975b). Total length, 9.5 to 10.7 mm (10.1).

19.16 *Selenophorus gagatinus* Dejean (1829:112)

According to Lindroth (1968) found on high, dry hills and to Larochelle (1974a) "a xerophilous species, occurring under stones, on gravelly or sandy places, with sparse vegetation . . . [on] hills and uplands." The beetles are fully winged and probably fly. Only one example was collected on the Island, in 1915 (EAS & HSB). There are no recent records. No teneral specimens seen. The single adult was collected in June. Hibernation takes place in the adult stage (Lindroth, 1968). Larochelle (1974b) found these beetles hibernating "in a field, under stones or dead leaves" in late October, in Quebec. Total length, 6.5 to 7.5 mm (7.0).

19.17 *Selenophorus pedicularius* Dejean (1829:100)

In Florida, found on road sides under prostrate grasses and running over the soil between grassy areas. These beetles are fully winged and fly; they are attracted to light. Only one example was collected on the Island, in 1905 (EAS). There are no recent records. No teneral specimens seen. The single adult was collected in June. The stage in which hibernation occurs is unknown. Total length, 4.6 to 6.5 mm (5.6).

19.18 *Selenophorus ellipticus* Dejean (1829:108)

According to Lindroth (1968) found on dry, sandy soil and in drift. These beetles are fully winged and do fly. Only one specimen was collected on the Island, in 1923 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in August. The stage in which hibernation takes place is unknown. Total length, 5.3 to 6.5 mm (5.9).

19.19 *Geopinus incrassatus* Dejean (1829:21)

According to Lindroth (1968) found on sandy, moderately dry ground with sparse vegetation and often near water. These beetles are excellent diggers and tunnel deep into the soil. They are fully winged and fly. According to HSB card file, EAS observed these on the Island but apparently did not collect any, ca. 1902. There are no recent records. No teneral specimens seen. According to Lindroth (1968) teneral specimens are found in late summer. Hibernation takes place in the adult stage (Larochelle, 1975b). Total length, 13.0 to 17.0 mm (15.0).

19.20 *Notiobia nitidipennis* LeConte (1848:388)

Found in open areas with short grasses or moss, with scattered shrubs on dry sandy soil (Lindroth, 1968; Noonan, 1973). These beetles are fully winged and fly; they are attracted to light. Several examples were collected on the Island and adjacent Maryland shore between 1902 and 1974 (HSB, HSB & EAS, WLM, TLE & DRW). No teneral specimens seen. Adults were collected in March, April, June, August, and September. Noonan (1973) indicates specimens have been collected in all months except January, and Lindroth (1968) indicates teneral specimens collected in November. Hibernation takes place as an adult. Total length, 7.0 to 9.0 mm (8.0).

19.21 *Notiobia terminata* Say (1823b:48)

According to Noonan (1973) found in numerous habitats but consistently in open land without dense forest cover. These beetles feed in part on vegetable material, e.g. flower heads, seeds, grass, and pollen and in part on animal matter, e.g. weevil larvae. The beetles are fully winged and fly; they are attracted to lights. Only two examples were collected on the Island, in 1902 (HSB, RPC). There are no recent records. No teneral specimens seen. Adults were collected in August, and according to Noonan (1973) for other areas, March to October. Hibernation takes place in the adult stage. Larochelle (1974b) found a specimen hibernating "along edges of wooden areas" in November in Quebec. Total length, 8.5 to 9.1 mm (8.8).

19.22 *Anisodactylus discoideus* Dejean (1831:831)

Found in drift at uppermost edge of primary flood plain in almost pure sand where there was little or no vegetation. According to Larochelle (1974a) found "at the borders of rivers, brooks, and ponds, on wet sandy soil, with sparse vegetation or none at all . . . understones . . . commonly with *Anisodactylus sanctaecrucis* Fabricius and *Stenolophus comma* Fabricius." These beetles are fully winged and fly; they are attracted to lights. They were also observed running in the sunshine (Larochelle, 1975a). Two examples were found on the Island, 1912, 1972 (HSB, TLE) and one on the Virginia shore, in 1905 (FK). No teneral specimens seen. Adults were collected in July, October, and November. According to Lindroth (1968) adults hibernate. Larochelle (1974b) found specimens hibernating six inches deep in "mounds," in November in Quebec. Total length, 10.0 to 12.2 mm (11.1).

19.23 *Anisodactylus carbonarius* Say (1823b:32)

Exact habitat unknown. These beetles are fully winged and fly; they are attracted to lights. Elsewhere (e.g. Kansas, Georgia) these beetles were found in grassland under sack traps and in soil under grass in peach orchards. Numerous examples were collected on the Island and adjacent Virginia shore between 1902 and 1932 (HSB, HSB & EAS, EAS, JLW, LLB). There are no recent records. No teneral specimens seen. The adults were collected in June, July, and September. Teneral specimens from elsewhere (e.g. Washington, D.C.) were collected in June and July. Hibernation takes place probably as an adult. Total length, 11.4 to 13.0 mm (12.2).

19.24 *Anisodactylus nigerrimus* Dejean (1831:842)

According to Lindroth (1968) found in old gravel pit with rich vegetation. This would indicate that areas of disturbance are suitable. P. Miliotis (pers. comm.) has collected these beetles in wet riverside situations. According to Larochelle (1974a) found "on open, very dry, sandy ground, with scattered vegetation . . . with *Anisodactyla merula* Germar and *A. rusticus* Say."

These beetles are fully winged and probably fly. Only five examples were collected, two from the Island in 1902 (HSB) and 1906 (HSB), and three from Virginia on the shore opposite the Island in 1902, 1921, and 1923 (HSB). There are no recent records. No teneral specimens seen. The adults were collected in April, October, and November. Teneral specimens from elsewhere (e.g. Maryland) were collected in June. Hibernation probably takes place as an adult. Total length, 9.2 to 10.8 mm (10.0).

19.25 *Anisodactylus melanopus* Haldeman (1843:302)

Exact habitat unknown. These beetles are fully winged and probably fly. They have been found in drift material on lake shores, and at Cabin John, Maryland, under stones. Only two examples were found on the adjacent Maryland shore, in 1907 and 1912 (WLM). There are no recent records. No teneral specimens seen. The adults were collected in March and April. Hibernation takes place as an adult, at least. Total length, 12.0 to 14.0 mm (13.0).

19.26 *Anisodactylus agricola* Say (1823b:33)

Found beneath stones in the forest above the secondary floodplain on sandy loam and in drift material on primary floodplain at the southeast corner of the Island where there was almost pure sand. These beetles have small wings, reflexed at the apex, but according to Lindroth (1968) they probably cannot fly. Several examples were collected on the Island and adjacent Maryland shore between 1912 and the present (HSB, JLW & HSB, PJS, TLE). One teneral specimen was collected in August. Adults were collected in March, May, August and October. Hibernation takes place as an adult. Total length, 11.0 to 14.0 mm (12.5).

19.27 *Anisodactylus rusticus* Say (1823b:32)

According to Lindroth (1968) found on dry, sandy soil in fields with sparse and sometimes high vegetation; they hide under the plants in the daytime. These beetles are fully winged and fly. They were also observed running in the sunshine (Larochelle, 1975a). Only one example was found on the Island, in 1908 (WLM). There are no recent records. No teneral specimens seen. The single adult was collected in April. Hibernation takes place in the adult stage (Lindroth, 1968). Total length, 8.8 to 11.0 mm (9.9).

19.28 *Anisodactylus verticalis* LeConte (1848:378)

Found in buried leaf litter mixed with layers of silt and sand on the upper edge of the primary floodplain at the southwest corner of the Island. According to Lindroth (1968) found in dark, moist woods on clay mixed with humus, and to Larochelle (1974a) "in deciduous woods, on moist clayey soil, often near water . . . under dead leaves and bark of fallen trees." These

beetles are fully winged and fly; they are attracted to lights. According to Lindroth (1968) the mouthparts of this species indicate a predatory mode of living rather than seed eating as in the preceding species. Two examples were collected on the Island, in 1905 (EAS) and 1974 (TLE & DRW). No teneral specimens seen. Adults were collected in May (Iowa, Washington, D.C.) indicating adult hibernation. Total length, 12.8 to 14.0 mm (13.4).

19.29 *Amphasia interstitialis* Say (1823b:57)

Found under leaf litter and logs on secondary floodplain in partial shade where the soil is sandy and in the woods above the secondary floodplain beneath stones in clay mixed with loam. These beetles are fully winged and probably fly. Numerous examples were collected on the Island and adjacent shores between 1905 and the present (HSB, EAS & HSB, WLM, PRM, ANC, PJS, GGP, TLE). Teneral specimens were collected in April. Adults were collected in February, March, April, May, August, September, and October. Hibernation takes place in the adult stage. Larochelle (1974b) found specimens hibernating on mounds and "in woods, under stones or vegetal debris" in November in Quebec. Total length, 8.5 to 10.2 mm (9.4).

19.30 *Bradycellus rupestris* Say (1823b:91)

Found in drift on almost pure sand on the uppermost primary floodplain at the southwest corner of the Island and according to Lindroth (1968) on open, gravelly, dry soil with sparse vegetation. These beetles are winged and fly; they are attracted to lights. One specimen was observed flying in the daytime (Larochelle, 1975a). Many examples were collected on the Island and adjacent shores between 1902 and the present (HSB & EAS, WLM, RSC, WVM, TLE). No teneral specimens seen. Adults were collected in February, March, April, May, June, July, August, and October. Hibernation takes place in the adult stage (Lindroth, 1968). Larochelle (1974b) found these beetles hibernating eight inches deep in, and on, "mounds" in November and December in Quebec. Total length, 3.9 to 4.7 mm (4.3).

19.31 *Bradycellus badipennis* Haldeman (1843:302)

Found in drift on pure sand at upper edge of primary floodplain on the southwest corner of the Island. These beetles are fully winged and probably fly. Only one example was collected on the Maryland shore in 1975 (TLE). No teneral specimens seen. The single adult was collected in March. Adults hibernate. Larochelle (1974b) found these beetles hibernating on "mounds" in November in Quebec. Total length, 5.1 to 5.7 mm (5.4).

19.32 *Bradycellus atrimedeus* Say (1823b:39)

Found on silt banks of the Channel in the primary floodplain area where it is still wet and there is no vegetation (see also Larochelle, 1972g), and in

drift on pure sand at the southwest corner of the Island. These beetles are fully winged and probably fly. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (EAS, WLM, HSB, TLE). No teneral specimens seen. Adults were collected in March, April, July, and November. Adults hibernate. Larochelle (1974b) found these beetles hibernating on and in "mounds" four inches deep in November and December in Quebec. Total length, 6.0 to 6.3 mm (6.2).

19.33 *Stenolophus ochropezus* Say (1823b:54)

Found on wet silt at the edges of the Channel in the lower primary floodplain; these beetles are best collected by splashing. They are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (HSB, HSB & EAS, TLE & DRW). No teneral specimens seen. Adults were collected in April, May, July, and August. According to Larochelle (1975b) adults hibernate. Larochelle (1974b) found a hibernating specimen on a "mound" in November, in Quebec. Total length, 4.8 to 6.7 mm (5.8).

19.34 *Stenolophus* "alpha"

This apparently undescribed species is represented by only one specimen. Exact habitat unknown. These beetles are fully winged and probably fly. Only one example was collected on the Virginia shore opposite the Island, in 1923 (HSB). There are no recent records. The single specimen is slightly teneral; it was collected in July. Hibernation probably takes place in the adult stage. Total length, 6.0 mm.

19.35 *Stenolophus plebejus* Dejean (1829:424)

Exact habitat unknown. These beetles are fully winged and probably fly. Only two examples were collected on the Island, in 1905, 1907 (HSB), and another from the Virginia shore, 1902 (HSB). The single specimen from Virginia is slightly teneral; it was collected in September. The others were collected in March and May. Hibernation probably takes place in the adult stage. Total length, 5.0 to 5.2 mm (5.1).

19.36 *Stenolophus humidus* Hamilton (1893:305)

According to Lindroth (1968) found on sandy soil in *Typha* marshes where there is plenty of water via streams. These beetles are fully winged and can probably fly. Only one example was collected on the Virginia shore opposite the Island, in 1921 (HSB). There are no recent records. No teneral specimens seen. The single adult was collected in October. The stage in which hibernation takes place is unknown. Total length, 4.2 to 5.0 mm (4.6).

19.37 *Stenolophus comma* Fabricius (1775:248)

Found commonly on the primary floodplain of the Channel and river under drift, by splashing the damp silt, and under dry silt cakes on the underlying sand. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent Maryland shore between 1903 and the present (EAS, HSB & EAS, WVW, TLE, TLE & DRW). No teneral specimens seen. Adults were collected in March through June and October. Hibernation takes place in the adult stage. Larochelle (1974b) found these beetles hibernating on "mounds" and in "mounds" seven inches deep in November and December, in Quebec. Total length, 5.5 to 7.7 mm (6.6).

19.38 *Stenolophus lecontei* Chaudoir (1868:164)

Found in the same places as the preceding species. These beetles are fully winged and fly. Many examples were collected on the Island and adjacent Maryland shore between 1903 and the present (HSB, HSB & EAS, WVW, WLM, JLW & HSB, OLC, TLE, TLE & DRW). No teneral specimens seen. Adults were collected in April, May, June, July, August, and October. It is likely that adults hibernate. Total length, 5.3 to 7.2 mm (6.3).

19.39 *Stenolophus rotundicollis* Haldeman (1843:302)

According to Lindroth (1968) found in gardens in "grass-heaps." Habitat in nature unknown. These beetles are fully winged and probably fly. Only one example was collected on the Island, in 1908 (WLM). There are no recent records. No teneral specimens seen. The single adult was collected in April. Hibernation probably takes place in the adult stage. Total length, 3.9 to 4.2 mm (4.1).

19.40 *Stenolophus conjunctus* Say (1823b:90)

According to Lindroth (1968) found in open, dry, usually sandy country with sparse vegetation. These beetles are wing-dimorphic; both the long- and short-wing individuals occur on the Island. The long-wing forms fly and have been collected in rotary traps. WLM collected one specimen "on mullen" (sic). They were observed running in the sunshine and mating on cloudy and rainy days (Larochelle, 1975a). Several examples were collected on the Island and adjacent shores between 1902 and 1963 (HSB, WLM, EAS, OLC, PJS & TPC). There are no recent records. No teneral specimens seen. Adults were collected in January, February, March, April, May, August, October, November. Hibernation takes place as an adult. Larochelle (1974b) found these beetles hibernating in a variety of habitats between November and March, in Quebec. Total length, 3.2 to 4.3 mm (3.8).

19.41 *Acupalpus* "alpha"

This apparently undescribed species is represented by only one specimen. Exact habitat unknown. This beetle is fully winged and probably flies. It belongs to the subgenus *Philodes*. The single example was collected on the Virginia shore, in 1921 (HSB). There are no recent records. The single nonteneral adult was collected in October. The stage in which hibernation takes place is unknown. Total length, 3.7 mm.

19.42 *Acupalpus* "beta"

This apparently undescribed species is represented by only one specimen. Exact habitat unknown. This beetle is fully winged and probably flies. It belongs to the subgenus *Philodes*. It differs from the preceding undescribed species by its pubescent abdominal sterna and the shape of the pronotum. Only one example was collected on the Virginia shore, in 1921 (HSB). The single nonteneral adult was collected in October. The stage in which hibernation takes place is unknown. Total length, 3.3 mm.

19.43 *Acupalpus hydropicus* LeConte (1863a:17)

Exact habitat unknown. These beetles are wingless and not capable of flight. Two examples were collected, one on the Island in 1912 (EAS & HSB) and one on the Virginia side of the river opposite the Island in 1921 (HSB). There are no recent records. No teneral specimens seen. The two adults were collected in July and October. The stage in which hibernation takes place is unknown. Total length, 2.5 to 3.1 mm (2.8).

19.44 *Acupalpus testaceus* Dejean (1829:460)

Exact habitat unknown. These beetles are fully winged and probably fly. Only one example was collected on the Island, in 1910 (EAS). There are no recent records. No teneral specimens seen. The single adult was collected in July. The stage in which hibernation takes place is unknown. Total length, 2.5 to 3.0 mm (2.8).

19.45 *Acupalpus pauperculus* Dejean (1829:463)

Found on primary floodplain in buried mats of leaf litter layered with silt; collected by splashing. These beetles are fully winged and fly; they are attracted to lights. Only one specimen was collected on the Island in 1974 (TLE & DRW). No teneral specimens seen. The adult was collected in May. Hibernation takes place as an adult. Larochelle (1972d) collected a specimen under snow in leaf litter at the edge of a eutrophic marsh in January, in Quebec; and (Larochelle, 1974b) under stones or leaves in a field in December, in Quebec. Total length, 2.9 to 3.4 mm (3.2).

MASOREINI. The "comb-spurred carabids" are a minor group of small beetles. It is not known what these beetles eat, but they are probably scavengers, egg-predators, or predators on small arthropods. They are either nocturnal or diurnal in habits, and most species are highly vagile dispersants. These beetles are xerophilous, often occurring on sand in the vicinity of water. The tribe is tropicopolitan in distribution, very few species occurring outside the tropics of Cancer and Capricorn. Only one species of this tribe occurs at the Plummers Island site.

20.01 *Tetragonoderus fasciatus* Haldeman (1843:298)

Found commonly on dry sand where there is sparse vegetation; often seen running in sunny spots, and near the river on wet sand also running in the sunshine. These beetles are fully winged and fly; they are attracted to lights. Numerous examples were collected on the Island and adjacent Maryland shore between 1903 and the present (HSB & EAS, EAS, WLM, PRM, TLE & DRM, TLE). No teneral specimens seen. Adults were collected in April through August. The stage in which hibernation occurs is unknown. Total length, 4.5 to 5.0 mm (4.8).

ODACANTHINI. The "long-necked carabids" are a minor group of medium-small beetles. These beetles are adapted to climbing in low vegetation, especially grasses in proximity to water. It is not known what they eat, but it likely they prey on small arthropods, such as aphids, which occur on vegetation. They are nocturnal in habits and are highly vagile dispersants. The tribe is tropicopolitan in distribution, very few species occurring outside the tropics of Cancer and Capricorn. Only one species of this tribe occurs at the Plummers Island site.

21.01 *Colliuris pensylvanica* Linné (1767:620)

According to Lindroth (1969) found in dry open grassland; found near the Island by JDH "on mullein." I found one example in leaf litter at the edge of the Pond. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent Maryland shore between 1905 and the present (HSB, JCC, WLM, JDH, TLE). No teneral specimens seen. The adults were collected in February, March, May, and July. Hibernation takes place as an adult. Total length, 5.8 to 7.2 mm (6.5).

LEBIINI. The "colorful carabids" are a major and diverse group of small to large beetles. Many groups of species are highly adapted arboricoles, others are terricoles. These beetles eat dead and dying arthropods or are specialized predators on particular kinds of prey. They are both nocturnal

and diurnal in habit, and many species are highly vagile dispersants (e.g. *Lebia* spp.), while others seem to be poor dispersants (e.g. *Agra* spp.). The tribe is cosmopolitan, but the greatest diversity occurs within the tropics of Cancer and Capricorn. Eighteen species in 8 genera are known from the Plummers Island site; 12 of these have not been seen recently.

22.01 *Lebia atriventris* Say (1823b:13)

According to Lindroth (1969) found in meadows and open forests often associated with the chrysomelid *Zygogramma heterothecae* which might be its host in the southern states. However, only *Z. suturalis* is common in the D.C. area, although I find no records from the Island. These *Lebia* beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island between 1902 and 1911 (HSB, EAS, HSB & EAS). There are no recent records. No teneral specimens seen. Adults were collected in April, May, June, and August. Hibernation takes place as an adult. Larochelle (1972a) collected a specimen under bark of a rotten tree stump in mid-November, in Quebec, and (1974b) on "mounds," "along edges of wooden [sic] areas," "swampy areas, in clumps of moss and grass," and "in a field, under stones or dead leaves" in October and November, in Quebec. Total length, 5.4 to 8.0 mm (6.7).

22.02 *Lebia tricolor* Say (1823b:11)

According to Lindroth (1969) found commonly on goldenrod flowers (*Solidago*). These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island between 1905 and 1919 (HSB, EAS, RCS, DHC). There are no recent records. No teneral specimens seen. The adults were collected in March, May, June, July, and October. Hibernation takes place as an adult (Larochelle, 1975b). Total length, 6.5 to 9.0 mm (7.8).

22.03 *Lebia grandis* Hentz (1830:255)

According to Lindroth (1969) found on goldenrod flowers (*Solidago*) in areas where the chrysomelid beetles of the genus *Leptinotarsus* live. In some areas, *Leptinotarsus decemlineata* is the host species for the *Lebia* larvae, and according to Lindroth (1969) other chrysomelids of this genus might serve as hosts. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent shores between 1902 and 1924 (EAS, HSB, WVW, WLM). There are no recent records. No teneral specimens seen. Adults were collected in May, June, and July. Hibernation takes place as an adult (Larochelle, 1975b). Total length, 8.5 to 10.5 mm (9.5).

22.04 *Lebia viridipennis* Dejean (1826:452)

Exact habitat unknown. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent Virginia shore between 1902 and 1930 (HSB, EAS, JCC, WLM, DHC, FEB). There are no recent records. One teneral specimen was collected in September. Adults were collected in May through September. Hibernation most likely takes place in the adult stage. Total length, 5.0 to 5.8 mm (5.4).

22.05 *Lebia viridis* Say (1823b:14)

According to Lindroth (1969) found in open sunny country on goldenrod flowers (*Solidago*) and on the leaves of *Alnus* and *Ulmus* in the company of chrysomelids in the genus *Altica*. These leaf beetles are the presumed host species. These carabid beetles are fully winged and fly; they are commonly found at lights. Many examples were collected on the Island and adjacent shores between 1903 and the present (HSB, EAS, PRM, WVW, WLM, RCS, FEB, HSB & JLW, VAR, DRW). Teneral specimens were collected in July and August. Adults were collected in April through September. Hibernation takes place in the adult stage. Larochelle (1974b) found these beetles hibernating in "swampy areas, in clumps of moss and grass" and "in a field, under stones or dead leaves" in November, in Quebec. Total length, 4.7 to 6.6 mm (5.7).

22.06 *Lebia analis* Dejean (1825:265)

Exact habitat unknown, but often found in the company of the flea beetles *Capraita obsidiana* and *Disonycha glabrata*. These *Lebia* beetles are fully winged and fly; they are attracted to lights. Many examples were collected on the Island and adjacent Virginia shore between 1902 and 1930 (HSB, HSB & EAS, EAS, JLW, RCS, FEB). There are no recent records. No teneral specimens seen. Adults were collected in May through September. Hibernation probably takes place as an adult, but this needs to be confirmed. Total length, 4.3 to 6.0 mm (5.2).

22.07 *Lebia solea* Hentz (1830:256)

According to Lindroth (1969) found on leaves of elder and other plants, and to Larochelle (1974a) "in deciduous forests, preferably maple forests, under dead leaves or on the flowers of the Blue-stemmed Goldenrod, *Solidago caesia* Linne." These beetles are fully winged and fly; they are attracted to lights. One specimen (HSB & EAS) is labelled "from dung in den of *Marmota*." Several examples were collected on the Island and adjacent Maryland shore between 1901 and 1930 (EAS, HSB, WLM, JLW & HSB, FEB). There are no recent records. One teneral specimen was collected in

August. Adults were collected in April through August. Hibernation probably takes place in the adult stage, but this needs to be confirmed. Total length, 4.5 to 6.2 mm (5.4).

22.08 *Lebia pectita* Horn (1885:133)

Exact habitat unknown. These beetles are fully winged and fly. Only two examples were collected on the Island, in 1902 (HSB) and 1905 (DHC). There are no recent records. No teneral specimens seen. The adults were collected in May and August. The stage in which hibernation takes place is unknown, however it is probably the adult. Total length, 5.6 to 7.1 mm (6.4).

22.09 *Lebia lobulata* LeConte (1863a:5)

Exact habitat unknown. These beetles are fully winged and fly. Numerous examples were collected on the Island between 1902 and 1960 (HSB & EAS, PRM, WLM, WP, FEB). Teneral specimens were collected in May, July, and August. Adults were collected in May through September. Hibernation probably takes place as an adult, but this needs to be confirmed. Total length, 3.0 to 4.0 mm (3.5).

22.10 *Lebia ornata* Say (1823b:13)

According to Lindroth (1969) found commonly on goldenrod (*Solidago*), and to Larochelle (1974a) "in deciduous and mixed forest . . . ." These beetles are fully winged and fly; they are attracted to lights. Many examples were collected on the Island and adjacent Maryland shore between 1902 and 1913 (HSB, WLM). There are no recent records. No teneral specimens seen. The adults were collected in May, July, September, and October. Hibernation takes place as an adult. Larochelle (1974b) found a specimen hibernating "in woods, under stones or vegetal debris" in November, in Quebec. Total length, 4.0 to 5.0 mm (4.5).

22.11 *Lebia pumila* Dejean (1831:388)

According to Lindroth (1969) found on goldenrod flowers (*Solidago*). These beetles are fully winged and fly. Only one example was found on the Island, in 1917 (GMG). There are no recent records. No teneral specimens seen. The single adult was collected in August. The stage in which hibernation takes place is unknown, however it probably is in the adult stage. Total length, 2.5 to 4.2 mm (3.4).

22.12 *Coptodera aerata* Dejean (1825:277)

Found running on logs which are held off the ground. These beetles are fully winged and fly; they are attracted to lights. Four examples were col-

lected on the Island between 1902 and 1922 (HSB, HSB & EAS). There are no recent records. No teneral specimens seen. The adults were collected in April, May, June, and July. Hibernation probably takes place in the adult stage, under bark. Total length, 5.5 to 6.5 mm (6.0).

22.13 *Dromius piceus* Dejean (1831:353)

Found under bark of hardwoods, and in British Columbia under the bark of *Pinus ponderosa* (Lindroth, 1969); in California under the bark of *Quercus*. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island and adjacent Virginia shore between 1905 and 1962 (HSB, EAS, JLW & HSB, HSB & EAS, KVK). There are no recent records. No teneral specimens seen. Adults were collected in April through August. Teneral specimens from elsewhere (e.g. Virginia) were collected in July. Adults hibernate. Larochelle (1974b) found one specimen "in woods, under stones or vegetal debris" in March, in Quebec. Total length, 6.3 to 7.8 mm (7.0).

22.14 *Apristus subsulcatus* Dejean (1826:451)

Found on dry sand mixed with gravel and silt about one meter from the river edge, by splashing. These beetles are fully winged, and they fly (Larochelle, 1975a). Two examples were collected on the Island, in 1906 (WLM) and 1974 (TLE & DRW). No teneral specimens seen. The adults were collected in April and August. Hibernation takes place as an adult (Lindroth, 1969). Total length, 3.2 to 4.4 mm (3.8).

22.15 *Calleida viridipennis* Say (1823b:9)

Found under bark of large dead walnut (*Juglans*) tree on the south slope below the cabin; the wood was still solid and dried out. Also found under bark of *Acer*. These beetles are fully winged and fly. According to Lindroth (1969) the beetles of this genus are predaceous on caterpillars of noctuid and pyralid moths. Many examples were collected on the Island between 1905 and the present (HSB, EAS, WLM, TLE). No teneral specimens seen. The adults were collected in February, March, May, June, and October. Hibernation takes place as an adult. Total length, 9.0 to 11.0 mm (10.0).

22.16 *Plochionus timidus* Haldeman (1843:298)

According to Lindroth (1969) found in damp places under bark and in webs of Fall Web-worm (*Hyphantria cunea*) where the beetles eat the caterpillars. These beetles are fully winged and fly; they are attracted to lights. Several examples were collected on the Island between 1909 and 1924 (HSB, EAS, JLW, LLB). There are no recent records. No teneral specimens seen. The adults were collected in June, July, and October. According to Lindroth (1969) adults hibernate. Total length, 6.5 to 7.5 mm (7.0).

22.17 *Pinacodera limbata* Dejean (1831:320)

Found in sparse, moist leaf litter beneath hickory trees (*Carya ovata*) in nearby Virginia. Also, according to Lindroth (1969) found under bark of trees and attracted to sugar baits for moths. These beetles are fully winged and fly; they are attracted to lights. Many examples were collected on the Island and adjacent Virginia shore between 1903 and 1917 (HSB, EAS, HSB & EAS). There are no recent records. One teneral specimen was collected in July. Adults were collected in June through September. Hibernation takes place in the adult stage. Total length, 8.5 to 10.5 mm (9.5).

22.18 *Apenes lucidula* Dejean (1831:320)

Found in leaf litter using a berlese funnel (PJS). According to Lindroth (1969) found in drier areas. These beetles are fully winged and do fly; they are attracted to lights. Many examples were collected on the Island and adjacent shores between 1902 and 1963 (HSB, HSB & EAS, EAS, PJS). There are no recent records. No teneral specimens seen. The adults were collected in March, April, June through September. Hibernation takes place in the adult stage. Total length, 10.0 to 11.5 mm (10.8).

ZUPHIINI. The "triangle-headed carabids" are a minor group of small beetles. These beetles are for the most part depigmented and have long sensory setae which led Lindroth (1969) to the conclusion that they are subterranean in habit. These beetles occur proximate to water and are highly vagile dispersants. Their food is unknown. They are nocturnal in habit. The tribe is tropicopolitan in distribution, very few species occurring outside the tropics of Cancer and Capricorn. Only one species of this tribe is known from the Plummers Island site and it has not been seen recently.

23.01 *Zuphium americanum* Dejean (1831:298)

Found in drift of small freshet by HSB & EAS and according to Lindroth (1969) under stones in open meadows. These beetles are probably more hypogean than most of our species. They are fully winged and fly. Only two examples were collected on the Island in 1911 (HSB & EAS). There are no recent records. No teneral specimens seen. Adults were collected in September. Elsewhere adults were collected in February and May. It is probable that hibernation takes place in the adult stage. Total length, 5.2 to 6.0 mm (5.6).

GALERITINI. The "false bombardier beetles" are a minor group of large to very large beetles. These beetles are true mesophiles, usually living in forests. It is not known what they eat, but they are likely to be discovered to be scavengers. They are nocturnal in habit and highly vagile dispersants. The tribe is found in all Regions except the Palearctic. Two species of this

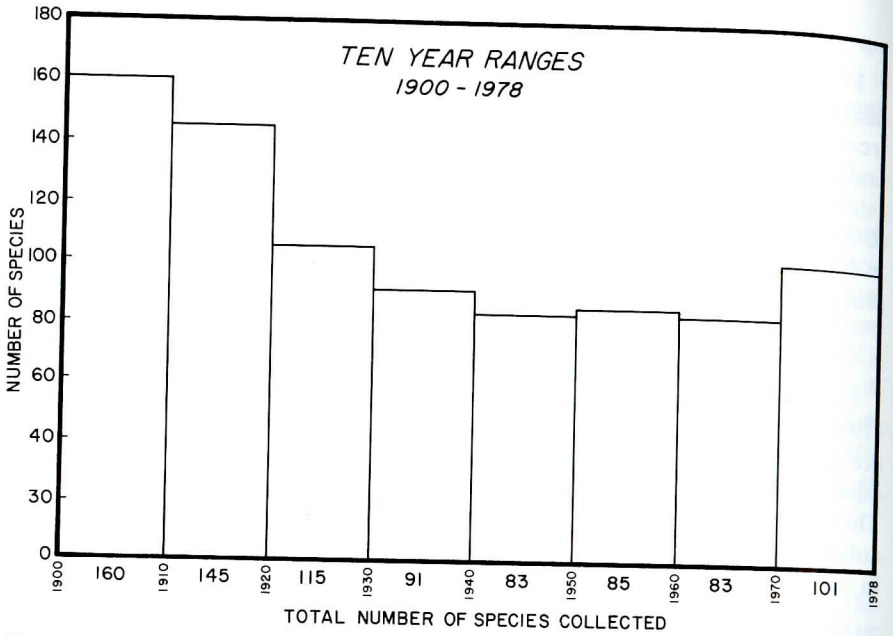

Fig. 7. Histogram of number of species found per decade at Plummers Island, Maryland.

tribe are known from the Plummers Island site; one of these has not been seen recently.

24.01 *Galerita janus* Fabricius (1792:136)

According to Lindroth (1969) found "under cover along fence rows and in deciduous woods," and to Larochelle (1974a) "in the mountains and uplands [of Quebec], under stones." Also abundant in drift on lake shores. These beetles are fully winged and fly; they are attracted to lights. Three examples were collected on the Island and adjacent Virginia shore between 1909 and 1922 (HSB, HSF). There are no recent records. No teneral specimens seen. The adults were collected in April, May, and June. Hibernation probably takes place as an adult, but this needs to be confirmed. Total length, 15.5 to 23.5 mm (19.5).

24.02 *Galerita bicolor* Drury (1770:94)

Found commonly under stones and beneath bark of rotting logs on the secondary floodplain and in the stable forest above the floodplain. These beetles are fully winged and probably fly. Numerous examples were collected on the Island and both adjacent shores between 1902 and the present (HSB, HSB & EAS, JLW & HSB, RCS, WMM, GGP, TLE). No teneral

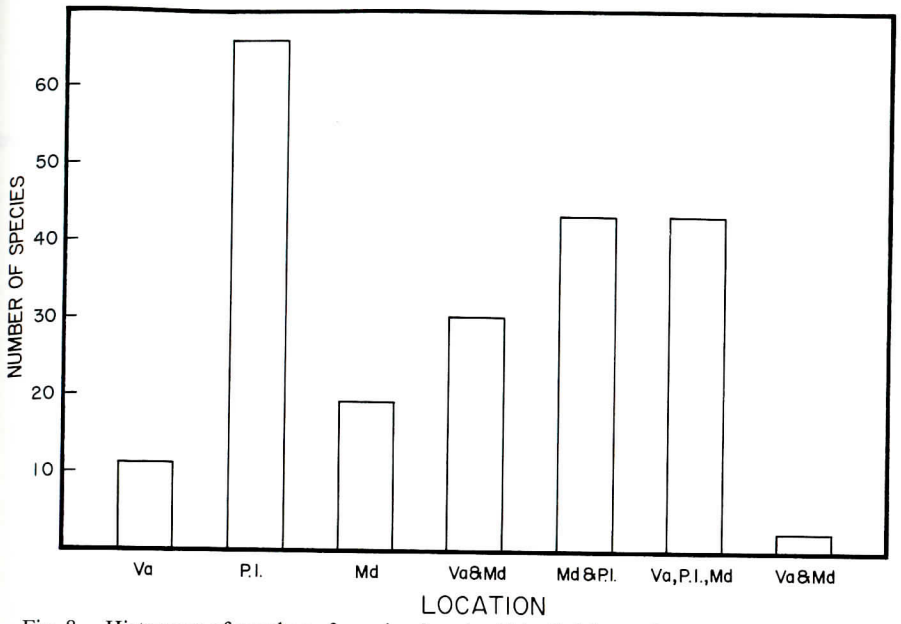

Fig. 8. Histogram of number of species found within divisions of study site or among one or more divisions (degree of local endemism); Virginia side of Potomac, Island, Maryland side of Potomac.

specimens seen. Adults were collected in March through September. Hibernation takes place as an adult. Total length, 17.6 to 22.1 mm (19.9).

Natural History

Size and Composition of Fauna.—The 214 species (plus one predicted species) represented in the study area are arrayed in 24 tribes, 69 genera (see checklist). Eleven large genera contain 51% of the fauna; 36 genera are represented by only one species. Members of ten of the large genera (8 or more species at the site) are mostly temperate terricoles (*Bembidion, Elaphropus, Agonum, Pterostichus, Amara, Chlaenius, Dicaelus, Harpalus, Anisodactylus, Stenolophus*). The other large genus is *Lebia,* whose members spend their adult life mostly on vegetation; *Lebia* diversity is greatest in the tropics and the group must be considered a tropical element. Although congeners in all of these large groups are diverse in their requirements, often many will be found together co-inhabiting the same microhabitats and eating the same foods.

The richness of the fauna at this small site is comparable to other well-collected places such as Barro Colorado Island, Panama, where I have recorded to date 287 species on ca. 1600 hectares, and Dobodura, Papua,

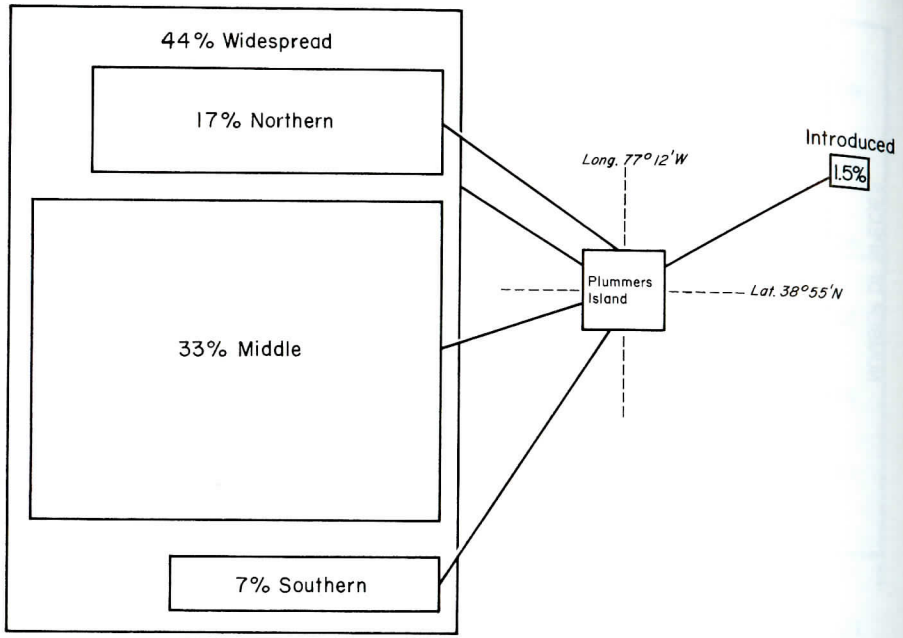

Fig. 9. Diagrammatic representation of affinities of Plummers Island fauna: "Northern" transect includes USA and Canada, America north of 45°N; "Middle" transect includes USA between 45°N and 35°N; "Southern" transect includes USA and points south, south of 35°N; "Widespread" indicates species in two or more transects; and "Introduced" indicates species probably coming from Europe via human transport.

where Darlington (1971) recorded 217 species in a couple of square miles (in 4 month's collecting!). Also, it should be noted that the total carabid fauna of the eastern Atlantic states from North Carolina to Canada does not exceed 350 species (my estimate). Lindroth's (1961b–1969) distribution records account for 297 species in this region, but he did not discuss predominately southern species; Lindroth's figure is based on species covered in his Canadian faunal project. Darlington's (1971) estimates for New Jersey, Indiana, and North Carolina were 300 to 400 for each state. I have reviewed all recent revisions and find 37 species not noted by Lindroth as possible elements of the Atlantic seaboard fauna, hence my figure of 350 as an upper limit. Therefore, the 23 hectare study site at Plummers Island has contained, over the past 79 years, about 60% of the carabid fauna of the eastern seaboard. During the first decade of this century (1901–1910) 160 species, or 45% (Fig. 7) of the possible eastern seaboard fauna occurred at the site. During the last decade (1965–1975), the number dropped to 101 species, or 28%, and the composition and mix of species changed.

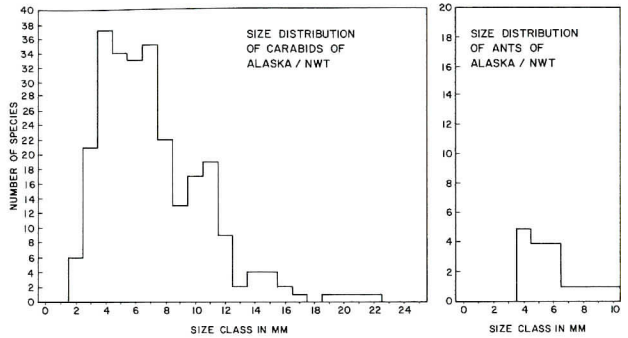

Fig. 10. Histogram of size classes (1.0 mm increments) and number of carabid and ant species of Alaska and Northwest Territories.

In total, the fauna is composed of several faunal elements (Fig. 8). The largest of these elements (44%) is made up of widespread or cosmopolitan species which have large ranges in North America. Another significant portion of the fauna (33%) is composed of species with general North American ranges confined to middle latitudes of the United States. Strictly northern elements make up 17% of the fauna; southern elements a mere 7%; and only a scant 1.4% are introduced by man, probably all from Europe. Thus the total fauna seems to be in balance with the site's generally mid-northern position on the continent; however, more southern elements could have been predicted. These elements are probably not present because of the site's position on the piedmont. A site closer to the coast, on the coastal plain, would have milder winters and perhaps allow more southern elements to become established and survive. Those southern elements which are, or have been, found at Plummers Island are mostly coastal plain or southern lowland species, for example, species of *Pasimachus, Megacephala, Loxandrus, Selenophorus,* and *Stenocrepis*.

Another aspect of the Plummers Island fauna is revealed in Fig. 9. Although collecting has been generally more intensive on the Island and Maryland shore, low percentages of local "endemism" indicate that the species in general are found throughout the study site. The faunal composition of the Virginia site has probably remained the most undisturbed due to limited accessibility, steep slopes, and lack of tree cutting; it is also the least well known.

This exceptionally large and rich fauna (for such a small area of the temperate region) reflects several things: 1) the continental aspects of the site, 2) the great diversity in habitats, 3) the mildness of climate, 4) the length of time covered by the study *and* accompanying change in general floral composition during that time (succession), 5) the age of the piedmont which has

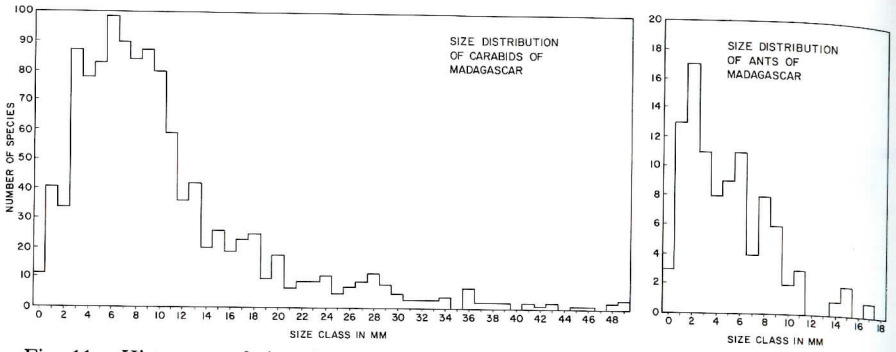

Fig. 11. Histogram of size classes (1.0 mm increments) and number of carabid and ant species of Malagasy Republic. Data from Jeannel (1946–1949) and Forel (1891).

lent stability to floral and faunal elements, 6) the proximity of both the coastal plain and nearby mountains which certainly must serve through time as source areas, and 7) the general location of the site which appears to be a transition between northern and southern elements.

Discussion of Taxa.—For purposes of discussions that follow, a synopsis of each carabid tribe and species represented at Plummers Island was given under "Annotated List of Species" above (see also checklist). This should help the reader in following these discussions. A brief tribal synopsis covering the global fauna is given in Erwin (1979).

Size of Individuals.—The size distribution of Plummers Island ground beetles is shown in Fig. 16. Comparative data are given in Figs. 10 to 15 for the faunas of Dobodura site in New Guinea, Madagascar, Great Britain, Sweden, and George Lake site in Alberta, and Barro Colorado Island, Panama.

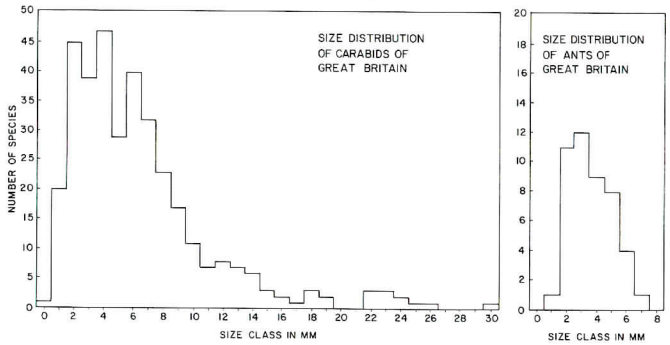

Fig. 12. Histogram of size classes (1.0 mm increments) and number of carabid and ant species of Great Britain. Data from Lindroth (1974) and Collingwood (1958).

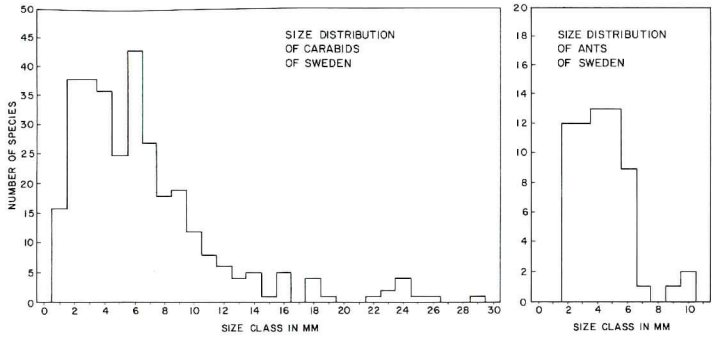

Fig. 13. Histogram of size classes (1.0 mm increments) and number of carabid and ant species of Sweden. Data from Lindroth (1961a) and Lindroth and Douwes (pers. comm.).

Darlington (1971) examined the size distribution of carabids of New Guinea and found that the resulting histogram was bimodal. Both the New Guinea fauna as a whole and the fauna occurring in about 5100 ha around Dobodura, New Guinea showed lack of species in the 3 to 5 mm total length (ABL) range. There are numerous species in the "under 3 mm" range and 6 to 8 mm range; above 8 mm the histogram decreases as in a normal curve. Remarkably, the size distribution of the Plummers Island site fauna is nearly identical to that of Dobodura (compare Figs. 10 and 16).

The size characteristics of the New Guinea fauna were accounted for by Darlington (1971) in several ways: Large forms were (are) excluded by a combination of factors such as "difficulty of access" to the island of New Guinea to members of continental faunas, "greater dispersibility of small as opposed to large Carabidae" over water gaps from continents, and

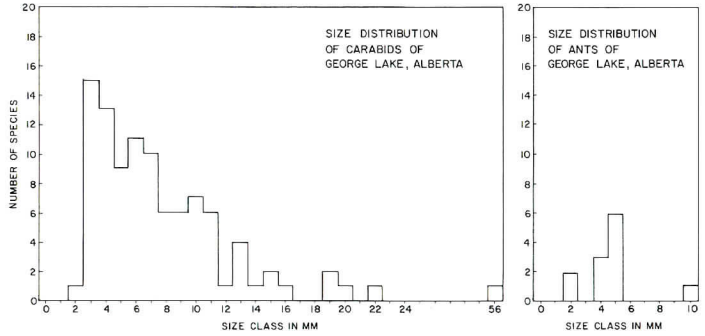

Fig. 14. Histogram of size classes (1.0 mm increments) and number of carabid and ant species of George Lake area, Alberta, Canada. Data courtesy of G. E. Ball and H. Goulet (pers. comm.).

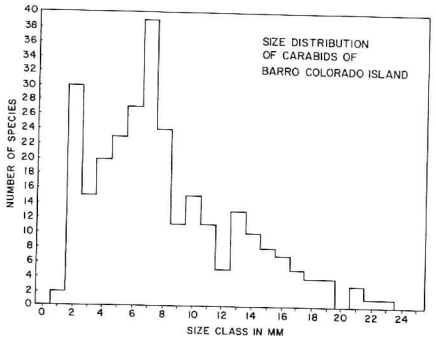

Fig. 15. Histogram of size classes (1.0 mm increments) and number of carabids at Barro Colorado Island, Panama. Ant data not available, but predictable.

relative recency of origin of the New Guinea fauna without "time to evolve large forms." To account for the bimodality of size distribution, Darlington thought that either the pressure of many small species of recently invading tachyines or an underlying relationship with ants (formicidae) caused the abnormal size curve.

Now that data are available for other faunas, both continental and islandic in nature, certain correlations make it apparent that large size (or that portion of the histogram over 7 mm) drops off in all faunas in the same fashion, that is the curve is normal. It is shifted to the right on Madagascar mostly due to the huge scaritines that live there. Since upper-range normal size distribution is common to all faunas tested (n = 7) it is likely that size is regulated by some commonality in the global environment or as part of the general structural or physiologic "ground plan" of carabid beetles. There-

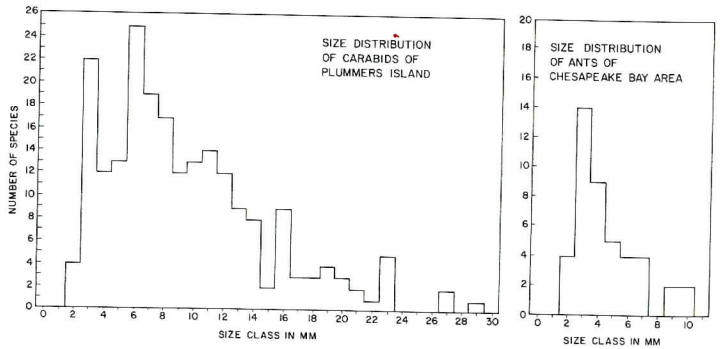

Fig. 16. Histogram of size classes (1.0 mm increments) and number of carabids at Plummers Island, Maryland and ant species of nearby Chesapeake Bay area. Ant data courtesy of J. Lynch (pers. comm.).

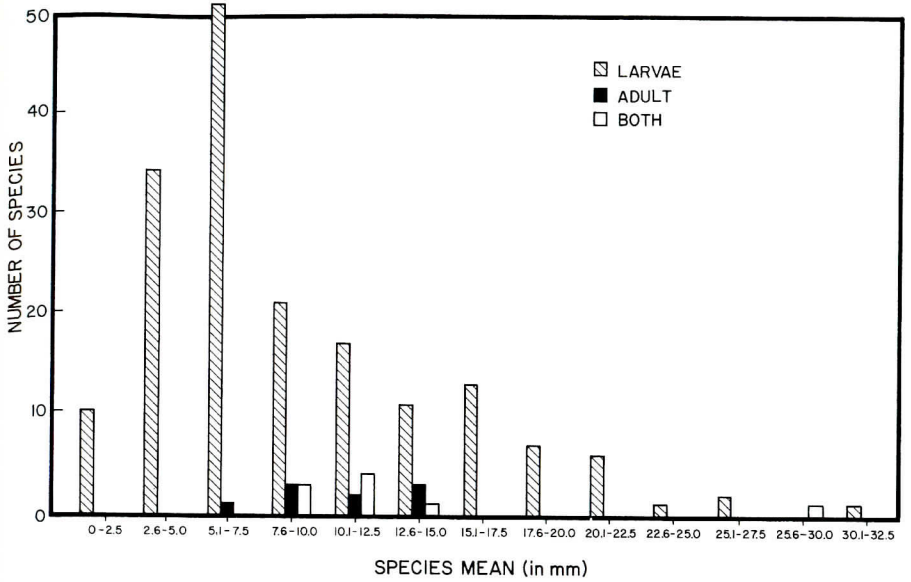

Fig. 17. Histogram of number of adult and larval hibernators per size class (1.0 mm increments) at Plummers Island, Maryland.

fore, Darlington's reasons (above) for deficiencies of large-sized species in the New Guinea fauna need not be invoked because that fauna is normal as compared to other faunas. His reasons may apply however to the apparent "skewness" toward small size. New Guinea and Madagascar have skewness in opposite directions, but their faunas are in balance with regard to size distribution. In sum, it is probable that Madagascar's fauna is very old and its components represent old lineages, while that of New Guinea is the opposite.

Table 5.—Hibernation stages of ground beetles at Plummers Island by number and percent of fauna in time.

	Total fauna 1901–1978		Early fauna 1901–1933		Continuous fauna 1901–1978		Late fauna 1959–1978	
Life stage	n	%	n	%	n	%	n	%
Larval	9	4.2	5	4.7	4	4.9	0	0
Adult	181	84.6	88	82.2	71	86.6	22	88.0
Both	9	4.2	3	2.8	5	6.1	1	4.0
Unknown	15	7.0	11	10.3	2	2.4	2	8.0
Total	214		107		82		25	

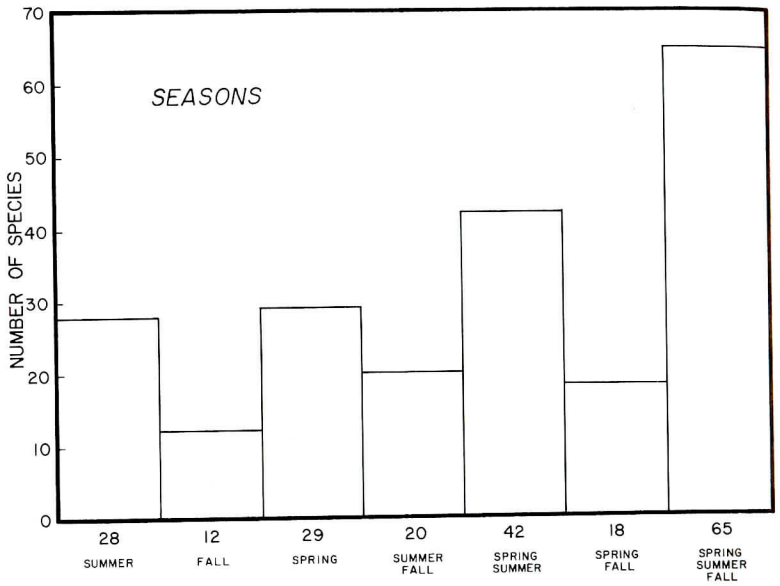

Fig. 18. Annual distribution of species as determined by when they have been collected.

The size distribution of Plummers Island carabid species is normal; mean length of early, late, and continuous faunal components lies between 5.1 and 7.5 mm (Fig. 21). Based on it and others (Figs. 10 to 15) predictions can be made following the observation that at the equator carabid faunas tend to be strongly bimodal in regard to size distribution of their species, this bimodality decreasing in faunas progressively away from the equator.

In seeking the causes of this phenomenon, I explored Darlington's suggestion that ants might exclude carabids of the same size from the fauna. Figures 10 to 16 also demonstrate that the peak of ant size distribution in

Table 6.—Vagility of ground beetles at Plummers Island by number and percent of fauna in time as determined by length of flight wings.

Wing length	Total fauna 1901–1978		Early fauna 1901–1933		Continuous fauna 1901–1978		Late fauna 1959–1978	
	n	%	n	%	n	%	n	%
Long	166	77.6	79	73.8	63	76.8	24	96.0
Short	35	16.4	22	20.6	13	15.9	0	0
Dimorphic	13	6.1	6	5.6	6	7.3	1	4.0
Total	214		107		82		25	

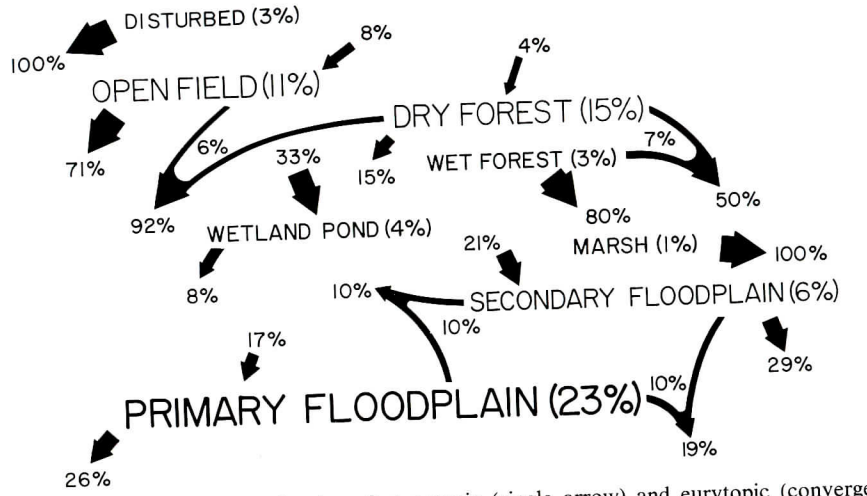

Fig. 19. Major losses and gains of stenotopic (single arrow) and eurytopic (convergent arrow) carabid species at specific habitats and habitat pairs at Plummers Island site. Downward arrows represent losses, upward arrows represent gains. Size of arrows and words represent relative losses and gains and portions of faunal components. See Table 7 for data.

various faunas is roughly correlated to the trough in the corresponding carabid fauna size distribution. This is particularly so at the Plummers Island site. In addition there is an inverse correlation with number of ant species and latitude, that is the higher the latitude the fewer ants (this is also true of mountains, that is, the higher the elevation the fewer the ants). This is directly correlated with decrease in carabid size bimodality toward the poles and up mountains. Although there seems to be correlation of statistics and observations, there is no strong reason to believe there is a direct interactive relationship among the organisms. No hypotheses have been tested. The question remains, could competitive factors allow ants to exclude other predator/scavenger terricoles at Plummers Island site or any other for that matter? Is there, in fact, a true interrelationship or is it just coincidence? What of the possible competition with spiders and rove beetles which occur commonly, evenly abundantly, in carabid (and ant) habitats? What of the predation pressure from birds and other predatory arthropods and vertebrates?

Ecologic Ranges.—Ground beetles, like other animals, are distributed in time and space geographically, and are said to occupy geographic ranges. These beetles are also distributed within communities in terms of microhabitats and roles they play in these microhabitats, and in addition, members of each taxon will have a definable set of interactions with other members of the microhabitat or community. This community distribution and role,

Table 7.—Specific habitat faunal components expressed as percentage in three time periods, late faunal additions, and percentage of total site fauna.

Specific habitats	n	Early component	Middle component	Total component	Late component	% Total fauna
Stenotopic Species						
Dry Forest Floor	28	15	4	43	4	15
Wet Forest Floor	5	80	0	20	0	3
Primary Floodplain	54	26	0	57	17	23
Secondary Floodplain	11	29	7	43	21	6
Woodland Pond	8	8	0	58	33	4
Open Field	24	71	4	17	8	11
Disturbed Areas	5	100	0	0	0	3
Marsh	2	100	0	0	0	1
Eurytopic Species						
Dry Forest/Open Field	12	92	0	8	0	6
Dry Forest/Wet Forest	14	50	7	43	0	7
Dry Forest/Pond	1	0	0	100	0	0.5
Dry Forest/Prim. Fpl.	2	0	0	100	50	1
Prim. Fpl./Secd. Fpl.	21	19	0	71	10	10
Prim. Fpl./Pond	7	0	14	86	0	4
Prim. Fpl./Open Field	1	100	0	0	0	0.5
Secd. Fpl./Pond	2	50	0	50	0	1

and this set of interactions at various levels is here regarded as an ecologic range (see also Darlington, 1971).

In order to gain insights about the faunal components of an area, various strategies can be adopted. Much can be gained by starting with museum collections if such are available for the area under study. These historic materials, if well documented with associated field data, can provide many basic observations necessary before erecting hypotheses that can be subsequently tested. For example, teneral specimens are readily detected in a collection and from these one can tell when immature stages are likely to be found in nature; also from these one can tell whether the species is a larval hibernator or adult hibernator. When collections have been made over a long period of time, faunal changes are readily detectable. And, if documentation is detailed enough one can go to precisely the habitat at the site and find the species of interest. A synthesis of specimen data and associated field data can lead to fruitful avenues of study. It is this collection-based approach that is employed here.

In total, the ground beetles of the Plummers Island site occupy all terrestrial habitats (except bare rock surfaces) and even one which might be described as subaquatic. These beetles can be classified as subxerophiles, mesophiles,

Table 8.—Invader species of carabid beetles at Plummers Island site unknown in the fauna before 1960 and which occur on primary or secondary floodplains.

Species name	Mean length in mm	First year discovered
Ardistomis viridis	5.8	1960
Bembidion honestum	6.2	1973
Bembidion rapidum	4.1	1974
Bembidion impotens	2.8	1972
Elaphropus vernicatus	2.1	1973
Paratachys obliquus	2.5	1960
Agonum tenue	8.8	1974
Agonum rigidulum	7.2	1972
Agonum excavatum	6.8	1974
Amara anthobia	6.5	1974
Chlaenius laticollis	15.5	1972
Bradycellus badipennis	5.4	1975
Acupalpus pauperculus	3.2	1974

arboricoles, and hydrophiles; most are restricted to one of these categories, a few have broader tolerances. Feeding habits range from herbivory to predation in both the larval and adult stages of species; most however can be regarded as omnivores or scavengers. Some carabid larvae are ectoparasitoids on specific hosts, such as water-beetle pupae (*Brachinus*) or leaf-beetle pupae (*Lebia*). Some carabid species are gregarious especially during hibernation, but most are found singly, even during hibernation. The Cychrini are known to aggregate during dry periods (Kavanaugh, 1977; Kavanaugh and Erwin, and Erwin, pers. obs.). It appears that carabid species, the members of which (even congenerically) live in guilds, have ecologic ranges which temporarily and spacially overlap to varying degrees. Observations to date are nearly all based on adults; it is likely that resources to these adults are for the most part somewhat unlimited for the number of adults in any certain space, for example, many eat "flotsam" along the shore, many use cracks in the soil as shelter during the day; neither of these is very scarce. Even to the casual observer, it is evident in the field that there are far more resources than needed by the number of adults present, thus limited resources are likely not important for adults. However, larval life systems may be limited in this regard and are probably more amenable for testing so-called "ecological principles" such as competition and exclusion, and there have been tests of such hypotheses elsewhere (Pearson and Mury, 1979; Pearson, 1980; Spence, 1979).

Succession at Plummers Island through the last 80 years has provided a great number of special habitats of which various guilds of carabids have taken advantage. In the following, I will discuss these habitats and the dominant carabid species which occupy (-ied) them.

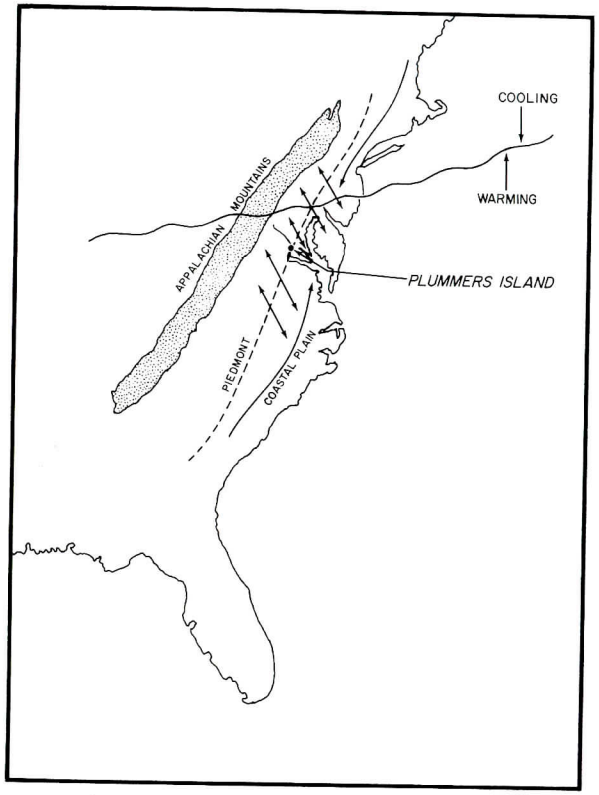

Fig. 20. Diagrammatic eastern seaboard of the USA with indication of climatic shifts and periodic faunal movements north and south and across the Fall line in area of Plummers Island.

In the first decade of this century, the top of the Island (Fig. 2) was covered with grass and scattered *Juniperus virginiana* trees, a typical pioneer vegetation in the area. This open habitat no longer exists at the site and many of its carabid species are locally extinct. Of the total 80-year fauna, 22 species were restricted to or at least found only in this habitat (11%), and an additional 17 species were part-time users of the open field community. Of the 22 species restricted to this habitat, only 3 are still present in marginal places. Of the 22 species, 14 have members which are generally regarded as seed-eaters (Harpalini and Zabrini).

These grassy areas underwent succession after the Island was purchased by the Washington Biologists' Field Club and now are covered with young climax vegetation of the area—Oak, Hickory, Maple forest. A small patch of Beech forest occurs near the tow path upslope from the ferry slip (Fig. 1a). These relatively dry and well-drained forest types together had in the

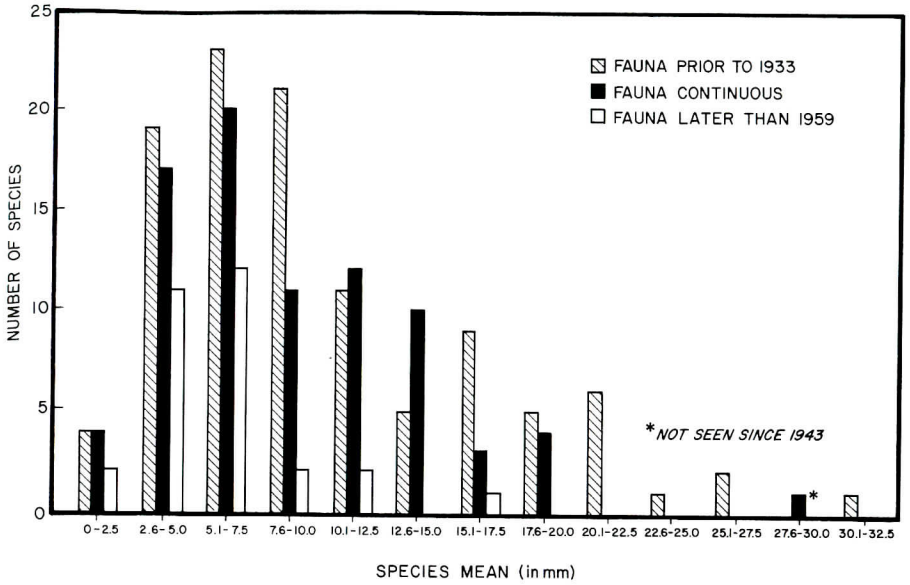

Fig. 21. Change in faunal classes through time at Plummers Island, Maryland.

first decade of this century 28 species of carabids restricted to them (15%) and an additional 30 species using them part-time. Another species was recorded for the first time in 1962. Of these 29 species, 13 are still present in the fauna. Members of all but three of these species are scavengers or predators, the remaining are seed eaters.

Wet forest occurs adjacent to the Pond and in low areas along the tow path. These areas have remained undisturbed since before the turn of the century. In them, 9 species of carabids occurred early in this century, 4 new ones were discovered in 1974; 5 have not been seen recently. Although this habitat constitutes a relatively very small area of the whole, it containe 7% of the 80-year fauna. All species have members which are either predaceous or omnivorous.

The primary and secondary floodplains of the Potomac River have not changed successionally since the turn of the century (Fig. 2). The primary floodplain is occupied by 45 indigenous species (23%), 9 of which arrived after 1960, with another 36 using it from time to time. The secondary floodplain is occupied by 11 species (6%), 3 of which arrived after 1970, with another 29 species using it. All feeding types are well represented in both areas. Thirteen species of the primary floodplain are no longer present in the fauna; 3 species of the secondary floodplain are no longer present.

The remaining habitat, if it can be called that, with moderately long-term stability is that of permanently disturbed areas. The tow path and its margins

Table 9.—Geographic distribution of generic groups of carabid beetles represented at Plummers Island site with relative size of genus within family Carabidae and northern limits in North America. H = Holarctic, N = Nearctic, Nt = Neotropical, E = African, Madagascan, O = Oriental, A = Australian.

Genus name	Distribution area	Relative size	Northern limits
Omophron	H, E, O	Small	Southern Canada
Brachinus	Tropicopolitan	Medium	Southern Canada
Nebria	H	Small	Arctic
Notiophilus	H	Small	Arctic
Elaphrus	H	Small	Arctic
Carabus	H	Medium large	Arctic
Calosoma	Cosmopolitan	Medium large	Middle Canada
Scaphinotus	N	Medium	Subarctic
Sphaeoderus	N	Small	Southern Canada
Megacephala	N, Nt, E, A	Medium	Middle USA
Cicindela	Cosmopolitan	Large	Subarctic
Scarites	Tropicopolitan	Large	Southern Canada
Pasimachus	N, Nt	Small	Southern Canada
Dyschirius	H, Nt, E, O	Medium	Arctic
Ardistomis	N, Nt	Medium	Middle USA
Clivina	Cosmopolitan	Very large	Southern Canada
Schizogenius	N, Nt	Medium	Southern Canada
Omoglymmius	Cosmopolitan	Very large	Northern USA
Clinidium	N, Nt	Medium	Northern USA
Bembidion	Cosmopolitan	Very large	Arctic
Anillinus	N	Small	Middle USA
Mioptachys	N, Nt	Large	Southern Canada
Tachyta	H	Small	Arctic
Elaphropus	Cosmopolitan	Very large	Middle Canada
Pericompsus	N, Nt, A	Medium	Northern USA
Paratachys	Cosmopolitan	Very large	Southern Canada
Polyderis	Cosmopolitan	Large	Southern Canada
Patrobus	H	Small	Arctic
Europhilus	H	Small	Arctic
Agonum	Cosmopolitan	Large	Arctic
Platynus	N, Nt	Very large	Arctic
Calathus	H	Large	Arctic
Synuchus	H	Small	Southern Canada
Olisthopus	H	Small	Southern Canada
Atranus	N	Small	Southern Canada
Loxandrus	N, Nt, A	Medium	Southern Canada
Myas	H	Small	Southern Canada
Pterostichus	Cosmopolitan	Very large	Arctic
Evarthrus	N	Medium	Southern Canada
Amara	H	Very large	Arctic
Chlaenius	Tropicopolitan	Large	Middle Canada
Oodes	Cosmopolitan	Small	Southern Canada
Stenocrepis	N, Nt	Small	Middle USA
Dicaelus	N	Small	Southern Canada

Table 9.—Continued.

Genus name	Distribution area	Relative size	Northern limits
Badister	H, Nt, E, O	Small	Middle Canada
Cratacanthus	N	Small	Southern Canada
Harpalus	H	Very large	Arctic
Episcopellus	N	Small	Southern Canada
Trichotichnus	H	Medium	Southern Canada
Selenophorus	N, Nt	Very large	Southern Canada
Geopinus	N	Small	Southern Canada
Notiobia	N, Nt, E, A	Medium	Middle USA
Anisodactylus	H, O	Large	Southern Canada
Amphasia	N	Small	Southern Canada
Bradycellus	H, Nt	Large	Arctic
Stenolophus	H, Nt	Large	Middle Canada
Acupalpus	Cosmopolitan	Very large	Southern Canada
Tetragonoderus	Tropicopolitan	Medium	Southern Canada
Colliuris	N, Nt	Medium	Southern Canada
Lebia	Cosmopolitan	Very large	Southern Canada
Coptodera	Tropicopolitan	Medium	Middle USA
Dromius	H, Nt	Medium	Southern Canada
Apristus	Cosmopolitan	Medium	Southern Canada
Calleida	N, Nt	Large	Southern Canada
Plochionus	N, Nt	Small	Southern Canada
Pinacodera	N, Nt	Small	Southern Canada
Apenes	N, Nt	Medium	Southern Canada
Zuphium	Cosmopolitan	Medium	Southern Canada
Galerita	N, Nt	Medium	Southern Canada

are now "maintained" by the National Park Service. Five species of carabids are known only from along this "roadway"; none of these have been seen after 1924, although I suspect some of them to be present.

The remainder of the species (36%) are found in more than one of these habitats, that is they each have a broader ecologic range than the stenotypic species discussed above.

Seasonality and Circadian Cycles.—As in most temperate climates, seasonality in the ground beetle fauna is well-marked and as far as is known all species are apparently univoltine, that is have only one generation per year (Thiele, 1979). Winter is a time of hibernation for all species, although some overwinter in different life stages than others (see Table 5, Fig. 17). Two breeding strategies exist in spring time: overwintering adults (adult hibernators, spring breeders) emerge from their winter cover, feed for some time and then lay eggs (if they were mated in the autumn) or search for mates, mate, then lay eggs; second, and by far the least common method is for larvae to overwinter (larval hibernators, autumn breeders), pupate when the ground warms, emerge in late spring as an adult, feed, mate, and

Table 10.—Summary of data in Table 9. Patterns of distributions represented by Plummers Island genera with number per type of distribution pattern and summary of generic northern limits per type of distribution.

Distribution	Number of genera	Summary of generic northern limits
H, O	1	1—southern Canada
H, E, O	1	1—southern Canada
H, Nt, E, O	2	1—Arctic; 1—middle Canada
N, Nt, A	2	1—southern Canada; 1—northern USA
N, Nt, E, A	2	2—middle USA
Tropicopolitan	5	1—middle Canada; 3—southern Canada; 1—middle USA
N	9	8—southern Canada; 1—middle USA
N, Nt	14	1—Arctic; 10—southern Canada; 1—northern USA; 2—middle USA
H	15	10—Arctic; 1—subarctic; 4—southern Canada
Cosmopolitan	15	3—arctic; 1—subarctic; 2—middle Canada; 8—southern Canada; 1—northern USA

lay eggs in the summer or fall. Regardless of method, the delicate larval stages are feeding in the summer, i.e., the most humid part of the year. Adults and larval stages overlap in late spring and summer and likely compete in part for the same food resources, although by this time there is plenty of food. According to Table 5 data, there has been a gradual tendency toward accumulation of adult-hibernating species, at the loss of larval hibernators and species that can do it either way. This trend probably is correlated with succession of habitat from open grassy areas to closed forest and the concomitant loss of seed eating carabids such as members of *Amara* and *Harpalus,* both of which often have larval hibernation.

Figure 18 shows annual distribution of the species in terms of when they are collectable (i.e., when they are active on the surface and likely to be collected). The largest percentage of species are active throughout the spring, summer, and fall. Eighteen species apparently enter summer diapause or aestivation and have never been collected during the hot months.

Ground beetles in general undergo various kinds of diapause and respond to various environmental factors (Thiele, 1979); however it is beyond the data avilable for the Plummers Island site for me to discuss these factors. The reader is referred to a wealth of European literature summarized by Thiele (1979) and Koch and Thiele (1980).

With regard to circadian cycles of Plummers Island ground beetles, I have knowledge of 171 species. Of these, 111 (64.9%) are nocturnal in habits, 27 (15.8%) are diurnal, and 32 (18.7%) are both nocturnal and diurnal. This ratio of 6:1:1 holds true for the early fauna as well as the late fauna, thus for this characteristic the fauna has not changed. Nocturnal species range

in size from 2.0 mm to 30.0 mm, the entire spectrum at the Island; diurnal species range from 2.0 mm to 13.0 mm; and either/or species range from 2.0 mm to 13.0 mm, plus 3 species of *Calosoma* which are 20.0 mm to 22.0 mm. These data apparently indicate that, except for *Calosoma,* species with large members (over 13.0 mm) are nocturnal in habits.

Vagility.—The nature of the fauna at Plummers Island is that of a vagile group of dispersant species; 77.6% of the fauna are long-winged and presumably capable of flight; an additional 6.1% are wing-dimorphic so that some individuals of each species at least can fly. Only 16.4% are wingless. According to Table 6, the components of the early fauna were less vagile than the later faunal introductions and no wingless species has arrived at the site after 1959; only one wing-dimorphic species arrived after 1959. Those species arriving after 1959 are mostly highly vagile dispersants (Table 8) associated with disturbed habitats in the sense of pollution and silting as opposed to vegetative cover removal.

Extinction and Invasion Patterns.—It has been through reduction in diversity of habitats that the fauna of carabids dropped from 160 species in the first decade of this century to 101 in the present decade (Fig. 7). The loss of open grassland accounts for most of the losses. Figure 19, based on data presented in Table 7, depicts graphically loss and gain in species from specific habitats. Although it is easy to understand that elimination of habitat directly results in reduction of species living in that habitat, it is not so clear why long standing habitats, such as primary floodplain, gained species during the same time period.

Relatively large gainers were the primary and secondary floodplains and the woodland pond, although both the former habitats lost more than they gained. Also the former two, during the last 80 years or at least until rather recently, have undergone great changes due to siltation and pollution. Such change would surely have a great impact on soil-living insects such as carabid beetles. Recently arrived species (within the last 20 years) are characteristically small and highly vagile (Table 8, Fig. 21). These kinds of carabid beetles are common in disturbed wet areas and would be predicted to invade strand with a covering of silt and organics such as is now the case with the Plummers Island shore. Concomitantly, larger species have been eliminated from the fauna (Fig. 21).

Largest losers, besides the habitats which are now virtually absent, are the dry and wet forests. Net loss in stenotopic dry forest species was 11%; of the eurytopic species shared with open fields, net loss was 92%. The wet forest lost 80% of its stenotopic species and 50% of its eurytopic species shared with the dry forest. The reasons for these dramatic losses are unknown. The dry forest is more extensive today and the wet forest is unchanged in visible quality or extent. Two possibilities could be explored: the dry forest today is a closed forest whereas in the first decade of the

century it was patchy with much more ecotonal area; Lawrey and Hale (1979) showed that heavy metals from the nearby freeway traffic have resulted in decreased lichen growth at critical life stages. The pertinent hypotheses for our purposes would be as follows: ecotonal areas adjacent to dry forest patches provide increased environmental diversity allowing more forest carabid species to exist in such patches; and/or carabids respond to heavy metal pollution as do lichens, the result of which is that numbers of species decrease.

Zoogeographic Aspects

Plummers Island is located along the Atlantic seaboard midway between northern and southern faunal-floral regions. Many groups of animals and plants common to the southern states have their northern limits in Virginia, Maryland, or southernmost Pennsylvania. Other groups common to northern regions have their southern limits in this area as well and extend south disjunctly only along the Appalachian uplands. Certainly the most important factor producing this distribution interface is the climate. Steering currents and the nearby mountains route most winter storms and really cold weather along the Pennsylvania border, rarely shifting south over the study site at Plummers Island and the lower Potomac River valley. Climatic cycles shifting this weather-interface a few miles south or north would, through time, allow certain beetle species (at their distributional limits) to shift in one direction or another for short periods of time (years or decades). These species would be noted in the local faunas some years and not others. Although collecting records and species monitoring are not yet sufficient to show climatic fluctuation, certain other zoogeographic aspects of the species at the Plummers Island site can be discussed here.

As shown in Fig. 8, of the 214 species at the site, 43.9% are widespread species occurring as far south as Florida and Texas or even transamerican and north to Canada; 32.5% are generally found at middle latitudes only in the eastern third or so of the continent, some reaching as far south as Georgia and north to New York or southernmost Canada; 16.8% are clearly northern elements which barely reach the study area via the Appalachian chain; 7.5% are clearly southern elements with centers in Florida or Gulf Coast states; 1.4% are introduced from Europe.

These data suggest the study site's fauna is more influenced by northern elements than southern ones and it was suggested (R. T. Allen, pers. comm.) that possibly the Potomac River's southeastward flow accounted for this by carrying elements down and depositing them on the Island. Another possibility is the location of the site on the Piedmont or lower-most slopes of the Appalachian chain just inside the Fall line (Fig. 20). East of the Fall line lies the coastal plain with its fauna and flora. Many of these elements overlap the Fall line, others do not and are restricted to one side or another.

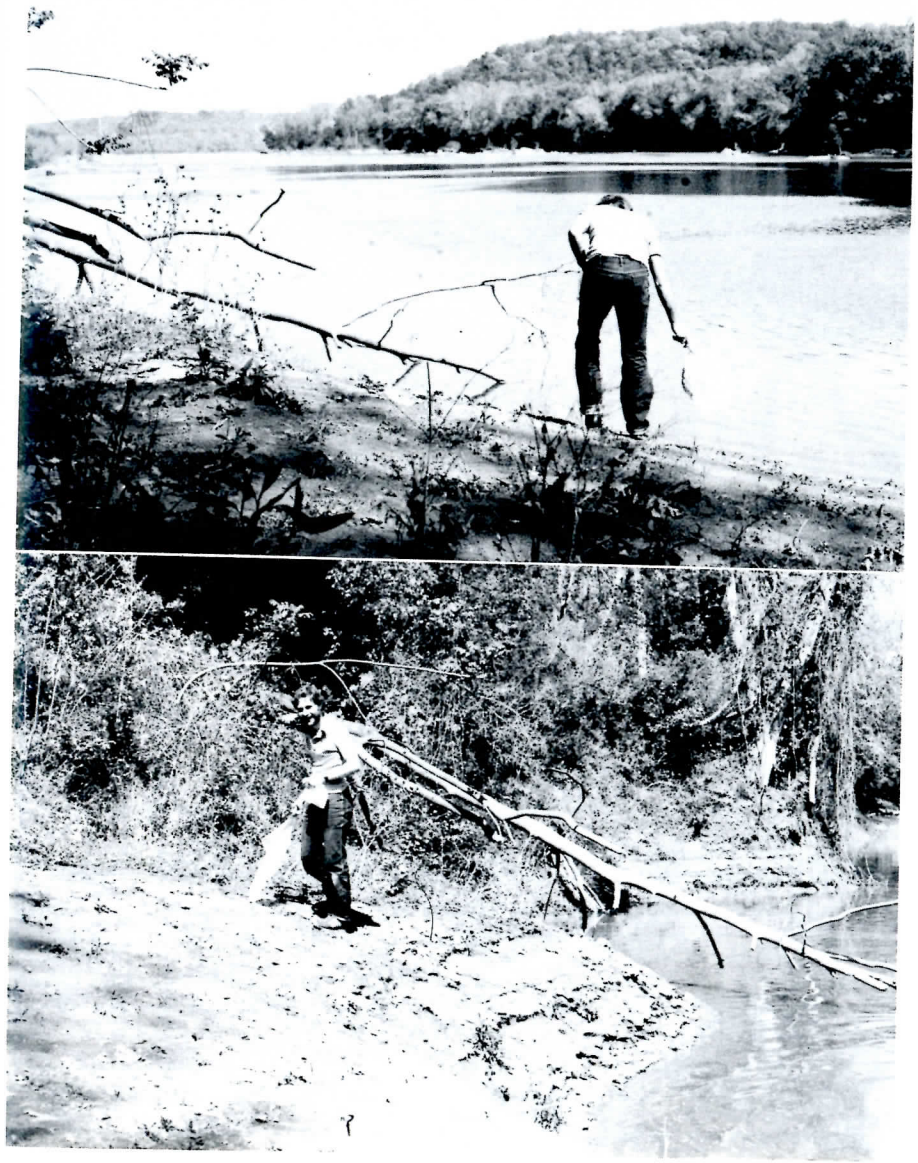

Fig. 22. Plummers Island, Maryland; primary floodplain along Potomac River, sand bank in April 1981.

Fig. 23. Plummers Island, Maryland; primary floodplain along Potomac River, gravel bar in April 1981.

Fig. 24. Plummers Island, Maryland; secondary floodplain along Potomac River in April 1981.

Fig. 25. Plummers Island, Maryland; primary floodplain along channel in April 1981.

Fig. 26. Plummers Island, Maryland; upland mixed forest in April 1981.

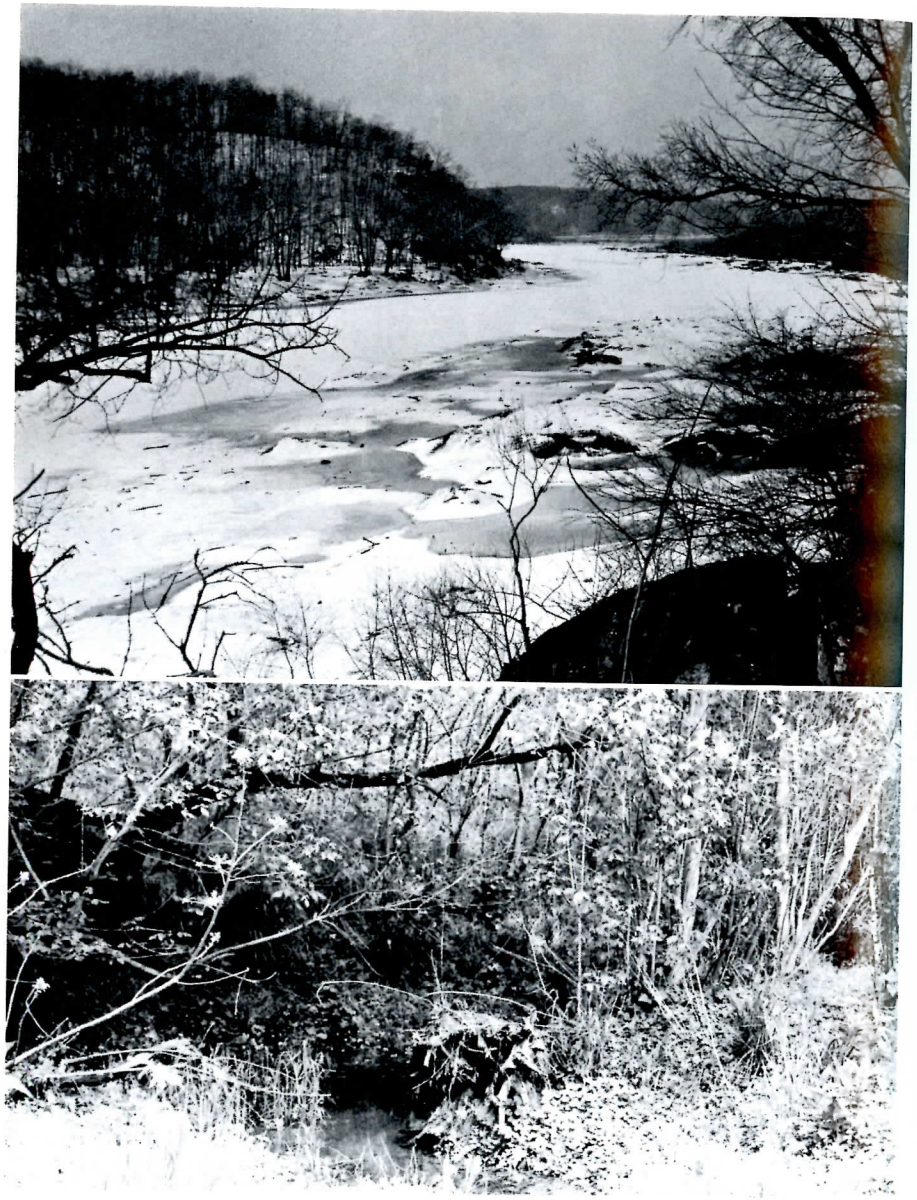

Fig. 27. Plummers Island, Maryland; shore and forested slope of Virginia side of river adjacent to Island in 1905; photograph by A. A. Doolittle.

Fig. 28. Plummers Island, Maryland; secondary floodplain pond at edge of mixed forest on Maryland side of river adjacent to Island in April 1981.

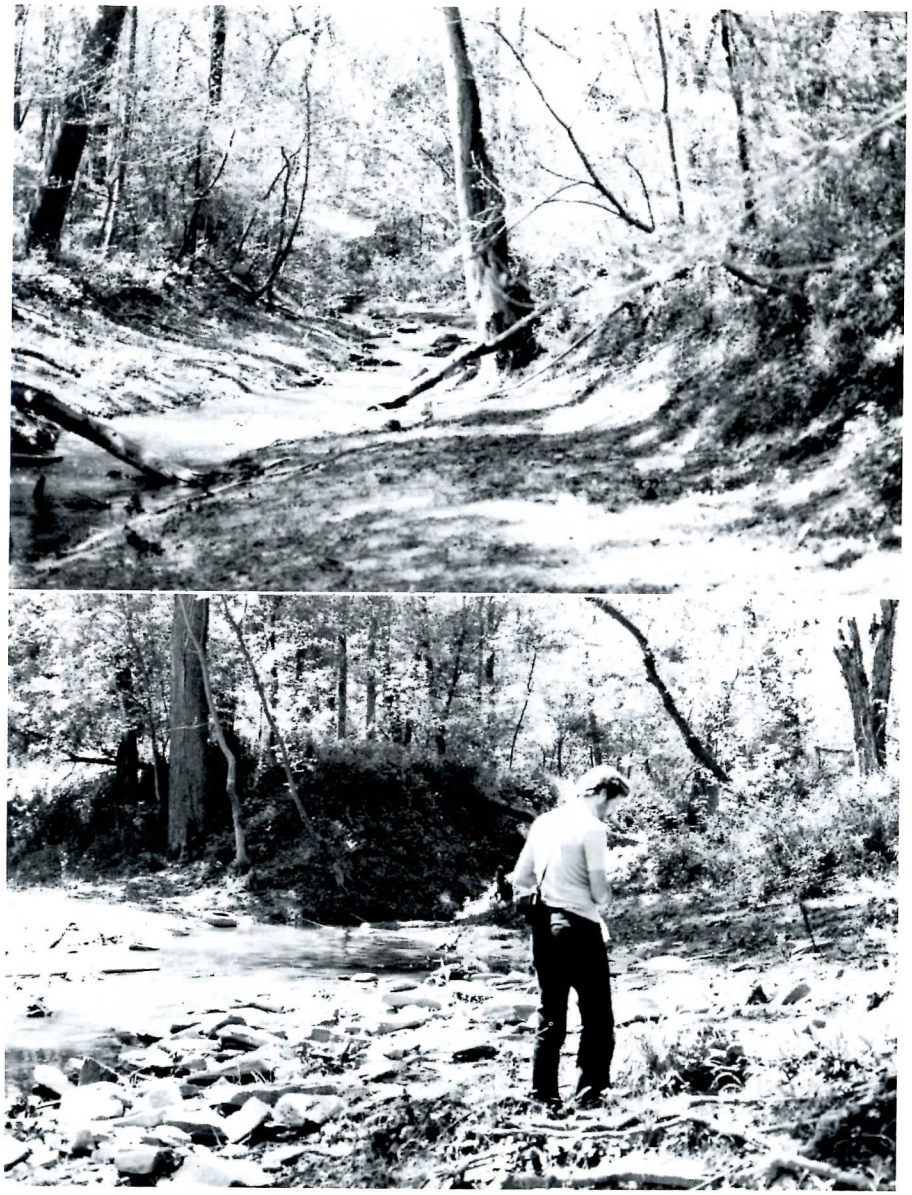

Fig. 29. Plummers Island, Maryland; Rock Run on Maryland side of river in April 1981.

Fig. 30. Plummers Island, Maryland; Rock Run delta on Maryland side of river in April 1981.

Fig. 31. Plummers Island, Maryland; young tertiary floodplain forest on Maryland side of river adjacent to Channel in April 1981.

Fig. 32. Plummers Island, Maryland; old tertiary floodplain forest on Maryland side of river adjacent to Channel in April 1981.

Fig. 33. Plummers Island, Maryland; xeric pine/sphagnum slope west of cabin on main island knoll in April 1981.

Fig. 34. Plummers Island, Maryland; deep leaf litter on moist-forest slope south of cabin on main island knoll in April 1981; habitat of *Harpalus viduus* LeConte.

Data in Table 9 indicate that the 69 genera represented at the site can be classified in 10 distributional patterns (Table 10). Of zoogeographic interest generally, are the numbers of genera which have northern limits in southernmost Canada or in the Arctic, and the patterns of northern limits expressed by genera in the distribution types. Forty-nine percent of the genera have their northern limit in southernmost Canada; 22% have arctic components and over half of these have Holarctic distributions! Three cosmopolitan genera have an arctic northern limit, as does one Nearctic-Neotropical genus.

During the last glacial advance of the Pleistocene, it is probable that 60–66% of the carabid *genera* spent the time south of the ice (all those listed in Table 9 from southern Canada south). Of those Holarctic elements which now extend as far as Plummers Island or even further south, and which now have species in the arctic zone, it is of interest to determine whether they stayed south of the ice or in northern refugia during glacial maxima. Of the 10 genera in question, all species represented at Plummers Island have ranges and relationships which indicate they were in a refugial area southeast of the main ice lobes (Kavanaugh, pers. comm.). Of these, 8 were most likely polycentric with regard to refugia and several had species in both western refugia south of the ice and refugia north and west of the ice. There is no evidence to date that would lead to the conclusion that any Plummers Island species is an invader from lineages which spent glacial time in northern or western refugia. All appear to be derived from an eastern Pleistocene fauna.

Evolutionary Considerations

If, as proposed elsewhere (Erwin, 1979, 1981; Erwin and Adis, 1981), the Taxon Pulse model is operable, the Plummers Island site is presently geographically located behind the front of major current temperate activity. During the peak of Pleistocene glaciations, Plummers Island lay south of the ice far enough that little disruption of the fauna probably took place, and the surviving fauna probably acted as a reservoir for advancement north as the ice receded. At present, 49% of the genera represented at Plummers Island have their northern limits in southernmost Canada (Tables 9, 10), 4% in the northern USA. It is these groups which are gradually advancing northward, or at least were doing so following the retreat of the ice. On the other side, Plummers Island is also located at the northern edge of what might be termed "northern limit of tropical groups," that is, a pattern exists, and is repeated in several tropical genera of carabids, as follows: large, lowland tropical genera have a center of species richness located usually adjacent to the equator and from such a center numbers of species decrease as counts are made toward the earth's poles. All neotropically centered genera dis-

appear at or before southernmost Canada. Six of these have their northernmost limits at about the latitude of Plummers Island (*Megacephala, Ardistomis,* "Anillina," *Stenocrepis, Notiobia, Coptodera*).

In the short term, the Plummers Island site represents a refugium for species restricted to climax eastern deciduous forest, secondary floodplain forest, woodland ponds, and mature beech forest. With increasing development in the area, pressure on such relatively undisturbed places will also increase. Although nearly 40% of the carabid species found at the site early in the century have now disappeared due to succession and subsequent loss of habitat diversity, those which are left approximate a natural ground beetle fauna in the eastern deciduous forest in a riparian setting.

Acknowledgments

I heartily thank the following people for aid and support during the study and writing of this project: La Verne J. Magarian (Erwin), for field work, critical review, and assistance in computer analysis; Donald R. Whitehead and Vera Krischik, for field work and many hours of discussions about data relevance; Lee-Ann C. Hyack, for helping me set up data categories and various computer services and for doing much of the liaison work between my desk and the computer; David R. Smith, James F. Lynch, Carl H. Lindroth, Henri Goulet, and George E. Ball for providing data about ants and/or carabids; Patty Wilkins and Daniel Thompson for preparation of specimens and/or researching literature; Gloria N. House and Janice C. Scott for searching the USNM collection for Plummers Island specimens; Gloria House for card punching measurement data; Linda Lea Sims, for bibliographic compilation, preparation of drafts of tables and graphs, and critical editing of the manuscript; Noreen Connell, Anne L. Halpern, and Joan B. Miles for the tedious task of typing and proofing the manuscript and tables through several early drafts; and George Venable for providing final illustrative material. This study was supported by the Washington Biologists' Field Club through funds provided for field work, technical assistance, and computer costs.

The following members and associates of the Washington Biologists' Field Club provided the specimens for this study: A. D. Appel, R. T. Allen, H. S. Barber, F. E. Blaisdell, L. L. Buchanan, A. Busck, O. L. Cartwright, E. A. Chapin, D. H. Clemons, T. P. Copeland, J. C. Crawford, R. P. Currie, T. L. Erwin, A. K. Fisher, W. S. Fisher, H. Frank, G. M. Greene, A. B. Gurney, P. Havenstein, G. F. Hevel, J. D. Hood, P. D. Hurd, L. O. Jackson, F. Knab, K. V. Krombein, W. L. McAtee, W. M. Mann, P. R. Myers, W. Palmer, G. G. Perrault, A. H. Pottinger, V. A. Roberts, E. A. Schwarz, R. C. Shannon, T. E. Snyder, P. J. Spangler, T. J. Spilman, W. H. Tyson, J. M. Valentine, W. V. Warner, D. R. Whitehead, J. L. Wrenn, and J. Zetek.

Literature Cited

Aldrich, J. W., and A. J. Duval. 1943. Breeding bird population of the Potomac River flood plain and adjoining uplands.—Bureau of Sport Fisheries and Wildlife. pp. 5–7.

Allen, R. T. 1972. A revision of the Genus *Loxandrus* LeConte (Coleoptera: Carabidae) in North America.—Entomologica Americana 46:1–184.

Andrewes, H. E. 1929. Coleoptera, Carabidae. *In,* Stephenson,J., ed. The Fauna of British India, including Ceylon and Burma 1:1–431.

Aneshansley, D., T. Eisner, J. M. Widom, and B. Widom. 1969. Biochemistry of 100°C: Explosive secretory discharge of Bombardier Beetles (*Brachinus*).—Science 165:61–63.

Ball, G. E. 1959. A taxonomic study of the North American Licinini with notes on the old world species of the genus *Diplocheila* Brulle (Coleoptera).—Memoirs of the American Entomological Society 16:1–258.

———. 1979. Conspectus of Carabid classification: History, holomorphology, and higher taxa. *In,* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history, and classification. Dr. W. Junk, Publishers. The Hague. pp. 63–111.

Beauvois, A. M. F. J. Palisat de. 1805. Insectes recueillis en Afrique et en Amérique, &c. Paris. 276 pp.

Bell, R. T. 1960. A revision of the genus *Chlaenius* Bonelli (Coleoptera: Carabidae) in North America.—Miscellaneous Publications of the Entomological Society of America 1(3):97–171.

———. 1970. The Rhysodini of North America, Central America, and the West Indies (Coleoptera:Carabidae).—Miscellaneous Publications of the Entomological Society of America 6(6):289–324.

———. 1979. Zoogeography of Rhysodini—Do Beetles travel on driftwood? *In,* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history and classification. Proceedings of the First International Symposium of Carabidology, Dr. W. Junk, Publishers, The Hague. pp. 331–342.

Bengston, S.-A., A. Fjellberg, and T. Solhøy. 1975. *Amara quenselii* Schn. (Coleoptera: Carabidae) new to Svalbard.—Norwegian Journal of Entomology 22(1):81–82.

Bland, J. H. B. 1863. Descriptions of a few supposed new species of North American Coleoptera.—Proceedings of the Entomological Society of Philadelphia 1:353–356.

Bonelli, F. A. 1813. Observations entomologiques.—Memorie della Reale Accademia della Scienze di Torino 20:433–484.

Burgess, A. P., and C. W. Collins. 1917. The Genus *Calosoma* including studies of seasonal histories, habits and economic importance of American species north of Mexico and of several introduced species.—United States Department of Agriculture, Bulletin 417:1–124.

Carr, M. E. 1950. The District of Columbia, its rocks and their geologic history. United States Government Printing Office. 59 pp.

Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America.—Memoirs on the Coleoptera 4:1–192.

———. 1918a. A Review of the North American Bembidiinae.—Memoirs on the Coleoptera 8:1–223.

———. 1918b. Studies among some of the American Amarinae and Pterostichinae.—Memoirs on the Coleoptera 8:224–393.

———. 1920. A revisional study of the American Platyninae.—Memoirs on the Coleoptera 9:1–132.

Chaudoir, M. de. 1843. Carabiques Nouveaux.—Bulletin de la Société Impériale des Naturalistes, Moscou 16(3):671–795.

———. 1868. Observations synonymiques sur les Carabiques de l'Amérique septentrionale et descriptions d'espèces nouvelles de ce pays.—Revue et Magasin de Zoologie, Ser. 2, 20:161–171.

Collingwood, C. A. 1958. A key to species of ants (Hymenoptera, Formicidae) found in Britain.—Transactions of the Society of British Entomology 13(5):69–96.

Csiki, E. 1930. Carabidae:Harpalinae. *In,* Schenkling, S., ed. Coleopterorum catalogus. Dr. W. Junk Publishers, Berlin. 2(112):529–737.

———. 1932. Carabidae:Harpalinae. *In,* Schenkling, S., ed. Coleopterorum catalogus. Dr. W. Junk Publishers, Berlin. 3(121):1023–1278.

Darlington, P. J., Jr. 1943. Carabidae of mountains and islands: Data on the evolution of isolated faunas, and on atrophy of wings.—Ecological Monographs 13:37–61.

———. 1952–1971. The Carabid Beetles of New Guinea. Parts 1–4.—Bulletin of the Museum of Comparative Zoology, 1952. Part 2, 107(3):90–252; 1962. Part 1, 126(3):321–564; 1968. Part 3, 137(1):1–250; 1971. Part 4, 142(2):129–337.

———. 1965. Biogeography of the Southern end of the world: Distribution and history of far-southern life and land, with an assessment of continental drift. Harvard University Press, Cambridge. 236 pp.

De Geer, C. 1774. Memoires pour servir à l'Histoire des Insectes. De l'imprimerie de Pierre Hesselberg, Publishers. Stockholm. 4, 456 pp.

Dejean, P. F. M. A. 1825. Spécies général des Coléoptères de la collection de M. le Compte Dejean. Paris. 1, 463 pp.

———. 1826. Spécies général des Coléoptères de la collection de M. le Compte Dejean. Paris. 2, 501 pp.

———. 1828. Spécies général des Coléoptères de la collection de M. le Compte Dejean. Paris. 3, 556 pp.

———. 1829. Spécies général des Coléoptères de la collection de M. le Compte Dejean. Paris. 4, 520 pp.

———. 1831. Spécies général des Coléoptères de la collection de M. le Compte Dejean. Paris. 5, 883 pp.

Drury, D. 1770. Illustrations of Natural History. London. 1, 130 pp.

Duftschmidt, C. E. 1812. Fauna Austriae. Linz, Leipzig. 2, 311 pp.

Eisner, T., T. H. Jones, D. J. Aneshansley, W. R. Tschinkel, R. E. Silberglied, and J. Meinwald. 1977. Chemistry of defensive secretions of Bombardier Beetles (Brachinini, Metriini, Ozaenini, Paussini).—Journal of Insect Physiology 23:1383–1386.

Erwin, L. J. M. 1976. Application of a computerized general purpose information management system (SELGEM) to a natural history research data bank (Coleoptera:Carabidae).—Coleopterists' Bulletin 30(1):1–32.

Erwin, T. L. 1970. A reclassification of Bombardier beetles and a taxonomic revision of the North and Middle American species (Carabidae:Brachinida).—Quaestiones Entomologicae 6:4–215.

———. 1972. Review—The Carabid Beetles of New Guinea by Philip J. Darlington, Jr.—Systematic Zoology 21(3):343–347.

———. 1974. Studies of the subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part II. A revision of the New World-Australian Genus *Pericompsus* LeConte.—Smithsonian Contributions to Zoology 162:1–96.

———. 1975. Studies of the Subtribe Tachyina (Coleoptera: Carabidae: Bembidiini), Part III: Systematics, Phylogeny, and Zoogeography of the Genus *Tachyta* Kirby.—Smithsonian Contributions to Zoology 208:1–68.

———. 1978. Techniques.—Coleopterists' Bulletin 32(4):372.

———. 1979. Thoughts on the evolutionary history of ground beetles: Hypothesis generated from comparative faunal analysis of lowland forest sites in Temperate and Tropical regions. *In,* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid

Beetles: Their evolution, natural history and classification. Dr. W. Junk, Publishers. The Hague. pp. 539–592.

———. 1981. Taxon pulses, vicariance, and dispersal: An evolutionary synthesis illustrated by carabid beetles. *In,* Nelson, G. and D. Rosen, eds. Vicariance Biogeography: A critique. Columbia University Press, New York. pp. 159–196.

———, and J. Adis. 1981. Amazonian inundation forests: Their role as short-term refugia and generators of species diversity and taxon pulses. *In,* Prance, G., ed. Biological diversification in the Tropics. Columbia University Press, New York (In Press).

———, and D. H. Kavanaugh. 1980. Systematics and zoogeography of *Bembidion* Latreille: I. The *carlhi* and *erasum* groups of western North America (Coleoptera: Carabidae, Bembidiini).—Entomologica Scandinavica. Supplement 15:33–72.

Evans, M. E. G. 1977. Locomotion in the Coleoptera Adephaga, especially Carabidae.—Journal of Zoology 181:189–226.

Fabricius, J. C. 1775. Systema Entomologiae, &c. Flensburg & Leipzig. 832 pp.

———. 1781. Species Insectorum. Hamburg & Kiel. 1, 552 pp.

———. 1787. Mantissa insectorum. Hafniae. 1, 348 pp.

———. 1792. Entomologia systematica. Hafniae. 1, 330 pp.

———. 1798. Supplementum entomologiae systematicae. Hafniae. 572 pp.

———. 1801. Systema eleutheratorum secvndvm ordines, genera, species adiectis synonymis, locis, observationibvs, descriptionibva. Kiel. 1, 506 pp.

Fall, H. C. 1901. List of the Coleoptera of Southern California with notes on habits and distribution and descriptions of new species.—Occasional Papers of the California Academy of Sciences 8:205–212.

Forel, A. 1891. Histoire naturelle des Hyménoptères. Vol 20. Les Formicides. *In,* Grandidier, A. Histoire physique, naturelle, et politique de Madagascar. Paris. 20(20):1–243.

Forster, J. R. 1771. Novae species insectorum. Centuria I. London. 100 pp.

Frank, J. H. 1971a. Carabidae (Coleoptera) as predators of the red-backed cutworm (Lepidoptera:Noctuidae) in Central Alberta.—Canadian Entomologist 103:1039–1044.

———. 1971b. Carabidae (Coleoptera) of an arable field in Central Alberta.—Quaestiones Entomologicae 7:237–252.

Freitag, R. 1969. A revision of the species of the genus *Evarthrus* LeConte (Coleoptera: Carabidae).—Quaestiones Entomologicae 5(2):89–212.

———. 1979. Carabid beetles and pollution. *In,* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history, and classification. Dr. W. Junk, Publishers, The Hague. pp. 507–521.

Greene, A. 1975. Biology of the five species of Cychrini (Coleoptera: Carabidae) in the Steppe Region of Southeastern Washington.—Washington State Entomological Society 19:1–43.

Haldeman, S. S. 1843. Descriptions of North American species of Coleoptera, presumed to be undescribed.—Proceedings of the Academy of Natural Sciences of Philadelphia 1:298–304.

Hamilton, J. 1893. Descriptions of some species of Coleoptera occurring near Allegheny, heretofore undescribed.—The Canadian Entomologist. London, Ontario 25:305–310.

Hayward, R. 1897. On the species of *Bembidium* of America North of Mexico.—Transactions of the American Entomological Society 24:32–143.

Hentz, N. M. 1830. Descriptions of eleven new species of North American insects.—Transactions of the American Philosophical Society 3:253–258.

Herbst, J. F. W. 1806. Natursystem aller bekannten in und äuslandischen Insekten, &c. Käfer. 285 pp.

Hinton, H. E. 1969. Diffraction gratings in burying beetles (*Nicrophorus*).—Entomologist 102:185–189.

———. 1970. Some little known surface structures. *In,* Neville, A. C., ed. Insect Ultrastructures. Royal Entomological Society, London. pp. 41–58.

Hlavac, T. L. 1971. Differentiation of the Carabid antenna cleaner.—Psyche 78(1–2):51–66.

Horn, G. H. 1885. Contributions to the Coleopterology of the United States. No. 4.—Transactions of the American Entomological Society and Proceedings of the Entomological Section of the Academy of Natural Sciences 12:128–162.

Jeannel, R. 1946–1949. Coléoptères Carabiques de la région Malgache. Parts 1–3. Faune de l'Empire Français, 1146 pp. 1946, Part 1, 6:1–371; 1948, Part 2, 10:373–765; 1949, Part 3, 11:767–1146.

———. 1963. Supplément a la monographie des Anillini (1): Sur quelques espèces nouvelles de l'Amérique du Nord.—Revue Française d'Entomologie 30(3):145–152.

Kavanaugh, D. H. 1977. An example of aggregation in the *Scaphinotus* subgenus *Brennus* Motschulsky (Coleoptera: Carabidae: Cychrini).—The Pan-Pacific Entomologist 53:27–31.

———. 1978. Nearctic species of *Nebria* Latreille Coleoptera:Carabidae:Lebriini): Classification, phylogeny, zoogeography, and natural history. Unpublished PhD dissertation. Department of Entomology, University of Alberta. xlviii + 1041 pp.

Killip, E. P., and S. F. Blake. 1935. Natural history of Plummers Island, Maryland. II. Flowering plants and ferns.—Proceedings of the Biological Society of Washington 48:118–137.

———, and ———. 1953. Natural history of Plummers Island, Maryland. X. Flowering plants and ferns. Supplement 1.—Proceedings of the Biological Society of Washington 66:31–38.

Kirby, W. 1837. Insects—Coleoptera. *In,* Richardson, J. Fauna Boreali-Americana; or the zoology of the northern parts of British America: containing descriptions of the objects of natural history collected on the late northern land expeditions, under command of Captain Sir John Franklin, R. N. Josiah Fletcher, Publisher. Norwich. pp. 1–165.

Kirchner, H. 1960. Untersuchungen zur Ökologie feldbewohnender Carabiden. Dissertation, Cologne.

Koch, D., and H.-U. Thiele. 1980. Zur ökologische-physiologischen differenzierung und speziation der Laufkafer-Art *Pterostichus nigrita* (Coleoptera:Carabidae).—Entomologia Generalis 6(2/4):135–150.

Krogerus, H. 1948. Ökologische Untersuchungen über Uferinsekten.—Acta Zoologica Fennica 53:1–157.

Krombein, K. V. 1964. Natural history of Plummers Island. XVIII. The Hibiscus wasp, an abundant rarity, and its associates (Hymenoptera:Sphecidae).—Proceedings of the Biological Society of Washington 77:73–112.

Laferté-Sénectère, M. F. T. de. 1841. Description de dix Carabiques nouveaux du Texas.—Revue Zoologique pp. 37–50.

Laporte, F. L. 1836. Études entomologiques, ou descriptions d'insectes nouveaux et observations sur la synonymie.—Revue Entomologique 4:5–60.

Larochelle, A. 1971. Notes on *Tachys obliquus* (Coleoptera:Carabidae).—Canadian Entomologist 103:1197–1198.

———. 1972a. Collecting hibernating Ground Beetles in stumps (Coleoptera:Carabidae).—Coleopterist Bulletin 26(1):30.

———. 1972b. Stridulation and flight in some *Omophron*.—Proceedings of the Entomological Society of Washington 74(3):320.

———. 1972c. Observations on the mating periods of some ground beetles (Coleoptera: Carabidae).—Proceedings of the Entomological Society of Washington 74(3):274.

———. 1972d. Collecting hibernating Carabidae under snow.—Proceedings of the Entomological Society of Washington 74(4):473.

———. 1972e. Notes sur les periodes d'accouplement de quelques Carabidae de Quebec.—La Naturaliste Canadien 99:61–63.
———. 1972f. Notes on the food of Cychrini (Coleoptera:Carabidae).—The Great Lakes Entomologist 5(3):81–83.
———. 1972g. Ecological notes on *Bradycellus atrimedius* Say (Coleoptera:Carabidae).—Coleopterist Bulletin 26(1):26.
———. 1973. Ground beetles flying under an electric light (Coleoptera:Carabidae).—Proceedings of the Entomological Society of Washington 75(4):424–427.
———. 1974a. On the habitat of some Carabid Beetles (Coleoptera: Carabidae).—Entomological News 85(7–8):205–207.
———. 1974b. Winter habits of carabid beetles (Coleoptera:Carabidae).—The Great Lakes Entomologist 7(4):143–145.
———. 1974c. The food of Cicindelidae of the world.—Cicindela 6(2):21–43.
———. 1974d. The American toad as champion Carabid Beetle collector.—Pan-Pacific Entomologist 50(2):203–204.
———. 1975a. Notes sur l'activité diurne de quelques Carabidae du Quebec.—Annales de la Societe Entomologique de Quebec 20:3–6.
———. 1975b. Les Carabidae du Quebec et du Labrador.—Departement de Biologie du Collège Bourget, Rigaud. Bulletin I:1–255.
Lawrey, J. D., and M. E. Hale, Jr. 1979. Lichen growth responses to stress induced by automobile exhaust pollution.—Science 204:423–424.
———, and ———. Retrospective studies of lichen lead accumulation in the northeastern United States.—Bryologist 85. In Press.
LeConte, J. L. 1844. Description of new species of North American Coleoptera.—Proceedings of the Academy of Natural Sciences of Philadelphia 2:48–53.
———. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains.—Annals of the Lyceum of Natural History of New York 4:173–474.
———. 1853. Notes on the classification of the Carabidae of the United States.—Transactions of the American Philosophical Society 10:363–403.
———. 1854. Synopsis of the species of *Platynus* and allied genera, inhabiting the United States.—Proceedings of the Academy of Natural Sciences of Philadelphia 7:35–59.
———. 1857a. Synopsis of the species *Clivina* and allied genera inhabiting the United States.—Proceedings of the Academy of Natural Sciences of Philadelphia 9:75–83.
———. 1857b. Catalogue of the species of *Bembidium* found in the United States and contiguous northern regions.—Proceedings of the Academy of Natural Sciences of Philadelphia 9:2–6.
———. 1863a. New species of North American Coleoptera.—Smithsonian Miscellaneous Collections 167:1–86.
———. 1863b. List of the Coleoptera of North America.—Smithsonian Miscellaneous Collections 140:1–49.
———. 1865. Notes on the species of *Harpalus* inhabiting America, North of Mexico.—Proceedings of the Academy of Natural Sciences of Philadelphia pp. 98–104.
———. 1880. Short studies of North American Coleoptera.—Transactions of the American Entomological Society 8:163–218.
Leonard, E. C. 1935. Natural history of Plummers Island, Maryland. II. Flowering plants and ferns.—Proceedings of the Biological Society of Washington 48:118–134.
———, and E. P. Killip. 1939. Natural history of Plummers Island, Maryland. VIII. Lichens.—Proceedings of the Biological Society of Washington 52:23–26.
———, and M. E. Pierce. 1939. Natural history of Plummers Island, Maryland. VII. Hepaticae.—Proceedings of the Biological Society of Washington 52:21–22.

Lindroth, C. H. 1945–1949. Die fennoskandischen Carabidae. Parts 1–3.—Goteborgs Kungeliga Vetenskaps-och Vitterhets-Samhalles Handlingar, Ser. B. 1945, pp. 1–709; 1945, pp. 1–277; 1949, pp. 1–911.
———. 1961a. Skalbaggar Coleoptera.—Svensk Insektfauna 9:3–209.
———. 1961b–1969. The Ground Beetles (Carabidae, excl. Cicindelinae) of Canada and Alaska. Parts 1–6.—Opscula Entomologica, 1192 pp. 1961, Part 2, Suppl. 20:1–200; 1963, Part 3, Suppl. 24:201–408; 1966, Part 4, Suppl. 29:409–648; 1968, Part 5, Suppl. 33:649–944; 1969, Part 6, Suppl. 34:945–1192; 1969, Part 1, Suppl. 35:i + xlviii.
———. 1974. On the elytral microsculpture of carabid beetles (Coleoptera:Carabidae).—Entomologica Scandinavica 5:251–264.
Linné, C. von. 1761. Fauna Suecica, &c. Stockholm. 578 pp.
———. 1767. Systema naturae, editio duodecima reformata 1(2):533–1327.
Mannerheim, C. G. 1843. Beitrag zur Käfer-Fauna der Aleutischen Insiln, der Insel Sitkha und Neu-Californiens.—Bulletin de la Société Impériale des Naturalistes de Moscou 26(1):175–314.
Moore, B. P. 1979. Chemical defense in Carabids and its bearing on phylogeny. *In,* Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history, and classification. Proceeding of the First International Symposium of Carabidology. Dr. W. Junk, Publishers, The Hague. pp. 193–203.
———, and B. E. Wallbank. 1968. Chemical composition of the defensive secretion in carabid beetles and its importance as a taxonomic character.—The Proceedings of the Royal Entomological Society of London (B), 37(5–6):62–72.
Newman, E. 1838a. A descriptive list of the species *Rhysodes*.—The Magazine of Natural History 2(2):663–667.
———. 1838b. Entomological notes.—The Entomologist Magazine 5:372–402.
Noonan, G. R. 1967. Observations on the ecology and feeding habits of adult *Scaphinotus punctatus* LeConte (Coleoptera:Carabidae).—Pan-Pacific Entomologist 43(1):21–23.
———. 1973. The Anisodactylines (Insecta:Coleoptera:Carabidae:Harpalini): Classification, evolution, and zoogeography.—Quaestiones Entomologicae 9(4):267–480.
Olivier, A. G. 1790. Entomologie, ou histoire naturelle des insectes, avec leurs caractères génériques et spécifiques, leur description, leur synonymie et leur figure enluminée.—Coléoptère, vol 2. Paris.
Pearson, D. L. 1980. Patterns of limiting similarity in tropical forest Tiger Beetles (Coleoptera: Cicindelidae).—Biotropica 12(3):195–204.
———, and E. J. Mury. 1979. Character divergence and convergence among Tiger Beetles (Coleoptera: Cicindelidae).—Ecology 60:557–566.
Perrault, G. G. 1973. A taxonomic review of the Eastern Nearctic species complex *Pterostichus* (*Haplocoelus*) *adoxus* (Coleoptera: Carabidae).—Quaestiones Entomologicae 9: 35–40.
Phillips, W. J. 1909. The slender seed-corn ground beetle.—United States Department of Agriculture, Bulletin 85:13–28.
Putzeys, J. A. A. H. 1846. Monographie des *Clivina* et genres voisins, précédée d'un tableau synoptique des genres de la tribu des scaritides.—Mémoires de la Société Royale des Sciences de Liège 10:521–663.
Say, T. 1823a. Descriptions of the Coleopterous Insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long.—Journal of the Academy of Natural Sciences of Philadelphia 3(1):139–216.
———. 1823b. Descriptions of insects of the Families of Carabici and Hydrocanthari of Latreille, inhabiting North America.—Transactions of the American Philosophical Society 2(1):1–109.

———. 1834. Descriptions of new North American insects and observations on some already described.—Transactions of the American Philosophical Society 4:409–470.

Shelford, V. E. 1908. Life-histories and larval habits of the Tiger Beetles (Cicindelidae).—Linnean Society Journal of Zoology 30:157–182.

Spence, J. R. 1979. Riparian Carabid Guilds—A spontaneous question generator. *In*, Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history, and classification. Dr. W. Junk, Publishers. The Hague. pp. 525–537.

Straneo, S. L. 1944. Note sui Pterostichini—IV, Su alcune specie del gen. *Pterostichus* Bon., subg. *Eufteronia* Cas.—Atti della Società Italiana di Scienze Naturali 83:126–130.

Thiele, H.-U. 1977. Carabid Beetles in Their Environment. Springer-Verlag Publishers. New York. 369 pp.

———. 1979. Relationships between annual and daily rhythms, climatic demands, and habitat selection in Carabid Beetles. *In*, Erwin, T. L., G. E. Ball, D. R. Whitehead, and A. L. Halpern, eds. Carabid Beetles: Their evolution, natural history, and classification. Dr. W. Junk, Publishers. The Hague. pp. 449–470.

Valentine, B. D. 1973. Grooming behavior in Coleoptera.—Coleopterist Bulletin 27(2):63–73.

Valentine, J. M. 1935. Speciation in *Steniridia*, a group of Cychrine beetles (Family Carabidae, Genus *Scaphinotus*).—Journal of the Elisha Mitchell Scientific Society 51(2):341–375.

Villa, A. 1833. Coleoptera Europae duplata in collectione Villa. Milano. pp. 1–36.

Weber, F. 1801. Observationes entomologicae, &c. Kiel. pp. 1–116.

Whitehead, D. 1972. Classification, phylogeny, and zoogeography of *Schizogenius* Putzeys (Coleoptera:Carabidae:Scaritini).—Quaestiones Entomologicae 8(3):131–348.

Willis, H. L. 1967. Bionomics and zoogeography of Tiger Beetles of saline habitats in the Central United States (Coleoptera:Cicindelidae).—University of Kansas Science Bulletin 47(5):145–313.

Zimmermann, C. 1869. Synonymical notes of Coleoptera of the United States, with descriptions of new species, from the MSS of the late Dr. C. Zimmermann. (Edited by John L. LeConte, M.D.).—Transactions of the American Entomological Society 2:243–259.

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