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Cover photograph – “Little Ricky” - juvenile dolphin, San Salvador, Bahamas (courtesy of Sandra Voegeli, 2003)

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NOTES AND PROPOSED STUDIES ON THE DARKLING BEETLES (COLEOPTERA: TENEBRIONIDAE) OF THE BAHAMIAN REGION

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ABSTRACT

This study reviews the known literature on Bahamian records of members of the beetle family Tenebrionidae, a large and diverse group of insects. Some background information on the life history, distribution, economic importance, techniques used to collect specimens, and biogeography is presented, in anticipation of future collaborative faunal surveys of the islands. Many new distribution records and undescribed species are represented in museum collections; these and future field collections will be studied in order to document the diversity of the Bahamian region and the faunal relationships among the islands and adjacent lands. Several flightless species have been described from a few of the islands of the Bahamas and are presumed to be endemic; these belong to the genera *Branchus*, *Diastolinus* and *Trientoma*, which are proving to be information-rich for biogeographic analyses. An ongoing study of the systematics of *Branchus* species, all of which are relatively large, burrowing beetles of coastal sandy scrub, suggests that a separate species occurs or will be discovered on islands of each of the historically isolated Bahamian banks.

INTRODUCTION

The fifth largest family of beetles, with approximately 19,000 described species worldwide (Aalbu et al. 2002), Tenebrionidae are a dominant part of many insect faunas, from deserts to rainforests. With a great diversity of body form and size in adult and larval stages (Lawrence and Spilman 1991; Medvedev 1965; Steiner 1995; Watt 1974), tenebrionids have become specialized in many substrates including soil, sand, rotten wood, woody fungi, and nests of other animals (ants, mammals, birds); a few are pests of stored grain and dry food products, and some will eat

lichens and live green plants. Caves and buildings may be inhabited by species which feed on bat guano and other organic material. Most species in forested areas feed either on fungi or rotten wood, but some tree-hole specialists, soil surface and nest scavengers are also represented. Species of desert and dry scrub habitats generally are scavengers living on or in sandy soils under leaf litter. They are often flightless, making them very useful in studies of island biogeography. Even small islands are inhabited by these beetles, which are often endemic to particular islands or island groups. Also of value as ecologic and biodiversity indicators, most are rather specific in habitat "preference" and sensitive to habitat change (Steiner 1999). Sampling techniques to survey their presence and abundance are easy to implement, should future monitoring be desired.

Published catalogs and taxonomic works record few species from the Bahamas but some preliminary island surveys and fieldwork focussed on this group indicate that many new records for the islands and a number of undescribed species are to be found. A study in progress on the Tenebrionidae of Grand Bahama alone has identified 31 species in 20 genera, including two species new to science (Steiner 2004c, ms. in preparation) but fewer than this are currently recorded from the entire Bahamian archipelago (including the Turks and Caicos Islands). Future surveys of other islands will likely yield similar results, as each visit to an island by a specialist targeting a particular group can add new species records (Browne et al. 1993; Morrison 1998). Patterns of distribution among the islands are beginning to emerge.

KNOWN RECORDS

Research on the literature of the Caribbean region's tenebrionid fauna has resulted in a list of

28 species recorded from the Bahama Islands and the Turks and Caicos Islands (Table 1). At least three of these are known to be introduced from other regions but the rest are probably native to the region, and more than half are presumably endemic (not known from outside the Bahamas). This low number of species might be expected, since islands of relatively small average size hold fewer species than do larger ones and mainland areas (MacArthur and Wilson 1967). The low percentage of endemics can also be attributed to the Pliocene inundation of the Bahamas (Browne et al. 1993). In addition, the Bahamas are of low elevation, not more than 65 m a.s.l., and with relatively simple topography (Shattuck and Miller 1905), offering insects fewer habitat types than would mountainous islands (Gillespie and Roderick 2002). However, except for a few monographic works for particular genera of the region, the Tenebrionidae as a whole have never been the focus of research in the Bahama Islands. While the first reported insect from the Bahamas was a small beetle (Elliott 2003), these receive less attention from collectors than do more colorful or larger insects. Even the cosmopolitan pest species of darkling beetles are not yet reported from the Bahamas, but they must certainly occur there.

Several Museum collections in the USA have small samples of Tenebrionidae from the Bahamas that remain unidentified. Preliminary examinations of these, along with current study of the species on Grand Bahama, ongoing analyses of samples from the Turks and Caicos Islands, and new collections made on San Salvador, show that the islands are much more rich than presently known. The scant opportunistic collections by general biological survey work are valuable for historical records and can mark those areas that warrant more sampling, but do not give sufficient collection records for describing species richness for and among islands.

The early Bahamian entomological notes of Wickham (1895) are of interest in that only two species of Tenebrionidae are mentioned, but he implied that others had been found; his collecting activities on the islands primarily used beating and hand-netting during the day, which are not

likely to yield many tenebrionids except for the *Hymenorus* species that he reported. He also notes a species of *Phaleria*, which would have been found under debris on open beaches (Triplehorn and Watrous 1979). However, he must have done some examination of leaf litter above the beach, as a few specimens of other genera taken by him are known (in the collection of the U.S. National Museum), including *Trientoma wickami* Casey (1907) from his samples on Egg Island. *Trientoma* species are all flightless geophiles and have been found in the scrub from the upper edges of the beach to interior sites with loose soils, but not on the open beach (WES, personal observations).

Another brief mention of Bahamian Tenebrionidae in the literature is that of Vaurie (1952) for species collected on the Bimini Islands in 1951, with notes on vegetation and habitats. Only one specific identification is mentioned in the text; with some question, thirteen unidentified species were listed, including 3 Alleculinae and one Lagriinae. Most of these specimens were collected at night on sheets illuminated by lanterns. These collections are in the American Museum of Natural History, New York. Lastly, records from Pigeon Cay, Andros, reported by Anderson (1996) included 3 tenebrionids previously reported from the Bahamas.

HABITAT DIVERSITY AND SPECIFICITY

With the many specializations for feeding and substrates inhabited by darkling beetles, the Bahamian Archipelago offers a wide array of habitats available for their colonization. Some islands offer more variety than others, since they vary greatly in size and to various degrees in other ways, e.g., topography, geological makeup and history, and vegetation cover (Sealey 1994). Nine or ten different plant communities are characterized (Correll 1979; Correll and Correll 1982; Nickrent et al. 1987) for the archipelago, with recognition that not all are to be found on any single island, but multiple zones or "formations" are described for relatively small islands (Coker 1905) and these can be further subdivided by dominant species associations.

Tenebrionid beetles represent trophic groups—the scavengers and fungivores—that are not yet represented among the insect taxa so far studied in the Bahamas. They are more specific to substrates, not host-specific, so are not likely to be tied to the distributions and origins of tree species, as has been postulated for Bahamian Cerambycidae (Browne et al. 1993). They can generally be categorized into two main ecological groups, the geophilous and lignophilous forms, depending on the habitats utilized for larval development. They can often be assigned to either of these at the tribal or subfamily level, e.g. the Opatrinae are all surface scavengers in soil or sand (geophilous), while members of the Coelometopinae inhabit rotten wood (lignophilous). Geophilous species generally inhabit more open, xeric habitats with loose substrates covered by some plant debris; these are often the dominant insects of desert and beach strand communities. Lignophilous species, including those which are host-specific fungus feeders, are most diverse in complex forest ecosystems but will be found in dry scrub forests as well. So, representatives of certain taxa may be present or absent from an island if certain habitat elements are present or not. An island with coastal sand formations as well as forested regions would be expected to not only hold more species but also have better representation of higher taxa. The habitat specificity and other characteristics of darkling beetles probably makes them a group for



Figure 1. Zones of beach strand drift and vegetation provide a variety of sites inhabited by darkling beetles. East Key, Dry Tortugas.

which habitat diversity may be more important than island size in determining species richness on a particular island (Ricklefs and Lovette 1999).

The islands with sand beach strands are proving to have a rich geophilous tenebrionid fauna. The species usually occur in a particular zone of the beach drift or vegetation, forming distinct species assemblages for each habitat zone (Figures 1, 2). Some species are strictly psamphilous and occur only under tidal debris (algal mats, driftwood, carrion) on the open beach, where they may partition themselves in narrow bands of a particular moisture level, either at the recent high tide line or at some dryer zone above it. Other species inhabit the zones of scrub vegetation and may or may not occur in a particular site depending on the amount of vegetation cover, leaf litter layer, soil moisture, depth and composition. The calcareous sand deposits of the Bahamas provide a mosaic of differing substrate deposits and textures due to storm action and sea level fluctuation (Multer 1977; Sealey 1994) and substrate characteristics are known to effect the occurrence, ecology and evolution of tenebrionid beetles (Doyen and Slobodchikoff 1984; Doyen and Tschinkel 1974; Medvedev 1965).



Figure 2. Beach strand shrub zone with an abrupt edge of shade cover on the primary dune crest. East Beach, San Salvador; photo. by J. M. Swearingen.

Geophilous beetles are often found to be most abundant at edges, i.e., the start of the shrub zone at the upper limit of the beach, or the zone of intermediate cover of leaf litter between shaded

ground and open, dry, sunlit gaps in the scrub. Some fossorial species move to varying depths in the sand and may locate near the interface of dry and moist sand. Sand grain size appears to have some effect on species assemblages. On hard clay soil or rocky ground without loose soil or sand, these species will not likely be found, but if there are small pockets of friable soil with moderate plant cover, this may provide enough stable microhabitat in which the larvae can develop.

Small sandy cays with no living vascular plant cover may even support some populations of beetles such as *Phaleria* spp., which apparently require only tidal drift deposits. The establishment of plants on small cays would, however, provide cover and organic material for additional species of psammophiles to colonize. With the island clusters and chains, diversity of island sizes and distances among them, the Bahamas offer opportunities for research on many questions in insular biogeography at many levels (e.g., see Gillespie and Roderick 2002; Morrison 1997, 1998). Patches or small clumps of plants on open sand flats (Figure 3) and localized deposits of sand can be viewed as ecological islands as well. Darkling beetles of low vagility can have restricted populations in such patches of suitable habitat (Doyen and Slobodchikoff, 1984).



Figure 3. Area of sand deposition on a small cay; isolated patches of vegetation collect wind-blown debris and provide "islands" of habitat for psammophilous beetles. East Key, Dry Tortugas.

The islands with pinelands (Figure 4) and tropical hardwood forests would be expected to harbor lignophilous species, including those that feed in the "conks" of woody fungi (Polyporaceae) that grow on dead wood. In members of the latter group, all life stages can be found in the fungal tissue. Adults of the wood-associated species hide during the day under loose bark or in cavities of dead wood and living trees; larvae also may be in these microsites, or tunnel in the wood being broken down by delignifying fungi. Some species only occur in wood of a particular stage of decay or moisture level. Dead standing wood appears to be more rich in species than fallen wood; dead branches on live trees are also utilized. The dry holes in trunks, either elevated or basal, with



Figure 4. Forest interior near Freeport, Grand Bahama.

accumulated loose debris in the bottom, are breeding sites for certain species, particularly some of

the Alleculinae, although many of these live in loose soils or sand (Steiner 1995).

Caves are a common feature in the islands and occur with great variety in all landscapes (Sealey 1994; Shattuck and Miller 1905); those with dry soil and any regular input of organic material, primarily bat guano, can support populations of certain darkling beetles. Caves in Cuba are known to harbor Tenebrionidae (Ardoin 1977) including some endemics known only from single caves, although these lack the characteristics of strict troglobites (Peck et al. 1999).

Human dwellings are inhabited by about 35 species (Spilman 1991) that are considered pests of stored food products, especially cereals, grains, and dried fruits. Most of these have become widely distributed through commerce and many have Old World origins. One notable species, *Ulomoides ocularis* (Casey), feeds in the pods of tamarind (Triplehorn and Weems 1964), which is planted widely in the Bahamas, so the beetle will be expected to occur at any sites where tamarind trees have been established and in stores of the pods.

SAMPLING TECHNIQUES AND SPECIMEN PREPARATION

Collecting and preserving specimens of Tenebrionidae for accurate identification and study can involve the use of many standard entomological techniques (Schauff 2001) but some are more appropriate or effective than others. Use of focussed hand-collecting methods in the habitats mentioned above is preferred, as it will optimize the capture of specimens and provide associated data on their natural history. Insect traps may capture many specimens but will generally not provide specific habitat information nor help in the association of life stages. A combination of trapping devices and techniques along with careful investigation of targeted habitats will provide the most robust results for island surveys, especially when the number of sampling days is limited. For example, a twelve-day survey of Navassa Island (5.2 km²) used such a combination of methods

and detected 541 species of insects among a total of 649 species of terrestrial arthropods (Steiner and Swearingen 2000; Swearingen 1999).

Even short visits of a few hours on small islands can yield important collections of darkling beetles when the most likely microhabitats are targeted. Scratching away the drift or leaf litter layer on sand to expose beetles, or looking under logs, stones, or in rotten wood and fungi are the best ways to find beetles and possibly their larvae and pupae. Notes (and perhaps samples) should be taken to document the type of substrate, host wood or fungus, and other ecologic information.

Most darkling beetles are active at night and the detection of many species can depend on the nocturnal activity of the collector. Beetles can be observed and sampled after dark on tree trunks, fungi, foliage, flowers, beach sand, etc. in such abundance that diurnal collecting, by comparison, may seem not worth the effort. A short-handled insect net is useful for catching falling beetles. This is a common escape tactic of tenebrionids on tree trunks, foliage or other surfaces—they drop to the ground when approached or disturbed (sometimes at flashlight exposure) and run into hiding, or take flight. Quickly positioning the net under the specimen can be crucial to its capture.

Use of black lights is especially effective for obtaining specimens of winged species, and some flightless individuals have been found as “walk-ins” at lights. Most beetles fly during the first hour of full darkness, making it important to have lights operating at dusk for best results. Artificial lights of other types, e.g., florescent lights on buildings, also attract beetles where they can be easily seen on walls and other surfaces. Placement of the light apparatus out of strong wind and in the proximity of source habitats for the beetles will increase the probability of captures. Edges or gaps in forest or scrub where visibility of the light across a broad area is possible are generally good sites. Light traps work well but catch many non-target insects (but this may be preferred if general survey collections are the goal). A light against a vertical white sheet hung over other sheets on the ground is preferred, as it allows selective capture

and preservation of specimens. Ground sheets are important because many small beetles land on the ground beneath the light and would go unseen.

Bait trails set out before dark can be used to attract the geophilous tenebrionids. A line of sprinkled corn meal or rolled oats across an open area of sand or other bare ground will intercept walking beetles, stopping to feed; specimens can be found on periodic examination by flashlight.

When several days or more can be spent at a single site or island, it is generally worthwhile to set traps of various kinds, which can be monitored daily or be picked up at the end of the sampling period. Pitfall traps made from nested plastic cups or bowls, inexpensive and light weight equipment, have been shown to be useful for sampling the geophilous Tenebrionidae. They can be placed in transects through the coastal scrub zones and so be informative as to habitat specificity. A few cm of sea water with a few drops of detergent in each trap will quickly drown insects; daily straining of the trap catch, rinsing of specimens, and preservation in ethanol is recommended.

Malaise traps and flight-intercept traps are somewhat productive for tenebrionids, especially the active, winged Alleculinae, some of which may be day-flying and so would be less likely to be found at night lights. The equipment is relatively light-weight, can be set up with little time and effort, and can obtain diverse samples of many insect orders in a short time. Pan traps can be placed along or under the mid-wall of the Malaise trap so as to capture beetles less likely to fly or climb upward to the trap bottle, but that drop into the pans of soapy saltwater. The preferred type of the Malaise trap is that of Townes (1972) because beetles are far more likely to be captured by this design; they are able to crawl up the fabric to the lateral entrance of the trap bottle and fall in, whereas the other type of bottle, with smooth horizontal or vertical funnels, probably prevents many beetles from being captured.

Ethyl acetate is the preferred killing agent for tenebrionid specimens. They can be left in the vials (containing absorbent tissue moistened with

the solvent) overnight, then transferred to 70-80 per cent ethanol for storage or transport. This also aids in "degreasing" specimens; darkling beetles, especially those from arid environments, have fat and oils in the body that often coat and discolor specimens as they dry. Several changes of ethanol during the following weeks (or perhaps years!) leading to final preparation will help leach out these oils; an initial preservation in a mixture of ethanol and small fraction of ethyl acetate will speed this process. Appendages of specimens are then more easily manipulated for mounting, and dissections of genitalia, often essential in specific identification and description, will be facilitated by this. If no ethyl acetate is available, direct preservation in the ethanol is next best, but beetles take longer to be killed and often die with wings open and appendages in stiff, unnatural positions. However, if future molecular studies are desired, some specimens should be initially preserved in ethanol (95 per cent) and not in ethyl acetate.

Larvae and pupae can be killed in ethyl acetate as well, but it is important to not leave them in the vial for more than an hour or two, as they become very soft and deformed. To avoid this and discoloration, placement briefly in boiling water is the preferred killing method for larval stages, then the specimens are preserved and stored permanently in ethanol. A pupa should have the associated larval skin (if found) kept and preserved with it.

Dry-mounting of adult Tenebrionidae uses standard techniques for pinning or pointing (Schauff 2001), but some special handling for certain ones should be noted. The Alleculinae are particularly fragile and should be pointed, not pinned, except for the very largest members, e.g., *Lobopoda* more than 12 mm long. For other groups, specimens up to about 8 mm should be pointed, and if the beetle is larger but slender-bodied, pinning should be avoided. Pinning of any small specimens can be very damaging as most tenebrionids have a hard exoskeleton; the pin may fracture the elytron and/or metasternum and the handling may break off appendages. Important taxonomic characters are often on the antennae and legs, which should be disentangled and posi-

tioned away from the body surface. Points can be trimmed to a truncated tip to match the space between the right middle and hind coxae, where the glue contact should be. Careful pointing without obscuring the ventral midline (Figure 5) of the beetles will aid identification.

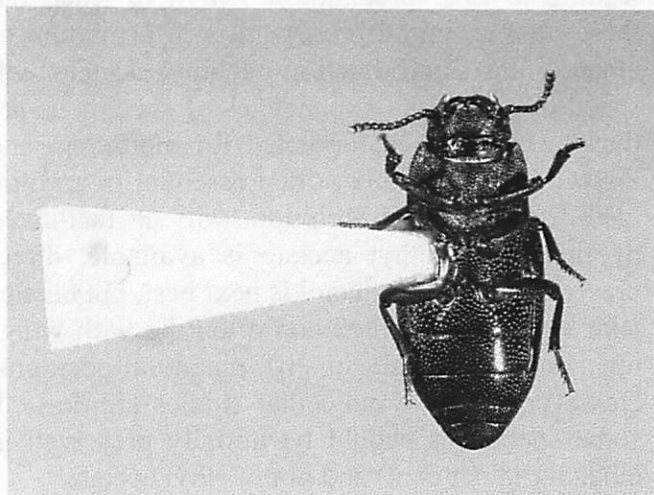


Figure 5. Underside of a point-mounted *Trientoma* sp., length 5.5 mm, showing proper position of point and glue contact.

When pinning beetles, prior alignment of the pin's path through the beetle is needed. Because many tenebrionids lack flight wings, the metathorax is shorter, with less room for the pin to properly exit between the middle and hind coxae (Figure 6). This often results in the pin exiting through the base of the abdomen or through the hind coxa and loss of the leg. Starting the pin entrance at a more lateral position, half way between the suture and lateral edge and at about the basal quarter or fifth of the right elytron, will reduce specimen damage.

Proper and prompt labeling of specimens is of utmost importance, especially when field trips include visits to many small islands during a short period and there is a likelihood of confusing localities. On temporary "field labels" as well as permanent museum specimen labels, the name of the island or cay is essential, followed by more detail, e.g., "western end" or "East Beach" and the

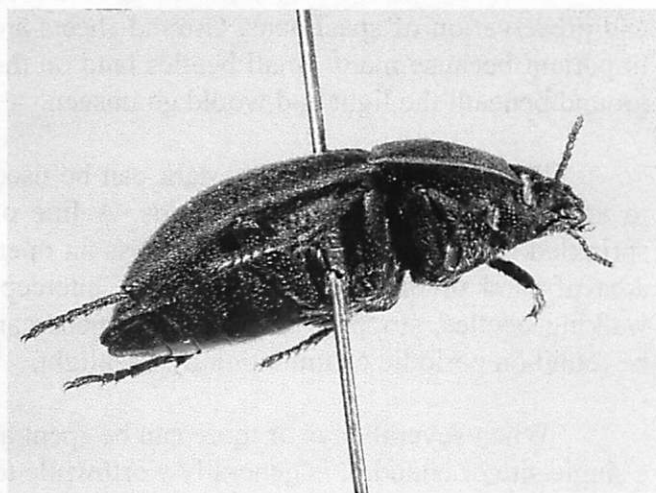


Figure 6. A specimen of *Branchus* sp., length 13 mm., showing proper position of the pin between the right meso- and metacoxae.

geographic coordinates of the site. If the locality is a small offshore cay, the name of it should be preceded by the name of the main associated island or island group.

DISTRIBUTION PATTERNS AND NOTEWORTHY TAXA

The nearest other land masses are to the south (Cuba and Hispaniola) and west (Florida) of the Bahamas, so it is logical to assume that these species-rich mainland (Peck and Thomas 1998) and large island (Blackwelder 1945) countries would be the primary sources of species that have colonized these islands. At the periphery of the West Indian region, the Bahamas are a terminus of distribution for species and higher taxa that display a "North American-Caribbean track" (Rosen 1976) of distribution. Studies of certain groups show that Bahamian insects are generally a subset of the faunas of either Cuba or Florida, or of the West Indian fauna in general. Examples of these include the Carabidae (Erwin and Sims 1984), Carabidae of the genus *Platynus* (Liebherr 1988), scaritine Carabidae (Nichols 1988), Formicidae (Morrison 1998), Cerambycidae (Browne et al. 1993), Halictidae (Eickwort 1988), Lygaeidae (Slater 1988) and the Tenebrionidae of the subfamily Alleculinae (Campbell 1971). Ex-

cept for the latter taxon, they often are represented by very few or no Bahamian endemics.

There are no endemic genera of insects known thus far from the Bahamas, and the few endemic species, e.g., among the longhorn beetles (Browne et al. 1993) and ants (Morrison 1998), generally belong to large and widespread genera. As discussed by these authors, this can probably be attributed to Pliocene submergence of the islands, their small size, low elevation and aridity when compared to the lands adjacent to them. Most of the members of the taxa studied are fully winged and so might be expected to be more vagile and widely distributed. The geophilous Tenebrionidae, however, being durable and long-lived xerophiles and able to colonize small patches of habitat, appear to have proliferated to a greater degree than have other insect groups in the Bahamian region.

Two genera of Alleculinae occur in the Bahamas and the great majority of the species are endemic (Campbell 1971). This seems unusual since they are all flying forms, but having functional wings does not necessarily indicate a greater dispersal ability (Gillespie and Roderick 2002). Members of one subgenus of *Lobopoda* are known only from Cuba and the Bahamas but with no species in common (Campbell 1971), indicating a close but isolated historical relationship between the two faunas. The more speciose genus *Hymenorus* also has four known Bahamian endemics (plus two undescribed ones, single specimens) and three others that occur in Florida and Cuba; one is said to have spread into Florida from the Bahamas (Campbell 1971). The variation in specimens of both genera from different islands described by Campbell suggests that isolates may be in the process of divergence.

All of the known members of the genera *Branchus*, *Diastolinus* and *Trientoma* lack flight wings and the elytra are at least partially fused. The three taxa are widely distributed in the West Indies and all species show a high degree of island endemism (Marcuzzi 1984) including those in the Bahamas. All are in need of systematic revision, and the generic status of *Diastolinus* is uncertain.

However, the Bahamian members of each appear to belong to single clades and may prove to be among the most information-rich beetles for studies of dispersal, speciation and other patterns among the islands.

Branchus beetles (Figure 7) are relatively large (to 15 mm long) burrowing forms that inhabit sandy scrub habitats. They are likely the largest native darkling beetles of the Bahamas, but *Branchus* specimens are not common in collections and rarely encountered in the field because of their secretive habits and specific habitat requirements. Sites where beetles occur appear to be usually limited to a narrow band of dune strand, generally on the back slope of the primary dune or the swale behind it, where dense scrub covers deposits of deeper, loose, rather coarse sand. The presence of spider lily, *Hymenocallis* spp., is a good indicator of suitable *Branchus* habitat. This zone is, however, often difficult to sample and study simply because of the hazardous vegetation, which includes the toxic *Hippomane*, *Metopium*, and thorny tangles of *Caesalpinia*.

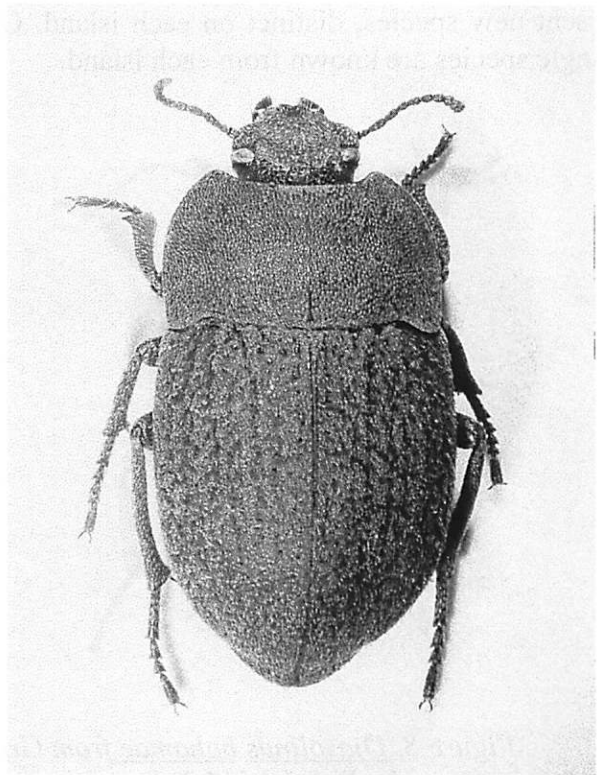


Figure 7. A *Branchus* sp. from Grand Bahama. Length of beetle, 13 mm.

Bahamian species of *Branchus* belong to the "floridanus group" (Steiner 1991), considered to be the most derived complex of species. With a revision of the genus in progress, some patterns of distribution are becoming clear as more material can be collected. Specimens of this group of *Branchus*, most representing undescribed species, are known from the Cayman Islands and Cuba eastward to the Turks and Caicos Islands. The type-species, *Branchus floridanus* Leconte is known from Miami to Key West, Florida (Triplehorn and Weems 1964). Described from New Providence, *B. woodi* LeConte (1866) appears to be represented on other islands of the Great Bahama Bank. It was also reported from Cuba based on a tentative identification by Spilman (1961), but Cuban specimens apparently belong to a separate species (Marcuzzi 1998; Steiner, personal observations). A new species is being named from Grand Bahama and Abaco, both of the Little Bahama Bank (Steiner 2004c, ms. in preparation) and the few known specimens of *Branchus* from other islands so far examined, e.g., San Salvador, Conception, Grand Turk and Providenciales, represent new species, distinct on each island. Only single species are known from each island.

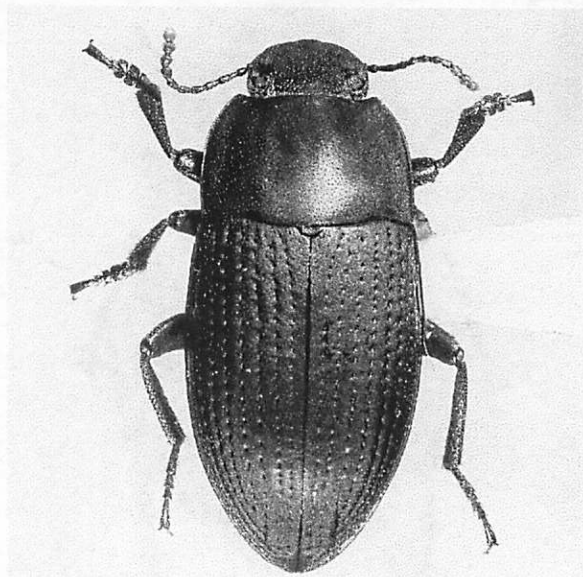


Figure 8. *Diastolinus bahamae* from Grand Bahama. Length of beetle, 7.5 mm.

Three species of *Diastolinus* (Figure 8) have been named from three Bahamian islands

(Marcuzzi 1965) and so far, each appears to be endemic to those islands (Table 1). Other material known in collections warrants more study. At least two species, probably undescribed, were discovered on San Salvador (during the course of this conference and seen in the collection of the Gerace Research Center). It is likely that members of this clade will show some patterns of speciation among islands, more so than the closely related *Blapstinus* species which can be fully winged.

Specimens of *Trientoma* under study from the Turks and Caicos Islands represent at least two species (Figure 9); these are distinct from *T. wickhami* from Egg Island (north of Eleuthera). On each of the two islands sampled so far, a small, punctate species co-occurs with a larger, smooth one; some differences in the microhabitats of each have been noted. Other islands probably harbor additional species that await discovery.

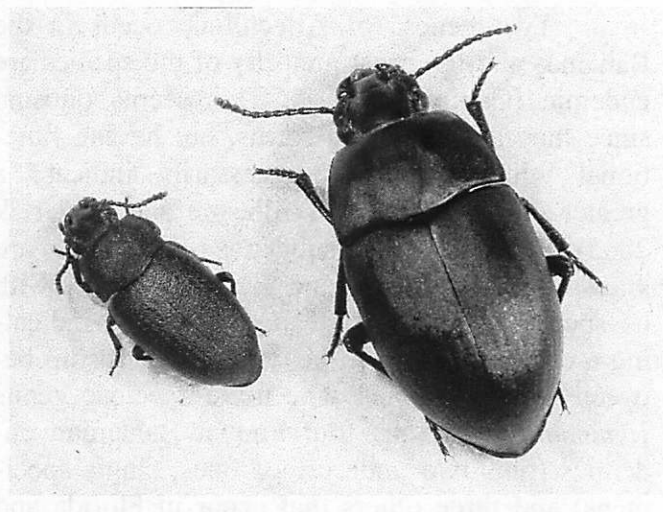


Figure 9. Two undescribed species of *Trientoma* from Providenciales. Length of beetles, left to right, 5.5 mm and 8.2 mm.

These and specimens of *Diastolinus* generally co-occur under leaf litter in the shrub scrub zones of coastal dunes and on sandy deposits inland. With thorough comparative and cladistic reviews, species in these genera and also the Bahamian *Branchus* will likely be found to have sister taxa in Cuba and possibly southern Florida. In the Turks and Caicos Islands, the possibility of sister taxa on nearby Hispaniola should be considered.

Undescribed species of the tribe Helopini are known from many Caribbean islands. Generic placement is unclear at present; absence or presence of flight wings has been used as a generic character, but it is apparent that single clades have members with either condition. The Bahamian members could be tentatively placed in *Nautes*, with more than 20 named Central American species and 3 from Cuba (Blackwelder 1945). One variable species is known to occur in Florida, Cuba, and Grand Bahama (Steiner 2004, ms. in preparation) and specimens of others are known from several other islands. Species of the northern "pine islands" are fully winged while those of the smaller scrub islands of the southern region appear to be flightless (Figure 10). This will be another useful group with which to study island biogeography.

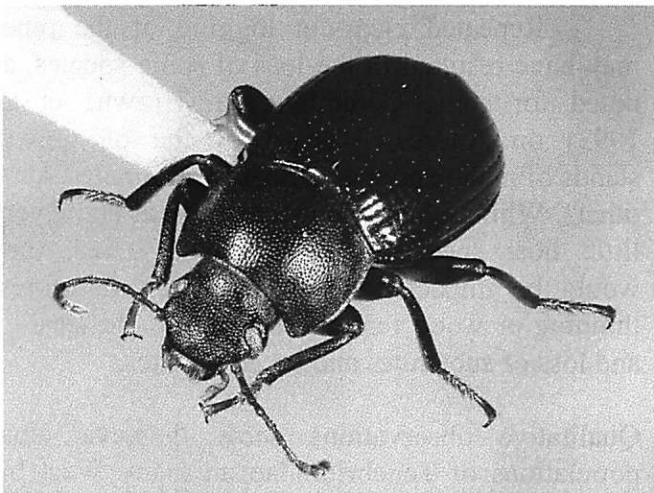


Figure 10. An undescribed member of the Helopini from Providenciales. Length of beetle, 6 mm.

Patterns of the distribution of flightless species in these groups are beginning to show a marked correlation to the geography of the "banks" (Shattuck and Miller 1905), elevated limestone platforms which were exposed at lower sea levels during the last glaciation (Olson and Pregill 1982; Pregill and Olson 1981) and this has been recognized as crucial to the understanding of insect species distributions, e.g., by Browne et al. (1993). Islands of the Great Bahama Bank, all interconnected as "Paleoprovidence" during the

Pleistocene, might be expected to share the same species, while the smaller banks and isolated islands with no historical land bridges (e.g. San Salvador and Conception) each have distinct endemic species, as suggested by the observations on *Branchus* made so far. These are probably the products of founder events as summarized by Gillespie and Roderick (2002).

The Bahamas are "Darwinian islands" (Gillespie and Roderick 2002) in having never been connected to neighboring lands that are the probable sources of their biota. The archipelago has islands of two different geological origins, the southern islands being remnants of a Cretaceous volcanic island arc, and the northern islands, an exposed part of continental shelf, and this may have influenced colonization (Browne et al. 1993). During the last glaciation, islands were closer to each other (or connected on the northern banks); Paleoprovidence was much closer to Cuba and Florida, facilitating overwater dispersal. The most likely dispersal method for tenebrionids is rafting, but the smaller winged forms may have arrived as "aerial plankton" (Peck 1991). Habitats available for colonization during this period probably favored the establishment of the xerophilous geophiles and not the forest species, which are probably more recent arrivals and have not undergone much divergence from source populations.

Pregill and Olson (1981) stressed the importance of xeric climatic conditions since the Pleistocene, with evidence that many endemic extant vertebrates in the Bahamas are relictual xerophiles. Flightless geophilous Tenebrionidae in eastern North America also have relictual post-Pleistocene distributions in coastal beach strands and inland barrens (Steiner 1999) and this may be the case for many island species. The smaller, drier islands of the southeastern Bahamian region appear to be as rich (if not more so) in geophilous species as the larger islands of the Great and Little Bahama Banks. This is the case with the herpetofauna (Pregill and Olson 1981) but these authors used fossil evidence, not available for Bahamian Coleoptera, to support their palaeoclimatic and relictual distribution picture. They note that the

smaller islands and rain-shadow areas of the larger Antillean islands have remained xeric through the climatic changes of the Pleistocene, so the beetle faunas may be represented by very old faunal elements as well as relatively recent island colonists, not relicts. Historically xeric parts of Cuba, for example, may be a source of ancestral forms that colonized the Bahamas and then differentiated at the species level on each of the isolated banks as autochthonous elements.

The larger islands of the Great and Little Bahama Banks were formerly larger, at times contiguous, and more xeric with open savanna and scrub woodland over vast low areas (Olson and Pregill 1982; Pregill and Olson 1981), offering xerophile insects more area of suitable habitat. Dominated by pine forest during relatively recent times, these islands would likely have xerophiles now restricted to coastal sands. These can be considered relictual in a local sense. The relatively mesic interior forest habitats would be colonized by widespread, vagile species (winged, mostly lignophilous beetles) and this has been the case among the assemblages noted on Grand Bahama (Steiner 2004c, ms. in preparation). Shifts in the abundance and range of xerophiles and moist forest species of island tenebrionids can be indicators of climate change (Geisthardt 2003).

Non-native species and inter-island introductions can confound zoogeographic analyses and their recognition is imperative. As knowledge of the faunas of lands adjacent to the area in question can be gained, oddities can often be identified. The Bahamian tenebrionid fauna is so far known to include adventive elements from the Old World (Steiner 2004a, 2004c, ms. in preparation; Triplehorn 1965), from South America (Steiner, unpublished data), and one of probable Antillean origin and recently detected as a "weed species" (Steiner 2004b, in press). Human travel to and among islands is the most likely dispersal agent for many of these species; maintenance of disturbed habitats around dwellings can aid their colonization.

HABITAT THREATS AND CONSERVATION

The flightless geophilous darkling beetles, with unique island endemics, are perhaps the most scientifically interesting and valuable elements of the Bahamian insect fauna. Unfortunately, they are among the most threatened of those elements. Their habitat specificity predisposes them to loss via a number of anthropogenic impacts. Beach strands and the higher dunes and swales behind them hold the greatest diversity of these specialized insects and these are the areas that are first and most occupied by humans. Coastal roads are often placed along these narrow strands, obliterating entire habitat zones from islands. Clearing of the vegetation among dwellings removes native cover and food sources, exposes the sand to rapid heating and drying through insolation, and opens areas to colonization by exotic species.

Repeated clear-cut logging of the pines may have resulted in the loss of some species, as noted for some Cerambycidae (Browne et al. 1993) on Andros. Harvest of the old-growth stands of mahogany has probably eliminated some others. While lignophilous tenebrionids show very little host specificity to particular trees, they would be impacted by the changes that forest thinning or wood removal brings, i.e. desiccation and loss of substrates and breeding sites.

Qualitative observations show, however, that populations of Tenebrionidae on many West Indian coasts are more greatly impacted by the spread and dominance of the exotic Australian pines (beefwood), *Casuarina* spp., which rapidly shade out and replace the diverse native strand vegetation (Steiner 1991). No beetles have been found living under the thick mats of *Casuarina* "needles" (Figure 11) but usually occur at the edges of stands if some native shrubs remain on sites with exposed soil. The introduction of this plant may have caused or will lead to the extinction of some species on islands, as it eliminates diverse ecologic communities in their entirety. Fortunately, the more xeric islands seem to be less impacted.



Figure 11. Shade and the thick mat of *Casuarina* branchlets has eliminated nearly all other beach strand vegetation. Loggerhead Key, Dry Tortugas; February 1989.

Seedlings spreading from planted *Casuarina* trees were first noted on Eleuthera and New Providence a century ago (Coker 1905); the resultant displacement of the native vegetation seen today is an abomination. Stands on small uninhabited cays demonstrate that plants can disperse and become “naturalized” on their own. No recent collections of *Branchus woodi* from New Providence have been seen. The threat to biodiversity, invasiveness, effects on coastal erosion, and other aspects are well documented (Hammerton 2001; Sealey, This Volume), but eradication of the trees is controversial and expensive.

A conservation strategy for these beetle species should include the preservation of at least some small section of each beach shoreline on islands, including the back-dune swales and crests, with periodic monitoring and removal of exotic plants. In degraded areas, restoration may be prudent if pockets of native vegetation and species of concern are found to be present. Raking and removal of beach drift and leaf litter beneath trees is a common daily practice at beach front resorts; these activities should be prevented in “off-limits” areas so that the full assemblage of maritime habitat zones and insect faunas is not impacted.

FINAL REMARKS

Compared with remote, ancient, oceanic archipelagoes that receive more attention from collectors and biogeographers, the Bahamas have been much neglected. The native Tenebrionidae of these relatively young islands, however, offer great promise for future mapping and understanding of zoogeographic patterns and vicariance among species on islands. Building and maintaining well-prepared and documented collections of these beetles from as many islands as possible will be paramount to this research. Their inclusion in any future island biodiversity surveys is strongly encouraged, as is the preservation of their native habitats.

It is not unreasonable to make the prediction that other new species will be discovered on islands not yet sampled, and even on relatively well-studied islands. Nearly all of the treatments of Bahamian insects cited above make clear the need for more sampling, and repeated visits to islands by specialist collectors continue to add new records. The Tenth Symposium on the Natural History of the Bahamas marked the one hundredth anniversary of the start of the surveys by the Geological Society of Baltimore in June of 1903 that produced the keystone descriptive work, “The Bahama Islands” (Shattuck 1905); it has been nearly three hundred years since the explorations of Mark Catesby (Coker 1905; Elliott 2003) and more than five centuries since Columbus made landfall on San Salvador, yet new entomological studies in the Bahamas demonstrate that the age of discovery is certainly not over.

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Table 1. Tenebrionidae recorded from the Bahama Islands.

| Species | Known Distribution | Source |
|--|------------------------------------|---------------------------|
| <i>Trientoma wickhami</i> Casey | “Bahama Islands (Egg Island)” | Casey 1907 |
| <i>Branchus woodi</i> LeConte | “New Providence, Bahamas” | LeConte 1866 |
| <i>Diastolinus bahamae</i> Marcuzzi | Grand Bahama | Marcuzzi 1965 |
| <i>Diastolinus dozieri</i> Marcuzzi | Grand Turk | Marcuzzi 1965 |
| <i>Diastolinus kulzeri</i> Marcuzzi | Mayaguana | Marcuzzi 1965 |
| <i>Blapstinus cubanus grand-turki</i> Marcuzzi | Grand Turk | Marcuzzi 1965 |
| <i>Blapstinus fortis</i> LeConte | “Bahamas” | Marcuzzi 1984 |
| <i>Phaleria picipes</i> Say | Rum Cay; South Bimini | Triplehorn & Watrous 1979 |
| <i>Phaleria punctipes</i> LeConte | 7 islands listed | Triplehorn & Watrous 1979 |
| <i>Phaleria testacea</i> Say | 6 islands listed | Triplehorn & Watrous 1979 |
| <i>Trachyscelis aphodioides</i> Latreille | Turks and Caicos Islands | Steiner 2004a (in press) |
| <i>Adelina bidens</i> (Schaeffer) | South Bimini | Vaurie 1952 |
| <i>Diaperis maculata</i> Olivier | “Bahama Islands: Nassau” | Triplehorn 1965 |
| <i>Neomida bicornis</i> Fabricius | “Bahama Islands: Andros” | Triplehorn 1965 |
| <i>Ulomoides ocularis</i> (Casey) | “Bahama Island: Nassau” | Triplehorn 1965 |
| <i>Glyptotus cribratus</i> LeConte | “Bahamas I.” | Marcuzzi 1984 |
| <i>Lobopoda androsi</i> Campbell | Andros, New Providence | Campbell 1971 |
| <i>Lobopoda bahamensis</i> Campbell | Andros, Eleuthera, South Bimini | Campbell 1971 |
| <i>Lobopoda cordata</i> Campbell | Mayaguana | Campbell 1971 |
| <i>Lobopoda nesiotica</i> Campbell | Andros, G. Bahama, Gt. Abaco | Campbell 1971 |
| <i>Hymenorus bahamensis</i> Campbell | 15 islands listed | Campbell 1971 |
| <i>Hymenorus convexus</i> Casey | 33 islands listed | Campbell 1971 |
| <i>Hymenorus densus</i> LeConte | 14 islands listed | Campbell 1971 |
| <i>Hymenorus farri</i> Campbell | Andros, G. Bahama, San Sal., Provo | Steiner 2004b (in press) |
| <i>Hymenorus insularis</i> Campbell | Long Cay; Crooked Island | Campbell 1971 |
| <i>Hymenorus minutus</i> Campbell | Crooked Island | Campbell 1971 |
| <i>Hymenorus pygmaeus</i> Campbell | West Caicos | Campbell 1971 |
| <i>Hymenorus transversus</i> Campbell | 5 islands listed | Campbell 1971 |