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**FLIGHTLESS BEETLES ON ISLANDS:
DISTRIBUTION AND LIFE HISTORY OF DARKLING BEETLES
OF THE GENUS *BRANCHUS* (COLEOPTERA: TENEBRIONIDAE)**

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ABSTRACT

Darkling beetles of the genus *Branchus* LeConte are flightless, each of the known species often being restricted to localized ecologic islands, semi-arid areas from Panama to southern Texas, and eastward through the Greater Antilles and southern Florida to the Turks and Caicos Islands. Species are proving to be unique to each island or bank of islands. The majority of known morphospecies in collections are represented by single or very few specimens, and many remain to be described. The known aspects of the life history of these secretive beetles are summarized, with notes on the larval and pupal stages, habitats, and threats to the survival of species.

INTRODUCTION

Darkling beetles (Tenebrionidae) of the American genus *Branchus* LeConte, with a nearly circum-Caribbean distribution, are all flightless soil-dwellers and have proven useful in studies of island biogeography in the Bahamas (Steiner 2006b). With two other closely related Central American genera they are placed in the Tribe Branchini of the Subfamily Pimeliinae (Aalbu et al. 2002; Matthews et al. 2010), but have been included as a subtribe in the closely related Coniintini (Doyen 1984).

Branchus specimens are not common in most museum collections, making systematic work on them difficult, especially because many are known only from single or very few specimens. Rarity is probably due to their restricted occurrence in habitats of loose sandy

soil “pockets” in narrow zones of suitable places which are often difficult to access or sample by collectors, such as dense coastal scrub vegetation dominated by thorny or poisonous plants, e.g., *Acacia*, *Caesalpinia*, *Hippomane* and *Metopium*. In addition, beetles are typically hidden under leaf litter and “play dead” when first exposed, and the soil encrustation makes specimens cryptic (and perhaps a not-so-appealing target to non-specialist collectors).

There are so far only 8 described *Branchus* species, but at least 20 other distinct undescribed forms are known. The closely related genera *Anectus* Horn, described from Honduras, and *Oxinthas* Champion from Mexico are monotypic at present, but several different forms of *Oxinthas*, probably representing additional species, are known in collections. Relationships among the three genera need study and it may be that synonymy and/or “splitting” of genera will be warranted.

DISTRIBUTION OF KNOWN SPECIES

Branchus specimens available for study show that members of the genus, including undescribed forms, occur from mainland Panama to southern Texas and Florida, USA, and on islands of the Caribbean (Greater Antilles and their associated smaller cays) and the Bahamian archipelago, but have not been found on Puerto Rico nor any of the Lesser Antilles, northern South America and associated islands (even though suitable habitats are available in many locations). The genus displays a “North American-Caribbean track” (Rosen 1976) of distribution, perhaps supporting the idea that the relatively primitive mainland forms

(Steiner 1991) dispersed eastward, colonizing islands probably by rafting on storm debris, and gave rise to the more derived forms of the Caribbean region. The 8 described *Branchus* species, listed by chronology of their publication, are:

- B. floridanus* LeConte, southern Florida and keys;
- B. woodi* LeConte, Great Bahama Bank;
- B. obscurus* Horn, Costa Rica to Honduras;
- B. opatroides* Champion, Mexico;
- B. jamaicensis* Marcuzzi, Jamaica;
- B. whiteheadi* Steiner, southern Texas;
- B. saxatilis* Steiner, Grand Bahama and Abaco;
- B. geraceorum* Steiner, San Salvador, Bahamas.

Mainland Species

From a localized dry forest area in Coclé Province, Panama, is an undescribed *Branchus* (Figure 1A) so far known only from a series collected by the author. With very rough and complex dorsal sculpture and less globular body form, the species was first mistaken for a member of the Asidini, but the apical (11th) antennomere is not reduced and recessed into antennomere 10, an important diagnostic feature of that tribe. Beetles were found under loose-leaf litter in depressions in dry sandy soil, in open edges and gaps among shrubs and small trees.

Branchus obscurus (Figure 1B) is fairly common in collections from dry forest areas of Costa Rica, Nicaragua and Honduras. Specimens are 12-15 mm long and vary in shades of brown to gray from site to site due to the color of the soil encrustation. A similar undescribed species is known in series from the semiarid areas of El Progreso, Guatemala, but has raised, polished lines on the elytra. Two other smaller Guatemalan species are represented by one and two specimens each: one beetle, exact origin unknown, was intercepted at Miami, Florida with a shipment of bromeliads; it is not soil-encrusted and has faint stripes of brown and black on the elytra; a pair of broadly

oval, finely scaled specimens is known from Sacatepequez, Cerro Alux.

In Mexico, several undescribed forms are present but each is represented by single or very few specimens. Most are small and robust with varying degrees of rough sculpture, belonging to the “*opatroides* group” (Steiner 1991) of species; *B. opatroides* was described from Veracruz and Jalisco. Among the smallest (6-8 mm long) of *Branchus* species, *B. whiteheadi* from southern Texas (and probably northern Mexico) belongs to this group. One species from Quintana Roo, however, known from a unique male, has some characters that place it in the “*floridanus* group”, most notably the lateral projections near the apex of the tegmen (see Steiner 2005a, 2006a).

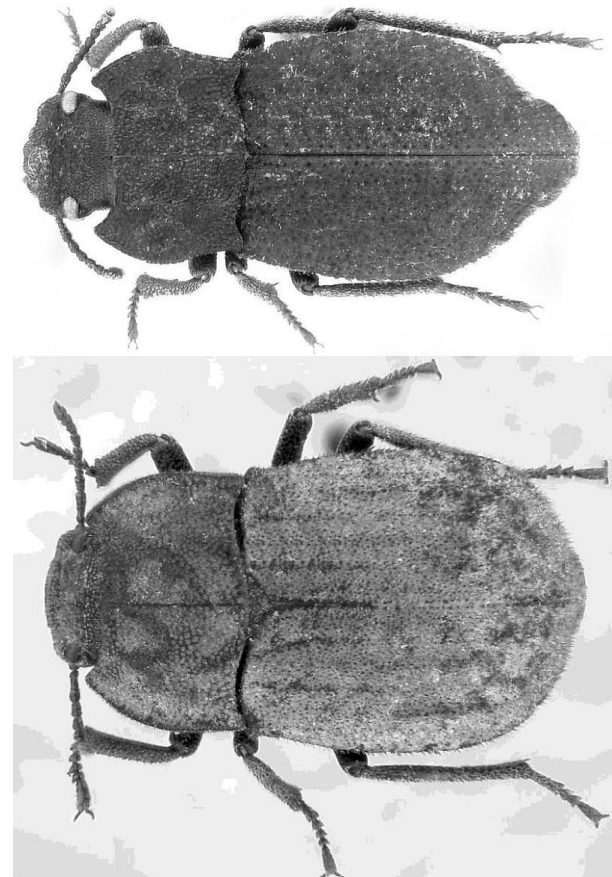


Figure 1A and B. A (upper), an undescribed *Branchus* from Panama; length of beetle, 13 mm. B (lower), *Branchus obscurus* from Costa Rica; length of beetle, 14 mm.

Branchus floridanus (Figure 2), the type-species, is endemic to southern Florida and has been considered rare in collections (Blatchley 1932; Triplehorn and Weems 1964), although soon after publication of the latter paper, the first author reported finding many specimens active during the day, crossing sidewalks and paths on Key West in April (C. A. Triplehorn, personal communication), suggesting that some *Branchus* can be locally abundant, but remain hidden until certain seasonal conditions trigger an event of “dispersal”. It is known from coastal localities in the Florida Keys and north along the Atlantic coast to Haulover Beach north of Miami and also the beach strand scrub at Cape Sable (W. Steiner, unpublished data). Beetles and associated larvae occur in rather coarse coral sand and may burrow several cm. deep under leaf litter accumulated at forest gap edges and in small depressions.

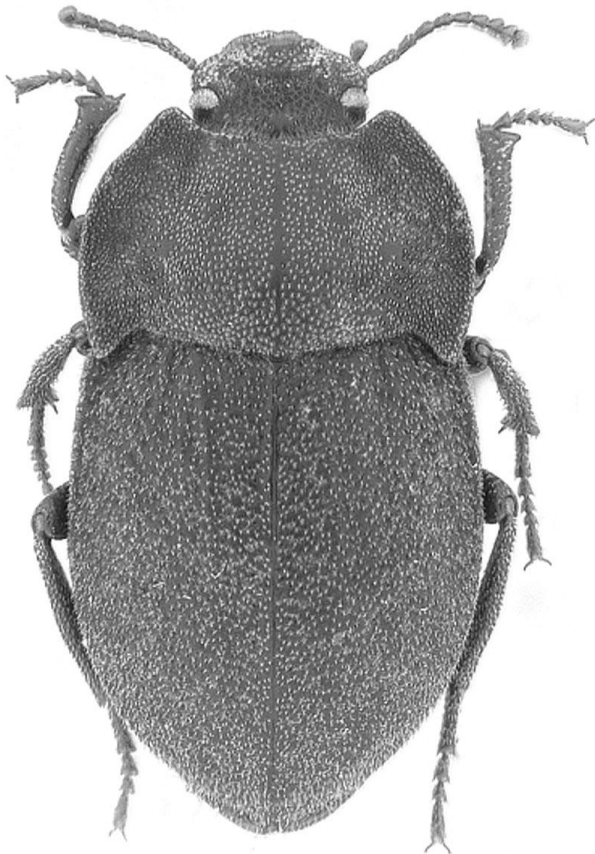


Figure 2. *Branchus floridanus*, specimen from Big Pine Key; length of beetle, 14 mm.

Antillean Species

Two species groups are represented in the Greater Antilles and associated smaller islands. Jamaica, the Swan Islands and Navassa each hold separate species which appear to be close relatives, all with similar male genitalia, the apex of the tegmen narrowly rounded and bifid (see Steiner 1991, Figs. 7 and 12), probably near or within the “*opatroides* group.” The only described form among them is *Branchus jamaicensis*, known from the dry coast of the Kingston area, but specimens at hand from the Morant Cays, about 50 km SSE, have slight differences in dorsal sculpture and scale-like setae and possibly represent a distinct species. Known from 5 specimens collected in 1929, the species from Swan Islands has more sulcate elytra, head and pronotum more distinctly contoured. Many more specimens of the Navassa species are available via the recent surveys of that island (Steiner and Swearingen 2000; Swearingen 1999); they are similar to *B. jamaicensis* but more broadly oval and with elytra carinate-sulcate.

The Cayman Islands, Cuba and Hispaniola are inhabited by members of the “*floridanus* group.” On each of the three Caymans lives a distinct form tentatively regarded as separate species: The Grand Cayman one has polished, broken ridges on the elytra while specimens from Little Cayman and Cayman Brac are only scaly, similar to *B. floridanus*. So far the only known specimens from Brac, a legless corpse and hind-body, do not provide enough material to assess species-level characters, but subtle differences in surface sculpture and setae are evident.

Specimens from Cuba are known from only a few singletons, some in poor condition (probably collected as corpses) and some not available for study. Two taxa have been listed from Cuba (Peck 2005) but there are problems: The record of *B. woodi* LeConte (Spilman 1961) is most likely a misidentification, this being known from islands of the Great Bahama Bank and nowhere else (Steiner 2006b; 2011); *B. cubensis* Marcuzzi is apparently a *nomen*

nudum. Two Cuban specimens examined at present each represent a distinct species, one from the north coast larger, globular; a smaller, more elongate one with sparse setae from an offshore Cay. From the north coast of the Dominican Republic is a poor image of a smooth, robust, somewhat shining *Branchus*, but no specimens have been examined.

Bahamian Species

All known *Branchus* from the Bahamian archipelago (Turnbow and Thomas 2008) belong to the “*floridanus* group” and those described include *B. woodi* LeConte (New Providence and other islands of the Great Bahama Bank), *B. saxatilis* Steiner (Grand Bahama and Abaco, of the Little Bahama Bank), and *B. geraceorum* Steiner (San Salvador). Localities, habitats and collection techniques have been described for these (Steiner 2005a, 2006a, 2011) and are similar to those observed for *B. floridanus*. Four other unnamed species, some mentioned previously, (Steiner 2005b, 2006b) are each known from separate isolated islands or banks.

Bahamian *Branchus* differ from each other in subtle ways, most easily seen in the relative density and forms of the scale-like dorsal setae, and to some degree in the shape of the curvature of the hind tibiae and apex of the tegmen in males.

Branchus geraceorum is the only known species of the Bahamas with raised, polished ridges on the elytra (Fig. 3); *B. saxatilis* and the slightly smaller *B. woodi* differ in density and size of dorsal punctures, color of setae, outline of the pronotum, and other comparative features, as do the four known new species.

A distinct and unique specimen with smooth elytra and evenly distributed scale-like setae is labeled “Anguilla Isl., B.W.I.” and it was thought at first to be from Anguilla in the northern Lesser Antilles, but no other *Branchus* are known from those islands, and searches for these beetles on Anguilla by the author and other collectors have proven negative, in spite of the presence of suitable habitats. The label is

now interpreted to refer to Anguilla Cay, in the Cay Sal Bank of the Bahamas, between Andros, Cuba, and Florida.

A similar species with tapered, pointed setae and faint elytral stripes lacking setae occurs on Conception Island. It is known from only 2 whole specimens and 2 hind-bodies. Conception is another small island on its own bank and, like San Salvador (Steiner 2006a, 2007), will likely hold other flightless endemic species.

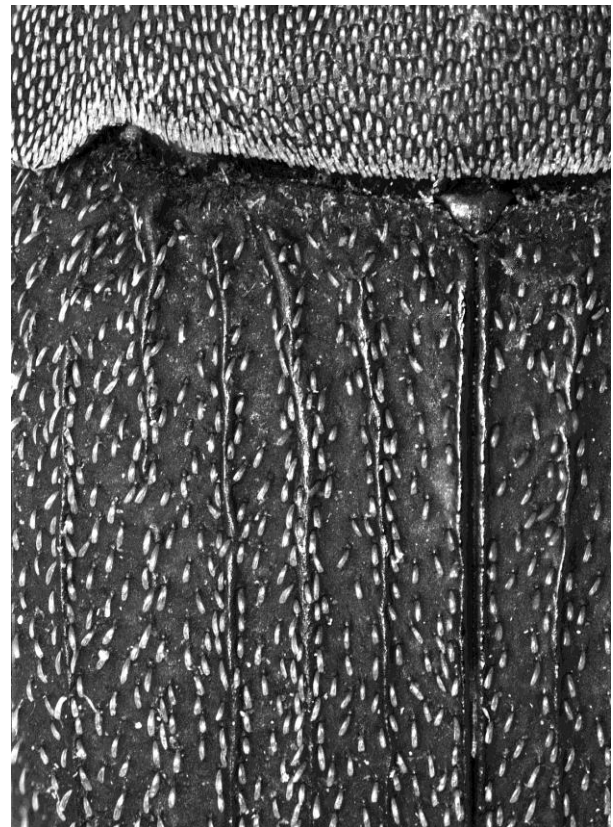


Figure 3. *Branchus geraceorum*, detail of elytral suture and posterior edge of pronotum, showing scale-like setae and raised, polished ridges. Actual size of area shown ca. 5 X 6 mm.

The Turks and Caicos Islands, on two separate banks separated by a deep sea channel, appear to display the same pattern of speciation in *Branchus*, the Caicos Islands sharing one distinct form, and the Turks Islands another. The two are very different in appearance (Fig.

4) and each has some derived characters for the genus, e.g., the Caicos species is very smooth, blackish because the setae are very fine and sparse and no soil encrustation is present; the Turks species has a rather broad, depressed body form and relatively slender legs. Both species are known from several sites on each island group and represented by series in most cases; larvae have been collected in association. Microhabitats include sites just past the first crest of dune scrub vegetation behind beaches as well as interior sites with deep loose sand deposits in partial shade.

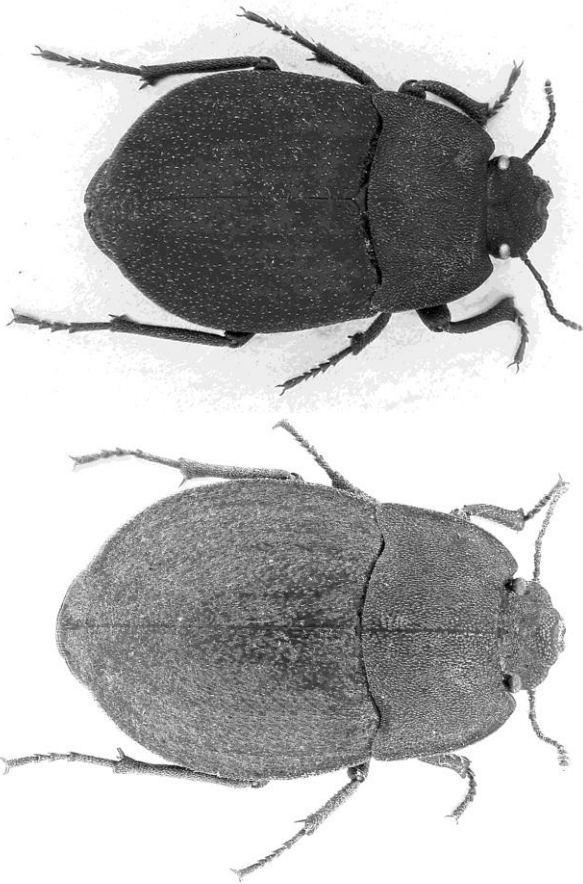


Figure 4. Undescribed *Branchus* species from Turks and Caicos Islands. Upper, specimen from Providenciales; length of beetle, 13 mm. Lower, specimen from Grand Turk; length of beetle, 13 mm.

BIOLOGY AND IMMATURE STAGES

These secretive beetles and their larvae live on and in loose sandy soils under plant debris in dry forest or beach strand habitats. They have been found under objects (wood pieces, stones, etc.) but usually are hiding under a layer of dry leaf litter only. Beetles may be concentrated in small depressions holding leaf litter and are usually exposed at the sand surface but nestled in small depressions or immediately under the sand surface. Members of the “*floridanus* group” tend to burrow, being found sometimes several cm in loose sand. Mainland species have been found on loose sandy soil microhabitats, often associated with riverbank bluffs with scrub vegetation or sparse tree canopy cover of tropical dry forest. *Branchus jamaicensis* has been found in similar microhabitats behind beach strands and also on elevated hillside locations near the coast. The species on Navassa, which lacks beaches, was found on a type of red oolitic soil accumulated in karst depressions. *Branchus floridanus* may be found behind sandy beaches but often occurs near rocky coasts without beaches or behind mangrove swamps on elevated sand deposits in maritime forest. Bahamian and Cayman Island specimens have been collected under leaf litter, palm thatch and wood debris on higher sandy ground behind the beach strand, in sites partly shaded by shrub or small tree canopy, e.g. *Bursera*, *Coccothrinax*, *Coccoloba* on deep, coarse, coral sand, often at edges of light gaps in dry sites.

Associated larvae occur deeper in the sand, usually 2-6 cm, and are often found in greater numbers than adults. They are apparently feeding on plant material, some decayed but also possibly live roots, newly fallen flowers or other parts. Pupation takes place (observed only a few times with captive larvae) in semi-moist sand in an elliptical cell prepared by the larva; adults emerge within 2 weeks, and are probably long-lived.

No larvae and pupae of *Branchus* have been formally described; this is a subject for future work, with larval material associated with

collections of *B. floridanus*, *B. woodi*, *B. jamaicensis*, *B. geraceorum*, and the species from Navassa, Grand Cayman and Turks and Caicos. A few pupae are also known for some of these taxa. A brief diagnosis of the immature stages follows.

The white, smooth, elongate-elliptical eggs (3.5 X 1.2 mm.) are known only for *B. floridanus*, obtained from captive adults that deposited them in semi-moist sand from the collection site.

The sand-burrowing larvae are slender, pale, cylindrical, up to 4.5 cm in length, with dark hardened head, prothorax and stout mandibles that form a scoop-like front for pushing sand. The prothoracic legs are much larger than the other 2 pairs, also modified for digging, with a very dark, curved, claw-like tarsungulus (Fig. 5). The abdominal apex (9th tergum) bears a characteristic “crown” of spines on a shovel-like platform (Fig. 6) with a patch of scattered stout spines across the middle. When exposed in the field, larvae have been found to be capable of burrowing both forward and backward into the loose sand. A violent defensive behavior has also been observed as larvae can wriggle rapidly, flip into the air, and land motionless; after many seconds they begin to burrow into the substrate.

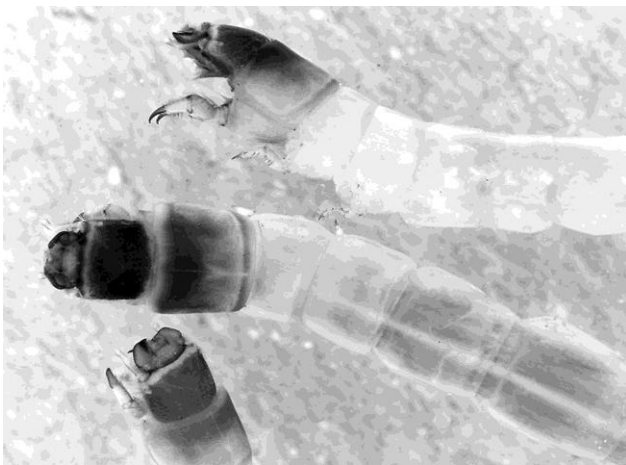


Figure 5. Larvae of *Branchus geraceorum*, anterior ends, showing dark heads and associated structures. Head of middle larva 2.7 mm wide.

Branchus pupae are similar to those known for the closely related genera *Coelus* and *Coniontis* (Steiner 1995) and a recently reared pupa of *Eusattus*. The apex of abdominal segment 9 (Fig. 7) is densely setose, rounded and without urogomphi except for a button-like median projection (more pronounced in *B. jamaicensis* and the Navassa species). Six pairs of “gin traps” are present between abdominal segments 1-2 through 6-7, the latter being much reduced with posterior tooth absent; anterior teeth have curved, finely serrulate to smooth blades and posterior teeth are small, single conical points. The body is cream-colored, mostly covered with fine erect setae; in

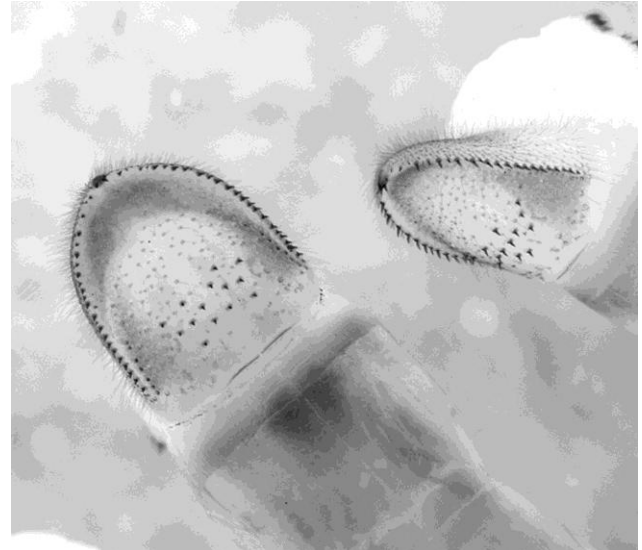


Figure 6. Larvae of *Branchus geraceorum*, posterior ends, showing arrangement of spines and setae on the 9th tergum. Width of segments (mature larvae), 3mm.

B. jamaicensis and the Navassa species there are also bands of small, dark, stout setae across the posterior dorsal surface of abdominal segments 1-6, but in *B. geraceorum* (*floridanus* group) these are lacking. Size generally matches that of the adult beetles of the species except that the deflexed head is not included in the length; pupae of *B. jamaicensis* and the Navassa species are 11-12 mm long; *B. geraceorum* (Fig. 7) is 14 mm long.

BRANCHUS HABITAT DYNAMICS AND THREATS

Branchus populations are often very restricted to small patches or strands of habitat in locations subject to storm events that would be catastrophic to the survival of most species. Hurricanes remove vegetative cover, flood dune habitats and deposit sand, woody and other debris on these sites. Observations indicate, however, that *Branchus* beetles are probably dependent on such events for habitat “renewal.” Sites sampled in Florida and the Bahamas for beetles prior to

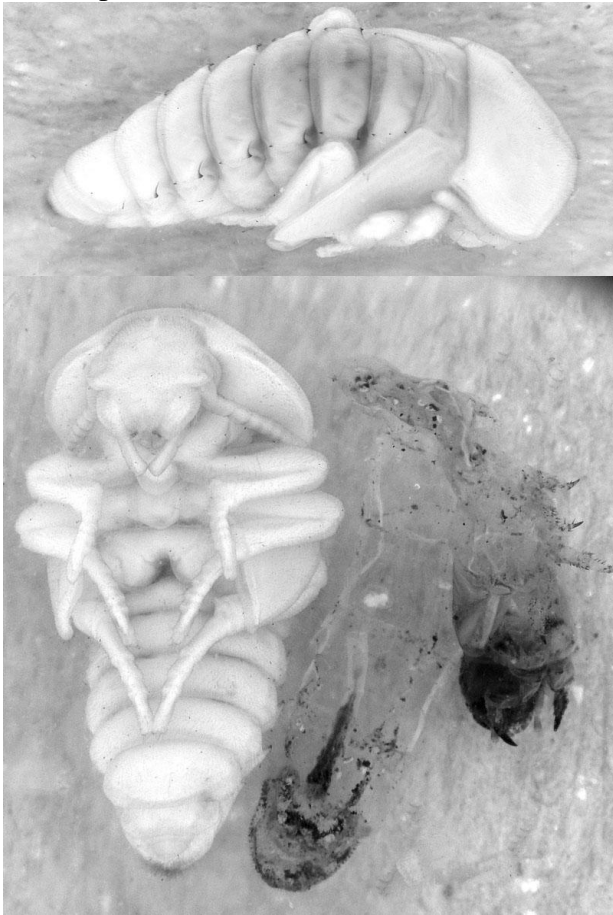


Figure 7. Pupa of *Branchus geraceorum*; upper, dorsolateral view; lower, ventral view and associated larval skin. Length of pupa 14 mm.

and after hurricanes show that local populations may be initially impacted (more difficult to find beetles and larvae within the year following a storm) but with new sand deposited and new

openings and edges created, numbers are seen to increase. Other species in this habitat assemblage apparently benefit as well. Survival periods during long exposure to sea water and, if beetles survive storm surge inundation by burrowing deeper in sand, are subjects for future studies. Storms may remove some individuals but also aid in dispersal and colonization; the flightless beetles (with fused elytra holding air) are likely very buoyant and could be carried during floods to new sites.

Threats to the survival of *Branchus* populations are primarily come from those human activities that cause habitat loss. Coastal roads are usually built along the high dune strand behind the beach, and with associated development this eliminates much, if not all, optimal habitat pockets for *Branchus* and other insects of this assemblage. Remnant populations can persist on small parcels, as long as native vegetation dominates and loose sand deposits are maintained.

The spread of introduced *Casuarina* trees which shade out and replace native vegetation is perhaps the greatest threat to native insect and plant assemblages, especially in coastal sandy areas of the Bahamas (Hammerton 2001). Exclusion of *Branchus* populations at sites over-grown with “Australian pine” has been noted previously (Steiner 1991, 2005a, 2011). In addition to the blanket of fallen *Casuarina* “needles” which smother the loose sand sites that geophilous beetles require, establishment of the trees leads to severe coastal erosion and complete loss of beach and dune strands (Sealy 2011). Extinction of populations (and species), especially on smaller islands, seems very likely but so far has not been documented. Restoration following removal of *Casuarina* from some sites has proven successful with re-colonization by native plants (Sealy 2011) and presumably the insects would likewise re-establish if nearby habitat refugia had survived the invasion.

CONCLUDING REMARKS

Studies on *Branchus* and other flightless arthropods have proven useful in mapping island biogeography in the circum-Caribbean region. Species of *Branchus* known in collections number about 30, but there are no doubt an unknown number of forms yet to be discovered. With what is known thus far about distribution of highly endemic forms, plus all of the entomologically unexplored islands and island habitats, *Branchus* beetles have led to a new view of “predictive biogeography” in the region. Additional species are likely to occur in the many isolated dry forest areas of Mexico and Central America, and on islands off the mainland coast such as San Andres and Providencia (Colombia), Cozumel (Mexico), Islas de la Bahia (Honduras), and Turneffe Islands (Belize). Cays off the coasts of Cuba and Hispaniola have yet to be surveyed. In the Bahamas, new undiscovered species of *Branchus* are waiting to be found on islands of unexplored smaller banks, e.g., Rum Cay, Samana, Crooked and Acklins, Mayaguana, Great and Little Inagua.

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