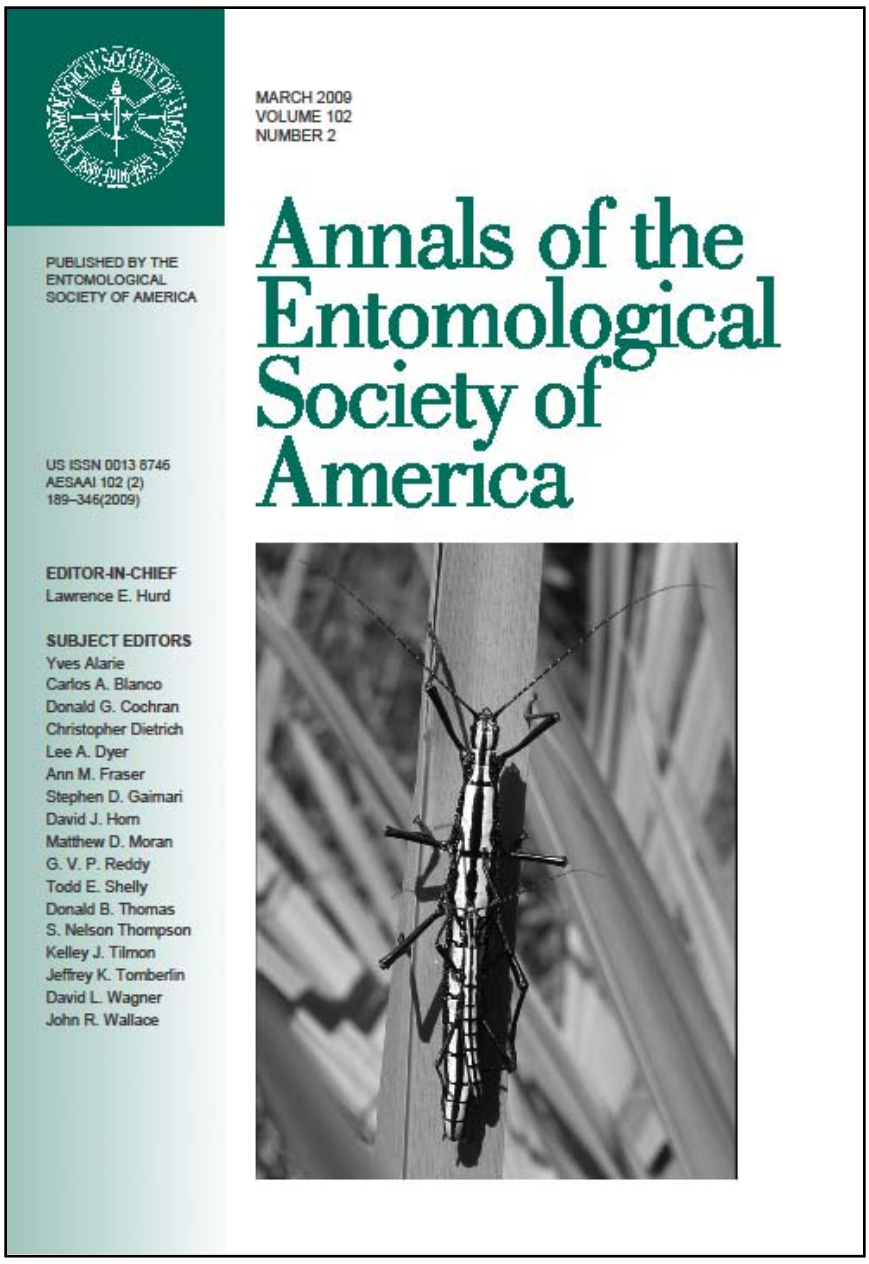

- Oskar V. Conle, Frank H. Hennemann, and **Aaron T. Dossey**, Survey of the Color Forms of the Southern Twostriped Walkingstick (Phasmatodea: Areolatae: Pseudophasmatidae: Pseudophasmatinae: Anisomorphini), With Notes on Its Range, Habitats, and Behaviors, (2009), ***Ann Entomol Soc Am***, 102, (2), 210-232. **Awarded "Editors' Choice Award" for best paper in 2009.**

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November 15, 2010

Aaron T. Dossey
University of Florida
3751 SW 20th Ave Apt 1
Gainesville, FL 32607-4301

Dear Dr. Dossey,

On behalf of the editors of Annals of the Entomological Society of America and the ESA, I am pleased let you know that you and your co-authors of the article cited below have been selected as the 2010 winners of the Editors' Choice Award for best paper in 2009.

Oskar V. Conle, Frank H. Hennemann, Aaron T. Dossey. 2009. Survey of the Color Forms of the Southern Twostriped Walkingstick (Phasmatodea: Areolatae: Pseudophasmatidae: Pseudophasmatinae: Anisomorphini), With Notes on Its Range, Habitats, and Behaviors. Ann. Entomol. Soc. Am. 102(2): 210-232.

As an award recipient, you and your co-authors each will receive an award plaque and a total of $1,000 ($334 apiece).

The Awards Ceremony will be conducted at the 2010 ESA Annual Meeting in San Diego, California during the opening plenary session on Sunday, December 12, 2010. The session will take place from 5:30 – 7:30 pm in the Golden Ballroom and the Pacific Salon One, Two, and Three at the Town and Country Resort and Convention Center.

If you have any questions regarding the award or the ceremony, please contact us at 301-731-4535 ext 3001 or awards@entsoc.org. Again, my warm congratulations on this honor.

Sincerely,

David B Hogg

Dr. David B. Hogg
2010 ESA President

Cc: Ann Kenworthy, Interim Executive Director

Survey of the Color Forms of the Southern Twostriped Walkingstick (Phasmatodea: Areolatae: Pseudophasmatidae: Pseudophasmatinae: Anisomorphini), With Notes on Its Range, Habitats, and Behaviors

OSKAR V. CONLE,[1] FRANK H. HENNEMANN,[2] AND AARON T. DOSSEY[3]

Ann. Entomol. Soc. Am. 102(2): 210–232 (2009)

ABSTRACT Numerous color morphs of the southern twostriped walkingstick (or "devil rider"), *Anisomorpha buprestoides* (Stoll, 1813) (Phasmatodea: Areolatae: Pseudophasmatidae: Pseudophasmatinae: Anisomorphini), predominantly from Florida, are described and illustrated. Three main color forms of *A. buprestoides* are recognized: white, orange and brown. Type specimens of *A. buprestoides* have been lost, but colored illustrations by its original describer are compared with the most similar color form described here. This is intended to support future selection of a neotype, which will become necessary for conducting any confirmed taxonomic studies. The common brown form is highly variable in size and coloration and exhibits a wide distribution, mainly throughout the more northern portions of the dispersal of *A. buprestoides*. The white and orange forms are restricted to rather small localities in central Florida and show affiliation with dryer habitats. The distribution of *A. buprestoides*, based on collecting records from various museum collections, extends as far south as Key West, FL, but the northern boundary of its range is unclear. The day-hiding, defensive, and oviposition behaviors are described and illustrated for the three recognized color forms and are shown to differ considerably with dependence on the respective habitat. A list of known host plants and alternative food plants used in captive breeding of *A. buprestoides* is provided, which proves this species to be rather polyphagous. Captive breeding on alternative food plants for three generations has shown the coloration to remain constant independent of food plant used. Our observations lead us to the conclusion that *A. buprestoides* is in every aspect capable of adaptation to ecological pressure.

KEY WORDS *Anisomorpha buprestoides*, color forms, intraspecific variation, ecology, host plants

The southern twostriped walkingstick, *Anisomorpha buprestoides* (Stoll, 1813) (Phasmatodea: Areolatae: Pseudophasmatidae: Pseudophasmatinae: Anisomorphini), is perhaps as well known in the United States as the widely distributed pest species, the walkingstick, *Diapheromera femorata* (Say, 1824). *A. buprestoides* (identified in this study by O.V.C. and A.T.D.) is abundant in the southeastern Gulf States, particularly in Florida. It is sometimes referred to as "devil rider" because 1) of its potent chemical defense spray and 2) because the males almost always being found riding the female (Eisner 2003). These insects are well known for their ability to defend themselves by spraying a particularly odoriferous and irritating chemical secretion from prothoracic glands. Numerous publications have dealt with its systematics and geographical range (Caudell 1903, Rehn and Hebard 1916, Conle and Hennemann 2002); external anatomy (Littig 1942, Happ et al. 1966); behavior, habitats, and host plants (Hetrick 1949a,b; Gunning 1987; Thomas 2001); chemical analysis of its defensive spray termed anisomorphal (Eisner 1965; Meinwald et al. 1962; Dossey et al. 2006, 2008), or injuries to the human eye caused by this secretion (Albert 1947, Stewart 1937, Paysse et al. 2001). Some studies have stated the adults show considerable color variability among populations. For example, Hetrick (1949a,b) reported a distinctive black and white form occurring only in the Ocala National Forest (Marion Co., FL). Dossey et al. (2008) also conducted a study of defensive secretion chemical variability among the three color forms studied here. However, so far no comprehensive and detailed survey of the ecology and behavior of the various color forms have been undertaken.

Field studies in more than eight different locations throughout Florida made by A.T.D. in summers 2006 and 2007 have shown the coloration and habits of *A. buprestoides* to vary considerably from locality to locality. Photographs and video were taken in the field by A.T.D. of live specimens by using a Canon Powershot S5 IS digital camera (5 megapixels, set to maximum resolution). Some of the laboratory photographs were taken by O.V.C. by using a Nikon D90 film camera. In addition to live specimens, extensive dried

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material from various museum collections in the United States (Academy of Natural Sciences, Philadelphia [ANSP]; Michigan State University [MSUC], and Florida State Collection of Arthropods, Gainesville [FSCA]) was examined to link certain color forms to localities. Captive breeding of all three color forms recognized herein was conducted to examine the constancy of the coloration. Furthermore, observation of live *A. buprestoides* in several locations throughout Florida has elucidated some interesting behaviors that are clearly specializations to specific habitats. The day-hiding and oviposition behaviors in particular are seen to differ considerably between specimens inhabiting semihumid habitats versus those occurring in more arid regions on sandy soil. Hetrick (1949a,b) previously described an unusual oviposition behavior of the distinctly black and white color form whereby females in mating pairs drop their eggs into indentations in sand or open spaces in leaf litter. This behavior is described and illustrated in detail in this study, and is shown to also frequently occur in the orange form at Archbold Biological Research Station (Highlands Co., FL). The brown form seems to prefer simply dropping their eggs to the ground while perched from a tree.

This article work provides the first illustrated survey of the various known color varieties of *A. buprestoides*, with emphasis on Floridian specimens, and it also takes into account their different habitats and behaviors. Three distinct color forms are recognized, and varieties from 10 localities throughout the distributional range of *A. buprestoides* are described and illustrated to show its range of variability.

Anisomorpha buprestoides (Stoll, 1813)

Synonyms

Phasma vermicularis Stoll, 1813.
Spectrum bivittatum Say, 1824.

The generic name "*Anisomorpha*" is a combination of the prefix "*A-*" (gr.=none) and the two Greek substantives "*isōs*" (=equal) and "*morphē;*" (=form). It means as much as "nonisomorphic" or "of unequal form" with which Gray, 1835 most certainly intended to refer to the remarkably bicolorous body of the type species *A. buprestoides.*

A detailed morphological study of *A. buprestoides* was presented by Littig (1942). Detailed descriptions of both sexes were provided by Conle and Hennemann (2002), who indicated the high intraspecific variability of the coloration by referring to a "Formenkreis *A. buprestoides.*" These authors have recognized the occurrence of at least two distinct forms and illustrated four distinct varieties from Florida, Georgia, and Mississippi (Conle and Hennemann, 2002, pl. IV: 37–41 and pl. V: 42–43). Body lengths of *A. buprestoides* are ♂♂ 38–52 mm, ♀♀ 58–85 mm.

Descriptions and illustrations of the eggs were published by Clark (1976) and Conle and Hennemann (2002). The latter authors recognized that the eggs also show considerable variation, even within a single population, and sketched four different varieties Conle and Hennemann (2002), figs. 157–164.

Differentiation. *A. buprestoides* is distinguished from *A. ferruginea* by the generally larger size, with ♂♂ being usually >40 mm and ♀♀ exceeding 60 mm; body comparatively more slender; head noticeably longer than wide; body with conspicuous and often very distinct longitudinal black dorsal and lateral stripes, the dorsal black stripe being continued on the anal segment. The eggs are similar to those of *A. ferruginea* but may be distinguished by their generally more elongate micropylar plate and longer median line (Conle and Hennemann 2002).

Two further species are presently recognized in the genus *Anisomorpha* Gray, 1835, neither of which occur in the continental United States. *Anisomorpha paromalus* Westwood, 1859 occurs in Mexico and Belize, and *Anisomorpha clara* Conle et al. (2006) is endemic to Hispaniola (Greater Antillean Islands).

Distribution. The limits of the range of *A. buprestoides* are not fully known, and there have been several erroneous records based on specimens confused with *A. ferruginea.* Records from North Carolina (Black Mountains) and Texas (Brazos and Galveston counties) are almost certainly *A. ferruginea. A. buprestoides* seems to be restricted to the southeastern states, ranging from South Carolina through Georgia, Alabama, and Florida, and as far west as southern Mississippi and the southeastern portions of Louisiana (Fig. 1). It is apparently most common and widespread throughout Florida, which is confirmed by the rich material in United States museum collections predominantly originating from Floridian locations. Thomas (2001) listed the following counties based on specimens in the FSCA: Alachua, Brevard, Broward, Collier, Columbia, Dixie, Escambia, Gadsen, Gulf, Highlands, Lake, Levy, Liberty, Marion, Miami-Dade, Monroe, Nassau, Orange, Osceola, Putnam, Santa Rosa, and St. John. The southernmost of these localities is Boca Chica Key in Monroe Co. (Thomas 2001).

Arment (2006) listed the following records for *A. buprestoides* from outside Florida: Alabama (Baldwin Co.), Georgia (Atlanta, Bibb, and Coweta counties.), Louisiana (Jefferson, Orleans, Rapides, and Terrebonne parishes), Mississippi (Harrison, Granada, and Jackson counties) and South Carolina (Anderson, Beaufort, Charleston, Hampton, Newberry, Oconee, and Pickens counties).

Specimens described and illustrated in the current study originated from the following locations (Fig. 2): Florida (Ocala National Forest in Marion Co. (29° 3′00″ N, 81° 38′50″ W), Archbold Biological Research Station in Highlands Co. (27° 10′50″ N, 81° 21′2″ W), Sanibel Island in Pinellas Co. (two locations: 26° 27′5″ N, 82° 00′57″ W and 26° 27′37″ N, 82° 09′25″ W), Gulf Hammock in Levy Co. (29° 14′46″ N, 82° 43′43″ W), and from various localities near Gainesville (Alachua Co.), e.g., Newnan's Lake (29° 38′11″ N, 82° 14′19″ W), near Gainesville Regional Airport (29° 44′3″ N, 82° 16′27″ W), and the University of Florida campus (29° 38′1″ N, 82° 22′11″ W), Georgia (Atlanta), and Mis-

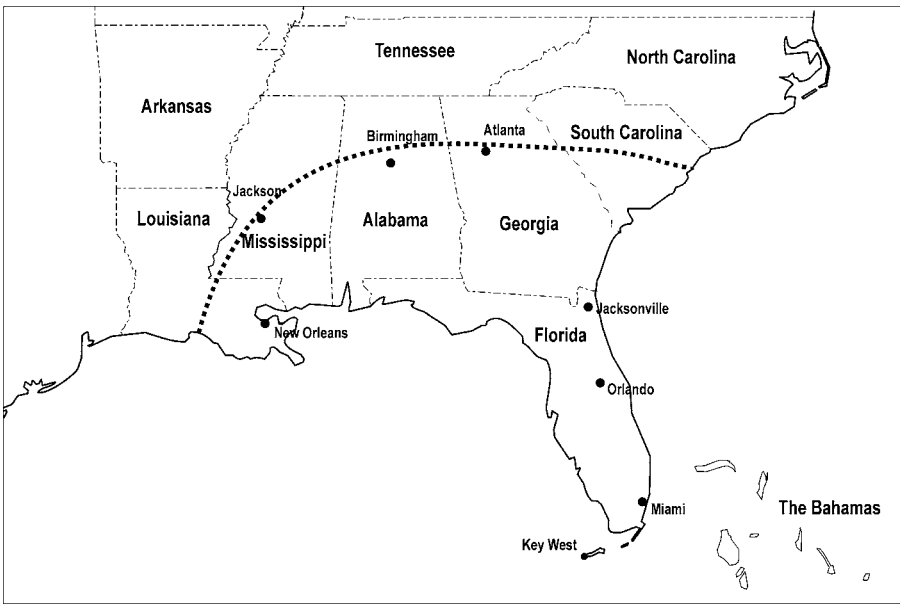


Fig. 1. Map showing the known distributional range of *A. buprestoides*. The dotted line indicates the still unknown northern boundary of its dispersal.

sissippi (Moss Point). Adults of *A. buprestoides* are usually found from July to November.

Host Plants. In its natural habitats *A. buprestoides* is known to feed on various oaks (Fagaceae), e.g., Chapman oak (*Quercus chapmanii* Sargent), myrtle oak (*Quercus myrtifolia* Willdenov), turkey oak (*Quercus laevis* Walter), and red oak (*Quercus rubus* [=*Quercus rubra* L.]); tree lyonia or staggerbush (*Lyonia ferruginea* (Walter) Nuttall; Ericaceae); various willows (*Salix* spp.; Salicaceae); sweetgum (*Liquidambar styraciflua* L., Hamamelidaceae); Florida rosemary or sand heath (*Ceratiola ericoides* Michaux; Em-

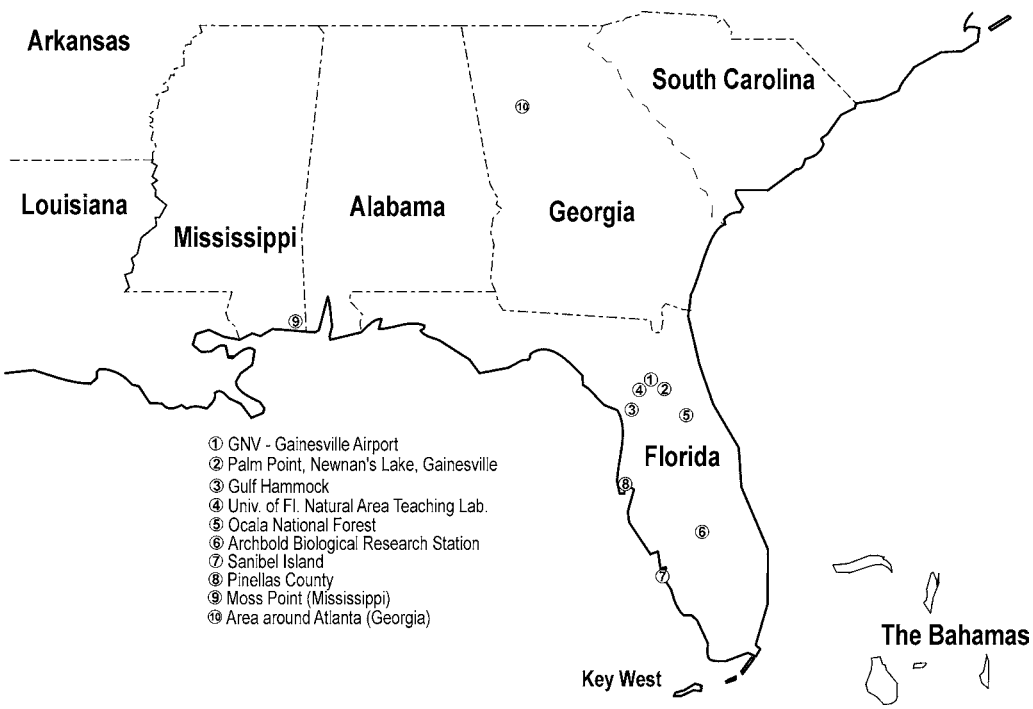
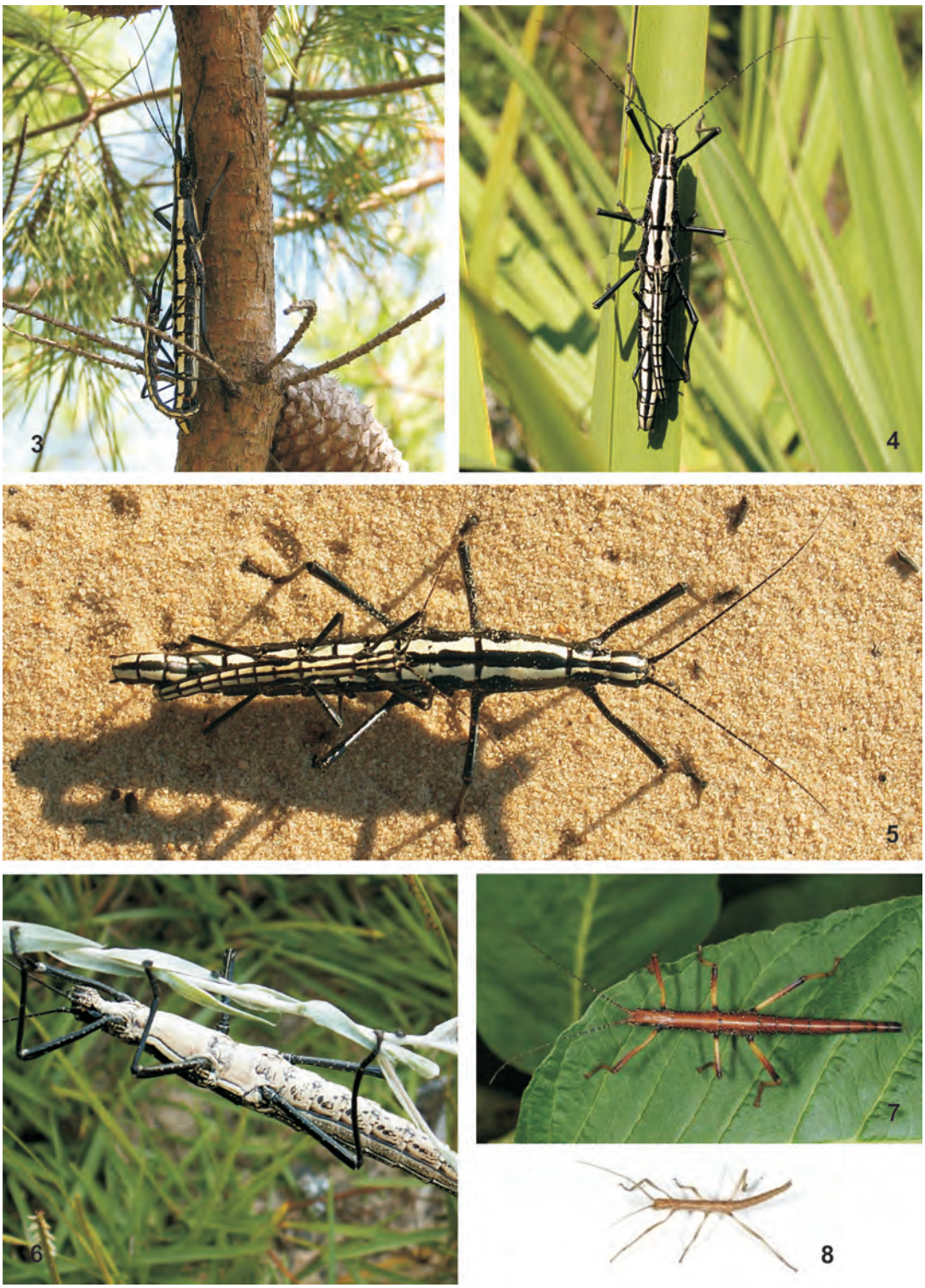
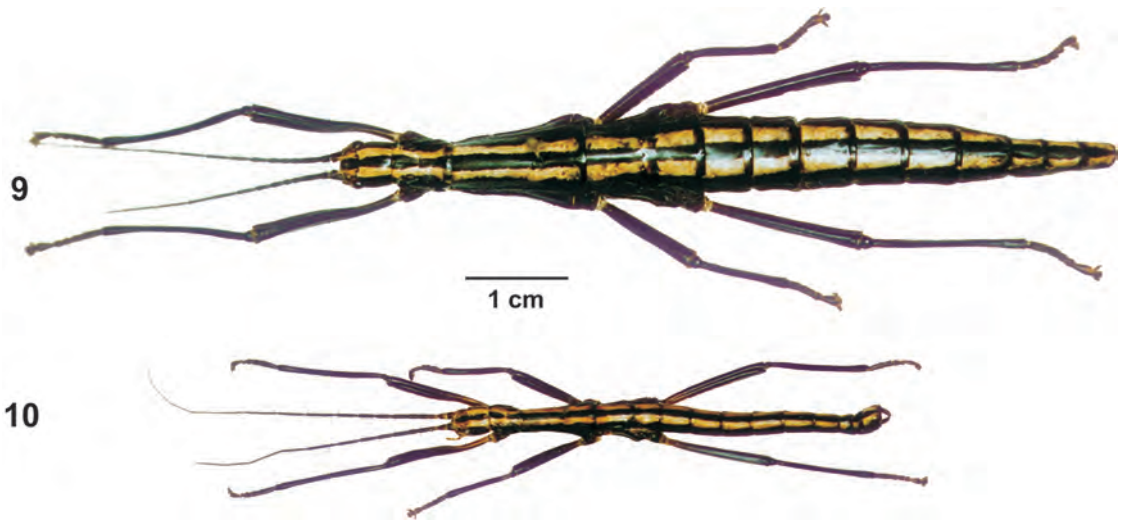


Fig. 2. Map showing the prospected areas and localities from which material was examined for this study.



Figs. 3–8. *A. buprestoides* white form from Ocala National Forest. 3. Mating couple resting on a sand-pine (plant identification by O.V.C.) in the day. 4. Mating couple resting on saw-palmetto (plant identification by O.V.C.) in the broad sun. 5. Mating couple walking on sand to search a suitable place for oviposition. 6. Ventral view of ♀ showing the distinct black mottling. 7. Fourth instar nymph with the typical whitish mottling. 8. Newly hatched nymph. Photographs 3–6 by A.T.D., photographs 7–8 by O.V.C.



Figs. 9–10. *A. buprestoides* white form. 9. Preserved ♀ in dorsal view (captive reared from unknown locality in Florida, coll. F.H.H.). 10. Preserved ♂ in dorsal view (captive reared from unknown locality in Florida, coll. F.H.H.). Photographs 9–10 by O.V.C.

petraceae); crepe myrtle (*Lagerstroemia indica* L.; Lythraceae); blackberry (*Rubus* spp.; Rosaceae); and roses (*Rosa* spp.; Rosaceae). Oaks seem to be the favored food plants in most localities, but various other plants are accepted alternatively in captivity, e.g., privet (*Ligustrum ovalifolium* Hasskarl, *Ligustrum sinense* Loureiro, and *Ligustrum japonicum* Thunberg; Oleaceae); ribwort plantain (*Plantago lanceolata* L.; Plantaginaceae); rhododendron (*Rohododendron* spp.; Azaleae); bramble (*Rubus fruticosus* L.; Rosaceae); raspberry (*Rubus idaeus* L.; Rosaceae); St. John's wort (*Hypercium patulum* Thunberg; Clusiaceae); and also European oaks (Fagaceae), such as stalk oak (*Quercus robur* L.) and swamp oak (*Quercus petraea* [Mattuschka] Liebl.). Although these insects are often found resting on the long lanceolate leaves of saw-palmetto (*Serenoa repens* [W. Bartram] Small; Arecaceae) or under loose bark of trunks of pine trees (e.g., sand-pine, *Pinus clausa* [Chapman ex Engelmann] Vasey ex Sargent; Pinaceae), neither of these plants seem to be part of their diet.

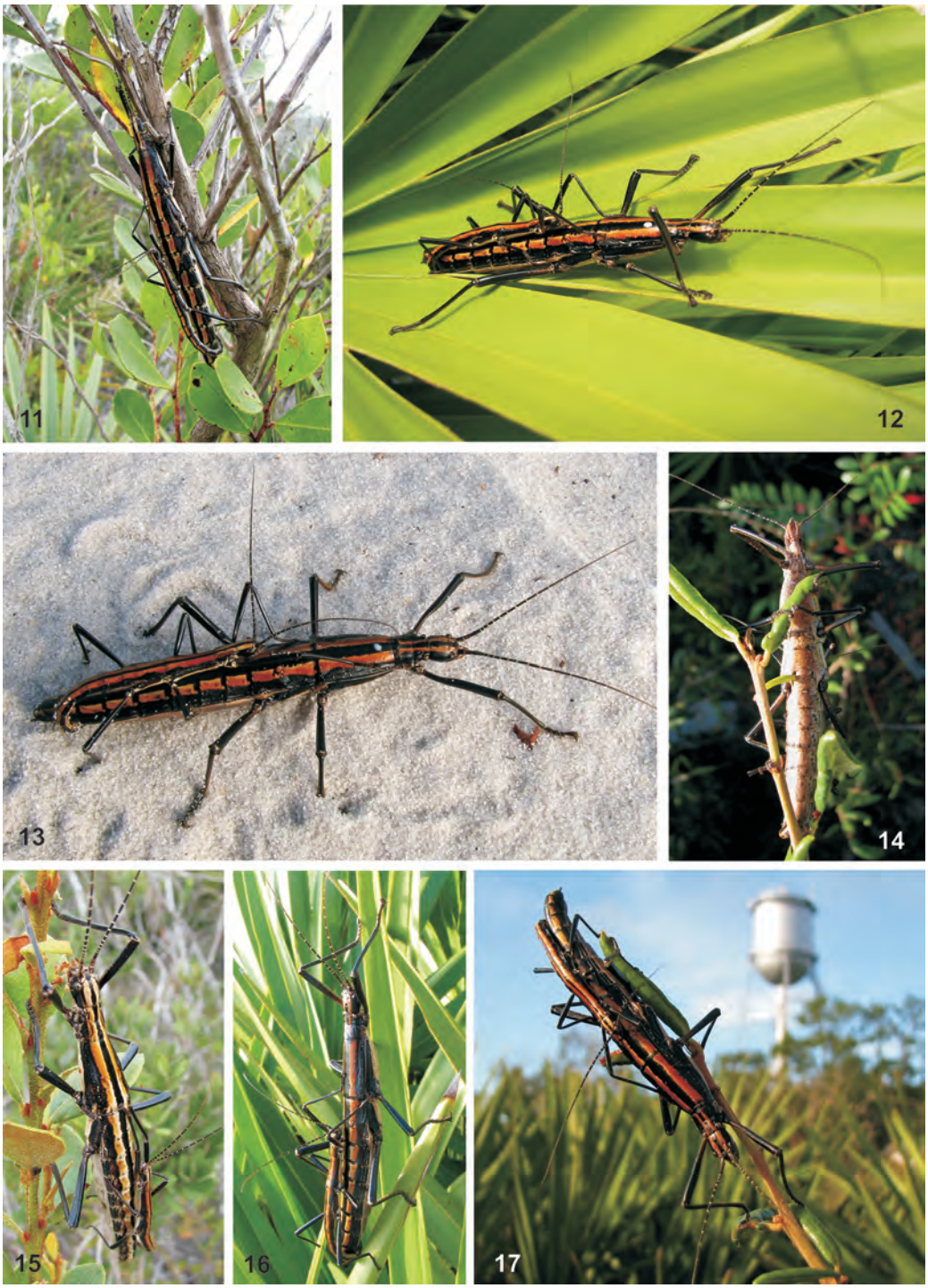
Survey of Color Forms. In general, *A. buprestoides* occurs in three distinct color forms: white, orange, and brown. These color designations refer to the color of the two lateral dorsal stripes. The brown form is widely distributed and commonly found throughout the entire range of the species. The other two forms are geographically restricted to rather limited areas in central Florida. The white form is only found in Ocala National Forest (Marion County) and adjacent areas, and the orange form occurs exclusively in the vicinity of Highlands Co., particularly around the Archbold Biological Research Station area.

All three forms have three conspicuous black longitudinal stripes, one stripe dorsomedial and one stripe along each lateral side. These stripes are well defined in the white and orange forms, but may be indistinct and more brown than black in certain morphs of the brown form. The dorsomedial stripe is always well defined and runs along the entire length of the body, whereas the lateral stripes often terminate on abdominal tergite IX in the brown form. The two pale dorsal stripes are always interrupted by black transverse bands between the body segments in the white and orange forms but rarely so in the brown form. The antennae and extremities are black in the white and orange forms, but are often blackish brown to mid-brown in brown forms.

The brown form shows considerable variation in the width and shape of the longitudinal stripes of the body and the stripe along the cheeks, degree and color of the lateral stripes of the body, as well as the color of the legs and antennae. Even the general coloration shows conspicuous variation and ranges from cream over pale grayish or yellowish brown to mid-brown. The coloration of adult and nymph specimens from all three color forms found at 10 localities is described in detail and illustrated below.

White Form. Ocala National Forest, FL (Figs. 3–8). This black-and-white morph is perhaps the most distinct of all color morphs known to occur in *A. buprestoides.* Its range seems to be restricted to Ocala National Forest (Marion Co.) and adjacent vicinity. In some years, it can be locally very abundant. During the day, adult couples are frequently found resting on palmetto and branches of various trees. In the late afternoon, they are seen alongside or crossing the sandy tracks leading through the National Park, and females can be observed laying eggs in depressions in the sand.

The two dorsal stripes range in color from creamy white or ivory to bright white with the dorsal and median stripes being very distinct, broad, and deeply black. The lateral stripes of the tergites, as well as the black meso- and metapleurae, are to a variable degree set with tiny white specks. The lateral stripes



Figs. 11–17. *A. buprestoides* orange form from Archbold Research Station. 11. Mating couple resting on staggerbush (identified by Dr. Mark A. Deyrup) in the day. The ♀ is seen to have the longitudinal stripes on the head pale cream instead of orange. 12. Mating couple resting on saw-palmetto (plant identification by O.V.C.) in the broad sunlight, the ♀ having a drop of its white defensive secretion on the mesonotum. 13. Mating couple walking on sand to search a suitable place for oviposition. 14. Ventral view of ♀. 15. Mating couple on *Lyonia* sp. (identified by Dr. Mark A. Deyrup), the ♀ representing the more rarely seen pale morph with the dorsal stripes not fully orange. 16. Mating couple resting on saw-palmetto (plant identification by O.V.C.). 17. Mating couple resting at the terminal of branch of sand heath (plant identification by O.V.C.). Photographs 11–17 by A.T.D.

Figs. 18–20. *A. buprestoides* orange form from Archbold Research Station. 18. Newly hatched nymph. 19. Several adults and nymphs forming an aggregation in the corner of their breeding cage. The ♀ in center is of the rare dark variety which has the longitudinal stripes on the thorax very narrow and the abdomen almost entirely black. 20. Mating couple, adult ♂ and two large nymphs forming a cluster. Photograph 18 by O.V.C. Photographs 19–20 by A.T.D.

are distinctly present on the anal segment. Cheeks are entirely black. Usually there is a longitudinal row of slightly enlarged white specks along the lateral margins of the mesonotum. The ventral body surface is pale creamy, often with a slight bluish or greenish wash, the hinder portions of the thoracic sternites and all abdominal sternites irregularly mottled with black (Fig. 6). Subgenital plate of ♀♀ and poculum of ♂♂, as well as cerci of both sexes are black. The antennae are black with pale joints. All legs and tarsi are black, the femora and tibiae set with a variable number of tiny white specks.

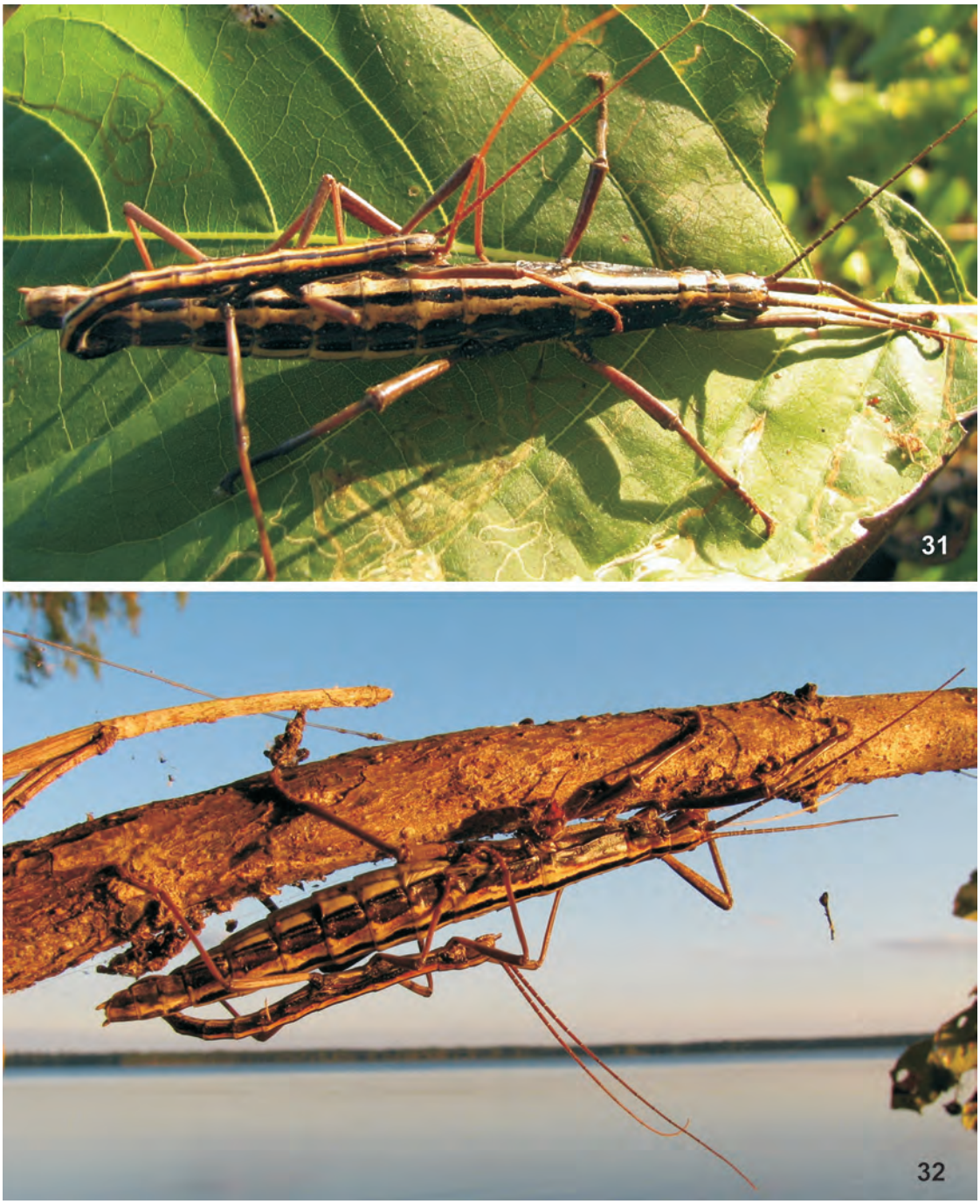
Newly hatched nymphs are creamy mid-brown with the basal sections of all femora and tibiae pale straw (Fig. 8). Nymphs between second and fifth stage have a color pattern rather unlike that of the adults. Their body has a rusty brown ground color with the lateral surfaces being darker and overlaid with many tiny white specks. Nymphal antennae are noticeably black with pale joints. The legs are drab yellowish with black knees and tarsi (Fig. 7). Nymphs of the white and orange forms look similar to each other.

Florida II (Figs. 9 and 10). This variety is very similar to the one found at the Ocala National Forest (Marion Co.), but it is of a more ivory-like coloration and has the black longitudinal stripes of the body very well defined. The lateral stripes are continued on the anal segment and the cheeks are black with the very lower portion mid-brown. The legs are black, except for the femora having some indistinct pale mottling on the ventral surfaces and being slightly reddish basally. Antennae are black with pale joints. In contrast, it lacks any white spots along the lateral surfaces of the body and the ventral body surface is creamy mid-brown with irregular paler mottling. Subgenital plate of ♀♀ and poculum of ♂♂ black apically but brown toward the base. All specimens at hand from the second author's collection (F.H.H., 2 ♂♂, 2 ♀♀) were captive reared in Europe. The exact origin of the culture-stock is unknown.

Figs. 21–26. *A. buprestoides* brown form from Gulf Hammock, FL. 21. Adult ♀ of the dark variety. 22. Adult ♀ of the dark variety. 23. Mating couple resting on the trunk of a pine tree (plant identification by A.T.D.). 24. Aggregation of specimens hiding on the trunk of a pine tree (plant identification by A.T.D.) and showing color variation is this population. 25. Fourth instar. 26. Newly hatched nymphs. Photographs 21–24 by AT.D. Photographs 25–26 by O.V.C.

Figs. 27–30. *A. buprestoides* brown form from site near Gainesville Regional Airport, FL. 27. Adult ♀ of the dark brown variety (dorsal view). 28. Lateral view of head and thorax of adult ♀ of the dark brown variety, showing the almost plain brown ventral body surface. 29. Mating couple resting in leaf-litter on the forest floor. 30. Mating couple of the pale brown variety in leaf litter on the floor of a pine forest. Photographs by A.T.D.

Orange Form. Archbold Biological Research Station, FL (Figs. 11–20). This form is generally similar to the white form found at the Ocala National Forest, but with bright orange instead of white dorsal stripes. It shows a great deal of variation in the width, shape and color of these stripes. They vary from dark reddish orange to bright orange (Figs. 12, 13, 16, and 17), but frequently specimens occur which have the stripes more of a cream color and only orange toward the outer borders (Figs. 15 and 56). Sometimes the part of the stripes on their head is a pale cream color, contrasting with the orange on the remainder of the body (Fig. 11). Rarely, very dark specimens are encountered that have the stripes only present and very



Figs. 31–32. *A. buprestoides* brown form from Newnan's Lake, FL. 31. Mating couple. 32. Mating couple. Photographs by A.T.D.

weakly defined on the thorax, and the dorsal surface of the abdomen is almost entirely black (adult ♀, Fig. 19). The distinct white specks seen on the legs of certain specimens of the white form from Ocala National Forest are not present in this orange color form; and, in contrast, the bases of all femora are dark reddish brown. The ventral side of the body is pale to mid-brown overlaid with irregular pale speckles and several black spots and markings, particularly on the abdominal sternites (Fig. 14). Throughout their entire development, nymphs are similarly colored to those of the white form from

Figs. 33–34. *A. buprestoides* brown form from Sanibel Island, FL. Mating couple resting on a solitary *Lyonia* sp. (plant identification by O.V.C) in the open land during the day. Photographs by A.T.D.

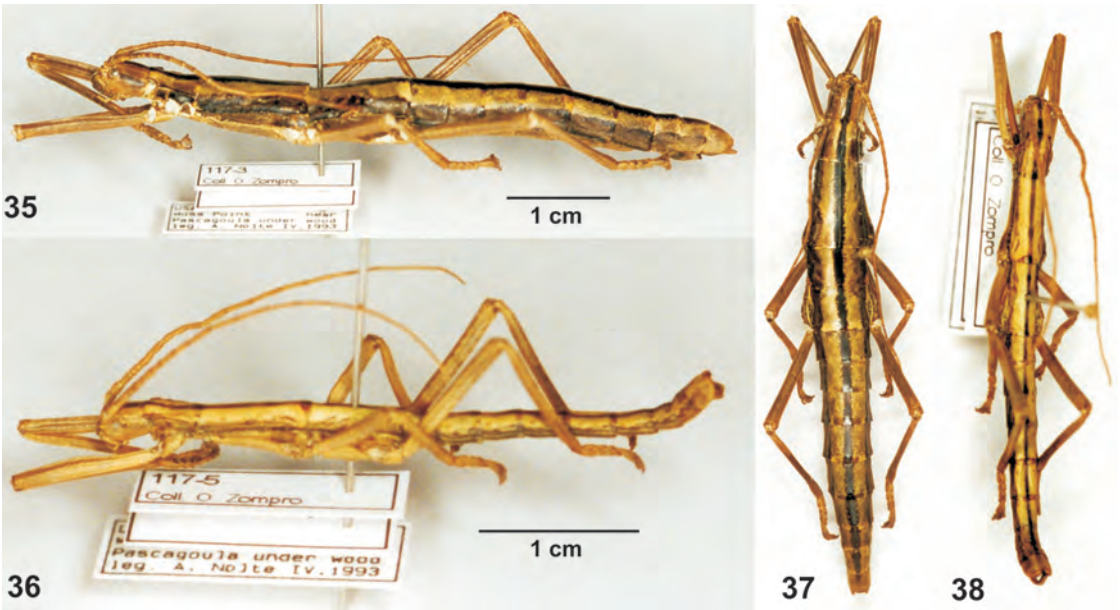
Ocala National Forest, but in general tend to be darker brown (Figs. 18–20).

Brown Form. In general, morphs of the brown form have the cheeks pale to dark brown or almost blackish but rarely as distinctly bicolored as in the white and orange forms. The lateral surfaces of the brown form body are much browner than black and the dorsal stripes are in general less sharply defined. The antennae and legs are never entirely black but vary from medium to blackish brown; the legs usually becoming paler brown (or even straw in pale specimens) toward the base. The subgenital plate of ♀♀, poculum of ♂♂, and cerci of both sexes are also never black as in the white and orange forms, but they exist in various shades of brown. In several localities (e.g., Gulf Hammock and Gainesville populations, Florida) the adult insects show remarkable color variation even within a single population, with pale and dark brown specimens occurring alongside one another (Fig. 24).

Gulf Hammock, FL (Figs. 21–26). Specimens from this locality are usually larger than specimens from other locations in this study and exhibit a great deal of color variation even within a small population (Fig. 24). The color of the two dorsal stripes of the body ranges from very pale creamy tan or grayish brown to sepia and reddish mid-brown. The black lateral and dorsomedial stripes are slightly less distinct than in the white and orange forms and may be interrupted in places. The ventral side of the body is more or less plain pale tan or grayish to mid-brown and to a various degree furnished with small darker sports. The cheeks are dark gray to blackish and become gray or brown ventrally toward the mouthparts. Subgenital plate of ♀♀ and poculum of ♂♂ pale brown to straw. The antennae range from pale tan or reddish brown to mid-brown and become darker toward the apices; the joints are pale. All legs and tarsi are brown to gray with the femora becoming darker toward the knees.

Newly hatched nymphs are pale to mid-brown and have the bases of the femora and tibiae indistinctly paler (Fig. 26). Later instars are uniform beige, reddish or tan to dark brown and lack the conspicuous white spots on the legs and body seen in nymphs of the white form. Late stage nymphs often have the dark dorsomedial stripe of the body quite well developed (Fig. 25).

Gainesville Airport and University of Florida Natural Area Teaching Laboratory (Figs. 27–30). Similar to the Gulf Hammock morph, but adult specimens in general are slightly smaller and have the dorsal stripes of the body better defined. Very dark varieties from these localities have the longitudinal stripes of the



Figs. 35–38. *A. buprestoides* brown form from Moss Point, MS [scale = 1 mm]. 35. Preserved ♀, lateral view (coll. O. Zompro). 36. Preserved ♂, lateral view (coll. O. Zompro). 37. Preserved ♀, dorsal view (coll. O. Zompro). 38. Preserved ♂, dorsal view (coll. O. Zompro). Photographs by O.V.C.

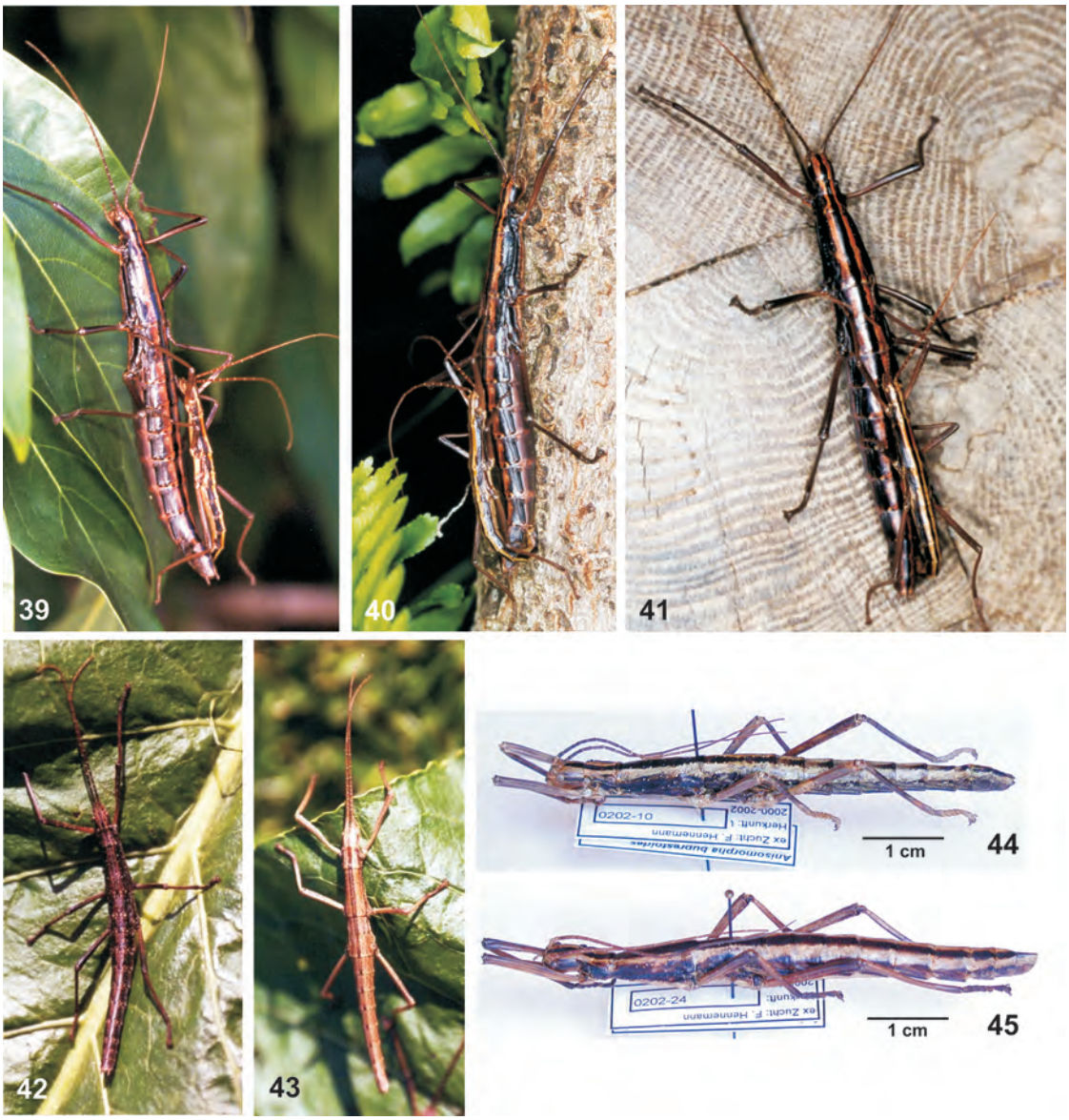
body and legs almost black with the femora becoming reddish brown toward the base, whereas these parts are brown in pale varieties (Fig. 30). This morph also shows a high variation of coloration, even within a colony on the same tree. Nymphs are similar to those of the Gulf Hammock morph. This variety is described from both wild and captive reared specimens.

Newnan's Lake near Gainesville, FL (Figs. 31 and 32). This variety is characterized by having the dark lateral stripes of the body rather broad and the black dorsomedial line comparatively narrow. The two pale stripes in between are very slender (particularly on the mesonotum) and pale creamy drab with the outer portion sepia. The cheeks are pale to mid-brown with only a very narrow longitudinal blackish brown postocular line. The antennae are yellowish to reddish mid-brown and the legs almost plain creamy mid-brown. The ventral body surface is creamy drab with some indistinct and irregularly set darker speckles. This variety was characterized from photographs of one adult pair in the wild.

Sanibel Island and Pinellas County, FL (Figs. 33–34). These specimens were similar to each other and resemble the typical form described by Stoll (1813) (Figs. 46–47). The color of the two pale dorsal stripes resembles that of the white form from an unknown locality in Florida described above (Figs. 9–10). The lateral and dorsomedial stripes of the body are sharply defined, of average width, and plain dark brown to almost black. The width of the dorsomedial stripe shows some variability, being increasingly narrow in some specimens. The two longitudinal stripes in between are rather broad and ivory to pale cream in some specimens, with the outer portion on the thorax bordered by a washed sepia brown line (Fig. 34). The cheeks have a broad dark brown to black postocular band that is brown in its lower portion and more pale cream colored at the very ventral margin of the head capsule. The legs are mid- to dark brown, with blackish brown tarsi. The antennae are reddish mid-brown and become darker toward their apices. The ventral body surface is pale cream to grayish pale brown and sparsely furnished with a few darker speckles, particularly on the abdominal sternites. The small nymphs (as early as first and second stage) show well-defined dorsal stripes. This variety was characterized from photographs and observation of three adult pairs in the wild as well as captive-reared specimens.

Moss Point, MS (Figs. 35–38). The coloration of this variety is a pale brown with faint washed mid- to dark brown lateral bands and is remarkable for the strikingly slender dorsomedial line of the body. The cheeks are pale to mid-brown and have the postocular stripe either very indistinct or lacking. The legs are plain pale to mid-brown, the antennae yellowish to reddish mid-brown. This form was described from dried specimens.

Atlanta, GA (Figs. 39–45). There are several culture-stocks from Georgia that have been kept by European breeders during the past 20 yr. No further details on the exact origin are available for most of them. One of the stocks was reared by O.V.C and F.H.H. between 1999 and 2002 and almost certainly originated from near Atlanta (perhaps from different localities), where *A. buprestoides* is frequently found. All known specimens from Georgia belong to the typical brown form, most of which are similar in colora-

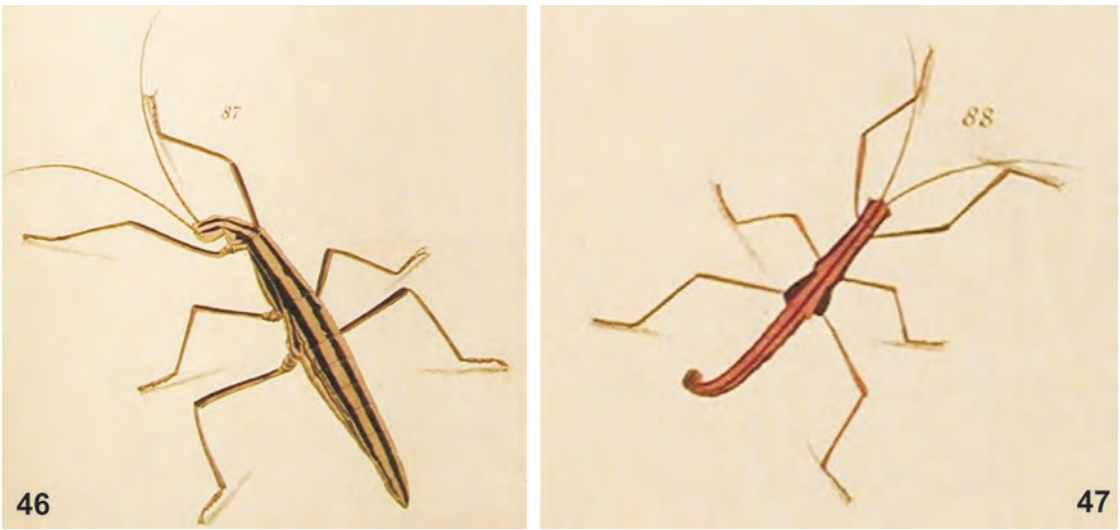


Figs. 39–45. *A. buprestoides* brown form from Georgia. 39. Mating couple of the dark orange brown variety (captive reared). 40. Mating couple of the dark orange brown variety (captive reared). 41. Mating couple of the dark orange brown variety (captive reared). 42. Third instar nymph showing whitish mottling. 43. Fourth instar having the dorsomedial stripe of the body quite well developed. 44. Preserved ♀, pale brown variety with the longitudinal stripes of the body rather undecided and irregularly separated (captive reared, coll. F.H.H.). 45. Preserved ♀, darker brown variety with the longitudinal stripes of the body well defined (captive reared, coll. F.H.H.). Photographs by O.V.C.

tion to the population described above from Gulf Hammock, FL.

Specimens of the stock reared by the authors showed a great deal of variation in coloration as well as the width and shape of the longitudinal stripes on the body. The dark lateral stripes range from mid-brown to almost black, the pale stripes from pale straw over tan and reddish mid- to almost dark brown. The dorsomedial stripe was always black, either broad and well defined (Fig. 45) or rather undecided and partly interrupted on the abdomen (Fig. 44). Some specimens had the cheeks broadly dark brown to black, others only with a rather narrow black postocular line (Fig. 44). The legs range from pale to dark brown with the apices of the femora and tibiae as well as the tarsi dark to blackish brown. The antennae are mid- to dark brown. This population is characterized mainly from captive reared stock.

Typical Form. *A. buprestoides* was first illustrated and described by Stoll (1813) as *Phasma buprestoides,*



Figs. 46–47. The typical form of *A. buprestoides*. 46. ♀ holotype of *P. buprestoides* (reproduced from Stoll 1788, pl. 23: 87). 47. ♂ holotype of *P. vermicularis* [=*buprestoides*] (reproduced from Stoll 1788 pl. 23: 88).

based on a single ♀. The corresponding ♂ was described by the same author as *Phasma vermicularis* (Stoll, 1813); this name consequently representing a synonym. The type locality of both species was stated to be "New Georgia." Unfortunately, the original type specimens have not been traced and are presumed lost. They are not present in the collection of the Natuurhistorisch Museum Leiden (RMNH, The Netherlands), which contains most of the types of species described by Stoll. However, Stoll (1813) provided colored illustrations of both species which in combination with the type locality help to attribute the type specimens to a certain color morph and define a typical form of *A. buprestoides.* This may serve for the future selection of neotypes required to fix these two taxa.

The original illustration of *P. buprestoides* by Stoll (1813) shows that the legs and antennae are brown, the cheeks with a slender postocular stripe, and the two lateral dark longitudinal stripes of the dorsal body surface terminate at the base of the anal segment. These features, in addition to the type locality New Georgia, match well with ♀♀ of the brown form found throughout Georgia and Florida. The color morphs from Sanibel Island, Florida, possibly come closest to Stoll's illustrations. Also a captive reared ♀ originating from Atlanta, GA, in the collection of O.V.C. (coll. F.H.H., no. 0202-19) has the coloration almost perfectly as shown in the illustration of the holotype of *P. buprestoides* by Stoll, except for the femora lacking the black dorsal surface. Thus, it is the pale variety of the brown form occurring in Georgia and certain localities in Florida, which must be regarded as "typical" *buprestoides.* Stoll's original illustrations of 1788 are shown here in Figs. 46 and 47.

Habitats and Behavior. The white and orange forms of *A. buprestoides* seem to prefer rather dry habitats in central and southern Florida and occur in geographically restricted areas with sandy soil. The brown forms are found in more humid habitats throughout the entire range of the species, such as oak–pine forests. However, no brown form specimens have been observed in areas where the white or orange forms occur. Furthermore, there are considerable differences concerning the day-hiding behavior of the brown form versus the more active daytime behaviors of the white and orange forms. Wild adults of the brown form usually hide in crevices of tree trunks or under loose bark and frequently aggregate in clumps or clusters of up to 100 specimens. Similar clustering is observed among captive-reared nymphs and adults. The white and orange forms are usually found as solitary individuals if nymphs, or as isolated mating pairs if adults. During the day the orange and white forms rest on the trunks of oak and pine trees or on saw-palmetto fronds often in broad daylight.

The white and orange forms exhibit the same distinctive oviposition behavior described for the white population from Ocala National Forest by Hetrick (1949a,b). This includes searching for a suitable locality, digging a pit in sandy soil, dropping some eggs into it, and covering the eggs and pit with sand, followed by a search for a new location. The reasons for this behavior are as yet unknown, and ♀♀ do not show any specializations of the front and mid-legs. It is quite likely, however, that covering the eggs with sand insures optimum conditions for incubation and hatching and protects them from winter predators, such as foraging ants, birds, and rodents. Winter fires frequently burn over the scrub areas of Ocala National Forest, where the white form of *A. buprestoides* is abundant. Hetrick (1949a,b) suggested the soil cover might also serve to protect the eggs from fire. This hypothesis has yet to be tested. In contrast to the white and orange forms, this striking oviposition behavior is not known for the brown forms. They are often seen


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Fig. 55. Close-up of a couple during oviposition affected by red parasitic mites (Erythraeidae) (identification by Dr. Michael C. Thomas). Photograph by A.T.D.

to simply drop their eggs to the ground from a location perched in a tree.

White Form. Ocala National Forest, FL (Figs. 48–54). The Ocala National Forest is situated in central Florida (Marion Co.) and covers an area of ≈607 square miles. The areas of the park where the white form of *A. buprestoides* is commonly found are very dry, excessively drained and sandy habitats (Fig. 48) dominated by saw-palmetto scrub, Chapman oak, myrtle oak, turkey oak, tree lyonia or staggerbush, Florida rosemary, and sand-pine (plant names provided by O.V.C.). Most of these plants, except the saw-palmetto and pines, seem to be part of the natural diet of the Ocala population. Hetrick (1949b) reported it to have been abundant near Salt Springs in October 1948 and at Juniper Springs in late 1947 (both in Ocala National Forest), with several thousand white form *A. buprestoides* couples observed in each locality.

These insects are usually found in solitary pairs or as solitary ♀♀ and not aggregated into clumps or clusters as typical in the brown form. This suggests that ♂♂ may be less numerous than ♀♀ in the Ocala population. There has been one report of an aggregation of this form hiding in a birdhouse (Chris Tozier, personal communication). During the day, they frequently rest in fronds of saw-palmetto scrub along the edge of the forest and along sandy trails and roads (Fig. 4) or in nearby oak and sand-pine trees (Fig. 3). In the late afternoon and evening, they leave their day-hiding places to feed and find a suitable place to lay their eggs. They are easily found as they cross the sandy trails and roads and leave distinctive trails in the sand (Figs. 49 and 50). These insects are often found walking "up high on their toes," probably to keep themselves off of the hot ground. Feeding takes place at night or after they have walked a long distance across a road or sand. Often the insects stop at the first

Figs. 48–54. Habitat and egg-laying behavior of the white form of *A. buprestoides* in the Ocala National Forest. 48. Preferred habitat with sandy tracks bordered by saw-palmetto scrub and flat-woods of sand-pine and oaks (*Q. laevis*, *Q. myrtifolia*, and *Q. chapmani*) (plants identified by O.V.C.). 49. Typical trails left by *A. buprestoides* crossing the sandy tracks throughout the Ocala Forest with a couple "in action" in the center. 50. Mating couple crossing a sandy track to search a suitable place for oviposition. 51. Mating couple burying a pit for oviposition under leaf litter of turkey oak (plant identification by O.V.C.). 52. ♀ with the abdomen curled upward over the head to throw an egg into the pit with its ♂ still attached. 53. ♀ during oviposition. The leaf litter indicates myrtle oak (plant identification by O.V.C.) to be the dominant tree in this particular locality. 54. Close-up of the oviposition pit and head of ♀. Several eggs can be easily seen lying in the sand. Photographs by A.T.D.

Fig. 56. Sandy track in the Archbold Biological Research Station (Florida) in the late afternoon, showing several mating couples of the orange form of *A. buprestoides* crossing on their search for food or a suitable place for oviposition (indicated by red arrows). The inserted picture in the left lower corner shows a couple burying a pit for oviposition (♀ is of the more rarely seen pale variation). Photograph by A.T.D.

suitable plant they find and start feeding, possibly due to being exhausted and hungry from the long walk.

Observation of the oviposition behavior in September 2006 has shown this to take place exactly as described and illustrated by Hetrick (1949a,b). ♀♀ search for a suitable place, dig small pits in the sandy soil, drop five to 10 eggs in it, and afterward cover them with sand. Sometimes preexisting depressions in the sand, such as tire tracks or holes, are also used as egg-laying sites. The details of the laying process are as follows: both the front and middle legs of the female are used for digging the pits and covering the eggs, the middle legs in particular for covering the eggs after they are laid (Fig. 52). If a couple, the ♂ frequently remains attached to the ♀ during this process but not in copula. He holds on tight to the ♀'s ventral abdominal segment VII by using its hook-like vomer. After a pit has been dug the ♀ remains motionless for a while with the head and prothorax facing downward into the deepest portion of the pit and with the abdomen kept in a normal straight position (Fig. 53). Then, the abdomen is slowly curled upward over the head and an egg is dropped into it the pit (Fig. 52). Just after releasing the egg, the insect returns its abdomen to the usual position, until the next egg is ready to be laid. Approximately five to ten eggs per pit have been observed, but no strict counts have been carried out. After the pit has been covered with sand, the ♀ moves away to search for another suitable location. (Supplemental data, a video clip of the egg laying procedure is available online: Ocala_Ntl_Forest_29-03-00N_81-38-50W_Sept_24_2006_31.MOV and also at http://media.phasmatodea.de/Ocala_Ntl_Forest_29-03-00N_81-38-50W_Sept_24_2006_31.MOV). Usually, no more than two or three pits are dug per day.

If disturbed, both nymphs and adults spray their defensive secretion toward the predator's eyes and then walk away quickly. If disturbed while resting on a branch or saw-palmetto leaf, the insects drop to the ground. The defensive spray of this form (wild adults) contains primarily isomers of anisomorphal (Dossey et al. 2008).

Enemies and Parasites (Fig. 55). Birds, reptiles and spiders are probably the main enemies of *A. buprestoides*, but personal communications with Ocala National Forest park staff revealed that also black bears like to eat them. Specimens from Ocala National Forest often bear many small red mites (Erythraeidae, probably *Leptus* sp.) (identification by Dr. Michael C. Thomas, Florida State Collection of Arthropods Museum, Gainesville). These mites were not observed in

Figs. 57–61. Habitat and day-hiding behaviors of the brown form of *A. buprestoides* at Gulf of Hammock, FL. 57. Trunk of a sweetgum tree (plant identification by A.T.D.) with a long vertical cavity fully "occupied" by *A. buprestoides*. 58. Closer view of the same trunk. 59. Cluster of specimens in the same cavity. Caused by the disturbance some specimens are seen to have drops of their white defensive secretion on their pronota. 60. Vine-covered trunk of an oak tree (plant identification by A.T.D.) with a sign nailed to it and several specimens of *A. buprestoides* resting underneath the leaves below it, indicating more specimens may be found nearby. 61. The same trunk with the plastic-sign bended over to show a cluster of >25 specimens is hiding behind it. Two of the ♂♂ are seen to have already made use of their defensive glands, seen by the white drops on their pronota. Photographs by A.T.D.

specimens of *A. buprestoides* from other localities examined for this study.

Orange Form. Archbold Biological Research Station, FL (Fig. 56). The Archbold Biological Research Station (Highlands Co.) is situated in central south Florida, some 290 km south of Gainesville. It covers an area of 2,104 ha (≈5,200 acres) and contains excellent examples of all the original upland habitats of the Lake Wales Ridge. These include sand pine scrub, scrubby flatwoods, bayhead woods, swales and seasonal ponds often exhibiting a rather unique flora. The habitats where *A. buprestoides* is found are similar to the habitats in the Ocala National Forest (Marion Co.), being relatively dry, sandy, and dominated by saw-palmetto scrub, rosemary balds (*Ceratiola ericoides* Michaux; Empetraceae), and flatwoods of Florida slash pine (*Pinus elliottii* Engelmann; Pinaceae) or Archbold oak (*Quercus inopina* Ashe; Fagaceae) (plant species names provided by O.V.C.).

As with the distinctly white form in the Ocala National Forest, specimens of this pretty orange population are frequently found resting on palmetto fronds during broad daylight but do not seem to feed on them. Occasionally, specimens may also be observed

Figs. 62–63. Day-hiding behaviors of the brown form of *A. buprestoides* at the University of Florida Campus, Gainesville, FL. 62. Trunk of a pine tree (plant identification by A.T.D.) with several specimens of *A. buprestoides* resting on it (red arrows). 63. The same trunk with the loose bark removed. Two ♀♀ (dark and pale variety) are seen to hide behind it and plenty of frass (red arrow) indicates this place to be frequently "occupied" by *A. buprestoides* during the day. Photographs by A.T.D.

feeding during the day. This population does not form aggregations or clusters of specimens when at rest during the day. Specimens are usually found as solitary mating pairs. Just as in the Ocala population, adult couples are frequently found walking "high on their toes" slowly on the sandy roads ≈2 h before sunset and throughout the night to search for suitable locations to lay their eggs (Fig. 56). They leave the same distinctive trails in the sand. The oviposition behavior is generally the same as described for the white form above (Fig. 56, bottom left corner). Wild individuals of this form produce anisomorphal as their primary chemical defense (Meinwald et al. 1962, Dossey et al. 2008).

Brown Form. Gulf Hammock, FL (Figs. 57–61). Gulf Hammock Wildlife Management Area is a 9,712 ha (24,000-acre) privately owned timber plantation in southwest Levy Co. consisting of planted pine, cypress swamp, and creekside hardwoods. *A. buprestoides* is rather abundant in the forests of this area, adults being found mainly from July to September. Both, adults and nymphs almost always form clumps or clusters of up to 100 specimens aggregating either on the bare bark of cypress (Cupressaceae), sweetgum, or oak trees (plants identified by A.T.D.), either on bare bark, among vines on a trunk, or behind something like a sign nailed to a tree (Figs. 60–61). Most of the adults are found as couples with some solitary ♂♂, which suggests ♀♀ are less numerous in the Gulf Hammock population.

If disturbed these insects directly spray their defensive secretion toward the predator's eyes and usually remain still. If the offending stimulus persists they will spray more and then walk up the tree they are on very quickly to get out of danger and then take the first opportunity to hide themselves again. Defensive sprays from wild adults from this population, sampled in the field, contain anisomorphal, peruphasmal, or some mixture of the two (Dossey et al. 2008). Nymphs produce variable mixtures of anisomorphal and dolichodial, with peruphasmal being present in only trace amounts (Dossey et al. 2006).

Campus of University of Florida, Gainesville (Figs. 62–63). Several adult couples were collected in the Entomology Department's Natural Area on the campus of the University of Florida. This area is dominated by pine flatwoods (Pinaceae). It is more humid than the habitats of the white and orange forms, with considerably more rainfall throughout the year, as is true of the habitat where most of the brown form populations occur.

During the day, groups of these insects are frequently found hiding in the bark of live trees or under the loose bark of dead trees, especially pine trees (Pinaceae), which have large crevices in their bark good for hiding. They are often found underneath vines on tree trunks. Substantial piles of frass (feces) are found in the bark crevices below their hiding-places and on the ground at the base of the tree, which indicates these sites to be frequently "occupied" by *A. buprestoides.* The hiding places seem to be only vacated at night to feed or search for a suitable place for oviposition. As many other wingless Phasmatodea do, these insects usually return to the same hiding places in the early morning rather than searching for a new one. However, further observation is needed to confirm that the same individuals return to the same hiding spots. Individuals in this population were observed at night feeding on sweetgum, but blackberry is also common in the area. The defensive spray from adults in this population contains either anisomorphal,

Fig. 64. Several specimens of the brown form of *A. buprestoides* hiding in a bee-hive at the collection site near Gainesville Regional Airport, FL (pale variety in the front and dark variety in the back). Photograph by A.T.D.

peruphasmal, or some mixture of the two (Dossey et al. 2008).

Near Gainesville Regional Airport, FL (Fig. 64). In the semihumid flatwoods around Gainesville Airport pines and sweetgum are some of the most common trees in the area (plants identified by A.T.D.). Additionally, large areas covered in blackberry (identified by A.T.D.) are present in the area where *A. buprestoides* was found. This species is moderately abundant in this area and often found in a similar manner to specimens in the Gulf Hammock area (Levy Co.) or the University of Florida campus. Some individuals of this variety were found in abandoned artificial beehives. These or similar constructions are obviously an attractive hiding place for *A. buprestoides*, because they are dark and provide good protection from predators. Wild adults from this population produce mainly peruphasmal for its chemical defense. Captive nymphs produce a variable mixture of anisomorphal and dolichodial until sexual maturity when all individuals analyzed began producing only peruphasmal (Dossey et al. 2008).

Sanibel Island and Pinellas Co., FL. This rather distinctive variety of the brown form is, as the pale cream colored stripes of the body suggest, found in dry sandy areas near the Florida west coast. Although it belongs to the brown form of *A. buprestoides*, this variety is exceptional in its day-hiding behavior, because several mating couples were found solitarily in the open field resting on isolated shrubs close to the ground. The defensive spray of individuals in this population contains mostly peruphasmal (Dossey et al. 2008).

Moss Point, MS. Specimens collected in April 1993 at Moss Point near Pascagoula, MS, were available for examination from the collection of Oliver Zompro (Kiel, Germany). They were found "under wood," which could have meant on tree trunks or under loose bark. The chemical defense of this form has not been studied.

Discussion

Examination of *A. buprestoides* from various localities throughout its distributional range and field studies in 10 locations in Florida have shown this species to have considerable variation concerning to its coloration (Fig. 65), and striking differences in day-hiding and oviposition behaviors. All are likely to be adaptions to their habitats, which range from semihumid pine or oak woods and coastal regions to rather arid and open-land with sandy soil.

Fig. 65. Direct comparison of the white form from Ocala National Forest (left) with a couple of the brown form from Gainesville, FL (right). Photograph by A.T.D.

The different color forms of *A. buprestoides* can be attributed to certain habitats, and, as usual in phasmatodeans, increase the camouflage to make the specimens visually disappear into their surroundings. Although the white form in the Ocala National Forest and the orange form in the Archbold Biological Research Station do not seem to make any effort at hiding in the day, the white form may be hard to see by a predator (e.g., a bird) on the white sandy soil, which dominates in the Ocala National Forest. However, any predators closer to the ground (e.g., small mammals or reptilians) should have no trouble finding them when the insects walk on the open sandy tracks to search for food or a suitable place for oviposition. The bright coloration of the orange form at Archbold Biological Research Station is odd and certainly does not serve for a better camouflage on the sandy ground. Instead, specimens are often found on plants with yellowish or orange young sprouts or flowers (e.g., staggerbush, *Lyonia ferruginea* [identified by Dr. Mark A. Deyrup] or sand heath *Ceratiola ericoides* [species name from O.V.C.]) and are usually observed to feed and rest on the leaves near the terminals often in broad daylight. Specimens were also seen resting on the same plants when they were completely green. As an alternative to the camouflage hypothesis, because these insects also produce a rather effective noxious defensive spray, the brighter coloration of the white and orange forms may also be a warning coloration for predators to "stay away."

In contrast, the coloration of the brown form, which has the dorsal stripes ranging from pale creamy to mid-brown, seems to be a much better camouflage in its natural habitats, which primarily includes semihumid pine or oak forests. These insects usually rest on tree trunks or hide in tree crevices, or under loose bark, or under leaf litter during the day. In these places the black and brown coloration provides good camouflage for avoiding notice by predators. Hence, their coloration is clearly an adaption to the general colors dominating their natural habitats and that of their preferred resting or hiding places. If disturbed, specimens of the brown form, instead of falling to the ground, spray their defensive secretion toward the predators' eyes and then very quickly walk up the tree they are on.

In addition to coloration, there are considerable differences concerning the day-hiding behaviors of the white and orange forms versus those of the brown form. As stated above, the white and orange forms seem to make little if any effort at hiding in the day and are frequently found in broad daylight resting in fronds of saw-palmetto scrub, sand heath, or in nearby oak and sand-pine trees (plant species names provided by O.V.C.). Instead of hiding, they often rest in quite visible places on top of the leaves or close to the terminals of branches and are usually found as solitary couples. There has only been one reported case of aggregation in the white form where many were observed hiding in a birdhouse (Chris Tozier, personal communication). In contrast to the white and orange forms, specimens of the brown form typically rest on tree trunks under vines, hide in crevices of tree trunks, under loose bark or leaf litter, and frequently aggregate in clumps or clusters of up to 100 specimens. The aggregation of clusters certainly increases the protection from predators, because several specimens can spray their defensive secretion once attacked and single insects are difficult to define.

Captive breeding of the three color forms recognized here has shown that alternative food plants (*Ligustrum* spp., *Rubus* spp., *P. lanceolata*, and *Q. robur*) (plant species names provided by O.V.C.) have no affect on the coloration and that a certain color form remains constant for at least two generations, but no long-term observations have been made. When the insects were given a large cage with plenty of floor-space and a layer of sand, the typical oviposition behavior of the white form was also observed in captivity. ♀♀ of the white form kept in smaller cages with insufficient floor space and without sand on the ground considerably reduced their egg productivity and they were often observed to simply drop their eggs. Specimens of the brown form frequently aggregated into clusters either in the corners of their breeding cage, or under pieces of bark if offered. As observed in the wild, the same hiding opportunities were rarely seized by specimens of the white form. These comparisons of captive-reared specimen coloration and behavior demonstrate that these traits are genetically programmed in the respective populations of *A. buprestoides* from which they came and are not a result of developmental environment, food-plant choice, or parental involvement. Cross-breeding of the white (Ocala National Forest) and brown color form (Gainesville) produced fertile hybrids in the breeding stocks of A.T.D. (USA) and O.V.C. (Germany). The fertile hybrids prove the differently colored colonies of the species to be only forms and not distinct species or subspecies.

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