2003

Acalypha deamii: distribution east of the Appalachians and comparative studies of reproductive anatomy

Patricia A. Truman

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ABSTRACT

Acalypha deamii (Euphorbiaceae), once thought restricted to flood plains of the Ohio and mid-Mississippi River systems, is now documented from similar habitats in Virginia, Maryland, and West Virginia along the James, Potomac, Rappahannock, Roanoke (Staunton), and Shenandoah rivers. This species is recognized by two-carpellate gynoecia, large seeds, and the routine occurrence of allomorphic flowers and fruits, features sporadically found within this large genus. In addition to documenting the newly recognized range extension of Acalypha deamii, this thesis also investigates the nature of its allomorphic reproductive structures. Staminate, pistillate, fruiting, and allomorphic reproductive structures of Acalypha deamii and a closely related species, Acalypha rhomboidea, were studied using LM and SEM. Staminate flowers are composed of four crystal-encrusted valvate sepals and eight stamens that bear divergent vermiform anthers with helically thickened endothecium, amoeboid tapetum, and tricolpate pollen. Pistillate flowers are bracteate, but otherwise naked, two-carpellate (Acalypha deamii) or three-carpellate (Acalypha rhomboidea), and have bitegmic, crassinucellate, anatropous ovules arising from an apical, axile placenta. Fruits from pistillate flowers are covered with trichomes, some gland-tipped, some simple and uniseriate. Internally, fruit walls bear a prominent inner-zone of sclerified cells involved in dehiscence and ballistic dispersal of seeds. Seeds are mottled tan to dark brown. Testa contains two prominent cell layers of the inner integument: the arcuate outer-most cells are sclerified and the inner-most cells are tracheid-like. Internal anatomy of allomorphic reproductive structures largely matches those of typical pistillate flowers and fruits. In contrast with pistillate flowers, allomorphic structures lack gland-tipped trichomes but have a markedly muricate surface, a one-carpellate
ovary that develops in a reflexed orientation, and more weakly developed mechanical layers in the fruit wall. Further, allomorphic seeds of *Acalypha deamii* possess weak sclerification within the testa. Notably, materials studied clearly show presence of embryos within allomorphic seeds of *Acalypha deamii* and *Acalypha rhomboidea*, evidence that these structures are fertile and viable.
ACALYPHA DEAMII: DISTRIBUTION EAST OF THE APPALACHIANS AND COMPARATIVE STUDIES OF REPRODUCTIVE ANATOMY

BY

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EXAMINING FACULTY:
ACALYPHA DEAMII: DISTRIBUTION EAST OF THE APPALACHIANS AND COMPARATIVE STUDIES OF REPRODUCTIVE ANATOMY

BY

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B. S., Meredith College, 1997

A Thesis
Submitted to the Graduate Faculty
of the University of Richmond
in Candidacy
for the degree of
MASTER OF SCIENCE
in
Biology

May, 2003

Richmond, Virginia
ACKNOWLEDGEMENTS

Special thanks are due to the persons who contributed in many ways to the completion of this work. I am indebted to Mr. Gary Fleming of the Virginia Natural Heritage Program for his contributions of *Acalypha deamii* collection data throughout Maryland, Virginia, and West Virginia and for his insightful comments about the ecology of this plant. For his expertise and assistance in generating a map of *Acalypha deamii* collections, I thank Dr. W. Michael Harrison, University of Richmond.

I am extremely grateful to the University of Richmond Graduate School of Arts and Sciences in generously providing a grant to fund this project. Special thanks are offered to members of the Biology Department at the University of Richmond for their support and help with this endeavor. I would also like to thank members of my committee for their help, suggestions, and generous support: Dr. Rafael O. de Sá and Dr. Gary Radice. For his assistance in the laboratory and for sharing information regarding other species of *Acalypha*, I would like to thank Chris Rigsby, an undergraduate student at the University of Richmond.

For her encouragement, I would like to thank Dr. Janice C. Swab, Meredith College. Her vitality was an inspiration to a budding young biologist.

To my advisor, Dr. W. John Hayden, I am grateful for his time, energy, advice, patience, and knowledge. His encouragement in support of this work was invaluable to me.

Finally, I am most grateful to my family for their love and support throughout this endeavor. Without their faith and assurance, I would not have had this opportunity.
# TABLE OF CONTENTS

Acknowledgments ........................................................................................................... ii

List of Figures ........................................................................................................... iv

Introduction ............................................................................................................... 1

Materials and Methods ............................................................................................... 6

Results and Discussion ............................................................................................... 9

- Geographic Distribution ....................................................................................... 9
- Staminate Flowers ............................................................................................... 10
- Pistillate Flowers ............................................................................................... 14
- Fruits .................................................................................................................. 16
- Seeds .................................................................................................................. 17
- Allomorphic Flowers, Fruits, and Seeds ............................................................ 19

Conclusions .............................................................................................................. 21

Literature Cited ......................................................................................................... 23

Tables ....................................................................................................................... 26

Figures ..................................................................................................................... 28

Appendix I ............................................................................................................... 54

Appendix II ............................................................................................................... 62

Curriculum Vitae ...................................................................................................... 64
<table>
<thead>
<tr>
<th>Number</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.</td>
<td><em>Acalypha deamii</em> shoot apex of mature, flowering individual</td>
<td>28</td>
</tr>
<tr>
<td>2.</td>
<td><em>Acalypha rhomboidea</em> shoot apex of mature, flowering individual</td>
<td>28</td>
</tr>
<tr>
<td>3.</td>
<td>Distribution map of <em>Acalypha deamii</em></td>
<td>29</td>
</tr>
<tr>
<td>4.</td>
<td><em>Acalypha deamii</em>, apex of staminate spike</td>
<td>30</td>
</tr>
<tr>
<td>5.</td>
<td><em>Acalypha deamii</em>, external surface of staminate flower bud</td>
<td>30</td>
</tr>
<tr>
<td>6.</td>
<td><em>Acalypha deamii</em>, section through sepal of staminate flower bud</td>
<td>31</td>
</tr>
<tr>
<td>7.</td>
<td><em>Acalypha deamii</em>, cruciate crystals on staminate flower</td>
<td>31</td>
</tr>
<tr>
<td>8.</td>
<td><em>Acalypha rhomboidea</em>, staminate flower primordium and bud</td>
<td>32</td>
</tr>
<tr>
<td>9.</td>
<td><em>Acalypha deamii</em>, staminate flower before anthesis</td>
<td>32</td>
</tr>
<tr>
<td>10.</td>
<td><em>Acalypha rhomboidea</em>, staminate flower before anthesis with abscission zone</td>
<td>33</td>
</tr>
<tr>
<td>11.</td>
<td><em>Acalypha deamii</em>, staminate flower before anthesis with abscission zone</td>
<td>33</td>
</tr>
<tr>
<td>12.</td>
<td><em>Acalypha rhomboidea</em>, staminate flower at anthesis</td>
<td>34</td>
</tr>
<tr>
<td>13.</td>
<td><em>Acalypha deamii</em>, anthers within a staminate flower bud</td>
<td>34</td>
</tr>
<tr>
<td>14.</td>
<td><em>Acalypha rhomboidea</em>, anther primordia</td>
<td>34</td>
</tr>
<tr>
<td>15.</td>
<td><em>Acalypha deamii</em>, young anther</td>
<td>35</td>
</tr>
<tr>
<td>17.</td>
<td><em>Acalypha rhomboidea</em>, nearly mature anther with amoeboid tapetum</td>
<td>36</td>
</tr>
<tr>
<td>18.</td>
<td><em>Acalypha deamii</em>, nearly mature anther with amoeboid tapetum</td>
<td>36</td>
</tr>
<tr>
<td>19.</td>
<td><em>Acalypha deamii</em>, nearly mature anther with tricolpate pollen</td>
<td>37</td>
</tr>
</tbody>
</table>
20. *Acalypha rhomboidea*, multi-lobed bract enclosing immature fruit ..........37

21. *Acalypha rhomboidea*, immature pistillate flowers ...............................38

22. *Acalypha deamii*, immature pistillate flowers ........................................38

23. *Acalypha rhomboidea*, stigmatic branches of pistillate flowers .............39

24. *Acalypha deamii*, young fruit and staminate spike .................................39

25. *Acalypha rhomboidea*, proliferation of inflorescence units .....................40

26. *Acalypha deamii*, buttressed trichomes on epidermis young fruit ............40

27. *Acalypha deamii*, buttressed trichome base from fruit wall .....................41

28. *Acalypha deamii*, pistillate flower bud ................................................41

29. *Acalypha deamii*, placental connection of ovules ..................................42

30. *Acalypha rhomboidea*, immature pistillate flower and ovules ..................42

31. *Acalypha rhomboidea*, young fruit and micropyle of ovules ....................43

32. *Acalypha rhomboidea*, inner micropyle, nucellar beak, and early embryo ...43

33. *Acalypha rhomboidea*, chalazal end of ovule ........................................44

34. *Acalypha deamii*, simple and glandular trichomes on fruit surface ............44

35. *Acalypha deamii*, fruit wall and testa ................................................45

36. *Acalypha rhomboidea*, fruit wall and testa ...........................................45

37. *Acalypha rhomboidea*, fruit wall ..........................................................46

38. *Acalypha rhomboidea*, base of fruit and seed ........................................46

39. *Acalypha deamii*, seeds ........................................................................47

40. *Acalypha rhomboidea*, seeds ..................................................................47

41. *Acalypha deamii*, arcuate sclereids from the outer-most layer of the inner

    integument ...............................................................................................................48
42. *Acalypha deamii*, base of ovule ................................................................. 48

43. *Acalypha deamii*, tannin-filled tracheids of inner-most layer of inner integument ................................................................. 49

44. *Acalypha rhomboidea*, tracheids of inner-most layer of inner integument ........................ 49

45. *Acalypha deamii*, endosperm cells of mature seed ........................................... 50

46. *Acalypha rhomboidea*, fruit and seed near maturity ............................................. 50

47. *Acalypha deamii*, allomorphic fruit .................................................................. 51

48. *Acalypha deamii*, allomorphic flower ................................................................. 51

49. *Acalypha rhomboidea*, testa and pericarp of allomorphic fruit .......................... 52

50. *Acalypha deamii*, muricate surface of allomorphic fruit .................................... 52

51. *Acalypha rhomboidea*, fruit wall and testa of allomorphic fruit ....................... 53

52. *Acalypha deamii*, allomorphic fruit and seed .................................................... 53
INTRODUCTION

"Being an unsightly Genus, it is neglected by the Botanists" (Rafinesque 1836)

_Acalypha_ is a genus of approximately 450 currently recognized species classified in the family Euphorbiaceae (Webster 1994). Most _Acalypha_ species inhabit tropical environments, however some species are found in temperate regions (Webster 1967). _Acalypha_ species are typically monoecious shrubs or herbs with apetalous flowers (Govaerts et al. 2000). Staminate flowers occur in spikes and pistillate flowers are bracteate either solitary or arranged in spikes (Fernald 1950). To date, systematic studies of the genus _Acalypha_ have focused largely on distinguishing species based on characters of gross morphology such as stem pubescence, petiole length, leaf shape, inflorescence architecture, and seed size (Pax and Hoffman 1924). Anatomical investigations, in conjunction with other approaches such as molecular systematics, hold much promise for clarification of relationships within the genus. This thesis features a comparative anatomical study of two species within the genus and also documents a recently recognized range extension for one, _Acalypha deamii_ (Weatherby) Ahles

The five species of _Acalypha_ indigenous to Virginia are classified series Brachylobae and series Sclerolobae. Locally, species of series Brachylobae, often referred to as the _Acalypha virginica_ complex, include _Acalypha deamii_, _Acalypha gracilens_ Gray, _Acalypha rhomboidea_ Raf., and _Acalypha virginica_ L.. The remaining local species is _Acalypha ostryaefolia_ Riddell, of series Sclerolobae.
Historically, most species in the *A. virginica* complex were considered to be varieties of *A. virginica* (e.g., Müller 1865, 1866). Rafinesque (1836) distinguished *A. rhomboidea* as a separate species from *A. virginica* based on pubescence of stem and other morphological characters. Weatherby (1927) recognized three species in the *A. virginica* complex: *A. gracilens* consisting of three varieties, *A. rhomboidea* consisting of two varieties [variety *rhomboidea* Raf. and variety *deamii* Weath.], and *A. virginica*. Ahles (1955) elevated Weatherby’s variety *deamii* to species, a disposition followed by many subsequent authors (Fernald 1950, Webster 1967, Gleason and Cronquist 1991, Levin 1999).

Common names for the local species of *Acalypha* include copperleaf or three-seeded mercury. These names apply particularly well to *A. virginica*. Foliage of this species turns coppery-red in late autumn. The basis for the name three-seeded mercury relates to a Mediterranean plant, *Mercurialis annua* L. (also Euphorbiaceae), commonly known as mercury. *Mercurialis* fruits produce only two seeds, whereas most Euphorbiaceae, *Acalypha* included, produce three. Hence, when North American *A. virginica* first came to the attention of European botanists its resemblance to and distinction from *Mercurialis* was reflected in the common name, three-seeded mercury. By extension, both common names have been applied to other species in the *A. virginica* complex regardless of leaf color or seed number.

The two species included in this study, *A. deamii* and *A. rhomboidea*, are generally similar in respect to habit and gross morphological features (figs. 1, 2), as well as the basic inflorescence organization. *Acalypha rhomboidea* and *A. deamii* produce pistillate flowers (and fruits) subtended by a staminate spike and a multi-lobed
bract. The bracts are deeply lobed in contrast to the shallowly crenate bract of *A. gracilens*. Further, both species have relatively short trichomes on their stems in contrast to the long, spreading, trichomes of *A. virginica*. Fruits from typical pistillate flowers of both species readily dehisce resulting in ballistic dispersal of seeds. Because of this overall similarity (figs. 1, 2), *A. deamii* was originally considered to be a variety of *A. rhomboidea* (Weatherby 1927).

Careful comparison of the morphological characteristics of *A. rhomboidea* and *A. deamii* allows the two taxa to be distinguished easily (Table 1). *Acalypha rhomboidea* is three-carpellate and three-seeded with seeds measuring 1.2 to 2.0 mm. In contrast, *A. deamii* is two-carpellate and two-seeded with larger seeds measuring 2.2 to 3.2 mm (Webster 1967). Allomorphic flowers and fruits rarely occur on *A. rhomboidea*, while these structures are characteristic of *A. deamii*. In addition, subtle differences exist in leaf size and shape. Leaves of *A. rhomboidea* are rhombic and horizontal with divaricate petioles (Gleason and Cronquist 1991), whereas the ovate leaves of *A. deamii* have a spreading petiole (Fernald 1950, Gleason and Cronquist 1991). Further, the leaf blades of *A. deamii* tend to droop somewhat (Fernald 1950, Gleason and Cronquist 1991), at least under relatively dry conditions. The leaf characters, however, do not always offer a clear-cut distinction between the two species. Carpel number and ovary/seed size provide the best field characters.

Knowledge of *A. deamii* and *A. rhomboidea* is restricted largely to alpha-taxonomy and floristics, i.e., nomenclature, gross morphology, and geographic distribution. *Acalypha deamii* was once thought to be restricted to mesophytic floodplain habitats of the mid-Mississippi and Ohio River systems west of the
Appalachian Mountains (Webster 1967). Recent fieldwork, however, indicates that the distribution of *Acalypha deamii* extends farther east, having been found in Maryland, Virginia, and West Virginia. Documentation of this newly recognized range extension east of the Appalachians is the focus of this thesis.

A second focus is to investigate the nature of allomorphic flowers of *A. deamii*. Although known to occur in several species of the genus *Acalypha* (Radcliffe-Smith 1973), allomorphic flowers are poorly understood. In fact, there is speculation in the literature about the sterility or fertility of allomorphic flowers; early references to certain tropical species of *Acalypha* suggest that they are sterile aberrations (Müller 1866) and this idea has been repeated more recently by Gamble (1967). Alternatively, Venkata Rao (1971) and Radcliffe-Smith (1973) indicate that allomorphic flowers produce viable seeds at least in certain tropical species. The fertility or viability of allomorphic flowers/fruits/seeds produced from temperate species of *Acalypha* has not been investigated. Thus, detailed anatomical developmental studies are clearly warranted. The foundation for such a study, however, must include an understanding of the structure and development of the ordinary staminate and pistillate flowers. In this regard, our knowledge is also somewhat rudimentary. The only publication on the subject is Landes’ (1946) study of seed development of *A. rhomboidea* (i.e., seeds produced by ordinary fruits). Notably, anatomical structures in Landes’ (1946) paper are documented solely by line drawings; neither photomicrographs nor electronmicrographs of flower, fruit, or seed structures have been published for the two species studied here. To understand better the nature of allomorphic flowers, the second focus of this study is to examine anatomically all reproductive structures, the
staminate, pistillate, and allomorphic flowers, as well as the fruits and seeds that develop from pistillate and allomorphic flowers. This study also included the same range of structures in the closely related species, *A. rhomboidea*, for comparative purposes.
**Materials and Methods**

**Geographic distribution.** Specimens of *A. deamii* collected by W. John Hayden, University of Richmond, and Gary Fleming, Virginia Natural Heritage Program were compiled to summarize the distribution of the species east of the Appalachian Mountains (Appendix I). Based on locality data for each collection, latitude and longitude for each site was determined. With the assistance of Dr. J. Michael Harrison, University of Richmond, latitude and longitude data for all collections were super-imposed on a base map featuring rivers of Maryland, Virginia, and West Virginia.

**Morphology and Anatomy.** Staminate, pistillate, and allomorphic reproductive structures of *A. deamii* and *A. rhomboidea* were examined using light microscopy and scanning electron microscopy. Collection data for specimens studied anatomically are listed in Appendix II. Specimens were preserved in the field using formalin-acetic acid-70% ethyl alcohol (FAA) solution (Johansen 1940, Berlyn and Miksche 1976). Each collection consisted of staminate, pistillate, and allomorphic flowers at various stages of development. Vouchers for each anatomical specimen were prepared and deposited in the University of Richmond Herbarium.

In the laboratory, the FAA solution was replaced with 70% ethyl alcohol for storage until processing. From each sample, some material was processed for observation via light microscopy and another portion was prepared for scanning light microscopy. A range of developmental stages was included among the materials prepared for detailed study.
For light microscopy, specimens were dehydrated in a graded series of tert-butyl alcohols and then embedded in paraffin in a 60°C oven (Johansen 1940, Berlyn and Miksche 1976). Following paraffin infiltration and casting, specimen blocks were trimmed and mounted on stubs for sectioning via rotary microtome. Ribbons produced by sectioning were reaaffixed to slides using Bissing's adhesive (Bissing 1974). Slides were stained using a combination of hematoxylin and safranin (cf. Johansen 1940, Berlyn and Miksche 1976) and mounted in Permount synthetic resin.

Digital photomicrographs were prepared using a Nikon Coolpix 950 camera and a Martin Microscopes MMCoolS/N:0120 photo ocular attached to a Nikon Labophot optical microscope. To ensure consistent magnification of images, the camera was always set at maximum zoom. The following camera settings were used: flash off, macro close-up focus, and enhanced contrast. The color images were saved as jpg files. The raw photomicrographs were converted into grayscale images and overall image tone was adjusted using Corel Photo House version 1.1. For each photographic image at a given magnification, scale bars were created from photomicrographs of stage micrometers at the same magnification.

For scanning electron microscopy (SEM), specimens were initially dehydrated to 100% ethyl alcohol and dried using an Electron Microscopy Sciences 850 Critical Point Dryer. Specimens were then mounted on a stub using aluminum tape and coated with a Hummer VII Sputter Coater to a thickness of approximately 75 nm. Observations were made using a Hitachi S-2300 SEM and electron micrographs were produced via Polaroid type 55 film.
SEM images were scanned with a Hewlett Packard Scanjet 4470C and saved as jpg images. For each electron micrograph, scale bars produced by the SEM were used to create new scale bars superimposed on the final images.
RESULTS AND DISCUSSION

Geographic Distribution

Figure 3 summarizes the known distribution of *A. deamii* east of the Appalachian Mountains. In addition to its previously known distribution in the Ohio and mid-Mississippi River systems, this species is now also known from the flood plains of the James, Roanoke (Staunton), Rappahannock, Shenandoah, and Potomac Rivers. Within these river systems, *A. deamii* inhabits only the piedmont region or in the case of the Shenandoah River, the Shenandoah Valley. The species is not known from the coastal plain nor in mountainous headwaters. Its preferred habitat, flood-plain forest with sandy soils and a preponderance of herbaceous annual understory plants, is common along rivers in the piedmont, but is seldom found in the coastal plain or mountains. Notably, *A. deamii* has not been found outside of this preferred riparian habitat. Its fidelity to a well-defined natural habitat both east and west of the Appalachian Mountains and its apparent inability to colonize areas of human disturbance anywhere within its range suggest that *A. deamii* is a native element of the flora. In this respect, the biology of *A. deamii* seems distinctly different from that of *A. rhomboidea*, an abundant weedy plant found in a wide variety of natural and disturbed habitats.

The floodplain habitats where *A. deamii* is found include a variety of deciduous woody species that can withstand periodic scouring by floods. Trees and shrubs such as *Acer saccharinum* Marshall, *Acer negundo* L., *Celtis occidentalis* L., *Toxicodendron radicans* L., *Lindera benzoin* (L.) Blume, *Fraxinus pennsylvanica* Marshall, *Platanus occidentalis* L., *Jugulans nigra* L., and *Ulmus americana* L. are commonly associated

**Staminate Flowers**

**Organography.** Staminate flowers of *Acalypha deamii* and *A. rhomboidea* are arranged in spikes that arise near the base of bracteate pistillate flowers. Peduncles of these spikes are minutely pubescent with uniseriate trichomes and bear staminate flowers towards the apex. The flowers are borne at a level above the bract that subtends the pistillate flower. Staminate flowers occur in small, bracteate clusters each of which possesses individual flowers at various developmental stages. For example, within a single cluster of flowers it is not uncommon to find a full developmental range from minute primordia to remnant pedicels of abscised flowers (fig. 4). Evidently staminate flowers are at anthesis for a relatively short period of time, thus routine observations reveal mostly buds and stump-like of pedicels of abscised flowers. Pedicels of nearly mature flower buds are 0.1 to 0.6 mm long. Perianth of staminate flowers consists of
four valvate sepals (fig. 5). External surfaces of each sepal exhibit an irregular surface, the result of cruciate crystals projecting from the epidermis (figs. 6, 7). These cruciate crystals are absent from sepal margins, but are frequent along the midvein. Stamens are eight and partially united, basally, by their filaments. Distally each filament bears a pair of divergent vermiform anthers (or anther sacs), yielding as many as sixteen anthers per flower. In some floristic literature (for example, Fernald 1950, Radford et al. 1964), stamen number for these taxa is reported as eight to sixteen. If sixteen stamens were truly present, there should be thirty-two individual anthers per flower, a number well above that observed in any flower in this study. The discrepancy may be explained in part by failure of some authors to distinguish anther number and stamen number, a critical factor for Acalypha because its stamens have divergent anthers. Present results (eight stamens and sixteen anthers) are consistent, however, with descriptions of stamen number by Gleason and Cronquist (1991).

**Histology.** At the earliest stage observed, staminate flowers consist of a central meristematic dome flanked by four sepal primordia that project to the same height as the dome (fig. 8). By the time sepal primordia converge, enclosing the floral bud, the eight stamen primordia are visible as lobes of the central dome. In early stages, sepal primordia are merely three cells thick (fig. 8). As development proceeds, sepal thickness increases, most markedly towards the apex. Shortly before anthesis, basal/proximal portions of the sepal remain relatively thin, perhaps three or four cells thick, whereas apical/distal portions become irregularly thickened, consisting of approximately twice as many cells (fig. 9). A portion of the extra thickness near sepal apices consists of relatively large cells forming buttress-like bases that support
epidermal cells bearing cruciate crystals. At their convergent tips, however, sepals are thinner than the surrounding buttressed regions (fig. 9). At anthesis, the cup-like sepals reflex along the pedicel such that sepal tips occupy a position about the same level as the receptacle (fig. 12). An abscission zone is visible in the pedicel at bud stages (figs. 10, 11). At anthesis, the abscission zone is prominent, staining darkly, forming a distinctly constricted band, observations consistent with the ephemeral nature of staminate flowers (fig. 12). Within each sepal, xylem was visible, but phloem was not detected. Xylem elements of the sepal are restricted to a few cells immediately adjacent to the inner epidermis (fig. 5). At bud stage, the inner epidermis equates with upper (adaxial) epidermis at anthesis, so xylem position in the sepals conforms with expected positions of xylem in foliar organs. A single vascular trace extends through the filament to the base of the anther.

Staminal filaments diverge from a basal androphore at two levels, four from its apex and four slightly lower from its perimeter. Sectioned anthers reveal a single tract of microspores or pollen grains. Since the anthers are paired, but diverge widely and are often somewhat pendulous (fig. 13), anther structure technically conforms with the bisporangiate condition. Bisporangiate anthers have been reported previously in Acalypha (Davis 1966), in contrast to the typical tetrasporangiate condition common to Euphorbiaceae (Kapil and Bhatnagar, 1994). Despite their small size and ab initio isolation as separate anther sacs, details of anther wall structure match well general patterns of development. In early stages, three distinct cell layers are visible corresponding to epidermis, primary parietal layer, and primary sporogenous layer; each of these layers is one cell thick (fig. 14). Eventually, the primary parietal layer will
form endothecium, middle layer, and tapetum (fig. 15). The anther portions of the stamen elongate as development proceeds resulting in somewhat curved, "vermiform," structures that loosely fill the space within the flower bud (fig. 13). During anther elongation, the epidermal layer fails to maintain continuity over the surface. Hence, at maturity endothecium frequently is the cell layer forming the surface of the anther. Endothecium is marked by helical thickenings (fig. 16). Although a middle layer is routinely visible, the origin of this layer (common with endothecium precursor or common with tapetum precursor) could not be determined based on the material available. Davis (1966) reports monocotyledonous anther wall formation in *Acalypha*, which is consistent with the single middle layer observed. The innermost layer of the anther wall consists of tapetum. In the species studied, tapetum is amoeboid which means that the protoplasts separate from their cell walls and intrude among the developing microspores/pollen grains (figs. 17, 18). In the material examined, amoeboid tapetum cells revealed no more than a single nucleus. In contrast, most species of Euphorbiaceae have been reported to have a 2 or 3-nucleate glandular (secretory) tapetum (Davis 1966, Kapil and Bhatnagar 1994). Pollen grains are tricolpate (fig. 19) and binucleate in agreement with previous reports (Kapil and Bhatnagar 1994).

In cross section, the stomium of anther walls is recognizable as a pair of lightly sclerified cells that protrude from the surface (fig. 18). Dehiscence is longitudinal. Because there is no floral advertisement nor obvious pollinator reward, pollen dispersal by wind has been assumed (Webster 1967, 1994). Once the pollen is shed, staminate flowers are promptly abscised.
Pistillate Flowers

**Organography.** In early stages, each pistillate flower and its associated staminate spike is partially enveloped by a leafy bract. Before anthesis, pistillate bracts diverge somewhat and the staminate spike emerges beyond the bract margin. Pubescence of the bract surface includes simple, uniseriate and/or glandular hairs (fig. 20). Early in the flowering season, these bract-flower-spike complexes occur singly at the nodes. As the season progresses, additional bract-flower-spike complexes proliferate. Further, from within pre-existing bracts, either secondary bract-flower-spike complexes may arise or additional ebracteate pistillate flowers may develop along with new staminate spikes (figs. 21, 22). At the time the pistillate flowers are receptive to pollen, bracts are relatively small and stigmas protrude beyond the bract tips (fig. 23). Pistillate flowers are naked and either two-carpellate (*A. deamii*) (fig. 24) or three-carpellate (*A. rhomboidea*) (fig. 25). Gynoecia bear thread-like stigmas that, for each carpel, branch several times. Ovary surface is uniformly pubescent; however, trichomes towards the apex arise from buttress-like papillate bases (figs. 26, 27). Several features of flowers and the fruits they produce are summarized in Tables 1 and 2.

**Histology.** The carpel wall of both *A. deamii* and *A. rhomboidea* is composed of three layers: a central mass of parenchyma (mesocarp) bounded by an outer epidermis (exocarp) and an inner epidermis (endocarp) (fig. 28). At anthesis, all cell layers of the carpel wall are uniform, with scarcely any sign of the stomates, trichomes, and buttressing that will develop on the outer epidermis, nor any sign of the sclerified mechanical tissue that will develop from the inner epidermis and the first two layers of
adjacent mesocarp (fig. 28). At this time, future vascular tissues of the mesocarp are largely procambial.

The anatropous ovules of both *A. deamii* and *A. rhomboidea* are solitary per locule and oriented in an anaxile position with the micropyle end towards the apex of the ovary and the chalazal end towards the base (Webster 1967, Landes 1946, Kapil and Bhatnagar 1994) (fig. 29). As is typical for most Euphorbiaceae at this stage, the ovules of *A. deamii* and *A. rhomboidea* are attached towards the apex of the locular space. However, as a result of differential growth, the placenta occupies a subapical position within the locule in fruit and seeds. Ovules are bitegmic (fig. 30). The inner portion of the micropyle formed by the inner integument projects more or less vertically. In contrast, as the micropyle passes through the well developed outer integument, it orients towards the floral axis terminating at the placental obturator (fig. 31). The ovules are crassinucellate with a small nucellar beak projecting towards the micropyle (fig. 32). Towards the micropylar end, nucellar cells adjacent to the embryo sac are densely cytoplasmic. At the chalazal end, nucellus is five or six cells thick; from among these cells the hypostase will develop (fig. 33).

Nucellar beaks are somewhat unusual among the angiosperms. However, this structure has been noted in a number of Euphorbiaceae and has been studied in some detail in this family (Kapil and Bhatnagar 1994). Generally, in Euphorbiaceae, the nucellar beak, derived from both dermal and subdermal cells, extends slightly beyond the micropyle and contacts the obturator (Kapil and Bhatnagar 1994). As such, the obturator and nucellar beak together function as a bridge for pollen tubes to traverse the distance between the base of the style to the female gametophyte. In contrast with most
Euphorbiaceae, the nucellar beak in ovules of *Acalypha* extends only to the inner aperature of the micropylar canal (endostome) (Davis 1966, Webster 1967, Kapil and Bhatnagar 1994); the ovules of *A. deamii* and *A. rhomboidea* conform.

Embryo sacs in the early stages of embryogenesis were not studied in detail, however, Landes (1946; and summarized by Davis 1966, Webster 1967) provides an outline of these stages in *A. rhomboidea*. Following meiosis, all four megaspores contribute to the development of the female gametophyte, thus development is tetrasporic which is evidently common for the genus (Kapil and Bhatnagar 1994, Webster 1967). There are two post-meiotic divisions resulting in a sixteen-cell female gametophyte conforming to the pattern known as the *Penaea*-type (as defined in Maheshwari 1950). Early embryos possess four suspensor cells, but are otherwise globose until cotyledons develop.

**Fruits**

At maturity, fruit wall conforms to the common pattern of exocarp, mesocarp, endocarp (figs. 35, 36). The exocarp consists of a simple epidermis bearing trichomes that are simple and uniseriate some with glandular tips (fig. 34). At the base of the fruit, trichomes are inserted between ordinary epidermal cells, however, towards the top of the fruit, trichome bases become prominently buttressed (figs. 26, 27), resulting in a somewhat muricate apex. External epidermis includes stomates. Mesocarp consists of parenchyma cells reminiscent of foliar mesophyll including intercellular spaces of irregular size (figs. 35, 36). The vascular tissue passes through the mesocarp. For each carpel, the median and marginal vascular bundles are detectable. Median carpel bundles are located at the outer extremity of each carpel. Marginal carpel bundles and
several others can be found within the septum (or septa). Marginal carpel bundles occupy a near-axial position where they supply the ovule/seed. In addition, several small vascular bundles are present in the septum and in adjacent regions of the carpel wall. Endocarp consists of three layers of sclerified cells which line the curved contour of the locular space (figs. 35, 36). Of these three layers, the outer- and innermost layers are perpendicular to the palisade-like middle layer (fig. 37). Whereas the long axes of outer- and inner-most cells are parallel to the locular surface, the long axes of these cells project along different vectors of the curved surface (fig. 35). The thickness of the palisade layer is not uniform throughout; it tapers towards the edges of the individual valves. Evidently, as the endocarp dries, the geometry of these sclerified cells orients the forces that contort the fruit wall and result in explosive dehiscence of the fruit and ballistic dispersal of the seeds.

Seeds

The ovoid seeds range in color from tan to black; they may be uniformly one color or mottled (figs. 39, 40). As the anatropous ovules mature into seeds, apical regions of the seed grow more rapidly than basal regions. Because of this allometric pattern of growth, the point of attachment to the placenta and hilum of seed is located at approximately one-third of the distance from the apex, whereas this point was apical in flowering stage. Another consequence of allometric growth is that the micropyle enlarges greatly, ultimately extending between the seed apex and the hilum (fig. 39). Landes (1946) interpreted the thickened micropyle as a caruncle, and Webster (1967) has characterized seeds throughout the genus as carunculate. Unlike the obviously carunculate seeds of *Ricinus communis* L. in which internal cells erupt through the
micropyle, structures observed in the present study suggest merely thickened integumentary cells of the micropyle (fig. 39). The fact that the nucellar beak extends only to the inner tip of the micropyle (fig. 32; Kapil and Bhatnagar 1994) and thus does not project through it, would be difficult to reconcile with characterization of the thickened integumentary cells on the seed surface as a true caruncle. Distinctive features of the ventral surface thus include micropyle, hilum, and a thin ventral raphe. Otherwise, seed surfaces are relatively smooth, but at modest magnification, small ripples formed by rows of integumentary epidermal cells are easily seen. Testa is composed of multiple layers of cells derived from the two integuments (fig. 38). The outer integument consists of two layers of cells: an outermost layer, variable in thickness, composed of unspecialized cells and a single layer of large, vacuolate, cuboidal cells. The inner integument consists of a layer of sclereids occupying the outer-most position, multiple layers of parenchymatous cells, and an inner-most layer of tracheids (figs. 35, 36). The sclereids occupying the outer-most position of the inner integument are sharply bent (fig. 41). The bending of these sclereids also results from the allometric growth of the ovules. Sclereids that constitute a major protective layer of mature testa derived from the outer-most portion of the inner integument appear to be widespread in uniovulate Euphorbiaceae (Jordan and Hayden 1992, and references cited therein). Tracheids of the inner integument, characterized by helical thickenings, are two to three times longer than their width. In *A. deamii*, these tracheids bear dense deposits of tannin (fig. 43), whereas these cells lack prominent contents in *A. rhomboidea* (fig. 38). In the chalazal end of the ovule the well-developed hypostase is continuous with tracheids of the inner integument (fig. 42). The sclerified cells of the
hypostase proper include xylem elements continuous with the vascular strand of the funiculus. In *A. deamii*, cells adjacent to the hypostase are tannin-rich (fig. 42), whereas those of *A. rhomboidea* are free of tannins (fig. 38). In agreement with descriptions of *A. rhomboidea* by Landes (1946), vascular tissue extends from the hypostase region into the nucellus. Endosperm of both *A. deamii* and *A. rhomboidea* is described as free-nuclear at formation, but it becomes cellular in later development (Davis 1966, Landes 1946). In the mature seed, endosperm cells are more or less isodiametric, contain large nuclei, and also possess abundant starch (fig. 45). The straight embryo is surrounded by endosperm and oriented with the radicle uppermost.

**Allomorphic Flowers, Fruits, and Seeds**

**Organography.** Allomorphic flowers and fruits of *A. deamii* and *A. rhomboidea* occur in the leaf axils occupying the lower-most to mid-region of the plant and can be intermixed with typical pistillate flowers. Whereas the ordinary pistillate flowers of the species studied are two- or three-carpellate and produce explosively dehiscent fruits, their allomorphic structures are one-carpellate, indehiscent, and produce only one seed (fig. 47). Moreover, stigmas of pistillate flowers diverge from the apex of the ovary, whereas allomorphic flowers are folded through approximately 180 degrees so that stigmas diverge from the base of the ovary near its attachment to the pedicel. Radcliffe-Smith (1973) noted that, when present, allomorphic flowers of several species of *Acalypha* are typically composed of one unilocular ovary. However, as described by Venkata Rao (1971), the allomorphic structures of *Acalypha indica* bear three carpels, but only one carpel produces a fertile seed. Several features of
allomorphic flowers and the fruits they produce are summarized in Table 2 for A. 
deamii and A. rhomboidea.

**Histology.** Overall, at the microscopic level, structures of allomorphic flowers and fruits are very similar to those of the ordinary pistillate flowers. At flowering stages, ovary wall is composed of largely undifferentiated parenchymatous cells (fig. 48). Likewise, cells of the two integuments are relatively uniform. Embryo sacs were observed, however most preparations revealed later stages of development and the material studied was inadequate for characterization of the female gametophyte of allomorphic flowers. At maturity, the cell layers of the ovary wall correspond well to those of the ordinary fruits (fig. 49). There are, however, three prominent differences. The surface of allomorphic fruits is pronouncedly muricate, more so than that of the ordinary fruits (fig. 50). Further, although allomorphic fruits are densely pubescent, gland-tipped trichomes are absent. In addition, allomorphic fruits possess only a weakly developed layer of sclereids corresponding to the sclereid layer of ordinary fruits that allows for dehiscence (fig. 51). Presumably, the weak development of this layer is responsible for the indehiscent nature of the allomorphic flowers. Testa of allomorphic seeds is very similar to that of seeds from ordinary fruits. The one prominent difference noted is that the sclereids making up the outer-most cells of the inner integument in A. deamii, though present, are only lightly sclerified (fig. 52). In A. rhomboidea, testa of ordinary and allomorphic seeds are essentially identical (fig. 51). At maturity, endosperm and embryo show no obvious differences between allomorphic and ordinary seeds for the two species studied.
CONCLUSIONS

*Acalypha deamii* is documented to occur in flood plain habitats of several major rivers east of the Appalachians in the mid-Atlantic region (Maryland, Virginia, and West Virginia). Locality data for the collections studied suggest this long-overlooked plant is a native element of the flora.

Proliferation of whole inflorescence units and individual staminate and pistillate flowers, features not previously recorded for these species, appear to be common characteristics of *A. deamii* and *A. rhomboidea*.

In contrast with earlier descriptions, seeds of *A. deamii* and *A. rhomboidea* lack caruncles. Instead, the small projection near the micropyle is merely composed of thickened outer integument.

Aside from differences in carpel number, the structure of ordinary staminate and pistillate flowers of *A. deamii* and *A. rhomboidea* are similar, even at the anatomical level. Allomorphic flowers, fruits, and seeds in these two species are likewise mostly similar except for minor difference in sclerification of testa. In general, allomorphic flowers, fruits, and seeds of the two species studied are similar to ordinary pistillate flowers, fruits, and seed. However, allomorphic structures differ as follows: they are one-carpellate, are oriented in a folded or reflexed position, lack glandular trichomes, bear weakly sclerified endocarp at fruiting stage, and are indehiscent; ovules are solitary and, in *A. deamii*, testa is weakly sclerified. Evidently, indehiscence of allomorphic fruits and weak sclerification of the endocarp are functionally correlated characteristics. Further study will be required to understand how flexure of allomorphic flowers develops and how the reflexed orientation impacts vascularization of the ovary wall.
Also, characterization of embryo sacs in allomorphic flowers and critical, early stages of reproduction remain unknown and deserve further examination.

Since allomorphic fruits of *A. deamii* and *A. rhomboidea* contain embryos, are indehiscent, and have a complex, muricate surface, it is reasonable to postulate that these structures in some way provide an alternative means of reproduction. Field based studies of the function (e.g. dispersal, seedling recruitment) of these allomorphic structures may prove insightful.


Müller, J. 1865. Vorläufige Mitteilungen aus dem für De Candolle’s Prodromus bestimmten Manuscript. Linnea 34: 1-126. [not seen]


Venkata Rao, C. Anatomy of the inflorescence of some Euphorbiaceae with a
discussion on the phylogeny and evolution of the inflorescence including the

Rhodora 29: 193-204.

Webster, G. L. 1967. The genera of Euphorbiaceae in the southeastern United States.

Table 1: Comparison of Morphological Features of *Acalypha deamii* and *Acalypha rhomboidea* (compiled largely from Fernald 1950, Webster 1967, and Gleason and Cronquist 1991)

<table>
<thead>
<tr>
<th>Feature</th>
<th><em>Acalypha deamii</em></th>
<th><em>Acalypha rhomboidea</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Leaf</td>
<td>Ovate leaves with spreading petioles</td>
<td>Rhombic and horizontal leaves with divaricate petioles</td>
</tr>
<tr>
<td>Carpel Number</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Style Tip</td>
<td>Highly branched</td>
<td>Branched twice</td>
</tr>
<tr>
<td>Seed Number</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>Seed Size</td>
<td>2.2 – 3.1 mm</td>
<td>1.2 – 2.0 mm</td>
</tr>
<tr>
<td>Production of Allomorphic Fruits and Flowers</td>
<td>Common</td>
<td>Rare</td>
</tr>
</tbody>
</table>
Table 2: Comparison of Ordinary Pistillate Flowers/Fruits of *Acalypha deamii* and *Acalypha rhomboidea* and Allomorphic Flowers/Fruits of Both Species

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Ordinary Pistillate Flowers/Fruits of <em>A. deamii</em></th>
<th>Ordinary Pistillate Flowers/Fruits of <em>A. rhomboidea</em></th>
<th>Allomorphic Flowers/Fruits of both species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carpel Number</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Carpel Orientation</td>
<td>Erect</td>
<td>Erect</td>
<td>Reflexed</td>
</tr>
<tr>
<td>Seed Number</td>
<td>2</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Fruit Surface</td>
<td>Pubescent and weakly muricate</td>
<td>Pubescent and weakly muricate</td>
<td>Pubescent and densely muricate</td>
</tr>
<tr>
<td>Trichomes</td>
<td>Simple and Glandular</td>
<td>Simple and Glandular</td>
<td>Simple</td>
</tr>
<tr>
<td>Dehiscence</td>
<td>Dehiscent</td>
<td>Dehiscent</td>
<td>Indehiscent</td>
</tr>
<tr>
<td>Seed Dispersal</td>
<td>Ballistic</td>
<td>Ballistic</td>
<td>Unknown</td>
</tr>
</tbody>
</table>
Fig. 1. *Acalypha deamii* (Hayden 4497); shoot apex of mature, flowering individual.

Fig. 2. *Acalypha rhomboidea* (unvoucher); shoot apex of mature, flowering individual.
Fig. 3. Distribution of *Acalypha deamii* in Maryland, Virginia, and West Virginia plotted on a base map of major river systems. ArcView map provided courtesy Dr. J. M. Harrison.
Fig. 4. *Acalypha deamii* (Hayden 4497); group of mature staminate flowers at tip of spike; note proliferating flower primordium on lower right.

Fig. 5. *Acalypha deamii* (Hayden 4497); external surface of staminate flower; note abundant cruciate crystals on the four valvate sepals.
Fig. 6. *Acalypha deamii* (Hayden 4497); section through sepal of staminate flower bud; note buttressed bases below cruciate crystals.

Fig. 7. *Acalypha deamii* (Hayden 5000); cruciate crystals on surface of staminate flower.
Fig. 8. *Acalypha rhomboidea* (Hayden 4498); staminate flower primordium (left) and young staminate flower bud with stamen primordia (right).

Fig. 9. *Acalypha deamii* (Hayden 4497); staminate flower shortly before anthesis.
Fig. 10. *Acalypha rhomboidea* (Hayden 4498); staminate flower shortly before anthesis; note abscission zone in pedicel.

Fig. 11. *Acalypha deamii* (Hayden 4497); staminate flower shortly before anthesis; note abscission zone in pedicel.
Fig. 12. Acalypha rhomboidea (Hayden 4498); staminate flower at anthesis; note reflexed sepals and abscission zone.

Fig. 13. Acalypha deamii (Hayden 5000); pendulous, vermiform anthers within a staminate flower bud.

Fig. 14. Acalypha rhomboidea (Hayden 4498); anther primordium showing epidermis (E), primary parietal layer (P), and primary sporogenous cells (S).
Fig. 15. *Acalypha deamii* (Hayden 4497); young anther; note endothecium (surface), middle layer (irregular ring), and amoeboid tapetal cells among the pollen grains.

Fig. 16. *Acalypha deamii* (Hayden 5000); nearly mature anther with well-developed endothecial thickenings.
Fig. 17. Acalypha rhomboidea (Hayden 4498); nearly mature anther; note amoeboid tapetum.

Fig. 18. Acalypha deamii (Hayden 4497); nearly mature anther; note amoeboid tapetum (arrows) and stomium (S).
Fig. 19. *Acalypha deamii* (Hayden 5000); nearly mature anther containing tricolpate pollen.

Fig. 20. *Acalypha rhomboidea* (Hayden 4498); multi-lobed bract enclosing immature fruit; note simple and glandular trichomes.
Fig. 21. *Acalypha rhomboidea* (Hayden 4498); two immature pistillate flowers proliferating from near the base of an older pistillate flower (upper-right).

Fig. 22. *Acalypha deamii* (Hayden 5000); two immature pistillate flowers proliferating from near the base of an older pistillate flower (upper-right).
Fig. 23. *Acalypha rhomboidea* (Hayden 5001); stigmatic branches of pistillate flower exserted beyond bract margins. [Image background digitally edited].

Fig. 24. *Acalypha deamii* (Hayden 3577); young fruit and staminate spike, both subtended by a multi-lobed bract.
Fig. 27. *Acalypha deamii* (Hayden 4497); buttressed trichome base of fruit wall.

Fig. 28. *Acalypha deamii* (Hayden 5000); pistillate flower bud; note undifferentiated, parenchymatous nature of future ovary wall.
Fig. 29. *Acalypha deamii* (Hayden 5000); oblique longitudinal section, two ovules, apical and axile placenta, chalaza lowermost.

Fig. 30. *Acalypha rhomboidea* (Hayden 4498); two ovules from ovary region of immature pistillate flower; note two integuments overgrowing the nucellus of each ovule.
Fig. 31. *Acalypha rhomboidea* (Hayden 4498); oblique section through upper portion of a young fruit, horizontal portion of micropyle and outer integument.

Fig. 32. *Acalypha rhomboidea* (Hayden 4498); inner sections of micropyle (M), nucellar beak (N), and globular embryo (E).
Fig. 33. *Acalypha rhomboidea* (Hayden 5000); procambial strand entering chalazal end of ovule and nucellar hypostase.

Fig. 34. *Acalypha deamii* (Hayden 5000); simple and glandular trichomes on fruit surface.
Fig. 35. *Acalypha deamii* (Hayden 5000); fruit wall with tapered zone of endocarp sclereids and testa with arcuate sclerified cells of the inner integument.

Fig. 36. *Acalypha rhomboidea* (Hayden 4498); fruit wall and testa as in Fig. 34; sclereids of inner integument perpendicular to plane of section; endosperm (top left).
Fig. 37. *Acalypha rhomboidea* (Hayden 4498); fruit wall with immature palisade-like sclereids of endocarp; note prominent nuclei.

Fig. 38. *Acalypha rhomboidea* (Hayden 4498); base of fruit and seed; from top, pericarp, testa, nucellus with hypostase, and endosperm.
Fig. 39. *Acalypha deamii* (Hayden 3577); seeds.

Fig. 40. *Acalypha rhomboidea* (Hayden 5003); seeds.
Fig. 41. *Acalypha deamii* (Hayden 5000); mature arcuate sclereids forming the outer-most layer of the inner integument.

Fig. 42. *Acalypha deamii* (Hayden 5000); base of ovule showing entry of funiculus into chalaza and tannin-rich cells adjacent to the hypostase; note nucellus (bottom).
Fig. 43. *Acalypha deamii* (Hayden 5000); tannin-filled tracheids of the inner-most layer of the inner integument.

Fig. 44. *Acalypha rhomboidea* (Hayden 4498); tracheids, without tannins, of the inner-most layer of the inner integument.
Fig. 45. *Acalypha deamii* (Hayden 5000); endosperm cells of mature seed.

Fig. 46. *Acalypha rhomboidea* (Hayden 4498); fruit and seed near maturity, embryo (center) surrounded by endosperm; note radicle is uppermost.
Fig. 47. *Acalypha deamii* (Hayden 3688);
allomorphic fruit; note midvein of the single carpel (horizontal groove near middle of image).

Fig. 48. *Acalypha deamii* (Hayden 5000);
allomorphic flower; note undifferentiated parenchyma cells of ovary wall.
Fig. 49. *Acalypha rhomboidea* (Hayden 5003); embryo (top), endosperm, remnants of nucellus, testa, and pericarp (bottom) of allomorphic fruit.

Fig. 50. *Acalypha deamii* (Hayden 5000); muricate surface of allomorphic fruit.
Fig. 51. *Acalypha rhomboidea* (Hayden 5003); fruit wall and testa of allomorphic fruit; note well-developed sclereids of inner-most layer of outer integument.

Fig. 52. *Acalypha deamii* (Hayden 5000); allomorphic fruit and seed; note light sclerification of inner-most layer of outer integument.
Appendix I: Hayden/Fleming Collections of *Acalypha deamii*

**Maryland**

- Washington Co., MD. Dry, sandy soil with sparse annual cover at C & O Canal ca 100 meters east (downstream) of Dam #4 and associated locks; edge of canal towpath and slope of canal bed. 17 October 1998, *W.J. and S. M. Hayden 4113* (URV).

**Virginia**


- Albemarle Co., VA. Howardsville, James River just below the mouth of the Rockfish River along the drawdown riverbank within ca 10 m of the boat ramp. 7 October 1998, *W. J. Hayden 4091 and Olga Troyanskaya* (URV).


- Appomattox Co., VA. Sandy silver maple forest along James River and Rt. 605, N of Bent Creek, 12 September 1997, *G.P. Fleming 14068* (GMUF, VPI, WILLI); *W.J. Hayden 3806* (URV).

• Bedford Co., VA. Sandy silver maple forest along James River at Holcomb Rock, NW of Lynchburg, 19 September 1997, G.P. Fleming 14160 and W.J. Hayden (GMUF).

• Botetourt Co., VA. Silver maple grove along James River below Rt. 609 E of Rocky Point, 19 September 1997, G.P. Fleming 14167 (GMUF); W.J. Hayden 3832 (URV).

• Botetourt Co., VA. Sandy silver maple forest along James River W of US Rt. 11 in Buchanan, 19 September 1997, G.P. Fleming 14172 (GMUF); W.J. Hayden 3837 (URV).

• Botetort Co., VA. James River, between Arcadia and Route I-81, east side of Route 614 bridge on riverbank. 19 September 1997, W. J. Hayden 3836 and Gary Fleming (URV).


• Campbell Co., VA. Sandy silver maple forest along James River at Joshua Landing off Rt. 726, opposite Joshua Falls, 19 September 1997, G.P. Fleming 14143 (GMUF, LYN, VPI, WILLI); W.J. Hayden 3814 (URV).


• Chesterfield Co., VA. Shaded area at Dutch Gap on the James River, along river bank path to Henricopolis site, about 60 meters upstream from point where path turns inland. 17 August 1996, *W. J. Hayden 3621* (URV).

• Chesterfield Co., VA. Dutch Gap on the James River, along river bank path to Henricopolis site, small eroding embayment about 50 meters downstream from boat launch area. 17 August 1996, *W. J. Hayden 3622* (URV).

• Chesterfield Co., VA. Dutch Gap on the James River, just downstream from the boat ramp, in the woods, east of the drainage ditch near trail to Henricopolis site. 21 September 1997, *W. J. Hayden 3840* (URV).

• Chesterfield Co., VA. Dutch Gap, edge of James River, along the path between boat launch and Henricus site (bluff). 16 October 1999, *W. J. Hayden 4228* (URV).

• City of Richmond, VA. Shady riparian woods on south bank of James River at James River Park, Huguenot Woods area, both sides of the steps at the canoe launch. 17 October 1994, *W. J. Hayden 3410* (URV).
• City of Richmond, VA. Shady riparian woods on south bank of James River at James River Park, Huguenot Woods area, on both sides of the steps at the canoe launch. 11 November 1994, *W. J. Hayden 3420* (URV).

• City of Richmond, VA. Huguenot Woods portion of James River Park, south bank of James River, about half way between the Huguenot Bridge and the canoe launch area. 5 October 1996, *W. J. Hayden 3687* (URV).

• City of Richmond, VA. Huguenot Woods, south bank of the James River about half way between the Huguenot Bridge and the canoe launch area. 14 October 1996, *W. J. Hayden 3688* (URV).

• City of Richmond, VA. Wooded flood plain at James River Park at Huguenot Woods area on south bank of James River. 31 August 1997, *W. J. Hayden 3735* (URV).

• City of Richmond, VA. Wooded flood plain at James River Park at Huguenot Woods area on south bank of James River. 4 September 1997, *W. J. Hayden 3746* (URV).

• City of Richmond, VA. Great Ship Lock Park, Chappel “Island”, along path near the Norfolk and Southern draw bridge over the canal. 21 September 1997, *W. J. Hayden 3845* (URV).

• City of Richmond, VA. James River Park along the riverbank between Ancarrow’s Landing the the I-95 bridge; clearing adjacent to path not far (about 50 m N or upstream) from vicinity of entrance to wastewater treatment plant. 27 September 1998, *W. J. Hayden 4077* (URV).
• City of Richmond, VA. James River Park at Belle Isle, east (downstream) tip of island, open sandy area. 29 September 1998, W. J. Hayden 4083 and Tihomir Kostadinov (URV).

• City of Richmond: James River Park, VA. Huguenot Woods, riverside trail just east (downstream) of the Huguenot Bridge. 3 November 1999, W. J. Hayden 4244 (URV).

• City of Richmond, VA. James River Park, VA. Huguenot Woods, riverside trail just east (downstream) of the Huguenot Bridge. August 2001, W. J. Hayden 4497 and Patricia Truman (URV).

• City of Richmond, VA. James River Park, VA. Huguenot Woods, riverside trail just east (downstream) of the Huguenot Bridge. 11 September 2001, W. J. Hayden 5000 and Patricia Truman (URV).

• Clarke Co., VA. Clay bank above river on west bank of Shenandoah River, about ¼ mile upstream of Route 50 bridge. 17 September 1998, W. J. Hayden 4035 (URV).

• Cumberland Co., VA. Silver maple woods on sandy flood terrace along James River, SE of Rt. 45 bridge, NE of Cartersville, 26 September 1995, G.P. Fleming 11409 (GMUF, VPI); verified by G.A. Levin (ILLS).

• Cumberland Co., VA. Forested alluvial terrace and banks along James River W of Rt. 690 bridge opposite Columbia, 6 October 1995, G.P. Fleming 11469 (FARM, GMUF, WILLI); verified by G.A. Levin (ILLS).
• Fairfax Co., VA. Sandy soil south bank of the Potomac River at Riverbend Park, about 300 m upstream of boat launch area. 22 September 1998, W. J. Hayden 4057 (URV).

• Fairfax Co., VA. Sandy alluvium at south bank of the Potomac River at Scott’s Run Nature Preserve, flood plain between the Scott’s Run waterfall (upstream) and the bluff (downstream). 22 September 1998, W. J. Hayden 4059 (URV).


• Goochland Co., VA. Sabot Hill Boat Landing on the James River south of Sabot Hill, west end of Sabot Island, about 30 yards from riverbank. 7 October 1997, W. J. and S. M. Hayden 3897 (URV).

• Halifax Co., VA. Sandy alluvial forest along Roanoke (Staunton) River, SW of Rt. 92 bridge, E of Clover, 10 September 1997, G.P. Fleming 14041 (FARM, GMUF, LYN, WILLI, VPI, URV).

• Halifax Co., VA. Sandy alluvial terrace along James River SW of Rt. 92 bridge, E of Clover, 10 October 1997, G.P. Fleming 14360 and T.F. Wieboldt (GMUF).

• Nelson Co., VA. Sandy silver maple forest along James River NE of confluence with Mayo Creek, N of Wingina, 12 September 1997, G.P. Fleming 14054 (FARM, GMUF, VPI, WILLI); W.J. Hayden 3752 (URV).


• Nelson Co., VA. Dry sandy soil at Wingina, boat launch area at Rt. 56 bridge. 7 October 1998, \textit{W. J. Hayden 4094} (URV).


• Powhatan Co., VA. Maidens Landing on south bank of James River at Route 522, between parking area and river. 8 October 1995, \textit{W. J. Hayden 3577} (URV).

• Rockbridge Co., VA. Sandy silver maple forest along James River at terminus of Rt. 790 below Skillern Mountain, George Washington National Forest - Smith Tract, S of Natural Bridge, 19 September 1997, *G.P. Fleming 14163* (GMUF); *W.J. Hayden 3828* (URV).

• Rockbridge Co., VA. Alluvial woods between railroad tracks and James River off Gillmore Mills Road (= Route 708), about 1.5 miles south from Rockbridge Station. 19 September 1997, *W. J. Hayden 3829 and Gary Fleming* (URV).

• Stafford Co., VA. Falmouth Riverside Park on the north bank of the Rappahannock River, access via Route 607 at parking area with squatt stone pillars, about midway between parking area and Route 607 embankment of recently installed rip-rap rock. 26 September 1997, *W. J. and S. M. Hayden 3867* (URV).

• Warren Co., VA. Sandy alluvium in South Fork of the Shenandoah River at route 613 bridge, west of Bentonville. 8 September 1998, *W. J. Hayden 4027* (URV).


**West Virginia**

Appendix II: Collections of *Acalypha deamii* and *Acalypha rhomboidea* Studied Anatomically

*Acalypha deamii*

- Powhatan Co., VA. Maidens Landing on south bank of James River at Route 522, between parking area and river. 8 October 1995, *W. J. Hayden* 3577 (URV).

*Acalypha rhomboidea*

- City of Richmond, VA. University of Richmond campus, west side of Gottwald Science Center. 4 September 2001, *W. J. Hayden and P. A. Truman* 4498 (URV).
• Berkeley Co., W. VA. Martinsburg, Travelodge Motel at junction of route 9 and I-81, edge of lawn. 5 October 2001, *W. J. Hayden and S. M. Hayden* 5003 (URV).

• Morgan Co., W. VA. Cherry Run Sportsman’s access to Potomac River. 6 October 2001, *W. J. Hayden and S. M. Hayden* 5008 (URV).
CURRICULUM VITAE

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