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Earl Core Student Award Report

Evolutionary implications of the lack of sexual reproduction in the Southern Appalachian endemic hornwort

Megaceros aenigmaticus

by Juan Carlos Villarreal

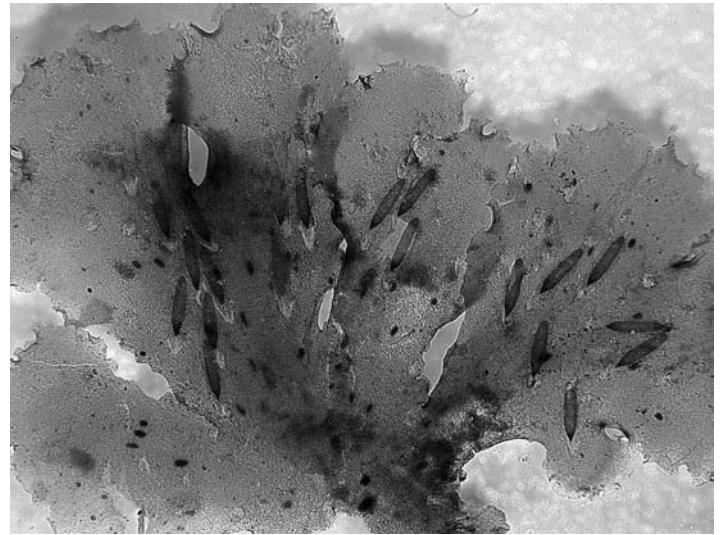
Juan Carlos Villarreal (University of Connecticut) received the Earl Core Student Award in 2008 and has been gracious enough to share this summary.

My research focuses on the evolutionary history of the haploid asexual hornwort *Megaceros aenigmaticus* R.M. Schust. It is currently reported as endemic to the Southern Appalachians (SA), where it is considered endangered (Schuster 1992a,b; Hyatt 2006; USDA website). This hornwort is dioecious, with male and female populations occurring in different watersheds (Renzaglia & McFarland 1999). Geographic isolation of the female and male gametophytes may account for the lack of sexual reproduction, which is further compromised by the premature abortion of male swimming gametes (Renzaglia & McFarland 1999). The species' survival is threatened immediately by habitat degradation due to an adelgid plague on hemlocks (Jacobs 2005; Hyatt 2006) and ultimately by the potential consequences of the lack of sexual reproduction. The consequences of this loss of sexuality on the genetic diversity and structure of the SA populations will be assessed with two main objectives, to:

- Reconstruct the phylogenetic origin of the species, and the time-frame of the loss of sexuality;
- Assess the population genetic structure of clonal populations of *M. aenigmaticus*.

Funding provided by the Southern Appalachian Botanical Society has been useful to complete the first part of the project and will also be used to finance a collecting trip during Spring 2009 in Georgia and North Carolina. I work in collaboration with Dr. Ken McFarland from the University of Tennessee.

The first part of the project was answered using a multilocus phylogeny: Data from three chloroplast, one nuclear and one mitochondrial locus have been used to reconstruct the phylogenetic relationships within the genus *Nothoceros*, including the American *Megaceros*. Based on the results (and supporting previous claims by Duff et al. 2007) American *Megaceros*, including *M. aenigmaticus*, belong to the genus *Nothoceros*. Formal nomenclatural changes will be made soon. In addition, *M. aenigmaticus* shares a recent common ancestor with populations collected in Neotropical alpine areas, suggesting that this species should no longer be considered a US endemic. Based on a Bayesian dating analyses (Drummond & Rambaut 2007; Villarreal et al. 2008) the approximate time for the dispersal to the SA is estimated to be the onset of the Pleistocene.



Female gametophyte of *Megaceros aenigmaticus* collected on a rock along a stream in the Joyce Kilmer Forest. Dark round spots are *Nostoc* (nitrogen-fixing cyanobacteria) colonies in the underside of the thallus. Note the elongated eggs inside of the thallus, presumably laid down by damselflies (K. Tennessen pers. com.). Further studies are needed to clarify the identity of the insect ovipositing on this hornwort. Photograph by Juan Carlos Villarreal

A Pleistocene origin of the SA lineage can also be considered as the maximum age for the loss of sexual reproduction of the SA *M. aenigmaticus*.

The next portion of the study will include a fingerprinting analysis using microsatellites of the SA *M. aenigmaticus* and conspecific sexually reproducing plants from the tropics. This will provide some genetic information on the impact of loss of sexual reproduction and will be critical in generating a conservation strategy for the plant. Manuscripts are in preparation!

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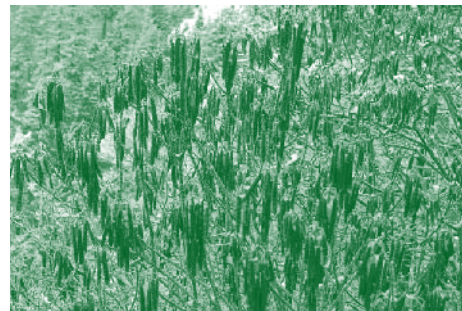
Letters to the editor

Hunkering Down

From Howie Neufeld

As a plant physiologist, I might take exception to several points that George Ellison makes regarding how plants tolerate the winter. For example, Erik Nilsen at Virginia Tech could not find an adaptive value for leaf curling by rhododendrons related to conserving moisture or changing leaf temperature (they are too thin). It might lower desiccation somewhat, but their stomata are completely closed in the winter, so that's probably not the reason. Rather, Erik found that curling reduced photoinhibition, which can be exacerbated in cold, sunny conditions. Leaves prevented from curling got brown spots and chlorotic. And the temperatures quoted for minima for trees seem somewhat too extreme for me. Don DeHayes found membrane damage and needle loss when temperatures hit -45°C in red spruce in NY. I think the -80°C is too low. Remember, that book he quotes is 21 years old now.

(Photo by Scott Ranger)



Field Notes on Three-birds Orchid brought several.

From John Bierhorst:

Your report on *Triphora* was forwarded to me yesterday by Steve Young of the NY Natural Heritage Program. I have monitored the *Triphora* colonies here in the eastern Catskills from the late 1960s, especially in the 1990s — about 6 colonies, 1000 stems, within a radius of 1 mile.

Your experience strikes me as unusual. Here the plants flower the second or third week in August, their main flowering. There is an earlier flowering around the first week of August, much smaller, and a later one around the first week of September, also small. The flowers all open at once. One year I compared the main flowering time with the Squam Lake *Triphora*

in New Hampshire, and it was exactly the same day. Other details seem aberrant: the near horizontal stems, the tendency to self pollination, the association with grape fern. You don't mention the "trigger": the cold night, after a period of warmer nights, followed the next morning by the main flowering. One year we observed it very definitely.

From Dennis Horn:

Your field notes on *Triphora trianthophora* were interesting to me. As you suggest much of the literature on the phenology of this species is probably without a strong scientific foundation. However there is some good information out there. You mention Leur. I think his observation is correct that all of the flowers in a colony, that are ready to open, will open the same day. There may be, and usually are, several waves of flowering within a colony of plants. These waves are usually 7 to 10 days apart.

I had three-birds in my front yard for a few years. The one year that I watched them closely, they flowered on August 10 (fully open only one day), then about 10 days later another wave, and finally a 3rd wave about 7 to 10 days after that. A cold front often seems to trigger flowering, but I'm not sure that is always reliable.

One account you should read is by Philip Keenan, *Wild Orchids across North America*, Chapter 22. He documents his observations over a 20 year period. He found that all three-birds in New England open the same day, in 3 or 4 waves from August 1 to the 1st week of September. Also Phil mentions that a plant brought home and placed on a window sill will flower on the same days as those in the field!

From Steve Evans:

I read your article in *Chinquapin* about the three-birds orchid and thought I might be a help to you. My wife is an orchid enthusiast and we have about 40 in our home. In these horticultural varieties, often many of the flowers do not open in what is called a "bud blast." It is the bane of most orchid growers. I am not sure if this is what is going on with your native orchids, but I

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Botanical Excursions

by George Ellison

Edwin Way Teale: An American Observer

From my perspective, the greatest literary naturalist in the English language was Gilbert White, author of *The Natural History and Antiquities of Selbourne*, which was published in 1789. White is the Shakespeare of nature writing...all else flows from him.

The British have, of course, produced a line of very fine literary naturalists since White. My favorite nineteenth century writer is W.H. Hudson, that low-key observer of the English countryside. One also has to mention the wildly romantic Richard Jefferies, author of *The Story of My Heart* (1883).

Nature writing in America inevitably flows from Henry David Thoreau, that sometimes cranky and always idiosyncratic observer of the commonplace. There is nature aplenty in that carefully contrived masterpiece *Walden* (1854), but the most memorable and heartfelt observations are to be found in Thoreau's journals. John Burroughs, his late nineteenth century follower, was the first professional nature writer in America, and he remains one of the most pleasurable to read. Then there is that forgotten gem of outdoor observations, Walt Whitman's *Specimen Days* (1882).



In the latter half of the twentieth century, we had a spate of self-conscious literary posers appear on the scene...and they are still going strong. These so-called New Naturalists have often been less interested in describing the natural world, as it exists, than in lovingly examining their own tender feelings and posteriors. Many in this tribe couldn't distinguish a trillium from a skunk cabbage, a warbler from a crow, a buzzard from a raven, or a bull from a bat. I exaggerate, of course, but not much.

The finest American nature writer of the 20th century was, hands down, Edwin Way Teale (1899-1980). If you doubt me, read anything that he wrote. I suggest that you start with *North With Spring: A Naturalist's Record of a 17,000 Mile Journey with the North American Spring* (1951), one of four volumes in a series—including *Autumn Across America: A Naturalist's Record of a 20000-Mile Journey Through the North American Autumn* (1956); *Journey Into Summer: A Naturalist's Record of a 19,000 Mile Journey Through the North American Summer* (1960); and, *Wandering Through Winter: A Naturalist's Record of a 20,000 Mile Journey Through the North American Winter* (1965)—which, collectively, won the Pulitzer Prize for General Non-fiction in 1966.

To whet your appetite, here are some excerpts taken almost at random from *North With Spring* that record Teale's observations made in Western North Carolina and the Great Smoky Mountains National Park, during the long journey with Nellie, his wife and constant companion, from Florida to Maine.

One of their stops was at Pearson's Falls Glen, located in the Pacolet River valley in southwest Polk County NC:

The coolness of the grotto surrounded us... Nowhere along the way did we find so glorious a wild flower garden as in this hidden nook among the North Carolina mountains... Conservationists have grown increasingly conscious of the importance of these small, 'type-specimen' sanctuaries. There is no finer example in the country of the value of such a preserve than the glen at Pearson's Falls... Our lives touched it at this one point, at this one time in spring when its magical beauty was unrivaled... At the head of the glen the path brought us to the white lace of Pearson's Falls.

It is lace formed of water by gravity on a loom of granite. In a thin, foaming layer the water slides down the face of successive shelves of rock. The sound of this falling water is murmurous, calming, companionable. Here is no mighty, roaring Niagara, no deep-tongued bellow. This was a sound for a glen to enclose... Night and day the falling water of Pearson's Falls generates a cool, moist breeze. It stirred the ferns and the lady-slippers and the pendant white flowers along the underside of branches of the silver-bell tree that leaned out over the pool."

(See www.pearsonsfalls.org.)

Along the Appalachian Trail in the Great Smokies north of Newfound Gap, Edwin and Nellie came to the dramatic overlook at Charlies Bunion:

Ridges, covered with red spruce and Fraser fir, extended away until they blurred into dark, smudgy lines in the distance. Seen from above, mountains become different mountains in different lighting... The scene changes with every movement of the sun. On this morning, under a leaden sky, in the breathless silence before a rain, the dull gray lighting stressed the wild and lonely character of our surroundings. In all the sweep of mountains and sky around us we saw no single sign of life... Then life appeared—a bird most fitting to that somber scene. Over the crags and blasted trees two dark birds, a pair of ravens, sailed past us. Their hoarse calls carried hollowly across the empty spaces... At intervals one of the birds would dive and twist in a wild display of aerobatics. There were times when the stunting bird was completely inverted, flying upside down. In the ecstasy of spring a number of birds loop or stunt or sail in inverted flight... but here, amid these crags that appeared as lonely as a moonscape and as devoid of active life, the aerobatics of the raven were superlatively impressive.

Many a New Naturalist, alas, would proceed to tell us of his or her flying dreams and then equate them to his or her quixotic search for a personal nirvana. But Edwin Way Teale simply records what he actually observed in the real world and lets it go at that. And therein lies all the difference. Gilbert White would approve.

Taxonomic Advisory!

by Alan Weakley

Change we can believe in?

“When botanists disagree on plant names the ordinary gardener keeps his head down, carries on using names to which he is accustomed and waits for the botanical flak to subside. However after reading the botanical salvos on ‘Hibernica’ in the last issue of the [British Ivy Society] Newsletter I feel I can lift my head from my slit trench, pick my way across the battlefield and examine the arguments” (Rose in Sulgrove 1984)

One frequently hears among botanists (defined for my purposes here as “any and all regular users of botanical taxonomy and nomenclature”) the suggestion—one might say “complaint”—that taxonomic changes are occurring at a rapid and unprecedented level. There are several variations to this charge:

- “I just wish the names would stay the same as they were when I was in college and first learned them” (*The Wistful*).
- “I know that names have to change because of improvements in our taxonomic understanding, but I just wish there weren’t quite so many changes” (*The Rationalist*).
- “I just wish the new names weren’t always longer and harder to pronounce than the old ones” (*The Frustrated*).
- “What the heck have they done now?” (*The Angry and Bewildered*).
- “What the heck have those Know-nothing, Molecular / DNA / Phylogeny people done now?” (*The [Angry] Traditionalist*).

Whatever the philosophic bent of the complainant, a frequent part of all the complaints is the idea that back in the good old days, taxonomic change occurred at a stately pace, following careful deliberation, and botanists were therefore able to absorb the (more carefully thought out and therefore clearly correct) changes more readily.

I thought it would be interesting to analyze the actual pace of taxonomic change in the eastern North American vascular plant flora to see if the perception that changes are more rapid now was true. To do so, I selected a series of influential floras and compared taxonomic usage in them, since floras summarize and synthesize taxonomic information and then serve as the primary source of taxonomic information for most users. Generally, a particular flora then serves as a sort of taxonomic standard for a generation. For comparison, I selected Weakley (2009), Radford, Ahles, & Bell (1968), Fernald (1950), Small (1933), and Chapman (1883), a set of regional floras in use over a 126-year period, and selected a random sample of 350 species (ca. 5% of the collective flora of the region) currently recognized in Weakley (2009), and compared their taxonomic treatment at species, genus, and family levels (see Table 1).

Table 1. Comparison of change in the taxonomy used in some eastern North American regional floras from 1883 to the present.

	RAB → Weakley	Fernald → RAB	Small → Fernald	Chapman → Small
intervening years	41	18	17	50
% species changed	42.3%	43.2%	51.8%	65.1%
% species changed / year	1.0%	2.4%	3.0%	1.3%
% genus changed	13.2%	3.3%	23.2%	28.8%
% genera changed / year	0.32%	0.18%	1.37%	0.58%
% family changed	9.7%	2.2%	33.3%	36.9%
% family changed / year	0.24%	0.12%	1.96%	0.74%

Of the random sample, a few examples will help illustrate the degree and nature of changes.

Diphasiastrum tristachyum



Chapman: *Lycopodium complanatum* (Lycopodiaceae). Not distinguishing “*tristachyum*” from “*digitatum/flabelliforme*”

Small, Fernald, RAB: *Lycopodium tristachyum* (Lycopodiaceae). Recognizing 2 species in eastern North America

Weakley: *Diphasiastrum tristachyum* (Lycopodiaceae). Segregate genera recognized based on lineages of great antiquity and fundamental differences in all ways.

Ilex amelanchier

Chapman, Small, Fernald, RAB, Weakley: *Ilex amelanchier* (Aquifoliaceae). No change at any taxonomic level from its naming by the Rev. Moses Ashley Curtis.

Platanthera lacera

Chapman: *Platanthera lacera* (Orchidaceae)

Small: *Blephariglottis lacera* (Orchidaceae). Genus change.

Fernald: *Habenaria lacera* var. *lacera* (Orchidaceae). Genus change again, and new variety recognized.

RAB: *Habenaria lacera* (Orchidaceae). Variety not recognized.

Weakley: *Platanthera lacera* (Orchidaceae). Genus change again... back to Chapman!

Galax urceolata

Chapman: *Galax aphylla* (Ericaceae).

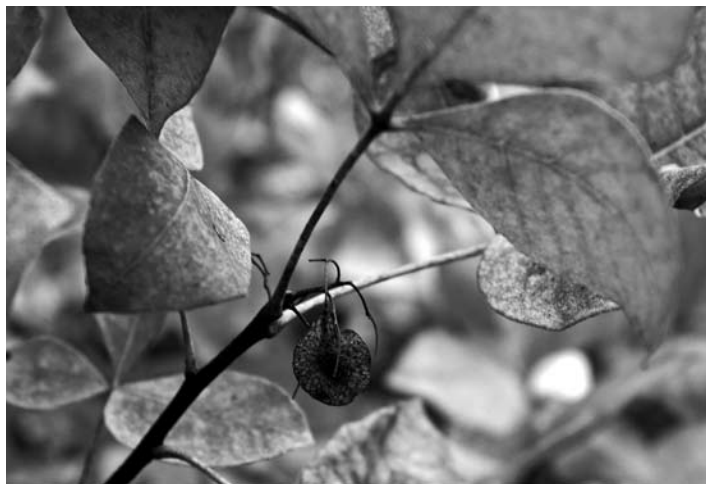
Small: *Galax aphylla* (Galacaceae). Family change.

Fernald, RAB: *Galax aphylla* (Diapensiaceae). Family change again.

Weakley: *Galax urceolata* (Diapensiaceae). Change in specific epithet based on nomenclatural factors.



Ptelea trifoliata



Chapman, Small: *Ptelea* several species (Rutaceae)

Fernald: *Ptelea trifoliata* several varieties (Rutaceae)

RAB, Weakley: *Ptelea trifoliata* s.l. (Rutaceae)

The results show a generally high (though variable) level of taxonomic change throughout the past 126 years' time, and at all levels (species, genus, and family). Certainly, there seems to be no basis for the belief that taxonomic changes at any taxonomic level are at unprecedented (or even unusual) levels in recent years. Without considering the differences in time intervals between these floras, change at all taxonomic ranks was greatest between Chapman and Small. When compensating for intervals by calculating a change per year value, per-year change at all taxonomic ranks was greatest from Small to Fernald. It is not clear to me which offers the better index of "psychological impact of taxonomic change," more simply labeled named Taxonomic Whiplash (TW): normalizing by annual rate makes sense in some ways, but for a Southeastern botanist born in 1840, who had used Chapman's various editions all of his life, the degree of change represented by Small's 1903 Flora would surely have hit like a ton of bricks!

The mention of the names Small and Fernald has to suggest the possibility that change is not necessarily a directional, even, and inspi-

rationally story of the steady onward march of scientific progress, but rather a reticulating process, with some streams antagonistic to one another, and some changes circling back by reversal. Small and Fernald were from opposing camps, centered at the New York Botanical Garden and the Gray Herbarium at Harvard University, respectively (Yankees and Red Sox, anyone?). Small and his colleague Per Axel Rydberg became famous (or notorious, depending on your camp) for taxonomic opinions at odds with the prevailing and dominant Harvard camp (so maybe the Yankees and Red Sox analogy should be reversed).

So, it is worthwhile to look at the degree of change spanning over that period, thus ignoring change from Chapman to Small that was then reversed by the time of Fernald and RAB. From Chapman to RAB, the level of family change was 7.9% (0.09% per year), genus change was 19.5% (0.23% per year), and species change 59.8% (0.7% per year), so the longer view does smooth out some level of Taxonomic Whiplash. My colleague Rogers McVaugh's 100th birthday is in May. In his professional career, he has seen the taxonomic standard for eastern North America start with Robinson & Fernald (1908) and Small (1913), published about 100 years ago, and go through a series of shifts. When I ask him about some taxonomic issue, he often will say things like "well, I always thought Small was probably right about that."

But whatever the era in which we live, or our lifespan, change (and overall, improvement, despite occasional blind alleys and reversals) in the taxonomic understanding of our flora is the order of the day.

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Photographs by Scott Ranger

Rare Plants

by Linda Chafin

Eastern Turkeybeard

Prescribed fire season is here—and every year seems to bring a greater understanding of the ecological importance of fire as well as broader applications of this landscape management tool.

The importance of fire to graminoid-dominated habitats in the Coastal Plain—sandhills, flatwoods, savannas, and bogs—has been understood for several decades, and its prescribed use is now widespread in these habitats on public lands throughout the South. The use of fire in montane habitats has been a harder sell but, where introduced, it has usually brought with it the same vigorous flowering and vegetative responses that follow prescribed fires in the Coastal Plain. Regardless of region, the benefits of prescribed fire are the same—more sunlight reaches the forest floor, nutrients are cycled back to the soil, and encroachment by woody plants on grass- and herb-dominated ground covers is reduced. As a result, some herb species thought to be rare and to flower infrequently are making a comeback in the Appalachians.

Eastern turkeybeard (*Xerophyllum asphodeloides*) could be a poster child for the campaign to return fire to the dry uplands of the Southern Appalachian Mountains. Turkeybeard is a perennial herb that forms large tussocks of long (up to 50 cm), very narrow (1 - 2 mm wide), evergreen leaves. Without fire, this may be all the field botanist ever sees of this plant. Plants can persist vegetatively for many years, waiting for fire or other disturbance to trigger flowering. The underground parts of turkeybeard – thick, ropy roots and a stout, woody rhizome topped by a bulb – are clearly adapted to survive fires. Following a spring fire, each plant produces one or more flower stalks up to 5 feet tall in the summer. Flowers are held in dense clusters at the top of the stalk. The flowers are about ½ inch across with 6 white tepals and produce small, 3-lobed capsules. After fruiting, the plant dies. Offshoots that did not bloom will live to flower in following years.

In recent years, fire was applied to turkeybeard habitat in the George Washington National Forest in Virginia, and, in the words of researcher Norman Bourg, there was “an immense flowering response.”

Thousands of plants burst into flower, some bearing hundreds of flowers. One plant produced 27 flower stalks! Nearby populations, left unburned, produced virtually no fruit or seeds. With a mass flowering event such as this, opportunities for cross-pollination and for recruitment of new, genetically distinct plants are greatly enhanced.

Turkeybeard is known primarily from the dry, rocky, pine-heath woodlands of the Southern Appalachians and the upper Piedmont of Georgia, North Carolina, South Carolina, and Virginia; it also occurs in disjunct populations in the Pine Barrens of New Jersey. A non-flowering tussock of turkeybeard can resemble one of the narrow-leaved bunch-grasses, but turkeybeard leaf bases are white, flattened, and lack sheaths.

Turkeybeard inflorescences are reminiscent of those of fly-poison (*Amianthium muscaetoxicum*), but these two species can be easily distinguished by their leaves. Turkeybeard leaves are narrow and stiff with finely toothed margins; fly-poison leaves are up to one inch wide with smooth margins. Turkeybeard occupies dry, pine woodlands, whereas fly-poison is a plant of moist, hardwood forests.

Turkeybeards (including the western species, *Xerophyllum tenax*) were long considered to be members of the lily family but recent molecular systematics research has placed these species in the tribe Xerophylleae within the bunch-flower family, Melanthiaceae; some botanists would place them in their own family, the Xerophyllaceae.

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Mystery Plants

by Dan Pittillo

For the last pair of mystery plants in Chinquapin 16(4), N° 1 was the bark pattern for *Diospyros virginiana* (clue by the deliquescent branched tree with fruits evident) and N° 2 was *Nyssa sylvatica* (clue of the branches extending at 90° from the trunk).

This time Kevin Caldwell, David Emory, Jim Rentch, Tracy Roof, Greg Schmidt, Susan & Alan Sweetster, and Stephanie Zuno all got both of them. And again, the Sweetsters lead with a perfect score of 8 for all four 2008 Mystery Plants pairs and will be given a book from my library of their choice.

2009 begins a new contest and here is a challenge that should be tougher than the persimmon and black gum!

These two twigs, though quite similar and seen throughout the East and into southern Canada.

No. 1 is a tree sapling while No. 2 is either shrubby or a climbing vine. Each of these were less than 0.5 m tall and found growing in the same habitat when photographed.

The twigs shown are about 30 mm long and 3-4 mm in diameter.



Name That Plant Contest

If you need more challenges for your identification skills, Richard Ware has it for you. Point your web browser to www.gabotsoc.org, the Georgia Botanical Society, and click on "Name That Plant".

Richard began the contest last August with a pair of easy plants, but they got a lot more difficult as the end of the year came along. He puts each month's contest on the website sometime during the first day of the month and the first person to correctly identify the plants (using scientific names only) wins a prize. There is also an annual contest for those who get the most right. Your editor won the annual contest with 9 of 10 correct. December's contest was particularly challenging and no one got both plants right, but Scott Ranger and Linda Chafin got mighty close! The challenging plant was *Eruca sativa*, garden rocket or arugula (left) that has now naturalized in north-west Georgia. Photo by Richard Ware.



Photo by Richard Ware.

Book Review

by Jim Rentch



A Field Guide to Surreal Botany, Illustrated by Janet Chui, Edited by Janet Chui and Jason Erik Lundberg. Two Cranes Press, ISBN 978-981-08-1017-7 \$12 USD (+\$3 USD s/h)

www.surrealbotany.net

Everything about this book suggests a real, if off-beat, botanical treatise of 50 very unusual plants from around the world. The drawings are excellent, and each entry has sections on taxa description and habitat, life cycle, and notes that describe weird (i.e., entirely imaginary but equally plausible) physiological, medicinal, historical, and/or behavioral properties. Plants are grouped by continent, and there are even some blank pages at the end of the book for your own "field notes." Everyone has their favorites. Mine is the baby cabbage (*Brassica homogenesis*). Its life cycle is described: "baby cabbage sprouts where both tears and human semen have fallen on the ground. Some observers (E. Bear, 2006) claim vigorous masturbation produces best results...the fruit bears in the form of a human baby, which can in fact be found under a cabbage leaf." Editor's note: go visit the website. It's fun!

Letters, continued from page 2

thought I might pass on a link from the American Orchid Society that might give you some ideas: http://www.aos.org/AM/Template.cfm?Section=Pests_and_Diseases&TEMPLATE=/CM/ContentDisplay.cfm&CONTENTID=5604.

From David C. Dister:

I enjoyed reading your thoughts about the enigmatic *Triphora trianthophora*. Have you read my Scientific Note about that species, *A New Population Maximum for Triphora trianthophora in Ohio*, in *Castanea* 71(4)?

I do have a few comments as well, which follow:

- I was also surprised to find flowering plants that were perhaps only 3 cm tall. Also, of the 2,600 + plants that I counted during the maximum year, a few had between 5 and 7 flowers per plant!
- My census broke out plants in "clusters," and it was also rare that plants occurred solitary.
- In this southwest Ohio population, I don't recall even a single cluster having a grapefern of any species associated with it.
- Self-pollination seems plausible since I rarely found more than a few plants in flower at the same time, and yet later in the summer it was common to find many plants with mature fruit pods.
- Only once in 9 years of observation did I encounter a mass synchronous flowering. This could be an overstatement as you suggest.

I now reside in northern Michigan and look forward to many encounters with boreal species at the southern limit of their ranges, or in the case of *Triphora trianthophora*, at its northern limit.

Hornwort, continued from page 1

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