PROC. ENTOMOL. SOC. WASH.
94(2), 1992, pp. 177–188

MIMICRY AMONG APOSEMATIC APPALACHIAN XYSTODESMID MILLIPEDS (POLYDESMIDA: CHELODESMIDEA)

Donald R. Whitehead[1] and Rowland M. Shelley

North Carolina State Museum of Natural Sciences, P.O. Box 27647, Raleigh, North Carolina 27611.

Abstract.—The Appalachian Mountains of eastern North America harbor a xystodesmid milliped fauna of more than 100 aposematically colored species-group taxa. They form interactive mimetic communities that share the same dorsal color pattern, if individuals are typically surface active, or the same lateral pattern including leg color, if they are cryptic and exposed by foraging predators. Lack of coloration in the non-aposematic genus *Nannaria* may constitute mimicry with unpigmented juveniles of aposematic genera. Boundaries of mimetic communities appear to be set by distribution limits of mid-size predator complexes; adjacent communities mimic, but distant ones are free to differentiate.

Key Words: Mimicry, aposematic, Xystodesmidae, banded, bimaculate, trimaculate

More than 100 aposematic species-group taxa of several xystodesmid milliped genera inhabit eastern North America. Unlike other eastern polydesmoids they produce benzaldehyde, which imparts an almond or cherry scent to their defensive secretions, so the bold colors may warn of this compound. A striking characteristic of this fauna is the frequent occurrence of sympatry among species of different genera, and many sympatric forms exhibit similar if not identical dorsal pigmentation patterns, suggesting mimetic convergence. In northwestern North Carolina, for example, *Sigmoria* (*Sigmoria*) *latior latior* (Brolemann), with black metaterga and red to yellow paranota, occurs sympatrically with forms of *Pleuroloma flavipes* Rafinesque with the same markings, and the various banded patterns of *Sigmoria* s. lat. in southwestern North Carolina and adjacent parts of South Carolina and Georgia overlap areas where such patterns are exhibited also by species of *Dynoria, Furcillaria,* and *Brachoria* (Shelley and Whitehead 1986). To the west in the Cumberland Plateau of Tennessee, sympatric representatives of *Brachoria* and *Sigmoria* (*Falloria*) display identical patterns of red paranota and blue metatergal bands, such that the genera can be distinguished only through details of the male genitalia. As these features are imperceptible to the unaided eye, one must undertake microscopic examination to determine the genus of field-collected specimens.

In addition to rather obvious instances of mimicry like the above are others in which the colors and patterns vary, both within polymorphic populations of individual species and among the entire mimetic complex. A few polydesmoids in other chelodesmoid families, for example *Euryurus* (Platyrhacidae) and *Eurymerodesmus* (Eurymerodesmidae), also display bold colors in parts or all of their ranges and may be components of the mimetic community when they occur

[1] Deceased, May 1990.

sympatrically with aposematic xystodesmids.

Despite the fact that mimicry has been suspected in this fauna for 30 or so years and alluded to generally in publications like that by Shelley and Whitehead (1986), the only specific reference to the phenomenon is by Hoffman (1971). He remarked that little "mimicry" appeared to be involved between *Brachoria hoffmani* Keeton and *Apheloria virginiensis corrugata* (Wood) near Haysi, Dickenson County, Virginia, whereas at Wytheville, Wythe County, the latter species and *B. separanda versicolor* Hoffman resembled each other closely. However, mimicry can occur in the lateral as well as the dorsal perspectives, so dissimilar dorsal pigmentation patterns do not necessarily indicate that the phenomenon is inoperative.

To document mimicry among these arthropods and ascertain its causes, Whitehead conducted field studies in the Appalachian Mountains during the period 1985–1989, primarily in Virginia and West Virginia. The objective at each productive collecting site was to gather a sample sufficient to gain an impression of the whole mimetic fauna and the variation of its members; population differences were assessed by sampling at nearby localities. All specimens were preserved in 70% isopropanol and deposited in the collection at the National Museum of Natural History, Smithsonian Institution, Washington, DC. Whitehead's investigations ended prematurely because of illness and subsequent death, and a draft manuscript of his findings that he had prepared was edited and developed into the present contribution by the second author upon request of colleagues in his institution, the Systematic Entomology Laboratory, U.S. Department of Agriculture. Whitehead's observations at seven principal sites—Mt. Rogers and High Knob, Virginia; Pinch, Centralia, and Alta, West Virginia; Wayah Bald, North Carolina; and Brasstown Bald, Georgia—are detailed herein along with his observations and conclusions about mimicry, an unexamined aspect of these arthropods. He died before he could test most of his ideas, and they are thus presented here as hypotheses for investigation by future students of Appalachian biology.

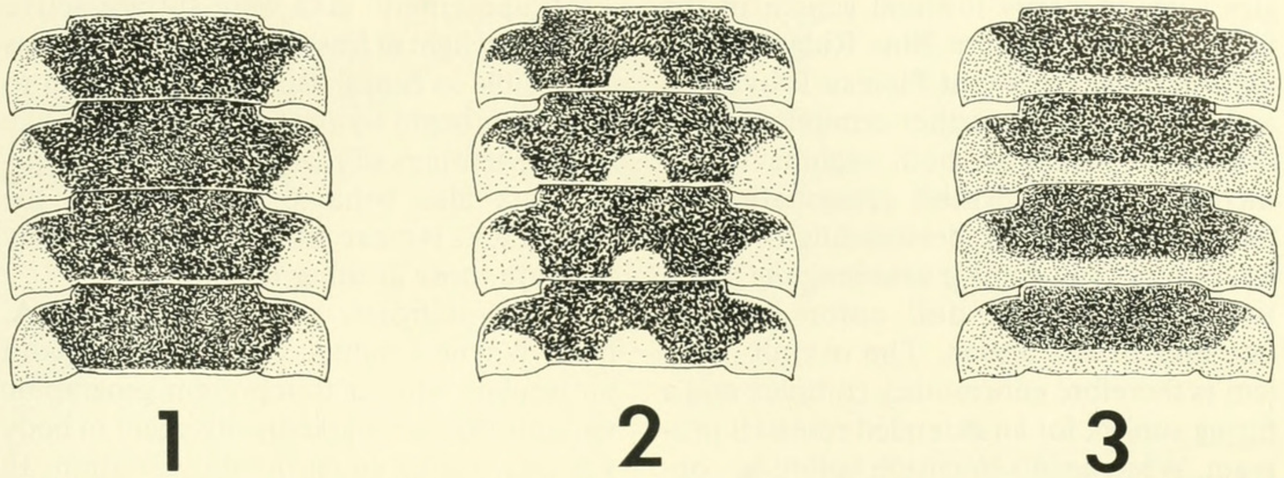
Color and Color Patterns

Figs. 1–3

Shelley and Whitehead (1986) distinguished three color patterns in *Sigmoria*—bimaculate, for paranotal spots only; trimaculate, for paranotal plus middorsal spots; and banded, for crossbands along the caudal metatergal margins (Figs. 1–3)—and developed a notation for representing the pattern and its colors. That for *S.* (*Falloria*) *nantahalae* Hoffman, with its unique combination of red paranotal spots and white metatergal crossbands, was "banded red/white." The present study shows that leg color is important also because coiled xystodesmids often roll on their sides revealing these appendages when disturbed, so the notations should include also leg pigmentation as the last item. Thus, for samples of *S.* (*F.*) *nantahalae* with red legs from Wayah and Brasstown Balds, the description becomes "banded red/white/red."[2] "Trimaculate yellow/yellow/yellow" describes *Cherokia georgiana* (Bollman) at these localities. Pigments must be noted in the field, at the time of collection, because they fade rapidly in preservative. The pattern is visible in alcohol months or years after collection, but the colors of the spots or bands typically fade after only a few days. Consequently pigmentation notes made on preserved specimens a week or more after collection are probably unreliable.

---

[2] The sequence of descriptors in these notations is the type of pattern (banded, trimaculate, or bimaculate) followed by the colors of the paranota, metaterga, and legs. The metatergal pigmentation is placed second in deference to the bimaculate pattern, in which the metaterga lack bright colors and exhibit the background color, usually black. "Bimaculate red/black/red" is preferable to "bimaculate black/red/red."



Figs. 1–3. Representations of the three principal xystodesmid color patterns. 1, bimaculate. 2, trimaculate. 3, banded. The size and shape of the middorsal spots varies in the trimaculate pattern from small, discrete circles to large, semilunar splotches.

Other descriptors, like subfasciate, for irregular crossbands formed of obvious middorsal and paranotal spots, and subvittate, if the middorsal spots are not confined to the metaterga, are unnecessary to describe visual impact. If the animal looked banded it was recorded so whether the band was irregular or entire; likewise, if the legs looked red they were described so even if ringed with white. If color is conspicuous, minor differences are irrelevant for the purposes of mimicry, although they help to evaluate variation and polymorphism. A population of sharply banded and sharply trimaculate individuals is probably polymorphic, with variation in the widths of the bands and the shapes and diameters of the spots. More commonly, the trimaculate condition involves variably transverse middorsal spots that expand laterad and often connect with the paranotal markings to form irregular crossbands.

Taxonomic Notes

The genus *Apheloria* is under study by R. L. Hoffman, so names are not assigned to the phena labeled as species A and B. They have similar gonopods and may be consubspecific with *A. virginiensis corrugata,* but they do not exhibit the banded pattern characteristic of this race. Also awaiting description are phena A and B of *Sigmoria* (*Rudiloria*), tentatively considered as new species.

Tribal compositions of the principal Appalachian xystodesmids are as follows: Chonaphini—aposematic, one genus (*Semionellus*); Rhysodesmini—aposematic, three genera (*Boraria, Pleuroloma,* and *Cherokia*), not aposematic, one genus (*Gyalostethus*); Nannariini—not aposematic, one genus (*Nannaria*); and Apheloriini—aposematic, three genera (*Apheloria, Brachoria,* and *Sigmoria*). Of these genera, *Gyalostethus* was not encountered in this study and is not considered. In the southern Appalachian periphery there are four other aposematic genera that probably demonstrate mimicry—*Erdelyia* (Rhysodesmini) and *Deltotaria, Dynoria,* and *Furcillaria* (Apheloriini) (Shelley 1981, 1984a; Shelley and Whitehead 1986). The last three genera extend into southeastern lowland physiographic provinces and are known to resemble sympatric species of *Sigmoria* in the Piedmont Plateau and Coastal Plain. Three apparently non-aposematic rhysodesmine genera also occur in coastal Georgia, Alabama, and Florida—*Caralinda, Gonoessa,* and *Lourdesia* (Hoffman 1978, Shelley 1979, 1984b, c, 1991), as does a fifth tribe, Pachydesmini, which ranges northward into the southern fringe of the Appalachians. Thus, the mimetic Appalachian fauna intermingles with primarily lowland genera in the fringes of the southern Blue Ridge Mountains and the Piedmont Plateau Provinces, and the picture is further complicated by sympatric genera in both regions whose members do not exhibit aposematic patterns. A complete understanding of mimicry would thus involve assessing the selective advantage of dull colors on the non-aposematic genera. The overall problem is therefore enormously complex and a fitting subject for an extended research program, Whitehead's intention before he contracted a terminal illness. This contribution outlining his observations and conclusions is intended to stimulate investigation on this topic.

Color Patterns and Mimetic Communities of Appalachian Xystodesmids

Fig. 4

A complete listing of species collected during this study is presented in Table 1, and the xystodesmids encountered in and near West Virginia are listed in Table 2. Figure 4 shows Whitehead's collecting localities in both the Appalachians and neighboring regions, and collections and observations at major sampling sites are described in the ensuing paragraphs.

Mt. Rogers, Washington Co., Virginia. One syntopic community included *Apheloria tigana* Chamberlin, *Boraria stricta* (Brolemann), and *Sigmoria* (*Dixioria*) *coronata* (Hoffman). Four other aposematic xystodesmids—*Brachoria ethotela* Chamberlin, *Pleuroloma flavipes, Sigmoria* (*Sigmoria*) *latior latior,* and perhaps even *Sigmoria* (*Rudiloria*) *trimaculata kleinpeteri* (Hoffman)—also occur in this general area and are likely components of the mimetic community (Keeton 1959, Hoffman 1971, Shelley 1980, Shelley & Whitehead 1986). All are bimaculate, known or predicted yellow/black/yellow. Northward, bimaculate taxa extend only to the southernmost counties of West Virginia, so this color pattern has pronounced geographical limits.

All aposematic taxa were surface-active during daylight at least occasionally and thus are visible in dorsal aspect often enough to be remembered by potential predators like birds. Members of this surface-active complex are also behaviorally mimetic; the whole fauna is more prone to surface display than are those at other localities.

Apheloria tigana and *Apheloria* sp. A, from Wayne County, West Virginia, both bimaculate, appear to represent geographic variants that are markedly divergent in body size but similar in chromatic variation. In three specimens of *A. tigana,* the paranotal spots are small and triangular, and in one they are connected by a narrow, inconspicuous metatergal band. In the three specimens of sp. A, the paranotal spots are proportionately much larger, and in two they are connected also by a fine transverse band.

Pinch, Kanawha Co., West Virginia. Mimetic forms of *Apheloria virginiensis corrugata* and *Sigmoria* (*Rudiloria*) *rigida* Shelley occur here, both displaying yellow crossbands and bright red legs. Only one specimen of the former was encountered, distinguished in the field as a larger, stouter animal, and the red paranotal markings were much more developed than in specimens of *A. v. corrugata* found elsewhere. In dorsal aspect the red spots blend with the legs to reduce apparent body size and form to that of the narrower-bodied *S.* (*R.*) *rigida.*

These xystodesmids seemed less surface-active than those at Mt. Rogers, raising the questions as to which predators the mimicry is directed and at what range. Collectors more often find these millipeds under leaves than on the surface, and certain predators hunt for prey by "scratching" in leaves. Thus, if millipeds are exposed in this manner, they are seen in dorsal aspect at short range and benefit from immediate recognition.

Centralia, Braxton Co., West Virginia. Upstream from Pinch on the Elk River, yellow banded *A. v. corrugata* and *S.* (*R.*) *rigida* were less precisely mimetic and were syntopic with trimaculate, yellow/yellow-red/

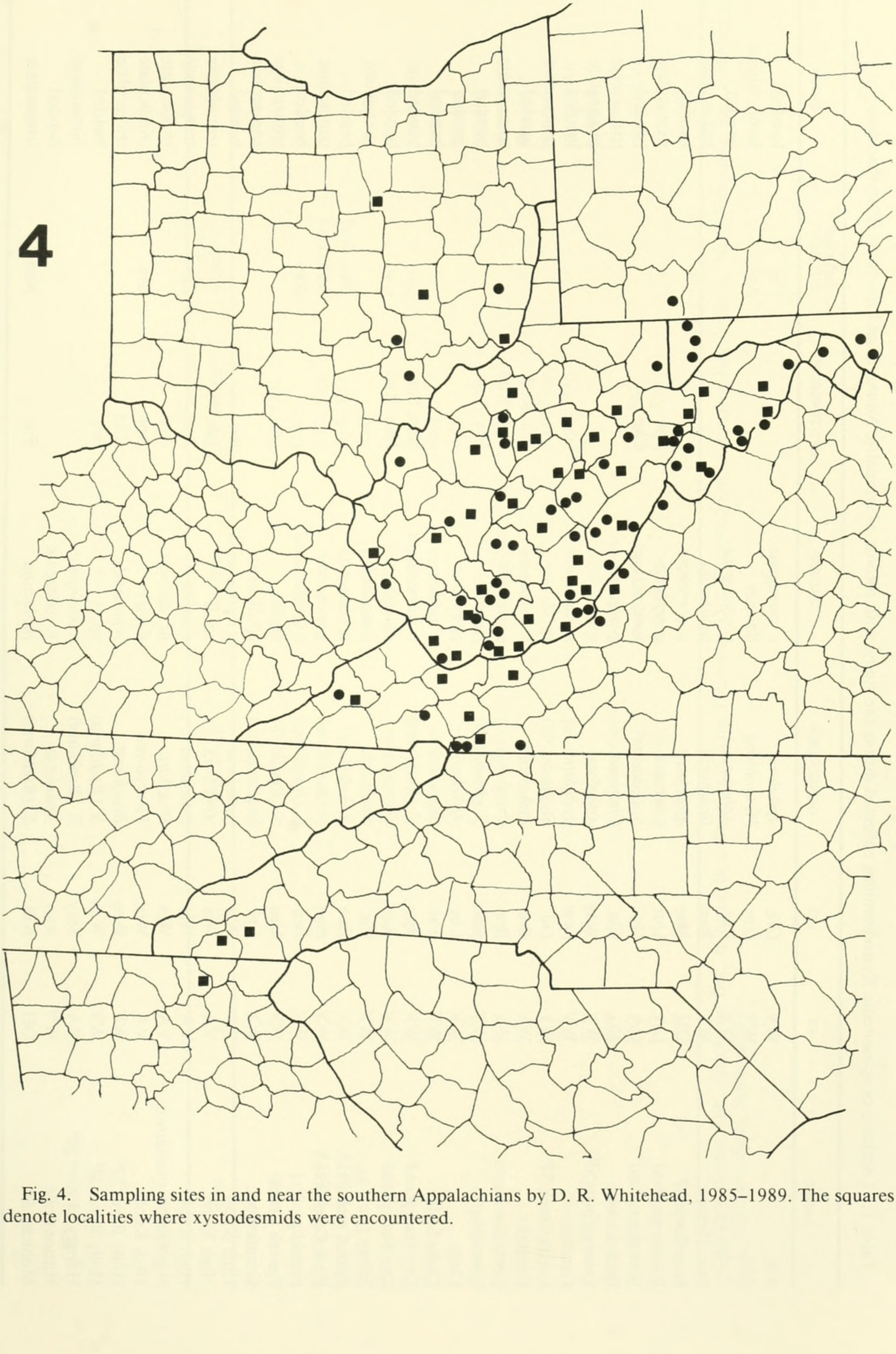


Fig. 4. Sampling sites in and near the southern Appalachians by D. R. Whitehead, 1985–1989. The squares denote localities where xystodesmids were encountered.

Table 1. Localities of aposematic Xystodesmidae collected during the study, with records of sympatric *Nannaria* and *Euryurus* (Platyrhacidae).

Locality	ST	CO	GENSUBGEN	SPSUBSP	SYNTOPGEN*	OTHGEN SUBGEN*	Pattern
Alta	WV	Gre	*Apheloria*	*v. corrugata*		Ple	banded
Alta	WV	Gre	*Pleuroloma*	*flavipes*		Aph	feebly trimac
Audra SP	WV	Bar	*Apheloria*	*v. corrugata*			banded
Bear Heaven	WV	Ran	*Brachoria*	*separanda*			trimaculate
Blue Rock SP	OH	Mus	*Apheloria*	*v. corrugata*			banded
Brasstown Bald	GA	Uni	*Cherokia*	*georgiana*	Fal		trimaculate
Brasstown Bald	GA	Uni	*S. (Falloria)*	*nantahalae*	Che		banded
Buck Creek	NC	Cla	*Cherokia*	*georgiana*			trimaculate
Cabwaylingo SF	WV	Way	*Apheloria*	sp. A			bimaculate
Camden	WV	Lew	*Apheloria*	*v. corrugata*			banded
Cedar Creek SP	WV	Gil	*S. (Rudiloria)*	sp. B			trimaculate
Centralia	WV	Bra	*Apheloria*	*v. corrugata*	Bra, Rud		banded
Centralia	WV	Bra	*Brachoria*	*separanda*	Aph, Rud		trimaculate
Centralia	WV	Bra	*S. (Rudiloria)*	*rigida*	Bra, Aph		banded
Clay	WV	Cla	*Apheloria*	*corrugata*			banded
Dolly Sods	WV	Tuc	*Semionellus*	*placidus*			banded
Dry Fork Road	WV	Ran	*S. (Rudiloria)*	*t. trimaculata*	Nan, Sem		banded
Dry Fork Road	WV	Ran	*Semionellus*	*placidus*	Nan, Rud		banded
Edray	WV	Poc	*Brachoria*	*separanda*			subfasciate
Fork Creek PHA	WV	Boo	*Apheloria*	*v. corrugata*		Nan, Rud	banded
Fork Creek PHA	WV	Boo	*S. (Rudiloria)*	*guyandotta*		Aph, Nan	trimaculate
Franklin	WV	Pen	S. (*Rudiloria*)	*t. trimaculata*		Nan	banded
French Creek	WV	Ups	S. (*Rudiloria*)	sp. B			trimaculate
Grantsville	WV	Cal	S. (*Rudiloria*)	sp. B			trimaculate
High Knob	VA	Wis	*Apheloria*	*v. corrugata*	Bra		banded
High Knob	VA	Wis	*Apheloria*	sp. B	Bra, Ple		trimaculate
High Knob	VA	Wis	*Brachoria*	*insolita*	Aph	Ple	trimaculate
High Knob	VA	Wis	*Brachoria*	nr. *dentata*	Aph		trimaculate
High Knob	VA	Wis	*Pleuroloma*	*flavipes*	Aph	Bra	trimaculate
Holly River SP	WV	Web	*Brachoria*	*separanda*	Rud		trimaculate
Holly River SP	WV	Web	*S. (Rudiloria)*	sp. A	Bra		banded
Hungry Mother SP	VA	Smy	S. (*Rudiloria*)	*t. kleinpeteri*			bimaculate
Huttonsville	WV	Ran	*Apheloria*	*v. corrugata*			banded
Mohican SP	OH	Ash	*S. (Rudiloria)*	*mohicana*	Eur	Nan	trimaculate

Table 1. Continued.

Locality	ST	CO	GENSUBGEN	SPSUBSP	SYNTOPGEN*	OTHGEN SUBGEN*	Pattern
Mount Nebo	WV	Nic	*Apheloria*	*v. corrugata*			banded
Mount Rogers	VA	Gra	*Apheloria*	*tigana*	Bor, Dix		bimaculate
Mount Rogers	VA	Gra	*Boraria*	*stricta*	Dix	Aph	bimaculate
Mount Rogers	VA	Gra	*Boraria*	*stricta*	Aph, Dix		bimaculate
Mount Rogers	VA	Gra	*S. (Dixioria)*	*coronata*	Aph, Bor		bimaculate
North Bend SP	WV	Rit	*Apheloria*	*v. corrugata*	Rud		banded
Panther SF	WV	McD	*Brachoria*	nr. *laminata*	Rud	Nan	banded
Panther SF	WV	McD	*S. (Rudiloria)*	*t. kleinpeteri*	Bra	Nan	bimaculate
Pinch	WV	Kan	*Apheloria*	*v. corrugata*	Rud		banded
Pinch	WV	Kan	*S. (Rudiloria)*	*rigida*	Aph		banded
Rinard Mills	OH	Mon	*Semionellus*	*placidus*			banded
Short Mountain	WV	Ham	*S. (Rudiloria)*	*t. trimaculata*			trimaculate
Spencer	WV	Roa	*Apheloria*	*v. corrugata*			banded
Stumptown	WV	Gil	*Apheloria*	*v. corrugata*	Rud, Nan		banded
Stumptown	WV	Gil	*S. (Rudiloria)*	sp. B	Aph, Nan		trimaculate
Twin Falls SP	WV	Wyo	*Apheloria*	*v. corrugata*			banded
Wardensville	WV	Har	*S. (Rudiloria)*	*t. trimaculata*			trimaculate
Wayah Bald	NC	Mac	*Cherokia*	*g. georgiana*	Eur, Fal		trimaculate
Wayah Bald	NC	Mac	*S. (Falloria)*	*nantahalae*	Che, Eur		banded
Williamsburg	WV	Gre	*Apheloria*	*v. corrugata*			banded

* Abbreviations: Aph, *Apheloria*; Bor, *Boraria*; Bra, *Brachoria*; Che, *Cherokia*; Dix, *Dixioria*; Eur, *Euryurus*; Fal, *Falloria*; Nan, *Nannaria*; Ple, *Pleuroloma*; Rud, *Rudiloria*; Sem, *Semionellus*.

Table 2. Aposematic Xystodesmidae in and near West Virginia; abbreviations as in Table 1.

GEN-SUBGEN	SPSUBSP	Locality	CO	ST	SYNTOPGEN	OTHGEN SUBGEN	Pattern
Apheloria	*v. corrugata*	Alta	Gre	WV		Ple	banded
Apheloria	*v. corrugata*	Audra SP	Bar	WV			banded
Apheloria	*v. corrugata*	Blue Rock SP	Mus	OH			banded
Apheloria	*v. corrugata*	Camden	Lew	WV			banded
Apheloria	*v. corrugata*	Centralia	Bra	WV	Bra, Rud		banded
Apheloria	*v. corrugata*	Clay	Cla	WV			banded
Apheloria	*v. corrugata*	Fork Creek PHA	Boo	WV		Nan, Rud	banded
Apheloria	*v. corrugata*	High Knob	Wis	VA	Bra		banded
Apheloria	*v. corrugata*	Huttonsville	Ran	WV			banded
Apheloria	*v. corrugata*	Mount Nebo	Nic	WV			banded
Apheloria	*v. corrugata*	North Bend SP	Rit	WV	Rud		banded
Apheloria	*v. corrugata*	Pinch	Kan	WV	Rud		banded
Apheloria	*v. corrugata*	Spencer	Roa	WV			banded
Apheloria	*v. corrugata*	Stumptown	Gil	WV	Rud, Nan		banded
Apheloria	*v. corrugata*	Twin Falls SP	Wyo	WV			banded
Apheloria	*v. corrugata*	Williamsburg	Gre	WV			banded
Apheloria	*tigana*	Mount Rogers	Gra	VA	Bor, Dix		bimaculate
Apheloria	sp. A	Cabwaylingo SF	Way	WV			bimaculate
Apheloria	sp. B	High Knob	Wis	VA	Bra, Ple		trimaculate
Boraria	*stricta*	Mount Rogers	Gra	VA	Aph, Dix		bimaculate
Boraria	*stricta*	Mount Rogers	Gra	VA	Dix	Aph	bimaculate
Brachoria	*insolita*	High Knob	Wis	VA	Aph	Ple	trimaculate
Brachoria	nr. *dentata*	High Knob	Wis	VA	Aph		trimaculate
Brachoria	nr. *laminata*	Panther SF	McD	WV	Rud	Nan	banded
Brachoria	*separanda*	Bear Heaven	Ran	WV			trimaculate
Brachoria	*separanda*	Centralia	Bra	WV	Aph, Rud		trimaculate
Brachoria	*separanda*	Edray	Poc	WV			subfasciate
Brachoria	*separanda*	Holly River SP	Web	WV	Rud		trimaculate
Pleuroloma	*flavipes*	Alta	Gre	WV		Aph	feebly trimac
Pleuroloma	*flavipes*	High Knob	Wis	VA	Aph	Bra	trimaculate
S. (*Dixioria*)	*coronata*	Mount Rogers	Gra	VA	Aph, Bor		bimaculate
S. (*Rudiloria*)	*guyandotta*	Fork Creek PHA	Boo	WV		Aph, Nan	trimaculate
S. (*Rudiloria*)	*t. kleinpeteri*	Hungry Mother SP	Smy	VA			bimaculate
S. (*Rudiloria*)	*t. kleinpeteri*	Panther SF	McD	WV	Bra	Nan	bimaculate
S. (*Rudiloria*)	*mohicana*	Mohican SP	Ash	OH	Eur	Nan	trimaculate

Table 2. Continued.

GEN-SUBGEN	SPSUBSP	Locality	CO	ST	SYNTOPGEN	OTHGEN SUBGEN	Pattern
S. (*Rudiloria*)	*rigida*	Centralia	Bra	WV	Bra, Aph		banded
S. (*Rudiloria*)	*rigida*	Pinch	Kan	WV	Aph		banded
S. (*Rudiloria*)	sp. A	Holly River SP	Web	WV	Bra		banded
S. (*Rudiloria*)	sp. B	Cedar Creek SP	Gil	WV			trimaculate
S. (*Rudiloria*)	sp. B	French Creek	Ups	WV			trimaculate
S. (*Rudiloria*)	sp. B	Grantsville	Cal	WV			trimaculate
S. (*Rudiloria*)	sp. B	Stumptown	Gil	WV	Aph, Nan		trimaculate
S. (*Rudiloria*)	*t. trimaculata*	Dry Fork Road	Ran	WV	Nan, Sem		banded
S. (*Rudiloria*)	*t. trimaculata*	Franklin	Pen	WV		Nan	banded
S. (*Rudiloria*)	*t. trimaculata*	Short Mountain	Ham	WV			trimaculate
S. (*Rudiloria*)	*t. trimaculata*	Wardensville	Har	WV			trimaculate
Semionellus	*placidus*	Dolly Sods	Tuc	WV			banded
Semionellus	*placidus*	Dry Fork Road	Ran	WV	Nan, Rud		banded
Semionellus	*placidus*	Rinard Mills	Mon	OH			banded

yellow-red *Brachoria separanda* Chamberlin. Legs of all 3 species varied from yellow to red. In dorsal aspect, *B. separanda* does not seem a member of the mimetic community, but membership becomes evident in side view. Increased variation in leg color in *S.* (*R.*) *rigida* at Centralia, compared with that found at Pinch, appears to reflect the presence of *B. separanda,* decreased reliance on precise dorsal mimicry, and increased reliance on mimicry in the lateral perspective.

High Knob, Wise Co., Virginia. Five phena, possibly in two parapatric communities, were discovered at four brief collecting stops within five miles of the summit. Site A, 2.9 miles north of the entrance to High Knob Lake Recreation Area, was occupied by boldly banded *A. v. corrugata* and trimaculate *Brachoria* sp. nr. *dentata* Keeton. The other three sites were 1–4 miles south of the entrance and harbored syntopic, trimaculate animals that are virtually indistinguishable in the field. Site B contained *B. insolita* Keeton, polychromic (yellow/yellow/yellow, yellow/orange/pink, pink/pink/pink). Sites C and D, where all specimens had yellow legs, contained the following: site C, *Apheloria* sp. B. and *Pleuroloma flavipes*; site D, *Apheloria* sp. B. and *B. insolita.*

Two of the three specimens of *Apheloria* sp. B displayed yellow middorsal spots on the proterga as well as the metaterga; the other had the middorsal and paranotal spots connected by a fine transverse band. As with the finely banded variants of the bimaculate *A. tigana* from Mt. Rogers and *Apheloria* sp. A from Wayne County, West Virginia, no color intergradation with the strongly banded *A. v. corrugata* was evident. These variations are unlike those found in *B. separanda* and *P. flavipes,* in which middorsal spots of some species are enlarged to connect with paranotal spots in an irregular band as a continuous series of intergrades.

Additional taxa may occur at High Knob, for example *Brachoria hoffmani* Keeton, which Hoffman (1971) recorded from another Wise County locality. His comment about lack of mimicry between this banded, polychromic species and *A. v. corrugata* was solely from the dorsal perspective and overlooked the possibility of lateral mimicry as seen by a litter-scratching predator.

Wayah Bald, Macon Co., North Carolina, and *Brasstown Bald, Union Co., Georgia.* Coiled specimens of trimaculate yellow/yellow/yellow *Cherokia georgiana* and banded red/white/red *Sigmoria* (*Falloria*) *nantahalae* presented similar outer spirals of alternating pale and dark. They thus appear to be functionally mimetic though differing in actual color and pattern.

Alta, Greenbrier Co., West Virginia. Body size of two species affects aposematism because if they are too different, mimicry will not work. Small size will correlate with reduced aposematism if mimicry develops primarily for side viewing. Because a 15–20 mm coil should be perceived much more readily by a potential predator than a 10 mm coil, the selective advantage of lateral mimicry will be reduced for small millipeds, and the metabolic cost of maintaining an aposematic color pattern will become too high. With reduction in selective advantage, aposematy for side viewing may be lost. However, if the millipeds are commonly surface-active, dorsal aposematy and mimicry provide useful visual impacts for much smaller animals. At Alta *P. flavipes* is not syntopic with either *A. v. corrugata* or with other species exhibiting a similar dorsal pattern; its smaller size prevents useful mimicry in side view as well.

A Preliminary Synthesis

Observations of geographically correlated color patterns and behavioral attributes of Appalachian xystodesmid species are explained readily and reasonably in terms of Mullerian mimicry, i.e. simplification of recognition of sympatric, specifically different groups of unpalatable organisms by potential predators. However, patterns among millipeds are varied, and as stated previously, a detailed understanding of the entire complex will require much additional research. At present, we offer the generalized thoughts that are summarized below.

Color pattern.—Because banded patterns are displayed by representatives of other diplopod orders and are more widespread in the class than spotted patterns, we postulate the banded pattern to be ancestral and that the interrupted patterns evolved in the sequence banded → trimaculate → bimaculate.

In *Apheloria,* selection for Mullerian mimicry apparently causes shifts from strongly banded to bimaculate and trimaculate patterns via loss of yellow pigment rather than through reduced intensity or dull color. In contrast, the bimaculate pattern of *S.* (*R.*) *trimaculata kleinpeteri* seems an extreme negative expression of the dull orange or red middorsal spots found in southernmost populations of *S.* (*R.*) *t. trimaculata* (Hoffman 1951) and *S.* (*R.*) *guyandotta* (Shelley and Whitehead 1986).

For taxa or populations whose principal mimetic aspect is lateral (see below), consistency of middorsal spots seems unnecessary to maintain the crucial expression of pattern. Maximum benefit in the territory of yellow banded *Apheloria* would be for a trimaculate species to have a large yellow spot, but this benefit may not justify the cost when mimicry occurs in a different perspective. Except for *Apheloria,* the middorsal spots in trimaculate taxa tend to vary from bright yellow to dull red, the latter perhaps representing drift away from mimetic control.

Aspect and mimicry.—Mimicry is expressed either in dorsal or lateral aspects of these xystodesmids. Dorsal mimicry appears to warn hunters like birds and possibly box turtles that normally do not search under leaves and logs; occasionally it may warn larger predators that might expose millipeds without disturbing them. However, foragers like grouse, turkey, raccoon, fox, and possibly shrews scratch in the litter and disturb the millipeds, which immediately coil and fall on their sides, where they are mimetic. They present a 15–25 mm spiral of legs, venter, and dorsal colors, with a notable periphery of alternating light and dark colors. Visual impact is sufficient to generate instant recognition and therefore avoidance at a distance of 6–12″ or more.

Loss of bright color.—Xystodesmid juveniles tend to lack bright colors, possibly because they are not surface active, too varied in size, and too transient in life stage to justify metabolic investment in aposematy. However, they are exposed by the same litter scratching hunters that find adults, are seen only at close range, and are recognizable immediately because the absence of bright colors and similarity in body form make them look alike.

Members of the small-bodied, non-aposematic genus *Nannaria* were notably pale and resembled juveniles of larger xystodesmids with which they were found. This appears to be a minor form of mimicry probably brought about by selection for reduction in pigment.

Body size and aposematy.—Body size appears to affect aposematy. Small size will correlate with reduced aposematy if mimicry develops primarily for side viewing. Because a 15–20 mm coil should be perceived more readily by a potential predator than a 10 mm coil, the selective advantage of lateral mimicry for small millipeds will be reduced, and the metabolic cost of maintaining an aposematic color pattern may become too high. With reduction in selective advantage, aposematy for side viewing may be lost. However, if these smaller millipeds are surface-active, dorsal aposematy and mimicry with larger species provide useful visual impacts to deter potential predators.

Community differentiation of Mullerian mimics.—Mimicry is a shared response of sympatric, specifically different prey populations to predator pressure, dependent upon range limits of pertinent predators, because it is the individual predator or its family group that is capable of learning to recognize and avoid distasteful prey. Some prey individuals will be sacrificed for this learning to occur, but the entire mimetic complex benefits. Pressures that drive sympatric mimetic populations toward a shared color pattern will decrease genetic continuity between such populations and their relatives in adjacent areas, which may be under the influence of different selective pressures caused by a different predator complex. Decreased genetic continuity among allopatric conspecific populations leads to their speciation. Thus, predator pressure may lead to evolution of the distinctive milliped communities reported here.

As indicated by their different color patterns, the faunas at High Knob and Mt. Rogers, Virginia, must be stressed by somewhat isolated sets of predator units. The sites are sufficiently remote to preclude frequent exchange of predator individuals, so the milliped fauna of each area is free to form a separate mimetic community. As the banded → trimaculate → bimaculate evolutionary sequence takes place, predatory selection at one site favors one color pattern while that at another favors another. In contrast, if xystodesmid communities are parapatric, as possibly at the three High Knob sites, they would benefit from shared mimicry patterns if they occur within the range of the same predator complexes.

Aposematy and diversity.—The number of aposematic taxa in an area correlates well with the amount of mimicry and localized gonopod differentiation, which is constrained by requirements unrelated to membership in the mimetic community. Bimaculate, trimaculate, and banded color patterns coexist among five genus-group taxa in central West Virginia, but east of Allegany Mountain, on the border between Allegany County, Virginia, and Greenbrier County, West Virginia, *Brachoria* and *Semionellus* disappear except for an isolated population of *S. placidus* in the northern and central Blue Ridge of Virginia. Otherwise, only two xystodesmid species occur in this region (*A. v. corrugata* and *S.* (*R.*) *t. trimaculata*), which vary less and typically are not mimetic. In contrast, Mount Rogers has seven taxa that share a single color pattern and differ phenotypically from taxa to the north.

Concluding Remarks

The search for understanding of phenomena that involve complex community interactions has led many biologists to tropical areas, where such interactions abound. Working in the tropics carries with it a variety of hardships ranging from risk of disease to struggles with bureaucratic regulations. The xystodesmid mimetic complex reported here offers a system for investigation that holds as much promise as a researcher could hope to find in the tropics, but one that can be investigated with comparative ease and little personal risk.

Understanding how speciation works among the aposematic Appalachian xystodesmids requires a comprehensive analysis of the entire aposematic fauna, which extends hundreds of miles in all directions to the Mississippi River, the Gulf of Mexico, the Atlantic Ocean, and nearly to Tampa Bay, Florida (Shelley and Whitehead 1986). Acquiring such knowledge could be a daunting task, for the eastern Xystodesmidae includes five tribes, numerous genera, and innumerable species. However, the fauna at each locality typically is uncomplicated taxonomically, having only one member of a given genus-group, and species-group taxa need not be syntopic nor share similar population structures to benefit from mimicry. Thus, analyses can proceed area by area in a sequence determined by the requirements and wishes of an investigator.

Acknowledgments

We thank G. E. Ball for helpful advice to the first author during the stages of his research and for an especially beneficial review of a draft manuscript; D. S. Lee and R. L. Hoffman, for commentary on drafts; and R. D. Gordon, for assistance in publication. Cathy Wood typed and retyped numerous drafts of the manuscript, and Figs. 1–3 were prepared by R. G. Kuhler.

Literature Cited

Hoffman, R. L. 1951. Subspecies of the milliped *Apheloria trimaculata* (Wood) (Polydesmida: Xystodesmidae). Chicago Academy of Sciences, Natural History Miscellanea 81: 1–6.

———. 1971. Millipeds of the genus *Brachoria* in Virginia (Polydesmida: Xystodesmidae). The Radford Review 25:83–99.

———. 1978. A new genus and species of rhysodesmine milliped from southern Georgia (Polydesmida: Xystodesmidae). Proceedings of the Biological Society of Washington 91: 365–373.

Keeton, W. T. 1959. A revision of the milliped genus *Brachoria* (Polydesmida: Xystodesmidae). Proceedings of the United States National Museum 109: 1–58.

Shelley, R. M. 1979. A new milliped of the genus *Caralinda* from north Florida (Polydesmida: Xystodesmidae). The Florida Entomologist 62: 183–187.

———. 1980. Revision of the milliped genus *Pleuroloma* (Polydesmida: Xystodesmidae). Canadian Journal of Zoology 58: 129–168.

———. 1981. A new xystodesmid milliped genus and three new species from piedmont South Carolina (Polydesmida). Proceedings of the Biological Society of Washington 94: 949–967.

———. 1984a. Revision of the milliped genus *Dynoria* (Polydesmida: Xystodesmidae). Proceedings of the Biological Society of Washington 97: 90–102.

———. 1984b. New records and species of the milliped genus *Caralinda* (Polydesmida: Xystodesmidae). The Florida Entomologist 66: 407–415.

———. 1984c. A new xystodesmid milliped genus and five new species from the Coastal Plain of Alabama (Polydesmida). The Florida Entomologist 67: 453–464.

———. 1991. A fourth genus of small-bodied xystodesmid millipeds from the southeastern Coastal Plain (Polydesmida). Proceedings of the Entomological Society of Washington 93: 244–247.

Shelley, R. M. and Whitehead, D. R. 1986. A reconsideration of the milliped genus *Sigmoria*, with a revision of *Deltotaria* and an analysis of the genera in the tribe Apheloriini (Polydesmida: Xystodesmidae). Memoirs of the American Entomological Society Number 35, 223 pp.