INSECT ENDEMISM IN THE INTERIOR HIGHLANDS OF NORTH AMERICA

ROBERT T. ALLEN
Department of Entomology
University of Arkansas
Fayetteville, AR 72701

ABSTRACT

Sixty-eight species of insects are considered endemic to the Interior Highlands of North America. The area encompassed by these species consists of the Ozark, Ouachita, Arbuckle, and Wichita Mountains of Illinois, Missouri, Arkansas, and Oklahoma. County maps are given for each species as well as maps showing the distribution of close relatives, where available. The hypothesis that all endemism in the Interior Highlands is the result of events associated with Pleistocene glaciation is questioned because the area has been an above water land mass since the Pennsylvanian era. Based on taxon/area cladograms of sixteen of the species, a biogeographic pattern is suggested. It is further suggested that only two vicariant events were necessary to account for the origin of the species represented in the taxon/area cladograms. The times at which these events may have occurred is uncertain. The first event may have been in the early cretaceous when the Interior Highlands was an isolated island surrounded by epicontinental seas.

Resumen

Seiscinta y ochenta especies de insectos se consideran endémicos al interior montañoso de Norte América. El área circundada por estas especies consiste de las Ozark, Ouachita, Arbuckle, y las montañas Wichita de Illinois, Missouri, Arkansas, y Oklahoma. Se proveyeron mapas de condados para cada especie así como mapas enseñando la distribución de parientes cercanos cuando estaban disponibles. La hipótesis de que todo el endemismo en el interior montañoso es el resultado de eventos asociados con la glaciación Pleistocena se pone en duda porque el área ha estado sobre el nivel del agua desde la era Pensilvánica. Basado en cladogramas del área por taxa de dieciséis especies, se sugiere un patrón biogeográfico. Se sugiere además que solo dos eventos vicariantes fueron necesarios para dar cuenta del origen de las especies representadas por cladogramas del área por taxa. Son inciertos los momentos en que estos eventos ocurrieron. El primer evento pudiera haber ocurrido temprano en la era cretácea cuando el interior montañoso era una isla aislada rodeada de mares epicontinentales.

As knowledge about the basic taxonomy and distribution of the North American biota has increased during this century, biogeographers have recognized a number of geographical areas containing significantly high numbers of endemic taxa. Three of the better-known North American areas of endemism are peninsular Florida, the southern Appalachians (especially the Great Smoky Mountains), and the Pacific Northwest. A less well-known area of endemism is the mid-continent, Interior Highlands occupying portions of Illinois, Missouri, Arkansas, and Oklahoma. There are over 200 species of plants and animals that appear to be endemic to the Interior Highlands (Allen, unpublished ms). Among the endemic animals are 68 species of insects. These species are distributed throughout the class Insecta, specifically in the following orders: Diptera, Microcoryphia, Ephemeroptera, Odonata, Plecoptera, Orthoptera, Hemiptera, Coleoptera, Trichoptera, Lepidoptera. This represents a significant number of endemic forms
and indicates that the Interior Highlands have played an important role in the evolution of the North American insect fauna.

A few insect systematists have discussed various insect taxa known to have endemic species in the Interior Highlands and suggested reasons for this endemism. Among these authors are: Ross, Trichoptera (1956, 1965); Ross & Ricker, Plecoptera (1971); McCafferty, Ephemeroptera (1977); McCafferty & Provonah, Ephemeroptera (1978); Freitag, Coleoptera (1969); Allen & Carlton, Coleoptera (1988). Many authors, noted throughout this paper, have described endemic Interior Highlands species.

When insect systematists have discussed the possible causal factors that have led to speciation in the Interior Highlands, the explanation has been the events associated with Pleistocene Glaciation (Ross 1965, Ross & Ricker 1971, McCafferty 1977). This Pleistocene explanation is certainly one possibility. However, the Pleistocene explanation fails to take into account that the Interior Highlands, specifically the Ozark and Ouachita Mountains, have been a positive feature on the North American continent since the Pennsylvanian (320 million years ago, mya). Thus the Interior Highlands have been subject to habitation by a land biota much, if not most, of this time, and this biota has been alternately connected and isolated from other North American biotas on numerous, separate occasions. One may conclude that, except for the Pleistocene, the vast majority of the geological and biological history of the Interior Highlands has been virtually ignored. If an accurate understanding of the origin and evolution of the Interior Highlands biota is to be formulated, then it will be necessary to consider the possible effect that such events as the late Tertiary rejuvenation of the Laramide revolution (beginning in the Mucene) and the formation of the prairie wedge (Cole & Armentrout 1979, Dickinson 1979) and the climatic and geological changes during and after the Cretaceous (130-63 mya) had on this Interior Highlands biota. Such a task will not be easy, but it is certainly necessary.

**Significance and Importance of the Interior Highlands Fauna**

The significance and importance of the endemic Interior Highlands biota has not been fully realized for a number of reasons. The descriptions and discussions of the Interior Highland endemic insects (as well as other animals and plants) have appeared in a diverse number of journals and books over an extended period of time. Specialists for one group, say the Coleoptera, may not be aware of the endemic species in other taxa.

A second factor that may have hindered work on the Interior Highlands insect fauna is that collecting in the area can be fortuitous if one does not visit the area at the “right time of the year.” Normally, the best collecting time for insects is from April until June, and from late September to mid October. This is when the most rainfall occurs. Because of the porous nature of the soils the surface dries rapidly, even after heavy rains in the spring, and insects become increasingly scarce as dry conditions prevail. A collector visiting the Interior Highlands in July or August normally would find a depauparate insect fauna except along the larger streams and around lakes or springs.

Some groups of insects seem to have significantly smaller populations in the Interior Highlands than in other areas of North America. Members of the ground beetle tribe Cycharini can be readily collected in the spring in the Great Smoky Mountains. In the Interior Highlands one is lucky to find more than one or two specimens after a hard day’s work of moving rocks, leaf debris, and rotting logs. The pselaphid genus Arianops is another example of the low population phenomenon. Three years of intensive collecting in the Interior Highlands has produced only six specimens belonging to this genus, whereas members of the genus seem to be more abundant in the Appalachian Mountains (Barr 1974).
All of the factors discussed tend to deter insect collectors from working intensively in the Interior Highlands. However, recent papers by a number of authors indicate that the insect fauna of the area can contribute a great deal to our overall understanding of the origin and evolution of the insect fauna of North America. Examples of some of the recent papers are those of Allen & Carlton (1988), Robotham & Allen (1988), Allen et al. (1988), Stark et al. (1983), Chandler (1988), Mathis & Bowles (1989).

The recent papers pertinent to the entomofauna of the Interior Highlands indicate that the area contains a rich, unknown group of endemic insect taxa. The endemism not only exists at the species level but also at the generic level (Chandler 1988, Mathis & Bowles, 1989). As these new forms are described, it would be profitable if workers would also analyze the cladistic/biogeographic affinities of the taxa. Such analyses would allow us to better understand the origin and evolution of this biota.

To hasten our understanding of endemism in the Interior Highlands, this paper summarizes what is currently known about the entomofauna. The biogeographic affinities of this fauna with other North American areas of endemism will also be discussed.

**Physical Composition of the Interior Highlands**

The Interior Highlands consist of a number of distinct geological provinces found in the states of Illinois, Missouri, Arkansas, and Oklahoma, Fig. 1. The Ozark Mountains

![Map showing the major geological divisions of the Interior Highlands.](image)

**Fig. 1.** Map showing the major geological divisions of the Interior Highlands. AKB = Arkoma Basin, ARB = Arbuckle Mountains, IOZ = Illinois Ozark Mountains, OUA = Ouachita Mountains, OZK = Ozark Mountains, WIC = Wichita Mountains.
extend from southern Illinois, through Missouri, into northern Arkansas and a small part of northeastern Oklahoma. The Ouachita Mountains lie mostly in southwestern Arkansas but extend into eastern Oklahoma. The Ozark and Ouachita uplifts are separated by the Arkansas River valley, known geologically as the Arkoma Basin. Erosion in the Arkoma Basin has formed isolated, positive, prominent features including Magazine Mountain, Petit Jean Mountain, and Mount Nebo.

Magazine Mountain, 2,753 feet, is the highest point in Arkansas and one of the highest points between the Appalachian and Rocky Mountains. At least 12 species are known to be endemic to Magazine Mountain including a tree, land snails, beetles, a mayfly, and a caddisfly.

The far western element of the Interior Highlands consists of two geological features in the southern part of Oklahoma. The Arbuckle and Wichita Mountains are now an area of relatively low relief but are, geologically (and probably biologically also), a part of the Interior Highlands uplift. They are on the southern edge of the formation and have received even less attention from biologists than the Ozark and Ouachita Mountains.

The geological areas composing the Interior Highlands have been positive features on the North American continent since the Pennsylvanian Period, arising some 320 million years before the present (Allen & Cox, in preparation). The areas surrounding the Interior Highlands have been periodically inundated by epicontinental seas or subjected to more xeric conditions than the highlands and, most recently flooded by melt water from glaciers. There is no evidence to suggest that the Highlands, including the southern Illinois segment, have ever been glaciated. Thus the Interior Highlands have been alternately isolated and reconnected with other land areas in North America. But the Highlands have remained above water and free of ice during their entire history (Allen & Cox, in preparation). The area was thus available for habitation by a diverse flora and fauna of both land dwelling and freshwater, aquatic taxa.

METHOD

Ideally, one would like to examine the cladistic and area relationships of the taxa endemic to the Interior Highlands and determine the distribution patterns exhibited by these taxa. This usually is not possible, however, because cladograms for the large majority of the taxa have not been constructed. An alternative, the one used here, is to map the distributions of the endemic forms, the distributions of their nearest relatives (if known), and use those cladograms where available in order to search for "suggested" distribution patterns. It is anticipated that this method will suggest fertile areas for future work as well as shedding some light on what we can now summarize about the evolution of the Interior Highlands insect biota.

Fig. 2. Distribution of endemic members of the order Diplura (Japygidae) in the Interior Highlands: Catajapsy eurige (circle), Eojapsy pedis (triangle), Occasijapsy carltoni (square), Occasijapsy n. sp. (diamond), (Campodeidae) Campodeida n. sp. 1 & 2 (erosa).

Fig. 3. Distribution of the genus Occasijapsy (Diplura: Japygidae) in North America.

Fig. 4. Pedetontus n. sp. (Microcoryphia: Machilidae) distribution in the Interior Highlands.

Fig. 5. Distribution of the genus Pedetontus (Microcoryphia: Machilidae) in North America.

Fig. 6. Distribution of endemic Ephemerebellidae (Ephemeroptera) in the Interior Highland: EphemereEB (Danwell) provonskai (circle); Paraleptothobia calcarica (cross); Habrophlebiodes annulata (circles).
Fig. 7. Distribution of the *Ephemrella* subgenus *Dannella* (Ephemeroptera: Ephemerellidae) in North America: *E. (Dannella) provonshai* (square); *E. (Dannella) simplex* (diamonds); *E. (Dannella) lita* (circles).

Fig. 8. Cladistic relationships of members of the *Ephemarella* subgenus *Dannella* (Ephemeroptera: Ephemerellidae).
The following section includes taxa considered to be endemic to the Interior Highlands. Distributions given here include both published and unreported county records following the state abbreviations.

**ENDEMIC INSECT TAXA**

**Diplura**

Relatively little is known about this order in North America. A series of papers by Smith recorded a number of new taxa in the family Japygidae, mostly from California. A few eastern North American species were also described by Smith. One of these species, *Eoajapyx pedis*, is known only from Missouri. At the present time there are four species of Diplura known from the Interior Highlands. These species may or may not prove to be endemic to the area. The two new species in the family Campodeidae represent the first record of the subgenus *Podocampus* north of the Rio Grande Valley.

**Japygidae**

*Catajapyx ewingi* Fox 1941:28. AR: Howard. Fig. 2.
*Eoajapyx pedis* Smith 1960:262. MO: Stoddard. Fig. 2.
*Occasjapyx* n. sp. AR: Garland. Figs. 2, 3.

**Campodeidae**

*Campodea (Podocampa)* n. sp. 1 and 2. AR: Logan. Fig. 2.

**MICROCORYPHIA**

**Machilidae**

There are five known North American species in the genus *Pedetontus*. The Arkansas species is most closely related to *P. persquamosus*, a species found in California, Fig. 4.

*Pedetontus* n. sp. AR: Logan. Fig. 5.

**Ephemeroptera**

There are three endemic species of mayflies in the Interior Highlands. A cladogram is available for only *Ephemerella (Dannella) provonshai* (McCafferty 1977). This species is most closely related to *E. simplex* confined to localities east of the Mississippi River.

**Ephemerellidae**

*Ephemerella (Dannella) provonshai* McCafferty 1977:886. AR: Johnson. Figs. 6, 7, 8.

**Leptophlebiidae**

*Paraleptophlebia calcarica* Robotham & Allen 1988:318. AR: Logan. Fig. 6.
*Habrophlebiodes annulata* Traver 1934:199. AR: Johnson, Scott. OK. Fig. 6.

**Odonata**

Only one dragonfly species is a known endemic of the Interior Highlands, *Con-
phurus ozarkensis. This species has a wide distribution in the Interior Highlands. Its
cladistic and biogeographic affinities are unknown.
Gomphurus ozarkensis (Westfall) 1975:91. Fig. 9.

Plecoptera

Several stonfly genera have endemic species in the Interior Highlands. Recent
work in Arkansas indicates that there are still a number of undiscovered and unde-
scribed species. Cladistic analyses of the genera Neoperla, Alloperla, and Isoperla are
needed.

Capniidae

Ross & Ricker (1971) discussed, at length and in some detail, their ideas concerning
evolution and speciation in Allocapnia. Basically, these authors suggested that specia-
tion in the Interior Highlands was the result of dispersal into and out of the area at
various times during the Pleistocene. Populations in the Interior Highlands became
isolated from those in the east and northeast and subsequently speciation occurred in
some lineages. The Illinois Ozarks were seen as a corridor with suitable habitats through
which Allocapnia populations could move. Ross (1956, 1965) had already discussed this
corridor in reference to caddisfly (Trichoptera) dispersal. McCafferty (1977) also thought
the Illinois Ozarks served as a dispersal route for at least one group of mayflies (Ephemeroptera).

The taxon most closely related to Allocapnia is the genus Capnia. Ross & Ricker
(1971) suggested that the Capnia vidua group, found in Europe, is the sister group of
Allocapnia. Thus Allocapnia species endemic to the Interior Highlands have a Euro-
pean/Interior Highlands/eastern North American distribution pattern.
A. oribata Poulton & Stewart 1987:296. AR: Searcy, Van Buren. Fig. 12.

Leuctridae

Ricker & Ross (1969) studied the basic taxonomy, distribution, and cladistic relations-
ships of the genus Zealectra. The distribution of the members of the genus is curious.
All the species occur north of the ancient demarcation line of the Pennsylvanian age
(320 mya) Ouachita/Marathon uplift areas in Arkansas, Oklahoma, and Texas. The range of
the genus now extends east of the Mississippi River. The distribution of the extant
despecies suggests that the evolution of this group may be associated with the long geologi-
cal history of this area.
Figs. 17, 18.
Strophopteryx cucullata Frison 1934:29. OK: Haskell, Latimer, Leflore, Pushmataha,
Sequoyah. Figs. 17, 18.

Perlidae

Neoperla harpi Ernst & Stewart, In Ernst et al., 1986:646. AR: Carroll, Clark, Craw.
Fig. 9. *Gomphurus ozarkensis* (Odonata: Gomphidae): general distribution in the Interior Highlands.

Fig. 10. *Allocapnia mohri* (Plecoptera: Capniidae) distribution in the Interior Highlands.

Fig. 11. Distribution of endemic *Allocapnia* (Plecoptera: Capniidae) species in the Interior Highlands: *A. warreni* (open square); *A. peltoides* (squares); *A. ozarkana* (diamond); *A. jeanae* (circles).

Fig. 12. Distribution of endemic *Allocapnia* (Plecoptera: Capniidae) species in the Interior Highlands: *A. sandersoni* (circles); *A. oribata* (square).
Fig. 13a, b. Distribution (13a) and cladistic relationships (13b) of members of the Allocapnia mohri (Plecoptera: Capniidae) lineage.

Fig. 14a, b. Distribution (14a) and cladistic relationships (14b) of members of the Allocapnia warreni-A. peltoides (Plecoptera: Capniidae) lineage.

Fig. 15a, b. Distribution (15a) and cladistic relationships (15b) of members of the Allocapnia ozarkana (Plecoptera: Capniidae) lineage.

Fig. 16a, b. Distribution (16a) and cladistic relationships (16b) of members of the Allocapnia sandersoni-A. jeanae (Plecoptera: Capniidae) lineage.
ford, Franklin, Howard, Nevada, Pike, Polk, Saline, Scott, Sevier, Stone, Van Buren, Washington, Yell. OK: Delaware. Fig. 19.

*N. robisoni* Poulton & Stewart, In Ernst et al., 1986:648. AR: Benton, Clark, Hot Spring, Izard, Johnson, Nevada, Ouachita, Pike, Sevier, Sharp, Yell. OK: McCurtain. Fig. 20.


*N. osage* Stark & Lentz 1988:372. AR: Montgomery, Washington, MO. Christian, McDonald. OK: Adair, Delaware. Fig. 22.

**Chloroperlidae**

*Alloperla wachita* Stark & Stewart, In Stark et al. 1983:56. AR: Montgomery. Fig. 23.

*A. caddo* Poulton & Stewart, 987:297. AR: Garland, Perry. Fig. 23.

**Perlodidae**

*Isoperla szczytkoi* Poulton & Stewart, 1987:298. AR: Logan. Fig. 23.

**Orthoptera**

**Acriddae**

Only one species in the order Orthoptera appears to be exclusively endemic to the Interior Highland. Its nearest relative is *Ereimacris superbium* known only from extreme southwest Texas.


**Hemiptera**

Only one hemipteran species is known to be endemic to the Interior Highlands. However, relatively little is known about the distribution of many of the taxa in the order that are soil dwelling forms. This may be a fertile area for investigation.

**Tingidae**

*Acalypta susanae* Allen, Carlton, Tedder 1988:126. AR: Logan, Polk. Fig. 26.
Fig. 23. Distribution of endemic Plecoptera *Alloperla* (Chloroperlidae) and *Isoperla* (Perlodidae) species in the Interior Highlands: *A. ouachita* (square); *A. caddo* (circles); *Isoperla seszytkoi* (diamond)

Fig. 24. *Eximacris phenax* (Orthoptera; Acrididae): distribution in the Interior Highlands.

Fig. 25. Distribution of the genus *Eximacris* (Orthoptera: [Family?]) in North America.
Coleoptera

The beetles are represented in the Interior Highlands by a number of endemic forms in several different families. As the beetle fauna is explored many additional endemic taxa may be discovered. Those taxa for which reliable cladograms are available are *Scaphinotus*, subgenus *Nomaretus* and the genus *Evarthus* in the family Carabidae and the genera *Arianops* and *Ouachitychus* in the family Pselaphidae.

Carabidae


*Scaphinotus* (*Nomaretus*) *infletus* Allen & Carlton 1988:132. AR: Newton. Fig. 27.

There are five species in the subgenus *Nomaretus*. Four of these species occur west of the Mississippi River, and the fifth species, *S. bilobus*, occurs both west of the Mississippi River and in previously glaciated areas in the East, Fig. 29a. The cladogram proposed by Allen & Carlton (1988) places *infletus* at the base of this monophyletic cluster of species.

Gidaspow (1973) noted that the subgenus "occurs in the Ozark Uplift (Missouri), except for *S. bilobus* which, following the retreating ice sheet, wandered to the region of the Great Lakes and the mountains of New York and New Hampshire." She also noted that *S. tiebeki* occurs in the South, in Texas and in one locality in Louisiana. It should also be noted that *S. fissicollis* and *S. cavicoloides* are found outside the Interior Highlands in Kansas and *S. cavicoloides* in Oklahoma. Because of the sympatry in these species it is not possible to suggest what events may have led to their isolation and evolution. However, consideration of the sister taxa of the subgenus *Nomaretus* does show a distinct disjunct distribution pattern in three monophyletic lineages.


*E. parasodalis* Freitag 1969:150. AR: Figs. 30, 32.

*Evarthus incisus*, occurring mostly north of the Arkansas River, is the sister species of *E. whitcombi* and occurs mostly south of the Arkansas River. There are five additional species in the monophyletic lineage that gave rise to *E. incisus* and *E. whitcombi*. These additional species all occur east of the Mississippi River. The cladogram of relationships proposed by Freitag (1969) would suggest that an original cosmopolitan eastern population was divided into eastern and western segments and that the eastern segment eventually gave rise to five species and the western segment evolved into *E. whitcombi* and *E. incisus*.

*Evarthus parasodalis* belongs to a monophyletic lineage composed of four other species: *E. sodalis* (with three subspecies), *E. furtivor*, *E. alternans*, *E. iuvensis*. The cladogram of relationships among these species and the distribution patterns, Fig. 32,
Fig. 30. Distribution of endemic species of Evarthrus (Coleoptera: Carabidae) in the Interior Highlands: E. parasodalis (squares); E. whitcombi (circles).

Fig. 31a, b. Distribution (31a) and cladistic affinities (32b) of members of the Evarthrus whitcombi (Coleoptera: Carabidae) lineage.

Fig. 32a, b. Distribution (32a) and cladistic affinities (32b) of members of the Evarthrus parasodalis (Coleoptera: Carabidae) lineage in North America.

Fig. 33. Distribution of endemic species of Dytiscidae (Coleoptera in the Interior Highlands: Hoperius planatus (circle); Hydroporus sulfurius (square); Hydroporus ouachitus (diamond).

suggests that this lineage had historically been divided into eastern and western populations by the Mississippi River Valley. These ancient eastern and western populations subsequently gave rise to a number of species from each population, Fig. 31a, 32a.

Dytiscidae

*Hoperius planatus* (Fall) 1927:178. AR: Hempstead. Fig. 33.
*Hydroporus sulfurius* Matta & Wolfe 1979:287. AR: Benton. Fig. 33.
*H. ouachitus* Matta & Wolfe 1979:289. AR: Polk. Fig. 33.
Pselaphidae


These two species are known from isolated, single localities in the Ouachita Mountains. _Arianops sandersoni_ lives in leaf litter and beneath stones on the north and east slopes of Magazine Mountain, Logan County, Arkansas. The genus _Arianops_ occurs in the Appalachian Mountains and seems to be confined to mountains in the Interior Highlands south of the Arkansas River. This distribution pattern may indicate an ancient connection between the southern Appalachians and the Ouachita Mountains across northern Alabama and Mississippi.


This endemic genus and species is also known only from Magazine Mountain, Logan County, in western Arkansas. The sister group of _Ouachitychus_ is the genus _Cylindracetus_ with 10 species in eastern North America. The biogeographic origins of _Ouachitychus_ are unclear.

Staphylinidae


Coccinellidae


Bruchidae

_Acanthoscelides schrankiae_ Horn 1873:331.

Chrysomelidae

_Pachybrachis pinicola_ Rouse & Medvedev 1972:82. AR: Nevada. Fig. 38.

_Lema maculicollis_ ab. _inornata_ Rouse & Medvedev 1972:81. AR: Montgomery. Fig. 38.

Trichoptera

There are at least 22 known endemic species of caddisflies in the Interior Highlands. These species are usually found in clear, fast-flowing streams or in isolated fresh water springs. Some of the large streams, such as the Buffalo River and the White River, flow throughout the year while many of the small streams have an intermittent flow—heavy in the spring and decreasing or drying up by late June or early July.

The origin and evolution of many of the Interior Highland endemic caddisflies has been discussed by H. H. Ross (1956). Ross thought that Pleistocene Glaciation played an important role in the isolation of Ozark/Ouachita Mountain populations. These isolated populations subsequently evolved into distinct taxa. This possibility will be discussed in greater depth in the discussion section of this paper.

Hydropsychidae


In her treatment of the genus _Ceunatopschye_, Gordon (1974) placed _C. rossi_ in a monophyletic lineage containing three other species. Two of the species in this lineage,
Fig. 34. Distribution of endemic species of Pselaphidae (Coleoptera) in the Interior Highlands: Arianops sandersoni (circle); Arianops stephani (diamond); Ouachitychus parvoculus (square).
Fig. 35. General distribution and cladistic affinities among genera closely related to Ouachitychus (Coleoptera: Pselaphidae).
C. smithi and C. logani are found only in the west, while C. pettiti is transcontinental. Since C. pettiti has a transcontinental distribution it is unclear where or when a once cosmopolitan population was first divided. The intermediate position of C. rossi in the cladogram does suggest that this Interior Highland endemic shares a close relationship and possible and immediate common ancestor with two western species. *Ceratopsycha piastris* (Ross) 1938a:148. AR: Fulton. MO: Oregon. Fig. 40.

Psychomyiidae

*Paduniella nearctica* Flint 1967:310. AR: Crawford, Johnson, Washington. Fig. 41.

This Interior Highland endemic represents one of the most interesting and provocative distribution patterns among the endemic fauna. The genus *Paduniella* is found in Ceylon, Java, Africa, India, Philippines, Indonesia, and the southern Usuri region of the Soviet Union. *Paduniella nearctica* is the sole representative of the subfamily Paduniellinae in North America. This suggests a very ancient geographic relationship—perhaps of pre-Cretaceous origin. *Paduniella nearctica* appears to be most closely related to *P. sanghamittra* Schmid from Ceylon (Flint 1967).

Philopotomidae

*Wormaita strata* (Ross) 1938c:11. AR: Johnson, Madison, Perry, Washington. Fig. 42.

Ross (1956) placed *W. strata* in a monophyletic lineage with 4 other species, fig. 42b. The pattern suggested by the cladogram indicates that at least two independent, transcontinental, eastern and western segments and gave rise to a number of separate but closely related species. One population gave rise to *W. thyria* and *W. hamata*, and the other population gave rise to *W. occidea*, *W. shawnee* and *W. strata*.

Glossosomatidae

*Agapetus arthes* Ross 1938a:106. MO: Oregon, Phelps. Fig. 43.

*A. illini* Ross 1938a:106. AR: Benton, Carroll, Crawford, Franklin, Garland, Johnson, Logan, Madison, Montgomery, Polk, Scott, Washington. IL: Hardin, Pope, Union. OK: Cherokee. Fig. 43.

*Agapetus medicus* Ross 1938a:107. AR: Benton, Clark, Hot Spring, Montgomery, Pike, Polk. Fig. 44.

Rhyacophilidae

*Rhyacophila fenestra* Ross 1938a:102. IL: Hardin, Jackson, Johnson, Massac, Pope, Tazewell, Union, Vermilion. Fig. 45.

*R. kiamichi* Ross 1944:37. AR: Crawford, Hot Spring, Johnson, Logan, Madison, Pike, Polk, Washington. OK: Cherokee, Haskell, Johnston, Latimer. Fig. 45.

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Fig. 36a, b. Distribution (36a) and cladistic affinities (36b) among North American species of *Ariaropus* (Coleoptera: Pselaphidae).

Fig. 37a, b. Distribution of *Derops divalis* (Coleoptera: Staphylinidae) in the Interior Highlands (37a); world wide distribution of the genus *Derops* (37b).

Fig. 38. Distribution of endemic Chrysomelidae (Coleoptera) in the Interior Highlands: *Pachybrachis pinicola* (circle); *Lema maculicollis var. inornata* (square).
There are two species in the genus *Rhyacophila* that are possibly endemic to the Interior Highlands. *Rhyacophila focontenta* has been reported from two localities outside of the Interior Highlands and is included here provisionally. Ross (1956) assigned these two species to his "Branch 6" of the genus. The two species were placed in a monophyletic lineage including *R. ledra*, *R. carolina*, and *R. teddy*, all found in eastern North America. The cladogram given by Ross (1956), Fig. 45b, suggests that the two Interior Highland endemics were isolated from one of the other eastern species, possibly *R. kiwami.*

**Brachyceridae**

*Micrasema ozarkana* Ross & Unzicker 1965:254. AR: Fulton. MO: Carter, Oregon. Fig. 46.

**Leptoceridae**

*Ceraclea nepha* (Ross) 1944:230. AR: Benton, Washington, White. OK: Pushmataha. Fig. 46.

*Setodes ozapia* (Ross) 1938b:88. AR: Benton, Washington. Fig. 46.

*Trianodes smithi* Ross 1959:40. IL: Union. Fig. 46.

**Helicopsychidae**

*Helicopsyche limnetla* Ross 1938a:179. AR: Benton, Carroll, Franklin, Garland, Hot Spring, Johnson, Madison, Montgomery, Ouachita, Sebastian, Washington. Fig. 47.

Ross (1938a) suggested that *H. limnetla* was so similar to its close relative *H. mexicana* (known from the southwest and Mexico) that the Ozark populations might only be a variation. However Bowles and Allen (in press) established the validity of *H. limnetla* and suggested a cladogram of relationships for the complex to which this interior Highland endemic belongs. *H. limnetla* represents a distinct type of Interior Highlands/Mexico vicariance pattern.

**Hydroptilidae**

*Ochrotrichia ariaca* (Ross) 1941:88. AR: Benton, Clark, Crawford, Garland, Johnson, Madison, Polk, Washington. IL: Union. OK: McCurtain. Fig. 47.

*O. contorta* (Ross) 1941:60. MO: Oregon. Fig. 48.

*O. union* (Ross) 1941:56. IL: Hardin, Jackson, Pope, Union. Fig. 48.

*O. weddleea* (Ross) 1944:274. AR: Hot Spring, Polk. OK: Latimer. Fig. 48.

*O. edalis* Ross 1941:62. OK: Johnson. Fig. 46.

*Neotrichia kita* Ross 1941:60. MO: Taney. Fig. 48.

*Paucicalcareia ozarkensis* Mathis & Bowles 1989:188. AR: Logan. Fig. 49.

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Fig. 39a, b. *Cheumatopsyche rossi* (Trichoptera: Hydroptilidae): distribution in the Interior Highlands (39a); cladistic and biogeographic relationships of the *C. petiti* lineage (39b); *C. smithii* (square); *C. logani* (closed circles); *C. rossi* (triangle); *C. petiti* (open circles).

Fig. 40a, b. *Ceratopsyche piaetra* (Trichoptera: Hydroptilidae): distribution in the Interior Highlands (40a); distribution of *C. piaetra* and its nearest relative (40b).

Fig. 41a, b. *Poduniella neoarctica* (Trichoptera: Psychomyiidae) distribution in the Interior Highlands (41a); world wide distribution of the genus *Poduniella* (41b).
LEPIDOPTERA
Papilionidae

Papilio joanae Hoitzman 1973:2 Fig. 50.

DISCUSSION

Sixty-eight species of insects are suspected to be endemic to the Interior Highlands of North America. Table 1 lists these species and summarizes the available information about close relatives occurring in eastern North America. Seven species have affinities with western taxa. The nearest relatives of 4 species occur outside of North America, and the close relative of 1 species is a boreal form. We do not know the close relatives of 18 of the Interior Highland endemic species.

An analysis of the geographic patterns of the Interior Highland endemics using taxon/area cladograms is difficult. The pattern that emerges is complex and not clearly defined. Several factors obscure the biogeographic pattern including the following: (1) the close relatives of the Interior Highland endemics occur in many different geographical areas in eastern and western North America; (2) the lack of cladograms for most of the Interior Highland endemics; (3) the detailed geological history of small individual areas in eastern North America is unknown in many cases. Nevertheless it may be instructive for future workers to scrutinize as closely as possible the data that is available.

Using a method proposed by Allen (1983), area cladograms are changed into a linear form (Fig. 51b) so that repetitious patterns may be discerned more readily and correlated with possible vicariant events. This linear form was proposed because taxa seldom, if ever, have relatives present in all the geographical areas under consideration. However, the cladistic/biogeographic relationships of the taxa and areas in which members do occur may remain the same. For example, even three taxa A, B, C that may or may not have members in areas a, b, c, d, e, f, it is possible to detect a repetitious pattern using linear relationships, Figure 51.

Using Figure 51 as a guide, a brief explanation may be helpful. Taxon A has members in areas a, c, d, and f, but not in areas b and c. Taxon B has members in three of the areas, b, e, and f, but not in a, c, and d. And taxon C has members in all of the areas except c. An important point to note is that the cladistic/area relationships remain the same in all of the taxon/area cladograms. That is, areas a and b share a common node (a common ancestor) in taxon A and taxon C and, in turn, the a, b, lineage shares a common node with d in both taxa. In taxon B, even though areas a, c, and d are missing the ancestor/descendent relationships of the areas present, b, e, and f, are the same as those elements (b, e, and f) in taxon A. This sharing of common nodes (or

Fig. 42a, b. Wormanida strata (Trichoptera: Philopotamidae) distribution in the Interior Highlands (42a); cladistic and biogeographic relationships of the lineage containing W. strata (42b).

Fig. 43. Agapetus artesus (circle) and A. illini (squares) (Trichoptera: Glossosomatidae) distribution in the Interior Highlands.

Fig. 44. Agapetus medicus (Trichoptera: Glossosomatidae) distribution in the Interior Highlands.

Fig. 45a, b. Distribution of endemic Rhycophila (Trichoptera: Rhyacophilidae) species in the Interior Highlands: (R. fenestra (squares); R. kiamichi (circles) (45a); cladistic relationships of members of Branch 6 of the genus Rhycophila (45b); see text for distribution data.
common ancestors), which is based on the principles of Hennigian phylogenetic systematics, is what makes it possible to detect common patterns as shown in Figure 51d.

If the pattern shown in Figure 51d was not present, then the taxon/area cladograms would have different ancestor/descendent relationships. For example, if we add taxon D, Figure 51e, with a different set of ancestor/descendent relationships it is obvious that taxon D belongs to a different pattern.

It should also be noted that terminal taxa (nodes) can be rotated 180 degrees such that the taxon/area cladograms can be written a, b, or b, a. Such a rotation does not affect the relationships of the taxa or the areas. Other nodes in the cladogram can also be rotated.

It might be argued that rotating the cladogram at different nodes changes the pattern. This is not true because the ancestor/descendent relationships at each node remains the same regardless of how the nodes may be rotated. For example, in taxon C rotating the a, b, d lineage so that it fits between e and f, Figure 51f, does not make f and a closer relatives. Area a still shares its closest relationship with b followed by d, followed by e, and then f. If such a rotation were done for taxon C, the same rotation could be done for the two other taxa A and B. The results would be the same area relationship pattern shown in Figure 51d, but written in a different sequence.

When using these taxon/area/linear diagrams it is important that the original data be presented so that other workers will be able to accurately and independently assess the validity of the conclusion, i.e. the biogeographic pattern.

Basically there appear to be three separate groups of species relationships: two species with distant Asian affinities, Derops divalis and Ephemeraella (Dannella) provonskai; several caddisfly lineages and the ground beetle subgenus Nomaretus with distinct western North American relationships (Figures 52 through 57); and the majority of the lineages with a complex eastern North American relationships (Figures 58 through 66).

The insect lineages with endemic Interior Highlands species that appear to have distinct western affinities are listed and shown in Figures 52 through 57. In these lineages we see five possible areas of endemism having relationships with one another (Figure 55); areas in western North America (NAw), the Interior Highlands (IH), areas east of the Appalachian Mountains (app.e), several restricted areas west of the Appalachian Mountains (app.w), western North American repeated (NAw), and widespread taxa in North America between the western edge of the Appalachians and the Mississippi River Valley (NAe, ws). One possible explanation for this pattern might be that

Fig. 46. Distribution of some endemic species of caddisflies (Trichoptera: Brachycentridae and Leptoceridae) in the Interior Highlands: Microsema ozarkana (Trichoptera: Brachycentridae) (diamonds); Ceraclea nepha (Trichoptera: Leptoceridae) (circles); Setodes oxapia (Trichoptera: Leptoceridae) (crosses); Triamodes smithi (Trichoptera: Leptoceridae) (square).

Fig. 47a, b. Helicopsyche timnella (Trichoptera: Helicopsychidae) distribution in the Interior Highlands (47a); cladistic relationships of species closely related to H. timnella (47b), see text for discussion of distribution data.

Fig. 48. Distribution of some endemic species of micro-caddisflies (Trichoptera: Hydroptilidae) in the Interior Highlands. Ochrostrichia unica (open circles); O. contorta (open squares); O. weddleae (closed diamonds); O. ellis (open square); Neotracheloba hiridae (cross).

Fig. 49. Paucicalcaria ozarkensis (Trichoptera: Hydroptilidae) distribution in the Interior Highlands.

Fig. 50. Papilio joanna (Lepidoptera: Papilionidae) distribution in the Interior Highlands.
<table>
<thead>
<tr>
<th>Table 1. Insect species endemic to the Interior Highlands, occurrence of nearest relatives, and availability of cladograms.</th>
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<tbody>
<tr>
<td><strong>IH ENDEMIC</strong></td>
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<tr>
<td>1. <em>Cataptyx ewingi</em></td>
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<td>2. <em>Eojapyx pedis</em></td>
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<td>3. <em>Occasypyx carltoni</em></td>
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<td>4. <em>Occasypyx n. sp</em></td>
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<td>5. <em>Camoecia (Podacampa) n.sp.1</em></td>
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<td>6. <em>Camoecia (Podacampa) n.sp.2</em></td>
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<td>7. <em>Pedeanthus n. sp.</em></td>
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<td>8. <em>Ephemerella pravonkai</em></td>
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<td>9. <em>Paraleptolebia calcyma</em></td>
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<td>10. <em>Habrophlebiodes annulata</em></td>
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<td>11. <em>Gomphurus ozarkensis</em></td>
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<td>12. <em>Allocapnia mohri</em></td>
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<td>13. <em>warreni</em></td>
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<td>14. <em>velia</em></td>
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<td>15. <em>ozarkana</em></td>
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<td>16. <em>jeanae</em></td>
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<td>17. <em>sandersoni</em></td>
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<td>18. <em>oribata</em></td>
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<td>19. <em>Zealeuctra wachta</em></td>
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<td>20. <em>cherokee</em></td>
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<td>21. <em>Strophopteryx cucullata</em></td>
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<td>22. <em>Neoperla hcpri</em></td>
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<td>23. <em>robisoni</em></td>
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<td>24. <em>fahayak</em></td>
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<td>25. <em>osage</em></td>
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<td>26. <em>Alloperla ovachita</em></td>
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<td>27. <em>coddio</em></td>
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<td>28. <em>Isoperla szczytki</em></td>
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<td>29. <em>Eximecris phenox</em></td>
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<td>30. <em>Acalypta susanae</em></td>
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<tr>
<td>31. <em>Phaenec ozarkensis</em></td>
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</tbody>
</table>
Fig. 51a, b, c, d. A hypothetical oct of taxon/area cladograms and their linear equivalents; see text for discussion.
Fig. 52-56. Taxon/area/linear cladograms of sister lineages [or "close relatives"] of the following endemic representatives in the Interior Highlands: 52 Wormaldia thyria; 53 Cheumatopsyche petitti; 54 Nomareus; 55 Rhacophila teddyi; 56 Helicyops rhoda. See figure 65 for location of areas: APPe = east of Appalachian Mountains. APPw = west of Appalachian Mountains, IH = Interior Highlands, NAw = western North America, NAw,ws = widespread in eastern North America between the Appalachian Mountains and the Mississippi River; cp = coastal plain.

Fig. 57. The general distribution pattern of lineages with endemic Interior Highland representatives and affinities with western North America. Fig. 58-64. Taxon/area/linear cladograms of sister lineages [or "close relatives"] of the following endemic representatives in the Interior Highlands: 58 Ailocapnia jeanae; 59 Ailocapnia sanderseni; 60 Ailocapnia malverna; 61 Ailocapnia frisoni & wazickei; 62 Ailocapnia illinoiensis; 63 Evarthus whitcombii; 64 Zeleuctra warreni.
Fig. 65. The principal areas of endemicity in North America showing relationships with endemic species in the Interior Highlands.

Fig. 66. The general distribution pattern of lineages with endemic Interior Highland representatives and affinities with eastern North America.

widespread, cosmopolitan species were first divided into eastern and western populations during the Cretaceous (100 mya) or possibly in the early Tertiary (90 mya). A second division into eastern and western groups could have occurred during the Miocene (12-25 mya) (Figure 5'). This possibility is in contrast to explanations offered by Ross (1956) suggesting a Pleistocene (1 mya) origin of the Interior Highland endemics. Whether an old (Cretaceous, Miocene) vicariance pattern or a relatively young (Pleistocene) explanation is correct will have to be settled by future research.

Turning to those insect lineages whose evolution occurred mostly in eastern North America (Figures 58-64), we see a complex of biogeographic relationships. We cannot hope to corroborate this pattern until many additional cladograms for other taxa are established, and more is known about the geological history of eastern North America and about areas of endemism within eastern North America. There are, however, a number of interesting points that can be considered.

It is noted that most of the Interior Highland endemic insect species have close relationships with species lying east of the Mississippi River Valley and west of the
Appalachian Mountains (app, w.), (Figure 66). It is also noted that there were apparently only two vicariance events that gave rise to Interior Highland endemics since this area of endemism is repeated twice in the linear sequence (Figure 66). Whether either or both of the events that isolated Interior Highland populations occurred during the Pleistocene is unclear. Such Pleistocene explanations have been offered by several workers as cited in the preceding text. We may also note that none of the lineages seem to have close or distantly related sister groups east of the Appalachian Mountains as we saw in the calidris and ground beetle taxa previously discussed.

Based on the cladistic/biogeographic data presented here and after a study of the geological literature it is not possible to suggest specific earth events occurring in eastern North America that may be correlated with the taxon/area/linear cladograms. It is suggested, however, that from the meager data available, a tentative biogeographic pattern is emerging (Figure 66). A great deal of additional work will be necessary before this pattern can be corroborated, rejected, or modified.

END NOTE

Distribution ranges shown for eastern North America are approximate. The reader is advised to consult the original citations for greater detail.

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