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# The Milliped Fauna of the Kings Mountain Region of North Carolina (Arthropoda: Diplopoda)

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**ABSTRACT.**—The millipeds of the Kings Mountain region of Cleveland and Gaston counties, one of five inselberg areas in the Piedmont Plateau of North Carolina, were sampled to determine seasonal variation in faunal composition. Comparative collections also were made at Spencer Mountain, an inselberg located northeast of Gastonia. Of 24 species taken, only *Narceus americanus* (Beauvois) and *Auturus erythropygos* (Brandt) were present as adults and juveniles in all three sampling seasons. The most diverse assemblage was encountered in October. Five species were more common in April and October than in July, four were more common in July than in either of the cooler months, and five others were collected in but a single season (three in July, two in October). A more diverse fauna was encountered in the contiguous Kings-Crowders ridge than at the isolated Spencer Mountain outcrop, from which three xystodesmids were conspicuously absent. A notable difference between millipeds of the two localities involved color pattern of the intergrades of *Sigmoria latior* (Brölemann). *Ptyoiulus* was the sole genus represented by more than one species, and the overall species/genus ratio is indicative of a lowland rather than a montane fauna.

The Kings Mountain region shares eight species with the eastern Piedmont and five with the Appalachian Mountains. Seven widespread species occur in all three regions, but three species are unique to the Kings Mountain region. This area is the northeastern range limit of the genus *Pachydesmus*; and the easternmost populations of four montane diplopods, the westernmost population of *Ptyoiulus ectenes* (Bollman), and the southernmost known locality of *Cleidogona medialis* Shelley, occur there. The conservation status of three species of concern to North Carolina is discussed, and the Kings Mountain region is considered a “cluster area” due to its unique diplopod fauna. The ranges of *Boraria stricta* (Brölemann) and *Deltotaria lea* Hoffman are extended into South Carolina. A key to genera and species is provided along with pertinent diagnostic illustrations.

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## INTRODUCTION

The importance of the Appalachian Mountains to the arthropod class Diplopoda has been evident since 1969, when Hoffman identified the mountains as a global center of milliped evolution. This opinion was based on the diversity and abundance of known indigenous taxa. Four other areas also were cited as important global centers of evolution and dispersal, and since all are mountainous to some extent, Hoffman surmised that vertical relief probably allows for a greater variety of ecological niches than occur in lowland or flat areas.

The Appalachian Highlands, one of eight physiographic divisions of the United States, is comprised of seven physiographic provinces (Hunt 1967). The most important in terms of known diplopod faunas are the Ridge and Valley and Blue Ridge Provinces, especially the southern section of the latter (the region south of the Roanoke River). The Xystodesmidae, the dominant Nearctic polydesmoid family, attains its greatest known diversity in the part of the southern Blue Ridge Province south of the Kanawha River System (Hoffman 1969). The bulk of the southern Blue Ridge Province is in western North Carolina, where it is demarcated from the Piedmont Plateau by a prominent escarpment, the Blue Ridge Front. Thus, for all practical purposes one of the five regions of greatest milliped diversity in the world lies in the western part of this state.

Although most of the mountains of North Carolina are west of the Blue Ridge Front, a number of prominent hills and ridges also occur to the east in the Piedmont Plateau. Some of these are quite properly called mountains and extend to altitudes of well over 300 meters. These isolated mountains protruding from a surrounding flat plain are known as inselbergs and are erosional remnants of previously more extensive mountain masses (Kesel 1974). Five main groups of inselbergs occur in Piedmont North Carolina (Fig. 1): the Sauratown Mountains of Stokes County (including Pilot Mountain, Surry County); the Brushy Mountains of Wilkes, Caldwell, Alexander and Iredell counties; the South Mountains of Burke, Rutherford, McDowell and Cleveland counties; the Kings Mountain region of Cleveland and Gaston counties; and the Uwharrie Mountains of Davidson, Randolph, Montgomery, and Stanly counties. The faunas of these inselberg regions are of particular biogeographic interest and raise a number of questions. Do they, for example, reflect previous direct connection with the Blue Ridge chain? If so, their later isolation may have separated previously continuous diplopod populations and led to speciation by geographical isolation. Accordingly, knowledge of the inselberg diplopod faunas may provide insights into processes affecting milliped evolution, and an investigation of one such area was conducted in this study.

The Kings Mountain region straddles the South Carolina border about 13 km southwest of Gastonia. Preliminary studies there had disclosed a milliped fauna with southern elements found nowhere else in

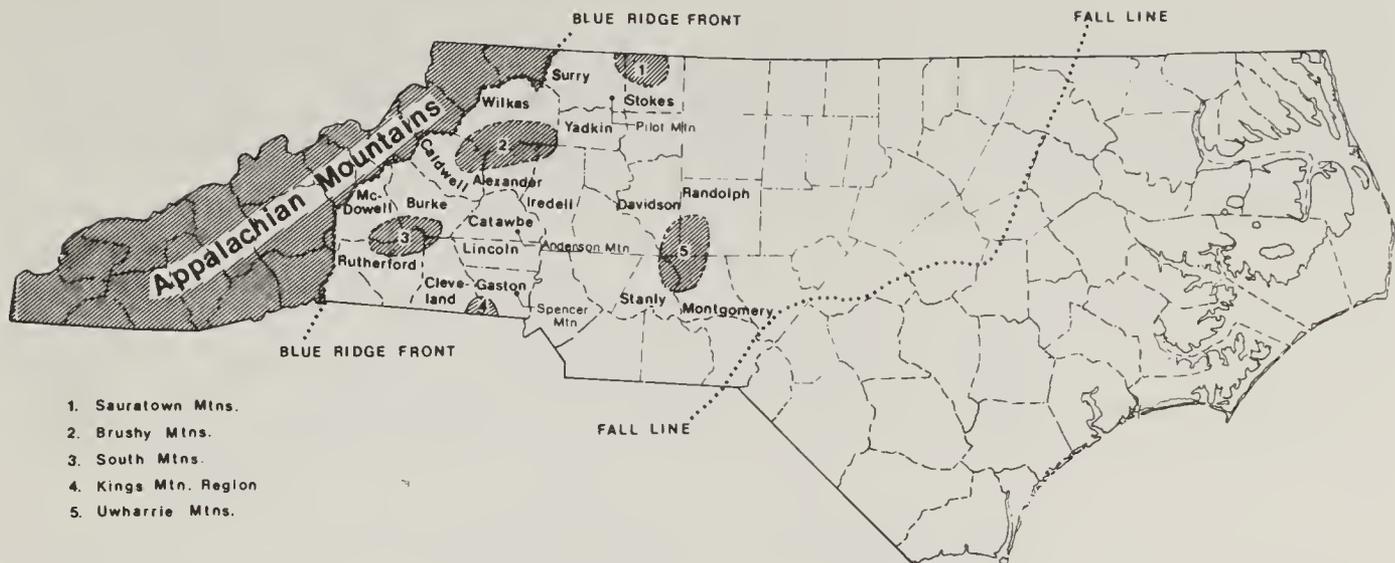


Fig. 1. Major inselberg regions of North Carolina.

North Carolina. The other inselberg regions have no faunas of such singular importance to the state. Information on unique areas in North Carolina is timely in regard to recent concerns about environmental management and planning, as reflected by the North Carolina Environmental Policy Act of 1971; the State Land Policy and Coastal Area Management Acts, both enacted in 1974; and the Symposium on Endangered and Threatened Biota of North Carolina (see Cooper et al. 1977). Moreover, the North Carolina Natural Heritage Program, administered by the Department of Natural Resources and Community Development through a contract with The Nature Conservancy, is presently conducting an inventory of the state's most significant natural areas. In order to realize the goals of these programs and to effectively manage the resources of the state, knowledge of its indigenous flora and fauna must be substantiated. Another objective of this project, therefore, was to furnish such knowledge for the Diplopoda of the Kings Mountain area, and categories of concern are suggested in some of the species accounts.

This report includes a key to genera and species, and gonopod illustrations to assist in determinations. Accounts are presented for each milliped species collected, along with synonymies for the two species previously reported from the region or vicinity. Numeric ratios of orders/families/genera/species (o/f/g/s) and species/genera (s/g) are used to show diversity and seasonal variation within the Kings Mountain fauna and to compare it with the faunas of the eastern Piedmont and the Great Smoky Mountains (Tables 10-12). Comments on seasonal occurrence of adults and juveniles are provided in the species accounts and summarized in Table 10. Noteworthy behavior and gonopodal variation are discussed for each species where appropriate. Localities are listed for species collected from fewer than six sites and for three diplopods considered of Special Concern in North Carolina, as defined in Cooper et al. (1977). Due to present nomenclatorial confusion and in deference to current work by other specialists, as explained in appropriate accounts,

specific names cannot be assigned for two millipeds and provisional names are used for two others. The major concern of this study was the fauna of natural habitats, and synanthropic diplopods were thus incompletely sampled. Additional species that might be discovered in future investigations are discussed in the final section.

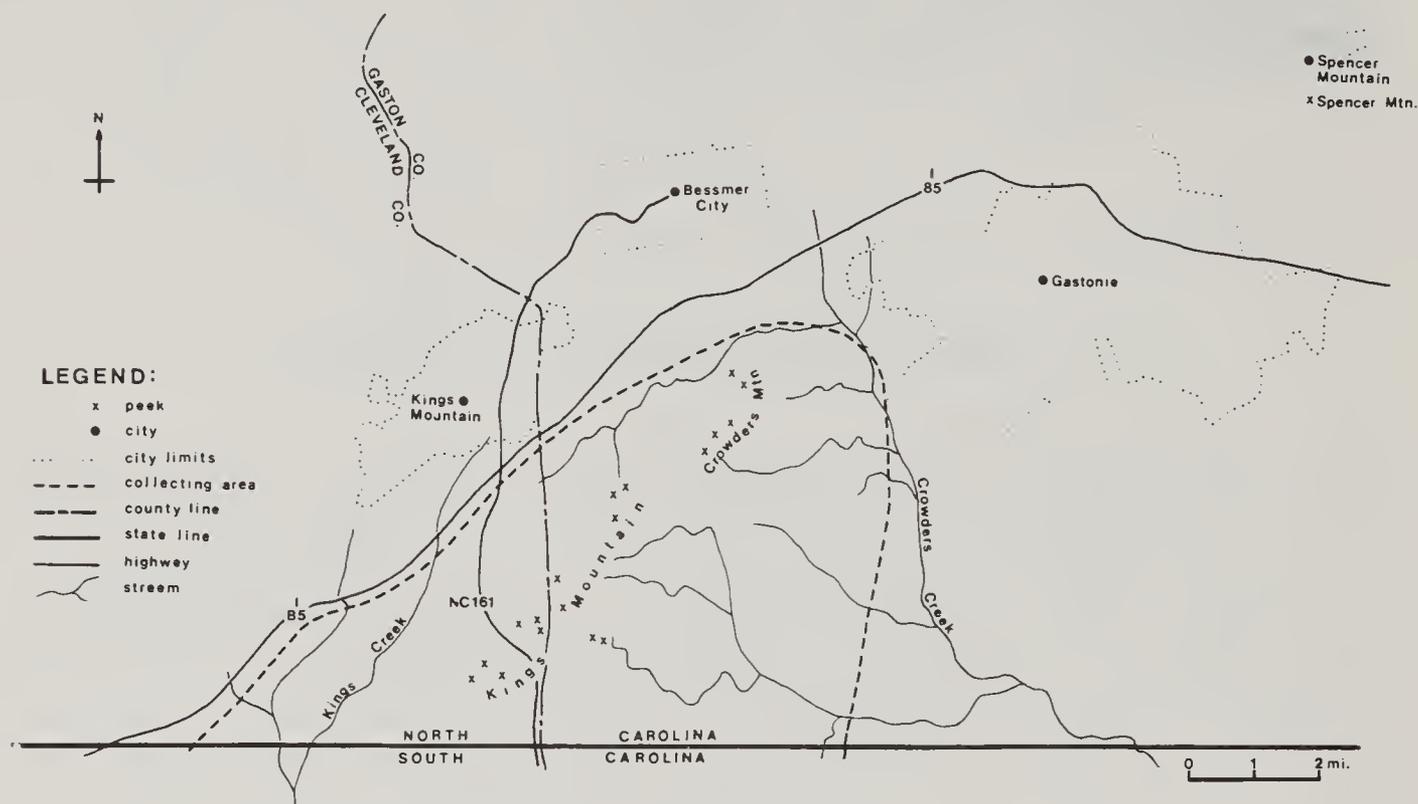


Fig. 2. The Kings Mountain region of North Carolina.

### THE KINGS MOUNTAIN REGION

The Kings Mountain range extends northeastward as a linear ridge some 26.5 km from the southern tip of Cherokee and York counties, South Carolina, to the southeastern corner of Cleveland and southwestern part of Gaston counties, North Carolina (Fig. 2). It is bounded on the east and west by Crowders and Kings creeks, respectively, and surrounded by Piedmont Plateau. Isolated outlying peaks, inselbergs of the Kings Mountain ridge, continue northeastward approximately 64 km to Anderson's Mountain in Catawba County. The bulk of the region is located about 136 km east of the Blue Ridge Front in Cleveland and Gaston counties, where it covers an area of approximately 3108 hectares. It consists of four main groups of lowlying peaks separated by gaps. Mean elevation is 361 m above sea level with maxima of 570 m (the Pinnacle) and 474 m (Crowders Mountain). Spencer Mountain, a 378 m high inselberg of the Kings Mountain ridge, is located about 14.5 km northeast of Crowders Mountain on the opposite side of Gastonia.

The Kings Mountain geologic belt, composing the range, is a narrow zone of metamorphosed sedimentary rocks (schist, marble, and quartzite) of Paleozoic age (Stuckey 1965). The porous nature of this rock produces a bountiful supply of ground water, and natural springs and seeps are characteristic of the area (Keith 1931). Soil composition

varies from thick black peaty humus in forested areas, to exposed red clays and yellow silts on eroded downslopes, to glittering micaquartzite sand along stream banks and on summits. Xeric scrub forests similar to those found in the Blue Ridge characterize these summits, and hardwood forests, remnants of the previous oak-hickory and beech-maple climaxes, distinguish relatively undisturbed regions on surrounding lower slopes. In clear-cut or burned areas, dense stands of Virginia pine, *Pinus virginiana*, and shortleaf pine, *P. echinata*, dominate to the exclusion of other species. Various pine-hardwood mixtures occur in disturbed areas throughout the Kings Mountain region (Burney 1974).

### MATERIALS AND METHODS

Millipeds were sampled in July and October 1976, and April 1977, to investigate seasonal variation in faunal composition. Collecting was done primarily in the contiguous ridge area around Kings and Crowders outcrops, but four sites around Spencer Mountain also were sampled for comparison. The South Carolina state line was selected as the southern boundary, and collecting limits were set in other directions using topographical and county road maps. Collecting sites, chosen to provide a maximum diversity of habitats, included pine, mixed pine-hardwood, and deciduous forests; banks of streams and ponds; seepage areas; borders of flat meadows; gradual slopes and steep hill terrains; bases, slopes, and summits of outcrops; and trash dumps. Climatic conditions varied from hot and dry in July to cool and damp in October and April.

Twenty-five sites were examined during the first trip (July). Five of these yielded few millipeds because of scant leaf litter, so only the twenty remaining sites were routinely sampled on all trips. Several new prospective sites were visited during each ensuing trip. Specimens were collected from beneath leaf litter, bark of decaying logs, and large rocks, and preserved in 70% isopropanol. Pine, hardwood, and mixed pine-hardwood litter samples were collected for extraction with Berlese funnels. Notes on color, behavior, and habitat were recorded at each site.

Measurements of length and width in mm were taken with vernier calipers. Drawings of most gonopods and all other structures were prepared with the aid of a grid reticle with 0.5 mm squares, but a camera lucida was used for the smallest gonopods, which were mounted temporarily in glycerine jelly and examined with a compound microscope. All other structures were examined using a stereomicroscope, with the specimens immersed in 70% isopropanol and stabilized by cotton. More than 1000 specimens were examined, some of which were collected in preliminary studies. All specimens are deposited in the invertebrate collection of the North Carolina State Museum of Natural History (NCSM), the invertebrate catalogue numbers of which are indicated in parentheses with appropriate citations. A single pertinent specimen was found in the collection of the American Museum of Natural History (AMNH).

In the species accounts and legends, CR means country road.

KEY TO GENERA AND SPECIES OF  
KINGS MOUNTAIN DIPLOPODS

1. Body soft, exoskeleton noncalcified; clusters of modified setae adorning head and tergites; terminal setal tufts present posteriorly; males without gonopods; adults less than 3 mm long (Penicillata, Polyxenida, Polyxenidae) . . . . . *Polyxenus fasciculatus* Say
- Exoskeleton hard, calcified; setae normal, scattered, males with gonopods on 7th or 7th and 8th segments; adults varying in size but always longer than 3 mm (Helminthomorpha) . . . . . 2
2. Head reduced; males with 8 pairs of legs preceding gonopods . . 3
- Head normal; males with 7 pairs of legs preceding gonopods . . . 4
3. Three pairs of ocelli present; paranota absent; segments arched, convex dorsally (Polyzoniida, Polyzoniidae) . . . . .
- . . . . . *Polyzonium strictum* Shelley
- Ocelli absent; paranota present, bilobed on segment five (Fig. 4); segments narrow, flattened (Platydesmida, Andrognathidae) . . . . .
- . . . . . *Andrognathus corticarius* Cope
4. Ocelli present; paranota absent; adults with more than 20 segments . . . . . 5
- Ocelli absent; paranota present; adults with 19 or 20 segments (Polydesmida) . . . . . 16
5. Segments with dorsal longitudinal crests . . . . . 6
- Without this character . . . . . 9
6. Collum enlarged, hoodlike, covering epicranial region of head . 7
- Collum reduced, head completely exposed (Callipodida, Caspiope-  
talidae) . . . . . 8
7. Epiproct trilobed (Fig. 11); adults with 30 segments; adult length not exceeding 26 mm (Chordeumida, Striariidae) . . . . .
- . . . . . *Striaria* sp.
- Epiproct entire; adults with more than 30 segments; adults 40-50 mm long (Spirostreptida, Cambalidae) . . . . *Cambala annulata* (Say)
8. Coxal process of gonopod thin, translucent, ensheathing stalk of telopodite; flagellum absent (Figs. 25-26) . . . . .
- . . . . . *Delophon georgianum* Chamberlin
- Coxal process of gonopod thick, opaque, bent laterad apically, not ensheathing stalk of telopodite; flagellum present (Fig. 20) . . . . .
- . . . . . *Abacion magnum* (Loomis)
9. Adults with 28-30 segments (Chordeumida) . . . . . 10
- Adults with more than 30 segments . . . . . 11
10. Ocelli arranged curvilinearly, 6 per row; adults not exceeding 5 mm long (Trichopetalidae) . . . . . *Trichopetalum dux* (Chamberlin)
- Ocelli in triangular patch, 26 per patch; adults longer than 5 mm (Cleidogonidae) . . . . . *Cleidogona medialis* Shelley
11. Coxae of legs 3-7 of males with lobed extensions (Fig. 16); ocelli in ovoid patch; gonopods concealed within body; adults large, robust, 80-100 mm long (Spirobolida, Spirobolidae) . . . . .
- . . . . . *Narceus americanus* (Beauvois)

- Coxae of pregonopodal legs of males without lobed extensions; ocelli variable in arrangement; gonopods completely visible or concealed within body; adults slender, never exceeding 5 mm long (Julida) . . . . . 12
12. Ocelli arranged linearly (Blaniulidae) *Nopoiulus minutus* (Brandt)  
Ocelli in triangular patch . . . . . 13
13. Gonopods completely concealed within body; first pair of legs of male reduced, hooklike, dorsum with 2 yellow longitudinal stripes containing narrow median black line (Julidae) . . . . .  
. . . . . *Brachyiulus lusitanus* Verhoeff
- Gonopods visible externally; first pair of legs of male enlarged; body uniformly gray in color, without stripes (Parajulidae) . . . . . 14
14. Epiproct decurved . . . . . *Teniulus* sp.  
Epiproct extending into straight spine . . . . . 15
15. Peltocoxites of anterior gonopods with flared, serrate calyx (Fig. 6)  
. . . . . *Ptyoiulus impressus* (Say)  
Calyx of peltocoxites cupped, smooth (Fig. 5) . . . . .  
. . . . . *Ptyoiulus ectenes* (Bollman)
16. Midbody metatergites with transverse groove; rim of paraprocts without setae (Paradoxosomatidae) . . . . . *Oxidus gracilis* (Koch)  
Midbody metatergites without transverse groove; rim of paraprocts with one pair of setae . . . . . 17
17. Prefemora of legs with ventrodiscal spines; gonopod usually bearing prefemoral process; adults large, robust, color bright yellow-black or yellow-brown (Xystodesmidae) . . . . . 18  
Prefemora of legs without ventrodiscal spines; gonopod without prefemoral process; adults slender, coloration otherwise . . . . . 22
18. Gonopods with coxal apophysis (Figs. 55-57) . . . . . 19  
Without this character . . . . . 20
19. Cranial setae present on frons and epicranium in both sexes; gonopods with one prefemoral and two tibiotarsal processes (Fig. 57); podosterna present . . . . .  
. . . . . *Pachydesmus crassicutis incurtus* Chamberlin  
Cranial setae absent from frons and epicranium in both sexes; gonopod with or without small prefemoral process; telopodite broadly curved, falcate in shape (Figs. 55-56); sterna unmodified . . . . . *Deltotaria lea* Hoffman
20. Telopodite of gonopod with irregularly notched expansion along proximomedial edge; prefemoral process large, extending beyond tip of telopodite (Fig. 54); membrane of cyphopod enlarged and folded, protruding through medial portion of aperture, . . . . .  
. . . . . *Croatania catawba* Shelley  
Without these characters . . . . . 21
21. Prefemoral process short, blunt, never two-thirds length of telopodite; telopodite curved, with medial flange at midlength (Fig. 60); adults 40-45 mm long . . . . . *Sigmoria latior* (Brölemann)

- Prefemoral process of gonopod acicular, approximately two-thirds length of telopodite; telopodite nearly straight, bent slightly mediodorsad distally, without flange (Fig. 47); adults 28-32 mm long ..... *Boraria stricta* (Brölemann)
22. Epiproct broad, truncate; adults gray with orange paranota and middorsal spots (Platyrrhacidae) .....  
 ..... *Auturus erythropygus* (Brandt)
- Epiproct subtriangular; adults with essentially uniform coloration (Polydesmidae) ..... 23
23. Adults with 19 segments; metatergites with four rows of small setiferous tubercles ..... *Scytonotus granulatus* (Say)
- Adults with 20 segments; dorsum without setae and distinct rows of tubercles ..... *Pseudopolydesmus branneri* (Bollman)

## CLASSIFICATION OF KINGS MOUNTAIN DIPLOPODS

### CLASS DIPLOPODA

#### SUBCLASS PENICILLATA

##### ORDER POLYXENIDA

###### Family Polyxenidae

*Polyxenus fasciculatus* Say

#### SUBCLASS HELMINTHOMORPHA

##### ORDER POLYZONIIDA

###### Family Polyzoniidae

*Polyzonium strictum* Shelley

##### ORDER PLATYDESMIDA

###### Family Andrognathidae

*Andrognathus corticarius* Cope

##### ORDER JULIDA

###### Family Blaniulidae

*Nopoiulus minutus* (Brandt)

###### Family Julidae

*Brachyiulus lusitanus* Verhoeff

###### Family Parajulidae

*Ptyoiulus ectenes* (Bollman)

*Ptyoiulus impressus* (Say)

*Teniulus* sp.

##### ORDER CHORDEUMIDA

###### Family Cleidogonidae

*Cleidogona medialis* Shelley

###### Family Trichopetalidae

*Trichopetalum dux* (Chamberlin)

###### Family Striariidae

*Striaria* sp.

## ORDER SPIROBOLIDA

Family Spirobolidae

*Narceus americanus* (Beauvois)

## ORDER CALLIPODIDA

Family Caspiopetalidae

*Abacion magnum* (Loomis)*Delophon georgianum* Chamberlin

## ORDER SPIROSTREPTIDA

Family Cambalidae

*Cambala annulata* (Say)

## ORDER POLYDESMIDA

Family Paradoxosomatidae

*Oxidus gracilis* (Koch)

Family Polydesmidae

*Pseudopolydesmus branneri* (Bollman)*Scytonotus granulatus* (Say)

Family Platyrhacidae

*Auturus erythropygos* (Brandt)

Family Xystodesmidae

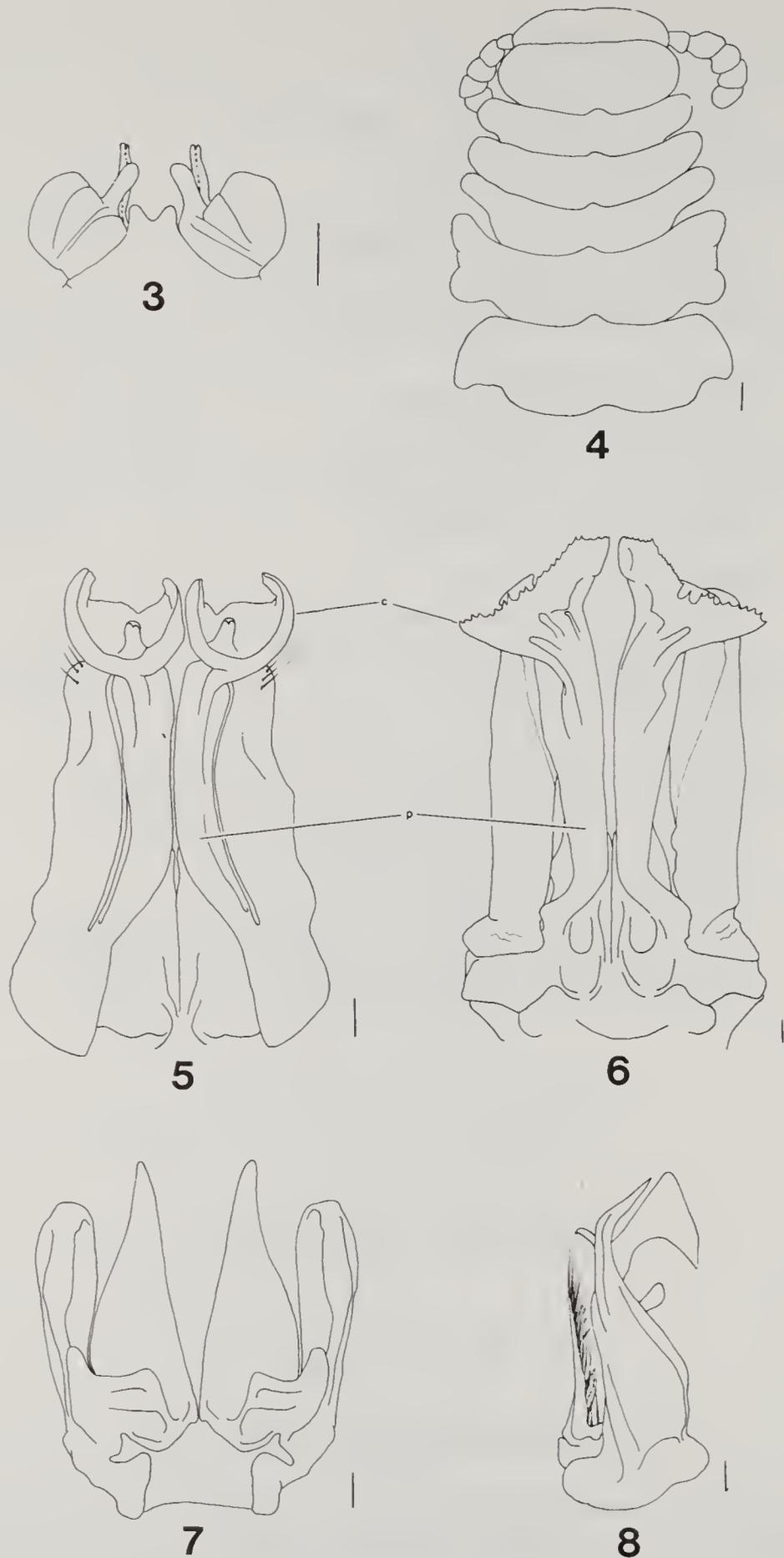
*Boraria stricta* (Brölemann)*Croatania catawba* Shelley*Deltotaria lea* Hoffman*Pachydesmus crassicutis incursus* Chamberlin*Sigmoria latior* (Brölemann)

## SPECIES ACCOUNTS

## Polyxenidae

*Polyxenus fasciculatus* Say, 1821

*Polyxenus fasciculatus*, a small, pale milliped, was recovered from pine and mixed pine-hardwood litter using Berlese funnels but was absent from hardwood litter. More adults and juveniles were taken in July than in October or April. Previous North Carolina records are from Duke Forest (Brimley 1938; Wray 1967) and the eastern Piedmont in general (Shelley 1978). The species is known to range from Long Island through the southeastern and midwestern United States to Texas (Chamberlin and Hoffman 1958). The presence of *P. fasciculatus* in the Appalachian Mountains is questionable, since Chamberlin and Hoffman (1958) reported it absent or very scarce there.



Figs. 3-8. 3, *Polyzonium strictum*, anterior gonopods, cephalic view. 4, *Andrognathus corticarius*, head and first six segments, dorsal view. 5, *Ptyoiulus ec-tenes*, anterior gonopods, caudal view, calyx (c) and peltocoxites (p). 6, *Ptyoiulus impressus*, anterior gonopods, caudal view, calyx (c) and peltocoxites (p). 7-8 *Teniulus* sp. 7, anterior gonopods, caudal view. 8, left posterior gonopod, lateral view. Scale line = 0.1 mm.

## Polyzoniidae

*Polyzonium strictum* Shelley, 1976

## Fig. 3

Yellow adults of *P. strictum* were taken from beneath the bark of decaying logs in July and October. A large number of juveniles was extracted from mixed pine-hardwood Berlese samples in October. In North Carolina *P. strictum* ranges from the mountains to the inner Coastal Plain, and it also occurs in the mountains of Virginia (Shelley 1976a).

## Andrognathidae

*Andrognathus corticarius* Cope, 1968

## Fig. 4

This slender, cream-colored diplopod typically occurs beneath the bark of decaying pine logs (Shelley 1978), a habitat that was examined extensively in the study area. Only two specimens were encountered, however, both in July from a single log at a Spencer Mountain site. Chamberlin and Hoffman (1958) reported *A. corticarius* from western Virginia, southeastern Kentucky, Tennessee, Georgia, and northern Florida. Gardner (1975) examined material from Graham and Madison counties in the Appalachian Mountains of North Carolina, and Shelley (1978) noted that the species was more prevalent in the southern subregion of the eastern Piedmont than north of the Deep-Cape Fear Rivers.

Locality. *Gaston Co.*—7.2 km NE Gastonia, along CR 2200, 2.2 km SW jct. NC Hwy. 7, base of Spencer Mountain, 2 ♀, 7 July 1976, M. Filka and W.W. Thomson (NCSM A1032).

## Blaniulidae

*Nopoiulus minutus* (Brandt, 1841)

This narrow brown milliped occurs in habitats similar to those of *A. corticarius*. Four immature specimens were encountered, in July and October, but no adults were found. The dearth of specimens in the Kings Mountain region contrasts markedly with the abundance of the species farther east in the fall zone region of North Carolina, where it also occurs in summer and autumn (Shelley 1978). *Nopoiulus minutus* is widespread east of the Great Plains, ranging from Illinois, Indiana, and Ohio south to Georgia (Enghoff and Shelley 1979).

Localities. *Cleveland Co.*—9.1 km SE Kings Mountain (town), along CR 2286, 1.6 km S jct. CR 2283, 8 July 1976, 1 juv., M. Filka and W.W. Thomson (NCSM A1973); and 1.9 km SW Kings Mountain (town),

along I-85, jct. NC Hwy. 161, 3 juvs., 18 October 1976, M. Filka and G. Wicker (NCSM A2197).

### Julidae

#### *Brachyiulus lusitanus* Verhoeff, 1898

*Brachyiulus lusitanus* is easily identified by its characteristic dorsal color pattern — two pale longitudinal stripes surrounding a narrow black mid-dorsal line. Introduced from Europe, *B. lusitanus* has been reported from developed areas of North America as far south as the “Triangle” (Raleigh-Durham-Chapel Hill) region of North Carolina, where it was erroneously reported as *B. pusillus* (Leach) by Shelley (1978). However, three females were encountered during this study, all in April, under debris at a public campsite. The Kings Mountain region thus becomes the southernmost known locality for *B. lusitanus* in the New World.

Locality. *Cleveland Co.*—1.9 km SE Kings Mountain (town), jct. I-85 and NC Hwy. 161, 3 ♀, 10 April 1977. M. Filka.

### Parajulidae

#### *Ptyoiulus ectenes* (Bollman, 1888)

##### Fig. 5

Juvenile and female *Ptyoiulus* are unidentifiable to species. Those found associated with males of a single species (all only in October) were adjudged to be that species and are so shown in Table 3. Those collected without associated males (all only in July) are tabulated by genus in Table 3. No juveniles or females were found with males of both species at a single collecting site. These identification problems may have influenced the apparent seasonal distribution patterns of both species of *Ptyoiulus* in the region, although examination of Table 3 reveals similar July and October patterns for the two. Adults of *P. ectenes* were most numerous in October but also occurred in April; immatures were found only in July and October. These data suggest that *P. ectenes* reproduces during fall and spring, and juveniles mature the following summer and fall. All specimens were collected from deciduous litter. Gonopods of the 31 males were examined but no variation was apparent.

This species was reported from the fall zone region as *Ptyoiulus* sp. by Shelley (1978) who declined to assign a specific name in deference to studies being conducted by the late Dr. Nell B. Causey. The oldest available specific name is in doubt, but that of Bollman is used tentatively here since it is one of the earliest names and the first applied to specimens from North Carolina. However, there is some question as to whether *ectenes* is referable to *Ptyoiulus*, since Bollman (1887) remarked that the

species differed in its "slender body and peculiar form of the male genitalia," which he neither illustrated nor described verbally in his description. Unfortunately, the male from the type series is lost, but collections made by Shelley in and around the type locality — Chapel Hill, Orange County, North Carolina — have produced male parajulids whose gonopods are virtually identical to that illustrated in Figure 5. This suggests that *ectenés* may be the species under consideration here, but a final judgment can only result from a comprehensive revision of *Ptyoiulus* in which female cyphopods are studied. Wray (1967) may have been correct in transferring *ectenés* to *Aniulus*, and this combination may be a senior subjective synonym of *A. orientalis* Causey, the only other parajulid known from the "Triangle" region of the state.

*Ptyoiulus impressus* (Say, 1821)

Fig. 6

Adults of *P. impressus* were abundant in October and absent in April and July; juveniles were taken only in July and October. Thus, *P. impressus* appears to have a slightly different life history from that of *P. ectenés*, with summer growth and maturation preceding fall reproduction. Both species are uniformly gray and both were found in deciduous forest litter. Adult *P. ectenés* are slightly smaller and less robust than adult *P. impressus*, although this difference can be misleading and should not be the sole criterion for identification. The most reliable character is the configuration of the calyx of the peltocoxites of the anterior gonopod (Figs. 5-6, c, p.), which is flared and serrate distally in *P. impressus* and cupped and smooth in *P. ectenés*. As with its congener, the gonopods of *P. impressus* were essentially uniform.

*Ptyoiulus impressus* ranges from the northeastern United States west to Indiana and south to western North Carolina and Kentucky (Chamberlin and Hoffman 1958). Shelley (1978) deleted this species from the eastern Piedmont fauna, stating that it was known definitely only from the mountains and western Piedmont. The Kings Mountain region is the easternmost authentic locality in North Carolina.

*Teniulus* sp.

Figs. 7-8

This uniformly gray species is similar in appearance to both species of *Ptyoiulus*, but is distinguished by the decurved epiproct. Adults were collected in October from moist deciduous leaf litter in association with both species of *Ptyoiulus*. No juveniles were found.

The genus currently contains only two species, *T. parvior* and *T. setosior*, both described by Chamberlin (1951) from Gatlinburg, Sevier County, Tennessee. Gatlinburg is about 200 km west-northwest of the

Kings Mountain region, and such wide geographic separation suggests that the forms in the two areas are not conspecific. If true, the Kings Mountain species is undescribed. However, drawings by Chamberlin (1951) accompanying the descriptions of the Tennessee species are unclear and were prepared from different views, which prevents close comparisons. Examination of the type specimens of both species by Shelley revealed that males and/or gonopods were absent. These two species may be synonymous, but adult males are needed before their identities can be determined and an accurate statement can be made on the status of the Kings Mountain form.

Locality. *Gaston Co.*—9.9 km S Bessemer City, along CR 1112, 0.3 km E jct. CR 1125, ♂, 5 ♀, 17 October 1976, M. Filka and G. Wicker (NCSM A2193).

### Cleidogonidae

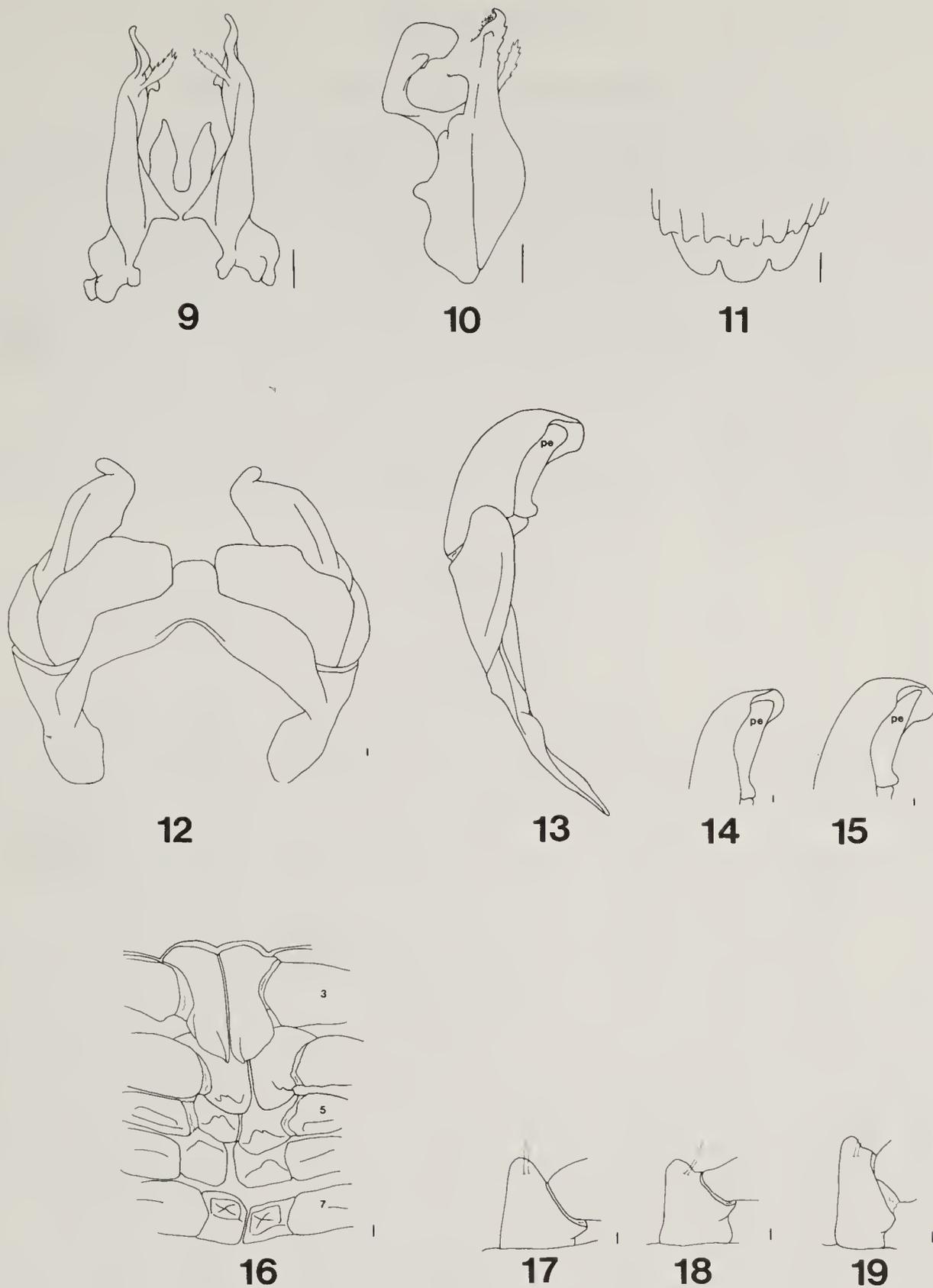
#### *Cleidogona medialis* Shelley, 1976

Figs. 9-10

The Kings Mountain region is the second known locality for this light brown chordeumid, whose range is now extended some 117 km from Blowing Rock, Watauga County, North Carolina (Shelley 1976b). The single male and female taken during this study and all those from the type locality were collected in October, suggesting autumnal maturation. Juveniles would therefore be expected in the summer; although none were encountered in July, they may be present in late August or early September.

The medial processes of the gonopods of the Kings Mountain specimen were more jagged than those of the holotype (Shelley 1976b, Fig. 10), which conforms to known variation in the species. A single oversized telopodite variant was reported in one male paratype, but those of the Kings Mountain male were as illustrated for the holotype. No other gonopodal variations were observed. Two additional records are cited below from material that has recently become available.

Localities. *Gaston Co.*—9.9 km SE Bessemer City, along CR 1126, 0.8 km SW jct. CR 1113, ♀, 16 October 1976, M. Filka and G. Wicker (NCSM A2770); and 9.9 km SW Bessemer City, along CR 1104, 1.3 km W jct. CR 1115, ♂, 17 October 1976, M. Filka and G. Wicker (NCSM A2771). *Davidson Co.*—Boone's Cave State Park, ♂, 6 November 1976, R.M. Shelley (NCSM A1434). *Watauga Co.*—16 km NE Deep Gap, ♂, ♀, 17 October 1965, J. & W. Ivie (AMNH).



Figs. 9-19. 9-11, Chordeumida. 9-10, *Cleidogona medialis*. 9, anterior gonopods, cephalic view, sternum broken in dissection. 10, left anterior gonopod, lateral view. 11, *Striaria* sp., epiproct, dorsal view. 12-19 *Narceus americanus*. 12, anterior gonopods, cephalic view. 13, left posterior gonopod, cephalic view. 14-15, distal portions of left posterior gonopods, cephalic views, showing variation in prefemoral endite (pe). 16, coxae and lobes of legs 3-7 of male, ventral view. 17-19, coxae and prefemora of left third legs of females, cephalic views, showing variation in coxal lobes. Scale line = 0.1 mm.

## Trichopetalidae

*Trichopetalum dux* (Chamberlin, 1940)

The specific identification of this milliped is tentative and based solely on previous North Carolina records. Only one female was collected, discovered in berlesate from a deciduous litter sample taken in Gaston County in April. This is the only species of *Trichopetalum* known from North Carolina, where it was previously reported from Duke Forest (Chamberlin 1940a; Wray 1967) and Chatham County (Shelley 1978). Positive identification of the Kings Mountain species awaits the collection of males.

Locality. *Gaston Co.*—8 km NE Gastonia, base of Spencer Mountain, along CR 2200, 1.7 km SW jct. CR 2003, ♀, 10 April 1977, M. Filka (NCSM A2185).

## Striariidae

*Striaria* sp.

## Fig. 11

*Striaria* is readily distinguished from the other chordeumids by its enlarged collum, crested segments, and trilobed epiproct. One adult female and two juveniles were taken in Gaston County in October and April, respectively. The adult female and one juvenile were brown with a pale white collum, while the other juvenile was uniformly brown. Three species of *Striaria* are known from North Carolina: two with a white collum — *S. zygoleuca* Hoffman, from Highlands, Macon County (Hoffman 1950; Wray 1967), and an undescribed form from High Falls, Moore County (Shelley 1978) — and one with a brown collum, *S. causeyae* Chamberlin, from eight counties in the eastern Piedmont (Shelley 1978). The presence of differently colored collums on the Gaston County material suggests the presence of at least two species, but again the absence of males precludes final determinations. For the purposes of this report, therefore, only one species is considered.

Localities. *Gaston Co.*—4.0 km S Bessemer City, along CR 1125, 0.2 km S jct. U.S. Hwy. 74-29, ♀, 17 October 1976, M. Filka and G. Wicker (NCSM A2215); juv., 9 April 1977, M. Filka (NCSM A2219); and 6.4 km SE Bessemer City, along CR 1103, jct. CR 1112, juv., 9 April 1977, M. Filka (NCSM A2202).

## Spirobolidae

*Narceus americanus* (Beauvois, 1805)

## Figs. 12-19, Tables 1-2

Body coloration of *N. americanus* is dark brown with the head, legs, and body segments bordered in red. As indicated in Table 3, this species is common in the Kings Mountain region, and adults and juveniles were



collected from a diverse array of habitats on each trip. Continuous breeding and maturation throughout the year is suggested by these data.

Two species of *Narceus* occur in North Carolina; *N. americanus*, known to range throughout the southeastern United States, and *N. annularis* (Rafinesque), known from the northeastern and midwestern United States (Chamberlin and Hoffman 1958). Both are reported from the mountains (Keeton 1960) and eastern Piedmont (Shelley 1978) of North Carolina.

In his monograph on the Spirobolidae, Keeton (1960) distinguished between *N. annularis* and *N. americanus* by a formula computing values based on somatic features (see footnote Table 1 for explanation) and by comparison of gonopodal characters. He found that differences were difficult to define due to overlap of characters. Consequently, identifications are difficult and distinctions between the species are vague, facts corroborated by the Kings Mountain material.

Thirty-four adults were collected but only 22 of these, 16 males and 6 females, were in sufficiently good condition for detailed study. As shown in Tables 1-2, the number of segments, clypeal setae, and labral setae of the Kings Mountain spirobolid are closer to the values for *N. americanus*; but the mean number of ocelli is closer to that for *N. annularis*. Mean length and width, the length/width ratio, and the formula value, also are nearer the figures for *N. americanus*.

The distal prefemoral endite of the posterior gonopod, normally rounded in *N. annularis* and acute in *N. americanus*, is rounded in 72% of the specimens (Figs. 13-14, pe) and acute in the rest (Fig. 15, pe). Likewise, the cephalic groove on the coxal lobes of the third pair of legs of males, a characteristic of *N. americanus*, is absent from all Kings Mountain males (Fig. 16). Furthermore, the third coxal lobe of adult females, enlarged in *N. americanus* but only slightly produced ventrad in *N. annularis*, conforms to the latter condition in all but one specimen (Figs. 17-19). The Kings Mountain spirobolid therefore could be identified as either species of *Narceus* depending upon the character used, and the question becomes one of the relative importance of the characters.

Although gonopods are the most important taxonomic character in the Diplopoda, many genera show few specific gonopodal differences whereas there is wide variation in body forms. This appears to be the situation in *Narceus*, and the few gonopodal similarities between the Kings Mountain spirobolid and *N. annularis* do not seem to outweigh the close agreement of nearly all the somatic features with those of *N. americanus*. Thus, the Kings Mountain spirobolid is identified as *N. americanus*. The great variability of the somatic features of *Narceus*, as demonstrated by Keeton (1960) and our tables, indicates a need for reassessment of the status of the two nominal eastern species. Such a study might show them to be conspecific.

Table 2. Comparison of length, width, and length/width ratio for the Kings Mountain spirobolid (KM), *Narceus annularis* (Nan) and *N. americanus* (Nam). Data for *Narceus* from Keeton (1960). d = difference from Kings Mountain spirobolid;  $\bar{C}\bar{X}$  = combined mean for both sexes; Cd = combined difference for both sexes.

		Length (cm)																				
		41-45	46-50	51-55	56-60	61-65	66-70	71-75	76-80	81-85	86-90	91-95	96-100	101-105	106-110	111-115	$\bar{N}$	$\bar{C}\bar{X}$	d	$\bar{C}d$		
KM	♂	1				3	5	3	2	2	1						16	75.1	76.0			
	♀						2	3									6	78.3				
Nan	♂	1	2	13	22	26	22	13	13	4	3	1	1				121	71.1	71.7	4.0		
	♀	1	4	16	19	21	23	18	13	9	5	2	1	1			133	72.2	71.7	6.1		
Nam	♂	2	2	4	6	4	4	6	1	3	2	4	1	1	1		37	78.5	78.5	3.4		
	♀	4	4	5	5	5	5	8	9	9	6	6	2				65	78.5	78.5	0.2		
		Width (mm)																				
		4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	$\bar{N}$	$\bar{C}\bar{X}$	d	$\bar{C}d$	
KM	♂				4	3	4	3	1		1							16	8.0	8.1		
	♀				1	3	1			1								6	8.2			
Nan	♂	2	15	42	40	36	9	3	1								148	6.0	6.3	2.0		
	♀	2	7	19	37	29	24	18	6	2	2						146	6.5	6.3	1.7		
Nam	♂	2	5	5	3	8	6	6	1	4	1	7	1	1			44	7.9	8.1	0.1		
	♀	1	1	3	4	9	8	9	9	10	6	6	2				68	8.2	8.1	0.0		
		Length/width ratio (%)																				
		7.0	7.5	8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	$\bar{N}$	$\bar{C}\bar{X}$	d	$\bar{C}d$
KM	♂	1				3	4	4	2	1									16	9.4	9.5	
	♀					1	3	2											6	9.5		
Nan	♂				1	2	3	8	20	21	24	30	9	7	1			3	129	11.9	11.6	2.5
	♀			2	1	1	15	26	29	33	11	5	4	2	1	1		2	133	11.2	11.6	1.7
Nam	♂			1	5	9	10	10	5	2	1								43	10.1	10.1	0.7
	♀	1	5	13	12	16	9	8	2	2									66	9.8	10.1	0.3

## Caspiopetalidae

*Abacion magnum* (Loomis, 1943)

Figs. 20-24

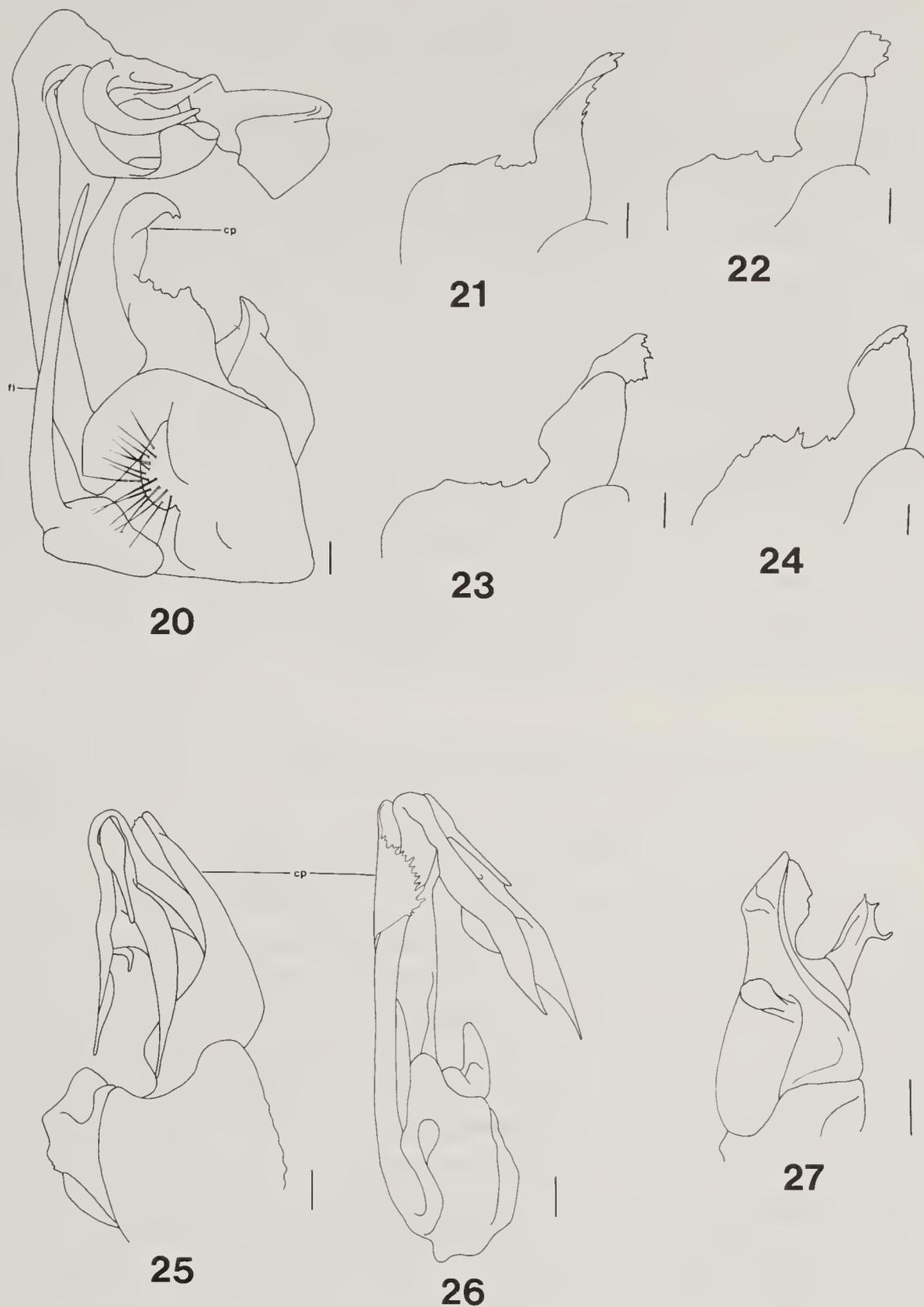
*Abacion magnum* is a crested diplopod, brown with a light middorsal stripe. It was one of the few species found in drier parts of deciduous, pine, and mixed leaf litter. Juveniles of the two callipodids, *A. magnum* and *D. georgianum*, could not be identified to species, but all were found with adult males of a single species and, as with *Ptyoiulus*, were identified as such. Adults of *A. magnum* were taken during all three months, while juveniles were collected only in July and October. This implies that reproduction and maturation occur throughout the year. The coxal processes of the gonopods of the eastern Piedmont specimens varied in degree of apical serration and configuration of the midlength angulation (Shelley 1978). These structures were found to vary similarly in the Kings Mountain specimens (Figs. 21-24). No other gonopodal variations were detected. This species has been collected in Macon and Transylvania counties in the North Carolina mountains (Hoffman 1950) and in eight counties of the eastern Piedmont (Shelley 1978).

*Delophon georgianum* Chamberlin, 1943

Figs. 25-26

This callipodid is similar in coloration to *A. magnum* but is smaller and differs in the structure of the gonopod. *Abacion magnum* has a flagellum and a serrate coxal process lateral to the telopodite (Fig. 20, fl. cp). *Delophon georgianum* lacks the flagellum, and its coxal process ensheathes the stalk of the telopodite (Figs. 25-26, cp) (Shelley 1979a). Little gonopodal variation was found in this study. Like *A. magnum*, adults of *D. georgianum* were taken on all three trips, but only one juvenile was encountered, in April. *Delophon georgianum* was typically found in moister habitats than *Abacion*.

This species has been previously reported from the mountains of North Carolina as *D. carolinum* Hoffman (Hoffman 1950; Chamberlin and Hoffman 1958; Wray 1967). However, Shelley (1979a) concluded that this binomial was a synonym of *D. georgianum*. The Kings Mountain population is disjunct from that occurring in the Appalachians, and no specimens have ever been taken in the intervening lowlands. Shelley speculated that the Kings Mountain population might be a Pleistocene relict that has survived due to a slightly cooler microclimate afforded by the peaks and coves of the area. Hardin and Cooper (1967) concluded that this was the explanation for the occurrence of several disjunct populations of montane plants, most notably *Tsuga canadensis* L. and *Pinus strobus* L., in the Piedmont.



Figs. 20-27. 20-26, Callipodida. 20-24, *Abacion magnum*. 20, left gonopod, caudal view, coxal process (cp), flagellum (fl). 21-24, coxal processes, lateral views, of four specimens from the Kings Mountain Region. 25-26, *Delophon georgianum*. 25, left gonopod, lateral view, coxal process (sheath) (cp). 26, left gonopod, caudal view, coxal process indicated. 27, *Cambala annulata*, left posterior gonopod, lateral view. Scale line = 0.1 mm.

## Cambalidae

*Cambala annulata* (Say, 1821)

Fig. 27

Shelley (1978) reported that *C. annulata* seemed to prefer cooler temperatures, and this was apparent in the Kings Mountain region where the dark purple adults were abundant in both April and October. Only one adult, a female, was collected in July. Juveniles were taken in July and October but not in April. Hoffman (1958) indicated that individuals of this species were usually found grouped together, but in the Kings Mountain region this was true only of females; adult males were always found alone. All stages were collected from moist humus. Hoffman found no gonopodal variation in material from high elevations, and Shelley (1979b) noted homogeneity in the gonopods of *C. annulata* throughout its range. This was evident in the Kings Mountain material, as the structures were virtually uniform. *Cambala annulata* has been reported from the northeastern and central subregions of eastern Piedmont North Carolina (Shelley 1978), and its distribution in the Appalachian Mountains was illustrated by Hoffman (1958).

## Paradoxosomatidae

*Oxidus gracilis* (Koch, 1847)

Causey (1943) reported nearly year around oviposition by *O. gracilis* under favorable conditions in a Durham County greenhouse, and Shelley (1978) collected fifth instar juveniles (adults are the seventh instar) in October from William B. Umstead State Park in the eastern Piedmont. The preponderance of juveniles in October and April and of adults in July and October in the Kings Mountain region suggests that maturation occurs in the fall and spring and breeding in the late summer and early fall. White juveniles often populated several square meters of deciduous leaf litter, and shiny black adults also were common. *Oxidus gracilis* is nearly worldwide in distribution, and was introduced into the United States from the East Indies via imported soil in greenhouses (Causey 1943).

## Polydesmidae

*Pseudopolydesmus branneri* (Bollman, 1887)

Figs. 28-40

*Pseudopolydesmus branneri* is the sole representative of its genus in the Kings Mountain region; neither *P. collinus* Hoffman nor *P. serratus*

(Say), both of which occur in the eastern Piedmont (Shelley 1978), were encountered during this study. This species has been previously reported from Rutherford, Wilkes and Alexander counties in the western Piedmont, as well as the mountains and eastern Piedmont (Shelley 1978), so its occurrence in the Kings Mountain region was expected. Juveniles and adults were collected in April and October, but none were found in July. Adults were dull reddish brown with light brown paranota, similar to Richmond County specimens (Shelley 1978). Material from the two areas was also similar in length.

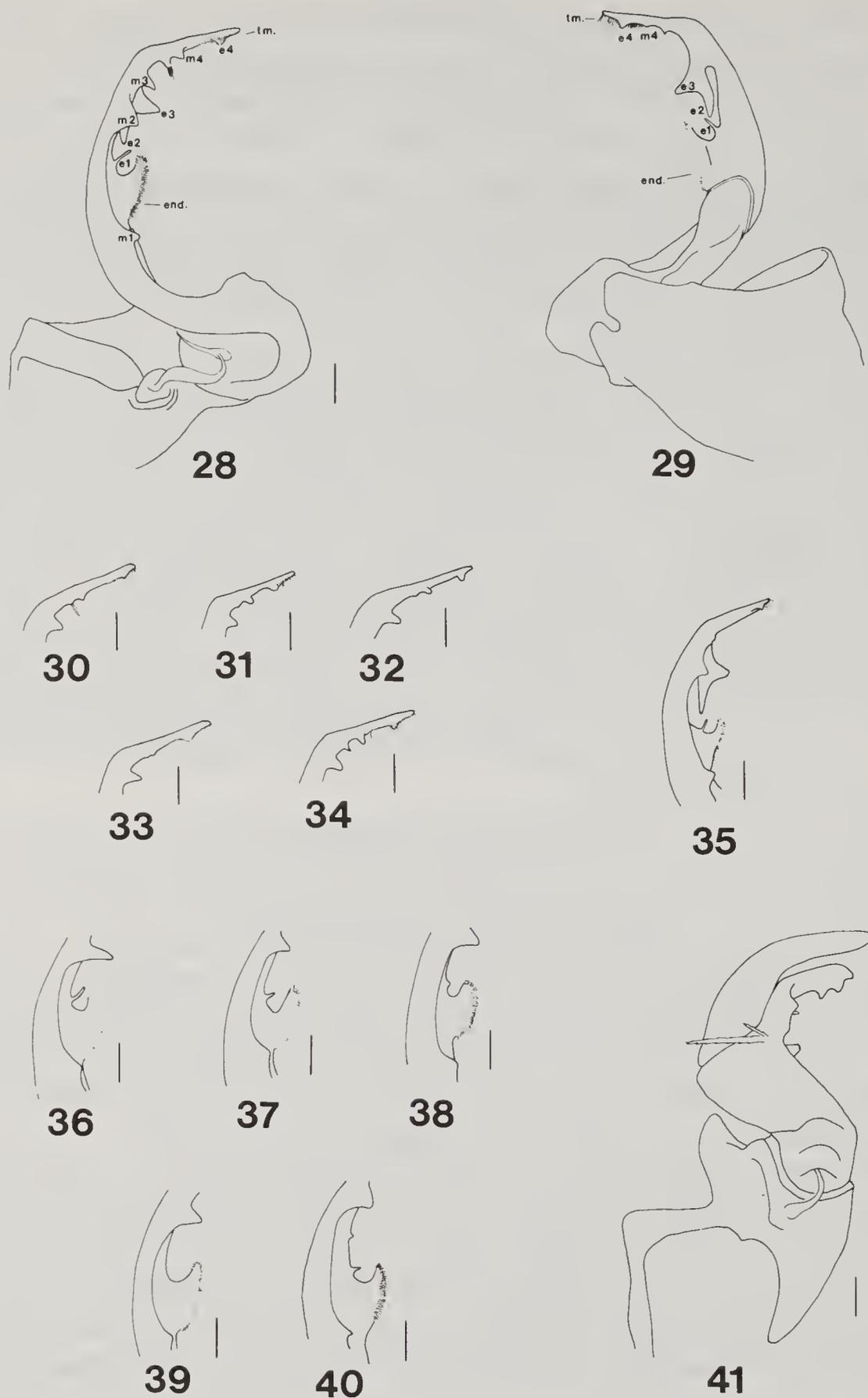
Past discussion of gonopodal variation in the Polydesmidae has been hampered by the absence of a standardized nomenclature for the spines, branches, and other projections of the posterior faces of the telopodites. Hoffman (1974) devised a labeling system based upon orientation of these processes, with letters "m" and "e" designating mesial and ectal position, respectively, and numbers indicating position relative to the base of the telopodite, the most proximal designated by 1. Thus, in *P. branneri* the four mesial processes are labeled m1, m2, m3, and m4; the four ectal processes are e1, e2 + 3 (indicating that they share a common pedicel), and e4 (Figs. 28-29). Examination of the left gonopods of 51 specimens collected from the Kings Mountain region revealed considerable gonopodal variation.

The only evident variation in the mesial processes involved suppression and division of m4. Nearly three-fourths of the individuals examined had a normal m4 lobe with a projecting setaceous shoulder (Figs. 28, 30, 34); the remaining individuals had a reduced or vestigial m4, with a shoulder lacking setae (Figs. 31-33). In 75% of the specimens, m4 consisted of a large lobe contiguous with a smaller shoulder (Figs. 28, 30-33). This lobe was divided into two separate processes in the remaining specimens (Fig. 34). The other mesial processes, m1-m3, were virtually uniform, although one individual lacked m2 (Fig. 35).

The most variable ectal process, e1, displayed four configurations; spiniform (Figs. 28, 36) in 31% of the males; reduced (Fig. 37) in 29%; vestigial (Fig. 38) in 18%; and absent (Fig. 39) in 18%. Two individuals (4% of the males) carried a vestigial secondary spine distal to a reduced e1 spine (Fig. 40). The other ectal processes, e2+3 and e4, were uniform.

Terminal macrosetae of the telopodite varied in abundance and distribution. Thirty-one percent of the males had numerous macrosetae occurring from just distal to m4 to the telopodite tip (Figs. 28-30, 33-34), and fifty-one percent carried fewer macrosetae distributed from e4 to the tip (Fig. 31). Most remaining individuals (14%) possessed very few macrosetae, occurring only apically on the telopodite (Fig. 35). Two individuals (4%) lacked terminal macrosetae (Fig. 32).

Hoffman (1974) reported that m2, m3, e2, and e3 were the most variable processes in *P. branneri*, but these were found to be the most stable in the Kings Mountain population, where most of the variation involved m4, e1, and the terminal macrosetae. Many combinations of these



Figs. 28-41. Polydesmidae. 28-40, *Pseudopolydesmus branneri*. 28, left gonopod, medial view. 29, the same, lateral view, medial processes (m1-m4), ectal processes (e1-e4), endomerite (end), terminal macrosetae (tm). 30-34, distal ends of telopodites, medial views, showing variation of m4 and terminal macrosetae. 35, distal half of telopodite, medial view, showing absence of process m2. 36-40, endomerite regions of telopodites, medial views, showing variation of process e1. 41, *Scytonotus granulatus*, left gonopod, medial view. Scale line = 0.1 mm.

gonopodal variants occurred, and there was no correlation between them. The length of the patch of terminal macrosetae and the configuration of m4 and e1 varied independently, and seem to be controlled by different genes.

These findings greatly expand current knowledge of variation for the species and illustrate the degree of variability that may occur within a local population. To Hoffman's (1974) characterization of *P. branneri* may now be added the occasional appearance of a new process, the secondary e1 spine, the division of a single process into separate components, m4 lobe and shoulder, and the occasional loss of all terminal macrosetae.

Hoffman (1974) described *P. collinus* as differing from *P. branneri* in the absence of m3 and either the absence or vestigial condition of e1. In the Kings Mountain specimens, e1 and/or m3 were present on all specimens, although e1 varied considerably in size. Consequently, only one species, *P. branneri*, is represented by this material.

*Scytonotus granulatus* (Say, 1821)

Fig. 41

This species was rare in the Kings Mountain region. Isolated brown adults were found in April and October, and white juveniles were taken in July. Both were found in moist humus. The widespread occurrence of the species in western North Carolina and several other states was noted by Hoffman (1962), and Shelley (1978) reported additional localities in eastern Piedmont North Carolina.

Platyrhacidae

*Auturus erythropygos* (Brandt, 1841)

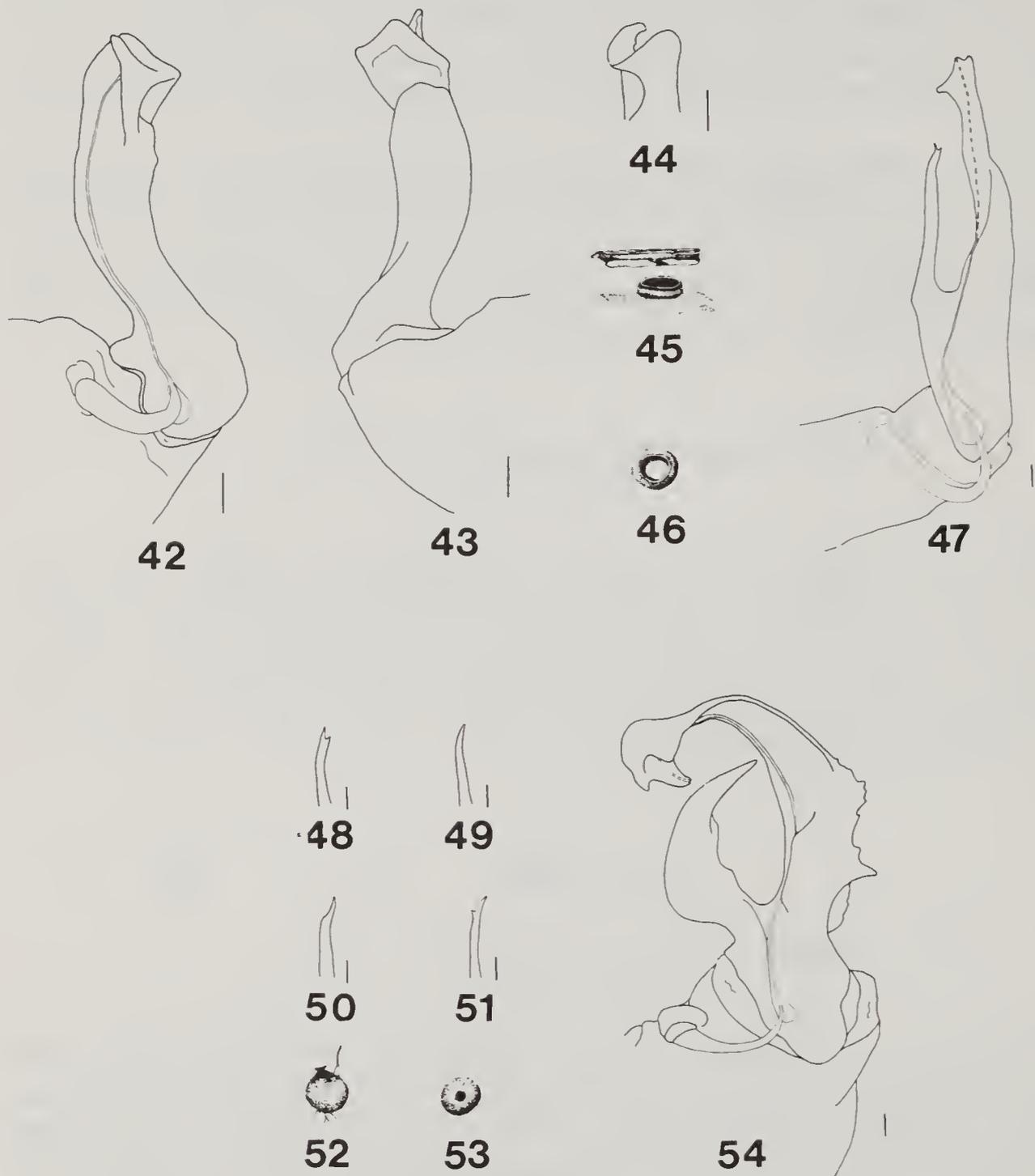
Figs. 42-46

Adults of *A. erythropygos* exhibit striking body coloration, with each blue-gray metatergite bearing a bright orange middorsal spot and orange paranota. Juveniles, though lighter, have a similar pattern. All stages were collected from under bark of decaying deciduous logs, in humus under logs, or in associated bark litter. Both adults and juveniles were most abundant in October, but the species was quite common in April and July.

Flattened, round molting chambers, built under the bark of logs inhabited by *A. erythropygos*, were observed on each collecting trip (Figs. 45-46). They are constructed of cemented wood particles and provide protection from desiccation and predation during intermolts. The dimensions were proportional to the inhabitant's size, the largest being 20-22 mm diameter. An adult or juvenile accompanied by cast exuvium was

seen in each chamber. The exoskeleton of newly molted individuals was whitish and incompletely sclerotized.

This species was unknown from North Carolina until reported from Northampton County by Shelley (1978), who listed it as *A. georgianus* Chamberlin, now considered a junior synonym.



Figs. 42-54. 42-46, *Auturus erythropygus*. 42, left gonopod, medial view. 43, the same, lateral view. 44, distal end of telopodite, cephalic view. 45-46, molting chamber. 45, side view *in situ* on log, bark lifted. 46, top view. 47-53, *Boraria stricta*. 47, left gonopod, medial view. 48-51, distal halves of prefemoral processes of left gonopods, medial views. 52-53, molting chamber. 52, side view *in situ*, attached to plant roots. 53, top view. 54, *Croatania catawba*, telopodite of left gonopod, medial view. Scale line = 0.1 mm.

## Xystodesmidae

*Boraria stricta* (Brölemann, 1896)

Figs. 47-53

The color of *B. stricta*, black with yellow paranota, is typical of most xystodesmid species in the Kings Mountain region. Adults were most abundant in April, and juveniles were common in October and April. Large colonies were discovered in wet mud-clay soils lining the banks of streams throughout the region. Individuals often were captured in tunnels beneath shallow layers of detritus. Round molting chambers, similar to those described for this species by Hoffman (1965), were observed in the vertical shafts of several tunnels in April (Figs. 52-53). Each chamber was formed of clay attached to exposed plant roots, and inhabited by a newly molted milliped with its cast exuvium. As can be seen by comparing illustrations (Figs. 45-46, 52-53), the molting chamber of *B. stricta* is spherical with an apical "chimney" and is attached at its base, whereas that of *A. erythropygus* is round, flattened in a vertical plane, and attached at both ends. These distinctions reflect the different biotopes inhabited by the species.

Hoffman (1965) reported that the known range of *B. stricta* coincided closely with the southern section of the Blue Ridge physiographic province and predicted only slight extensions at the northern and southern extremities. Discovery of the species in the Kings Mountain region represents an extension of slightly less than 64 km east into the Piedmont Plateau. The species was not reported by Shelley (1978) from the fall zone region, and extensive investigations in the Uwharrie Mountains also have failed to produce it. Hence, the Kings Mountain population is the easternmost known and is probably peripheral. Specimens also have been collected from a number of other Piedmont localities in the past eight years by Shelley, and since the Piedmont is geologically and climatically distinct from the southern Appalachians, material from the entire range was examined to determine if recognition of geographic races was warranted. Hoffman (1965) noted the homogeneity of *B. stricta* gonopods, with only slight differences detected. The lobes of the distal subhastate end of the telopodite varied in size relative to each other, and the degree of bending at midlength of the telopodite and apically on the prefemoral process varied. These differences were scattered and inconsistent, not conforming to any geographic pattern. The prefemoral processes of seven percent of males in the Kings Mountain population (including material from York County, South Carolina), however, were apically bifurcate (Figs. 47-48, 51), a condition never before reported for either the genus or species. These bifurcate males were intermixed with normal individuals, although there were differences in the apical prefemoral bend of the latter (Figs. 49,50).

In summary, no significant geographical variation was observed in

*B. stricta*, and the homogeneity noted previously by Hoffman (1965) also applies to Piedmont populations. The bifurcate prefemoral process is new, however, and its occurrence solely in the Kings Mountain population may represent a peripheral population effect. This occurs in too small a sample of the Kings Mountain population, however, to justify taxonomic recognition. The known range of *B. stricta* is expanded considerably to include Gaston and Cleveland counties, North Carolina, and York (Kings Mountain State Park) and Spartanburg (Croft State Park) counties, South Carolina.

*Croatania catawba* Shelley, 1977

Fig. 54

*Croatania catawba* Shelley, 1977:306, Figs. 1-2, 7, 11-12, 16.

*Croatania catawba* was one of the few millipeds encountered primarily in July; only three adults were found in April and October. The preference of species of *Croatania* for hot, dry conditions was discussed by Shelley (1977), who also presented a description of the habitat at the type locality in Cleveland County. Individuals collected during the present study, however, were taken from cool, moist seepage areas under deciduous leaf piles and from under large, decaying deciduous logs. As reported by Shelley (1977), adults were typically black with lemon yellow paranota and a variable yellow stripe along the anterior edge of the collum. One female displayed an orange tinted collum stripe similar to that reported by Shelley for two Union County, South Carolina specimens. No significant gonopodal variation was discerned.

Shelley (1977) suggested that the distribution of *C. catawba* in North Carolina might be associated with the Kings Mountain range, which extends northeastward through a series of hills and ridges to Anderson Mountain in Catawba County. Except for one Lincoln County specimen taken in 1952, however, the milliped has not been collected in North Carolina outside the contiguous ridge portion of the range in Cleveland and Gaston counties. *Croatania catawba* is thus essentially restricted to this small area in North Carolina, and therefore is considered to be a species of special concern in the state, as defined by Cooper et al. (1977).

Localities. *Cleveland Co.*—9.3 km S Kings Mountain (town), along CR 2245, 0.2 km N jct. CR 2288, 9 ♂, 5 ♀, 16 September 1975, R.M. Shelley and J.C. Clamp (NCSM A450) TYPE LOCALITY; 1.9 km SW Kings Mountain (town), along I-85, jct. NC Hwy. 161, ♀, 10 April 1977, M. Filka (NCSM A1040), ♂, ♀, 7 July 1976, M. Filka and W.W. Thomson (NCSM A1048), and 5 ♂, ♀, 6 juvs., 10 July 1976, M. Filka and W.W. Thomson (NCSM A1049). *Gaston Co.*—7.7 km SW Gastonia, along CR 1131, 0.2 km NW jct. CR 1133, ♀, 9 July 1976, M. Filka and W.W. Thomson (NCSM A1340); and 7.2 km S Bessemer City, along CR 1125, jct. CR 1106, ♀, 16 October 1976, M. Filka and G. Wicker (NCSM A1418).

*Deltotaria lea* Hoffman, 1961

Figs. 55-56

*Deltotaria lea* Hoffman, 1971:33, Figs. 1c, 3a.

Only ten specimens of *D. lea*, all adults, were collected in this study, all during the cooler weather of April and October. No juveniles were encountered. The original description by Hoffman (1961) was based on a single preserved male, and specimens from the Kings Mountain region supplement knowledge of the species in live coloration and gonopodal variation. Adults are black with yellow paranota and broad yellow stripes along the caudal edges of the metaterga and the anterior edge of the collum. All specimens display a metallic sheen quite unlike the glossy surfaces of species like *C. catawba*. Gonopodal variations included presence or absence of a minute prefemoral process, dimension of the distal end of the telopodite, and diameter of the telopodite arc (Figs. 55-56).

In North Carolina, *D. lea* is known to be concentrated in the Kings Mountain region. Like *C. catawba*, it also was collected in Lincoln County in the 1950's but has not been found there recently. Thus, in North Carolina *D. lea* also may be restricted to the Kings Mountain region and is considered of special concern in the state. The species has been collected from three South Carolina counties by Shelley, as reported below.

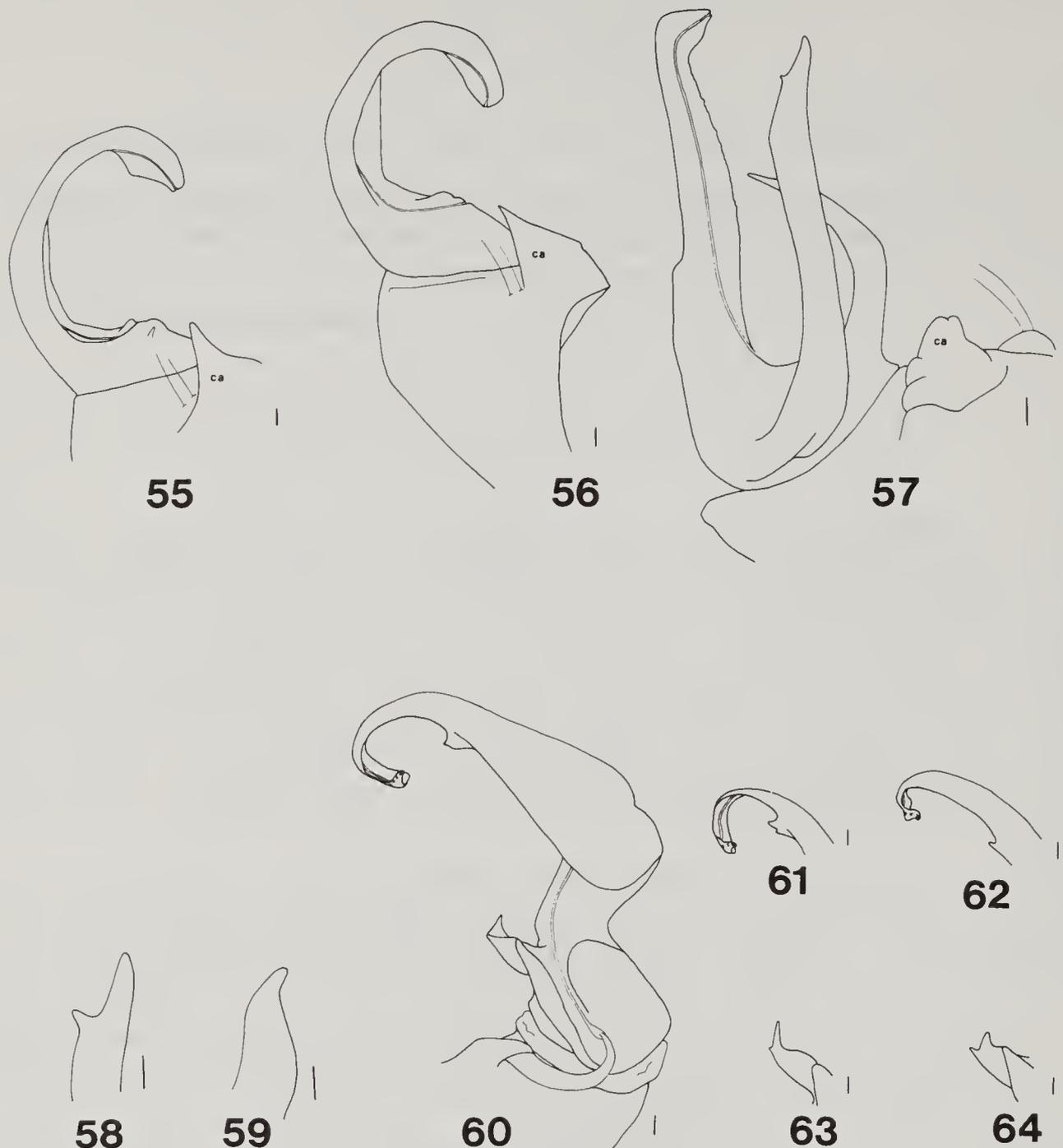
Localities. NORTH CAROLINA. *Cleveland Co.*—1.9 km SE Kings Mountain (town), along I-85, jct. NC Hwy. 161, ♂, ♀, 18 October 1976, M. Filka and G. Wicker (NCSM A2284); 6.5 km SW Kings Mountain (town), along CR 2245, 0.3 km N jct. CR 2283, ♂, ♀, 30 April 1976, R.M. Shelley (NCSM A720); 9.3 km S Kings Mountain (town), along CR 2245, 0.2 km N jct. CR 2288, ♂, 30 April 1976, R.M. Shelley (NCSM A723); 6.2 km S Kings Mountain (town), along NC Hwy. 161, 0.3 km S jct. CR 2354, 2 ♂, 30 April 1976, R.M. Shelley (NCSM A725); and 6.2 km SE Kings Mountain (town), along NC Hwy. 161, 1.6 km S jct. CR 2289, ♂, 8 April 1977, M. Filka (NCSM A2204). *Gaston Co.*—2.4 km NE Crowders Mountain, along CR 1122, 0.2 km N jct. CR 1131, ♂, 18 April 1976, M.R. and J.E. Cooper (NCSM A733); and 13.6 km SW Gastonia, along CR 1104, 0.5 km S jct. CR 1115, ♂, 29 April 1976, R.M. Shelley (NCSM A713).

SOUTH CAROLINA. *York Co.*—Kings Mountain State Park, ♂, 30 April 1977, R.M. Shelley (NCSM A1479). *Cherokee Co.*—7.4 km SE Blacksburg, along SC Hwy. 5, 0.5 km S jct. SC Hwy. 68, ♂, 10 May 1977, R.M. Shelley (NCSM A1480). *Chester Co.*—17.9 km NE Chester, along SC Hwy. 32, 1.1 km N jct. SC Hwy. 46, ♂, ♀, 1 May 1977, R.M. Shelley (NCSM A1498); and 19.8 km W Lowrys, along SC Hwy. 9 at Broad River, ♂, 1 May 1977, R.M. Shelley (NCSM A1501).

*Pachydesmus crassicutis incurtus* Chamberlin, 1939

Figs. 57-59

This is the largest polydesmoid milliped in North Carolina and is



Figs. 55-64. 55-56, *Deltotaria lea*, left gonopods, ventrolateral views, coxal apophysis (ca). 57-59, *Pachydesmus crassicutis incursus*. 57, telopodite of left gonopod, lateral view, coxal apophysis (ca), primary tibiotarsus (ptt), second tibiotarsus (stt). 58-59, distal ends of secondary tibiotarsi, lateral views. 60-64, *Sigmorita latior*. 60, telopodite of left gonopod, medial view. 61-62, distal ends of telopodites, medial views. 63-64, prefemoral processes, medial views. Scale line = 0.1 mm.

known definitely only from the Kings Mountain region (Shelley and Filka 1979). It is approximately 7 cm long, and dusky brown with yellow paranota. As with *C. catawba*, most specimens were found in July, concentrated in wet spots such as seepage areas. Shelley and Filka presented illustrations of gonopodal variation and showed changes in body dimensions that occur with latitude. Individuals of both sexes are larger and

more brightly colored in the Kings Mountain region than farther south in South Carolina, probably a reflection of more favorable environmental conditions in the former area.

Gonopod comparisons revealed variation in primary and secondary tibiotarsi (Figs. 57-59, ptt, stt). As reported by Shelley and Filka, the sub-terminal process of the secondary tibiotarsus was pointed, blunt, or absent. Since, in North Carolina, *P.c. incursum* is apparently restricted to the Kings Mountain region, it is considered to be endangered within the state, as defined in Cooper et al. (1977).

Localities. *Cleveland Co.*—6.6 km SW Kings Mountain (town) along CR 2245 at Dixon Branch Creek, 0.8 km NW jct. CR 2283, 2 ♂, 2 ♀, 1 juv., 16 August 1975, R.M. Shelley and J.C. Clamp (NCSM A537); 9.3 km S Kings Mountain (town), along NC Hwy. 245, 0.2 km N jct. CR 2288, 3 ♀, 16 August 1975, R.M. Shelley and J.C. Clamp (NCSM A541); 9.1 km SW Kings Mountain (town), along CR 2283, 1.3 km NE jct. NC Hwy. 216, ♂, 8 July 1976, M. Filka and W.W. Thomson (NCSM A1060); and 4.8 km S Kings Mountain (town), along CR 2289, 1.0 km W NC Hwy. 161, 2 ♀, 18 October 1976, M. Filka and G. Wicker (NCSM A2239). *Gaston Co.*—8.5 km SW Gastonia, along CR 1122, 1.4 km w jct. CR 1131, along Crowders Creek, 2 ♂, 2 ♀, 16 August 1975, R.M. Shelley and J.C. Clamp (NCSM A547); 6.4 km SW Gastonia, along CR 1126, 0.8 km S jct. CR 1113, ♀, 16 August 1975, R.M. Shelley and J.C. Clamp (NCSM A549); 7.7 km SW Gastonia, along CR 1131, 0.2 km NW jct. CR 1133, ♀, 8 July 1976, M. Filka and W.W. Thomson (NCSM A1091); and 1.9 km W Gastonia, along CR 1106, 2.4 km E jct. CR 1236, ♂, 16 October 1976, M. Filka and G. Wicker (NCSM A2255).

### *Sigmoria latior* (Brölemann)

Figs. 60-64

This was the most common xystodesmid in the region of study. Adults and juveniles were discovered beneath deciduous leaf litter and on open substrate in July, but only four adults were taken in both April and October. In North Carolina the species ranges from the northwestern mountains to the eastern Piedmont, and intergrades of the three subspecies were reported from McDowell County eastward to Scotland and Hoke counties (Shelley 1976c), an area which includes the Kings Mountain region.

Shelley (1976c) noted that all specimens available from south of the Catawba and Deep-Cape Fear rivers, including intergrades of *S. l. latior* (Brölemann) X *S. l. hoffmani* Shelley, had stripes along the caudal edges of the metaterga. The nominate subspecies, occurring north of these rivers, lacked stripes. During our study, however, specimens of both color patterns were discovered. At Spencer Mountain they exhibited the striped pattern, whereas around Kings-Crowders ridges the metaterga

were black and without stripes. In both areas the stripe and/or paranotal color was yellow and did not vary through shades of orange-red, as reported by Shelley for the nominate subspecies and intergrades.

Since this is the first report of unstriped specimens in the zone of intergradation, the gonopods of 18 striped and 13 unstriped males were examined for possible differences. Depth of the flange and broadness of the distal curvature of the telopodite varied, but the flange always extended below the tip of the telopodite (Fig. 60). The subterminal tooth varied in prominence and was double in two individuals (Figs. 60-62), and the prefemoral process ranged from simple to bifurcate with variation in the relative lengths of the components, although the vertical branch was always larger (Figs. 63-64). All are typical intergrade variations and do not correlate with either color pattern. Thus, the solid black metatergal color is interpreted to represent the nominate subspecies trait, just as some intergrade gonopods more closely resemble those of one subspecies than the other two.

## DISCUSSION

### SEASONAL VARIATION OF THE FAUNA

Although the Kings Mountain region was not sampled quantitatively and only limited conclusions can be drawn concerning numbers of species present in each season, the area was studied with sufficient intensity to reflect general trends in seasonal differences (Table 3). The overall abundance of millipeds increased from April to October, with only two species, *Narceus americanus* and *Auturus erythropygus*, present as both adults and juveniles in all three months. Adults of other species varied seasonally, with juveniles present simultaneously or in other months. The more common species that particularly exemplify these seasonal variations are discussed by month below.

Diplopods were least abundant in April. Adults of *Pseudopolydesmus branneri* and *Boraria stricta*, and juveniles of *Oxidus gracilis*, dominated the fauna, while adults and juveniles of *N. americanus*, and adults of *Cambala annulata* and *A. erythropygus* were moderately abundant. Adults of *Ptyoiulus ectenes*, *Delophon georgianum*, and *Deltotaria lea* were less common, and juveniles of these species were absent or nearly so. Only a few specimens of the remaining species were found. Adults of *D. georgianum*, *P. branneri*, *B. stricta*, and *D. lea*, and juveniles of *Striaria* sp., *O. gracilis*, and *B. stricta* were more numerous in April than in any other month. Two species, *Brachyiulus lusitanus* and *Trichopetalum dux*, were collected only in April.

A different group of diplopods dominated the fauna in July. *Narceus americanus*, *Abacion magnum*, *O. gracilis*, *A. erythropygus*, *Pachydesmus crassicutis incurtus*, and *Sigmoria latior* were the prevalent adult forms, while *Polyxenus fasciculatus*, *Ptyoiulus* sp., and *N. americanus* were common in immature stages. Intermediate numbers of *A. erythropygus* and



*S. latior* juveniles also were present, and the remaining species were represented only by scattered individuals. Five species, *P. fasciculatus*, *A. magnum*, *Croatania catawba*, *P.c. incursus*, and *S. latior* were more abundant as both adults and juveniles during July than at any other time. Immatures of *Nopoiulus minutus* and *Scytonotus granulatus* also were most numerous in July, although juveniles of the former were taken in October as well. Species more common as adults in July than in April included *Polyzonium strictum*, *N. americanus*, and *O. gracilis*. Species less common as adults during July than in October or April included *C. annulata* and *B. stricta*. Three species — *P. ectenes*, *P. branneri*, and *D. lea* — were absent from the July collections. *Andrognathus corticarius* was collected only in July.

The greatest abundance and diversity of species occurred in October. Those most abundant as adults were *Ptyoiulus ectenes*, *P. impressus*, *C. annulata*, *P. branneri*, and *A. erythropygos*. Those most common in immature stages were *P. ectenes*, *O. gracilis*, *P. strictum*, *N. americanus*, and *A. erythropygos*. More juveniles of the last three species were encountered in October than in either of the other months. The first two species were moderately abundant as either adults or juveniles. Both *Teniulus* sp. and *Cleidogona medialis* were found only in October and as adults. Millipeds less common in the adult stage in October than in July included *N. americanus*, *A. magnum*, *O. gracilis*, *C. catawba*, *P.c. incursus*, and *S. latior*.

The species/genus ratio (S/G) for all three months (1.04) was essentially unity (April and July S/G = 1.00, October S/G = 1.05), with the slightly higher fraction of October reflecting the presence of both species of *Ptyoiulus*. Seasonal changes in the faunal composition ratios (orders/families/genera/species, O/F/G/S) from April to October were more significant than changes in the S/G ratios. One more order, the same number of families, and one less genus and species occurred in July (8/12/16/16) than in April (7/12/17/17). The same number of orders, one more family, four more genera, and five more species occurred in October (8/13/20/21) than in July. Thus, the spring and summer faunas were less diverse than the October fauna. These fluctuations reflect variations in times of maturation and breeding of the different species.

The overall O/F/G/S ratio for the three months combined (9/16/23/24) showed one more order, three more families, three more genera, and three more species than occurred in any single month. This reflects the appearance and disappearance of species during the year, which is also indicated by the following seasonal trends. Five species — *P. ectenes*, *C. annulata*, *P. branneri*, *B. stricta* and *D. lea* — were more common in April than in July and again increased in abundance during October. A different five species — *P. strictum*, *P. ectenes*, *C. catawba*, *P.c. incursus* and *S. latior* — were more common in July than in either of the cooler months. Three species — *P. strictum*, *P. ectenes*, and *P. impressus* — were most abundant in October, and two — *N. americanus* and

*A. erythropygus* — were common in all three months as both juveniles and adults. Seven diplopods were encountered rarely (less than ten specimens) and were collected during only one month (*A. corticarius*, *B. lusitanus*, *Teniulus* sp., *C. medialis*, and *T. dux*), or two months (*N. minutus*, and *Striaria* sp.) These data indicate that milliped faunas should be sampled on a seasonal basis, a practice not generally followed to date, and that collections in spring and fall may produce species not available in summer.

#### COMPARISON OF FAUNAS AND SIGNIFICANCE TO NORTH CAROLINA

Spencer Mountain is separated from the contiguous Kings-Crowders ridge by approximately 15 km of urbanized Piedmont, and as shown in Table 4 fewer milliped species occur at the inselberg. At both Spencer Mountain (S/G = 1.00) and Kings-Crowder ridge (S/G = 1.05) every genus is represented by one species with the sole exception of *Ptyoiulus*, for which both species are present at Kings-Crowders ridge. At Spencer Mountain, however, three less families, seven less genera, and eight less species (8/11/14/14) were encountered than at Kings-Crowders ridge (8/14/21/22). The two areas had 12 species in common — *P. fasciculatus*, *P. ectenes*, *N. americanus*, *A. magnum*, *D. georgianum*, *C. annulata*, *O. gracilis*, *P. branneri*, *S. granulatus*, *A. erythropygus*, *B. stricta*, and *S. latior*. Two species collected only at Spencer Mountain, *A. corticarius* and *T. dux*, were found in such low numbers (Table 3) that their absence from the Kings-Crowders ridge could well be a collecting artifact. The same is true of the apparent absence of six species from Spencer Mountain — *P. strictum*, *B. lusitanus*, *N. minutus*, *Teniulus* sp., *C. medialis*, and *Striaria* sp. Of the remaining five species absent from Spencer Mountain, *P. impressus*, *B. stricta*, and *P.c. incurtus* have western or southern ranges that may well end at Kings-Crowders ridge. Two xystodesmids, *C. catawba* and *D. lea*, could occur at Spencer Mountain, since both were collected from Lincoln County in the 1950s. Their presence seems doubtful, however, since the extensive searches for diplopods at Spencer Mountain would surely have revealed these large, brightly colored, and obvious millipeds. Thus, the absence of these five species from Spencer Mountain may be real.

In addition to faunal distinctions between the two areas, color pattern variation was noted in *S. latior*. As discussed in the species account, specimens from Spencer Mountain displayed yellow paranota and stripes along the caudal edges of the metaterga, whereas those from Kings-Crowders ridge had yellow paranota but lacked the metatergal stripes. No anatomical differences were detected, and both color patterns are representative of intergrades. This is the first report of *S. latior* intergrades without stripes, a trait characteristic of the nominate subspecies.

The diplopod fauna of the Kings Mountain region is also compared with the faunas of the eastern Piedmont and Appalachian Mountains (numerical data for the Great Smoky Mountains) in Table 4, and is

Table 4. Comparison of the diploped faunas of Spencer Mountain and the Kings-Crowders Ridge with those of the eastern Piedmont and Appalachian Mountains of North Carolina.

Kings Mountain Fauna	Spencer Mountain	Kings-Crowders Ridge	Eastern Piedmont	Appalachian Mountains
<i>Polyxenus fasciculatus</i>	X	X	X	?
<i>Polyzonium strictum</i>		X	X	X
<i>Andrognathus corticarius</i>	X		X	X
<i>Nopoiulus minutus</i>		X	X	
<i>Brachyiulus lustratus</i>		X	X	
<i>Ptyoiulus ectenes</i>	X	X	X	
<i>Ptyoiulus impressus</i>		X		X
<i>Teniulus</i> sp.		X		X
<i>Cleidogona medialis</i>		X	X	X
<i>Trichopetalum dux</i>	X			
<i>Striaria</i> sp.		X	?	?
<i>Narceus americanus</i>	X	X	X	X
<i>Abacion magnum</i>	X	X	X	X
<i>Delophon georgianum</i>	X	X		X
<i>Cambala annulata</i>	X	X	X	X
<i>Oxidus gracilis</i>	X	X	X	X
<i>Pseudopolydesmus branneri</i>	X	X	X	X
<i>Scytonotus granulatus</i>	X	X	X	X
<i>Auturus erythropygos</i>	X	X	X	X
<i>Boraria stricta</i>	X	X	X	
<i>Croatania catawba</i>		X		X
<i>Deltotaria lea</i>		X		
<i>Pachydesmus crassicutis incurvus</i>		X		
<i>Sigmoria latior</i>	X striped	X solid	X	
Total number of species	14	22	35 <sup>a</sup>	53 <sup>b</sup>
Species in common with Kings Mountain region	—	—	15(1)	13(1,2)
Order/family/genus/species ratio	8/11/14/14	8/14/21/22	9/19/29/35 <sup>a</sup>	17/33/53 <sup>b</sup>
	9/16/23/24			
Species/genus ratio	1.00	1.05	1.21 <sup>a</sup>	1.61 <sup>b</sup>
		1.04		

<sup>a</sup>from Shelley (1978) for the eastern Piedmont<sup>b</sup>from Hoffman (1969) for the Great Smoky Mountains, ordinal figure not provided.

shown to have a lower S/G ratio and fewer taxa below the level of order than either. Comparison with the entire eastern Piedmont is somewhat misleading, however, since the land area investigated by Shelley (1978) was much larger and contained a greater variety of biotopes than the Kings Mountain region. A more meaningful comparison is with the three smaller areas that he sampled in detail — Medoc Mountain and William B. Umstead state parks, and the hardwood locality near Ellerbe — each more comparable in size to the Kings Mountain region. The ratios for these three sites are as follows: Medoc Mountain State Park (5/6/7/7, S/G = 1.00); William B. Umstead State Park (8/12/14/15, S/G = 1.07); and Ellerbe (7/10/12/12, S/G = 1.00). The Kings Mountain fauna is higher in each taxonomic category than any of these sites, but their S/G ratios still reflect the occurrence of essentially one species per genus. Only *Ptyoiulus*, with *P. ectenes* and *P. impressus* in the Kings Mountain region, and *Narceus*, with *N. americanus* and *N. annularis* in Umstead State Park, are represented by more than one species at a site. The greater numbers of taxa in the Kings Mountain region may reflect its mountainous character, but the region is still unable to support significantly more than one species per genus. Compared to the Appalachian Mountains in general and the Great Smoky Mountains in particular, the Kings Mountain region has fewer taxa in every category (the number of orders for the Great Smoky Mountains was not reported by Hoffman 1969) and a much lower S/G ratio. Many Appalachian genera are represented by more than one species, a reflection of the greater variety of niches afforded by the rugged, heterogeneous terrain.

Despite the numerical differences, however, there are similarities between the Kings Mountain region and the other areas. Eight species of widespread distribution are common to all three: *P. strictum*, *A. corticarius*, *N. americanus*, *A. magnum*, *C. annulata*, *O. gracilis*, *P. branneri*, *S. granulatus*, and one or possibly two species of *Striaria* (taxonomic problems exist within this genus). Some of the 24 species found in the Kings Mountain region also occur in one of the others but not both. Seven typically Piedmont inhabitants currently unknown from the mountains are shared with the eastern Piedmont — *P. fasciculatus*, *N. minutus*, *B. lusitanus*, *P. ectenes*, *T. dux*, *A. erythropygos*, and *S. latior*. Most were expected in the Kings Mountain region at the outset of the study. Five species are likewise shared with the Appalachians — *P. impressus*, *Teniulus* sp., *C. medialis*, *D. georgianum*, and *B. stricta*. Their discovery in the Kings Mountain region was a complete surprise and a significant range extension for each. Fifteen species reported from the eastern Piedmont by Shelley (1978) were not found in the Kings Mountain region, although three, *Cylindroiulus truncorum* (Silvestri), *Ophiulus pilosus* (Newport), and *Apheloria tigana* Chamberlin, are considered potential inhabitants. The first two are synanthropic millipeds that could have been overlooked in our study since we did not sample urban environments. *Apheloria tigana* is so common in the eastern Piedmont and in the

more proximal Uwharrie Mountains that it must be considered a possibility for the Kings Mountain region. Five millipeds known from both the Appalachian Mountains and eastern Piedmont must also be considered potential occupants of the Kings Mountain region due to its location between these two areas. These five species are *Polyzonium rosalbum* (Cope), known from Madison and Moore counties (Shelley 1976a, 1978); *Cleidogona caesioannulata* (Wood), reported from Macon, Jackson, Transylvania, and Swain counties (Shear 1972) and Granville, Orange, Durham, and Johnston counties (Shelley 1978); *Branneria carinata* (Bollman) cited from Transylvania and Macon counties (Shear 1972), and Wake County (Shelley 1978); *Pseudopolydesmus serratus*, collected in 14 eastern piedmont counties (Shelley 1978), and reported generally from the mountains (Chamberlin and Hoffman 1958); and *Pleuroloma flavipes* Rafinesque, recorded as *Zinaria brunnea* from Watauga and Moore counties (Wray 1967) and as *Pleuroloma* sp. from Orange and Wake counties (Shelley 1978).

In addition to species shared with the eastern Piedmont and/or Appalachian Mountains, a fourth group of three xystodesmids is unique to the Kings Mountain region: *C. catawba*, *D. lea*, and *P.c. incurtus*. The last is known in North Carolina only from the contiguous Kings-Crowders ridge, but the others also have been recorded from Lincoln County (Shelley 1978; Hoffman 1961), in the area that is the north-eastward extension of the range to Anderson Mountain, Catawba County. *Croatania catawba* and *P.c. incurtus* are more common in South Carolina and are basically southern forms which extend into North Carolina along the Kings Mountain range. Together these two millipeds lend a southern aspect to the Kings Mountain fauna, which is not found in any other part of North Carolina. *Deltotaria lea* appears to be endemic to a narrow section of the Carolinas, ranging from Lincoln County, North Carolina, to Chester County, South Carolina.

Thus, the Kings Mountain milliped fauna is characterized by its own species and the transitional ones it shares with the eastern Piedmont Plateau and Appalachian Mountains, together and separately. Only five of these species, however, are shared with the Appalachians alone. This, plus the low diversity and the lowland nature of the fauna militate against a prior direct topographic connection between the Blue Ridge Front and the Kings Mountain region. Aside from a general Cretaceous peneplain there is no geological evidence for such a connection, just as there is no faunal evidence from the diplopods. Unlike the Appalachians, the Kings Mountain region does not seem to have ever been a center of milliped evolution and dispersal. The five Appalachian species in the area may be relicts of a continuous Pleistocene or pre-Pleistocene distribution, as suggested by Shelley (1979a) for *D. georgianum*. The most significant aspect of the Kings Mountain region is its position at the known range periphery of several diplopods. It is the northern distribution limit of *P.c. incurtus* and the northeastern of the genus *Pachydesmus* (Shelley and

Filka 1979), and two montane millipeds, *D. georgianum* and *B. stricta*, reach their eastern terminus in the area. It is also the easternmost limit for *P. impressus* and the genus *Teniulus*, the southeasternmost known site for *C. medialis*, and the western limit for *P. ectenes*. The Kings Mountain region is therefore a unique area in North Carolina, in the southern elements of its milliped fauna, in being a transitional area between predominantly eastern and western faunas, and in forming a part of the range periphery for four genera.

Teulings and Cooper (1977) used the term "cluster areas" to denote places in North Carolina where species of concern are grouped. Four rivers systems and four land areas in the Piedmont Plateau Province were so identified. In a preliminary report, Filka and Shelley (1977) indicated that, on the basis of its diplopod fauna alone, the Kings Mountain region also would qualify as a cluster area. Three species considered of concern in North Carolina occur in the region — *P.c. incursus* (endangered), and *C. catawba* and *D. lea* (special concern). Moreover, the range peripheries of *P. ectenes*, *P. impressus*, *Teniulus* sp., *C. medialis*, *D. georgianum*, *B. stricta* and *P.c. incursus* lie there. The area also contains a unique gonopod variant of *B. stricta*, and is distinguished by southern elements of its fauna (*C. catawba* and *P.c. incursus*). As far as millipeds are concerned the Kings Mountain region is of singular importance to North Carolina, and investigations of other animal groups may provide further evidence of its uniqueness. One state park, Crowders Mountain, exists in the area, and every effort should be made to expand it to include the deciduous bottomlands where most milliped species occur, including those now considered of concern in the state. No millipeds were found during this study in the dry, predominantly pine habitats of the existing park.

One objective of this study, that of gaining insight into evolutionary processes affecting millipeds in the southern Appalachians, went unmet. With only five species in common and a lowland-type faunal diversity, the Kings Mountain region adds little to current knowledge of milliped biogeography that might be applied to such an objective. Moreover, none of the five shared species belong to the xystodesmid tribe Aphelorini, which is the single most diverse and abundant element of the Appalachian fauna. Aside from the ubiquitous *Sigmoria latior*, which ranges from the mountains of West Virginia to the Coastal Plain of southern South Carolina (Shelley 1976c), the great southeastern aphelorine fauna is absent from the Kings Mountain region.

The study was, however, the first attempt to document seasonal occurrence of milliped species in a discrete part of the southeast, an endeavor that should receive more attention. Seasonal sampling of juveniles and adults can yield valuable information on life histories, for example, and basic biological knowledge of this type has never been determined for most North American diplopods. Although direct rearing of larvae and adults, and breeding experiments, would provide the best such information, inferences can nevertheless be gained from seasonal collections.

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# Electrophoretic Analysis of Three Species of *Necturus* (Amphibia: Proteidae), and the Taxonomic Status of *Necturus lewisi* (Brimley)

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**ABSTRACT.**—Electrophoretic analyses of 10 *Necturus maculosus* from Minnesota, 10 from Massachusetts, and 1 from the Mills River, Henderson County, North Carolina, were compared with those of 20 *Necturus lewisi* and 8 unspotted *Necturus punctatus* from the Neuse River drainage and 8 spotted *N. punctatus* from Naked Creek, Robeson County, North Carolina. Evaluation of 17 loci showed that the three samples of *N. maculosus* were indistinguishable (Nei's  $D = 0.000$ ) while *N. lewisi* were unequivocally different from *N. punctatus* at four loci and from *N. maculosus* at six loci. The two *N. punctatus* populations were indistinguishable from each other but were distinguishable from *N. maculosus* at 6 loci. These data indicate that *N. maculosus*, *N. lewisi* and *N. punctatus* are distinct, long isolated species.

## INTRODUCTION

*Necturus lewisi* is one of several endemic species of vertebrates and invertebrates found in the Tar and Neuse River drainages of North Carolina. This waterdog was originally described by Brimley (1924) as a subspecies of *Necturus maculosus* because of the "spotted larvae". Viosca (1937) briefly described the previously unknown striped larvae of *N. lewisi* and used its medium size and overall spotting as the apparent criteria for elevating it to full species status. Ashton and Braswell (1979) compared *N. lewisi* hatchlings and striped larvae with larvae of *N. maculosus* and *N. punctatus*, and found that the striped larvae of *N. lewisi* were quite distinctive. No electrophoretic studies in the genus have been reported. Our study compared electrophoretic data for all three of these *Necturus* species, in an attempt to evaluate the taxonomic status of *N. lewisi*.

## METHODS AND MATERIALS

Ten *N. maculosus* from Minnesota were obtained from Nasco, Fort Atkinson, Wisconsin and ten from Massachusetts were purchased from Connecticut Valley Biological Supply Company, Southampton, Massachusetts. One additional *N. maculosus* was collected in the Mills River, Henderson County, North Carolina. Twenty *N. lewisi* and eight unspotted *N. punctatus* were captured in the Neuse River drainage. Eight

spotted *N. punctatus* were collected from Naked Creek, PeeDee River drainage, in the Sandhills region of Robeson County, North Carolina. Animals were killed in the laboratory and an organ homogenate prepared from the heart, liver, rinsed stomach and upper part of intestine, and kidney and tongue of each. The specimen remains are housed in the North Carolina State Museum collection. The tissues of individual animals were then homogenized in an equal volume of 2% 2-phenoxyethanol and centrifuged at 25,000 g at 4° C for 45 minutes. The supernatant of soluble proteins was then decanted and stored at -70° C until used a maximum of 48-hours following preparation.

The 17 loci coding for proteins consistently resolved are as follows: malate dehydrogenase (NAD-dependent) (*Mdh-1*); indophenol oxidase (*Ipo-1*);  $\alpha$ -glycerophosphate dehydrogenase ( $\alpha$ -*Gpdh-1*); isocitrate dehydrogenase (NADP-dependent) (*Idh-1*); phosphoglucomutases, three loci (*Pgm-1*, *Pgm-2*, *Pgm-3*); glutamate oxalate transaminases, two loci (*Got-1*, *Got-2*); glutamate dehydrogenase (*Gdh-1*); phosphoglucoisomerase (*Pgi-1*); malic enzyme, two loci (*Me-1*, *Me-2*); 6-phosphogluconate dehydrogenase (*6-Pgdh-1*); sorbitol dehydrogenase (*Sdh-1*), glyceraldehyde-3-phosphate dehydrogenase (*G-3-pdh-1*); and lactate dehydrogenase (*Ldh-2*).

Techniques of horizontal starch gel electrophoresis and protein staining were similar to those described by Selander et al. (1971), with the following modifications: *Idh*, *Pgm*, *Mdh*, *Gdh*, and *Me* were examined with their continuous tris-citrate buffer (pH 8.00); *6-Pgdh*, *Got*, *Sdh* and *G-3-pdh* were demonstrated with the tris-borate-EDTA buffer of Ayala et al. (1973). Staining methods for *Gdh*, *G-3-pdh* and *Sdh* were as described by Brewer (1970). All gels were 12.5% starch (Electrostarch Lot #307).

Genetic inferences from electrophoretic results are based on the patterns being consistent with known molecular configurations for the proteins analysed, i.e. two-banded patterns are observed for the heterozygotes for a protein that is a monomer and three-banded patterns are observed for a dimeric heterozygote. The genes coding for each enzyme are represented by italicized abbreviations.

If several forms of the same enzyme are present and each is controlled by a separate gene locus, the hyphenated numeral serves to differentiate the loci. The enzyme with the greatest anodal migration is designated one, the next two, and so on. When allelic variation occurs, the allele with the greatest anodal migration is called *a*, the next *b*, and so on.

## RESULTS

The two *N. maculosus* samples were essentially identical genetically (genetic distance,  $D = 0.000$ ; Nei 1972). One heterozygote was found at each of the two loci (*Pgm-2*, *Idh-1*) in the Massachusetts sample, the only heterozygotes found.

The only variants found in the *N. lewisi* sample were at the Got-1 locus. Six individuals were heterozygous for the *a* and *b* alleles, one was homozygous for *b*.

Two unspotted *N. punctatus* were each heterozygous at single loci (Pgi-1, Pgm-2). The only difference between the spotted and unspotted samples was in the frequency of the Pgi-1 alleles (Table 1).

Table 1. Fixed genetic differences in three *Necturus* species.

Locus	Allele			
	<i>N. lewisi</i>	<i>N. maculosus</i>	<i>N. punctatus</i> spotted	<i>N. punctatus</i> unspotted
Mdh-1	<i>b</i>	<i>a</i>	<i>b</i>	<i>b</i>
Me-2	<i>a</i>	<i>b</i>	<i>b</i>	<i>b</i>
Got-1	<i>a</i> (0.80) <i>b</i> (0.20)	<i>c</i>	<i>b</i>	<i>b</i>
Got-2	<i>b</i>	<i>c</i>	<i>a</i>	<i>a</i>
Ldh-2	<i>c</i>	<i>b</i>	<i>c</i>	<i>c</i>
Pgi-1	<i>b</i>	<i>a</i>	<i>c</i> (0.81) <i>d</i> (0.19)	<i>d</i>
Me-1	<i>a</i>	<i>a</i>	<i>b</i>	<i>b</i>

The three species were unequivocally different at four (*N. lewisi* vs. *N. punctatus*) or six (*N. maculosus* vs. *N. lewisi* or *N. punctatus*) of the seventeen loci investigated; alleles were not shared at these loci (Table 1). Nei's standard genetic distance estimates between each pair of species (Table 2) are indicative of a long history of isolation of the gene pools. Electrophoretic examination of one *N. maculosus* from the Mills River, Henderson County, North Carolina confirms the genetic distinction found between the larger samples of allopatric *N. maculosus* and *N. lewisi*.

Table 2. Standard genetic distance (D) between species of *Necturus* examined.

	1	2	3	4
1. <i>N. lewisi</i>	0.0			
2. <i>N. maculosus</i>	0.435	0.0		
3. <i>N. punctatus</i> (unspotted)	0.348	0.435	0.0	
4. <i>N. punctatus</i> (spotted)	0.339	0.426	0.040	0.0

## DISCUSSION

Electrophoretic analysis of ten individuals from each of two populations of *N. maculosus* and one individual from a third population showed that they were indistinguishable using this technique. *Necturus lewisi* and *N. punctatus*, however, were highly distinguishable from each other and from *N. maculosus*, indicating that each species has been genetically isolated for some time. Two populations of *N. punctatus*, the spotted form inhabiting the Sandhills region of North Carolina and the uniformly gray-black form inhabiting the Neuse River, were indistinguishable from each other.

In conclusion, the specific status of *N. lewisi* is confirmed by electrophoretic data as well as by the distinct larvae described by Ashton and Braswell (1979). Further, *N. punctatus* appears to have been reproductively isolated from sympatric *N. lewisi* and from allopatric *N. maculosus* for a considerable period of time, and spotted *N. punctatus* from the PeeDee River drainage (North and South Carolina) appear on the basis of electrophoresis to be genetically similar to the unspotted populations of the Neuse River system.

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# Vertebrates of the Okefenokee Swamp

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**ABSTRACT.**—Four hundred nineteen vertebrate species and subspecies are known from the Okefenokee Swamp region of Georgia and adjacent Florida. These include 36 fishes, 37 amphibians, 66 reptiles, 232 birds, and 48 mammals. The vertebrates occurring in the Okefenokee represent a typical southeastern Atlantic Coastal Plain fauna. There are no endemic species. Eleven species, recognized as threatened or endangered under state and/or federal guidelines, occur in the swamp.

## INTRODUCTION

The Okefenokee Swamp region of southeastern Georgia and adjacent Florida contains an extremely diverse vertebrate fauna. However, with the exception of biological surveys conducted by Cornell University in the early decades of this century, that fauna has received little attention. At present there exists no comprehensive information on the vertebrates of the swamp. Most of the available literature is semipopular, anecdotal, or, at best, outdated.

Accurate faunal information is essential to understanding the Okefenokee Swamp ecosystem. The long term value and credibility of the systems ecology studies presently being undertaken in the swamp will, in large part, be determined by the extent to which base level natural history information can be incorporated into definitive analyses and models. Base level faunal surveys provide information on species diversity and patterns of habitat use that are crucial for biogeographic and systematic research. Furthermore, comprehensive faunal studies serve also as dated testaments to species composition and distribution within specific habitats, which are crucial for environmental impact assessments associated with management practices.

For these reasons, we have undertaken vertebrate faunal surveys within the Okefenokee Swamp and surrounding uplands. We report here the results of these surveys. We present, too, a review of pertinent historical foundations of our present knowledge of the swamp's vertebrate fauna, a comparison of the fauna with that of adjacent southeastern regions, and a preliminary analysis of habitat distributions of vertebrates known to occur within the swamp.

### GENERAL HABITAT CHARACTERISTICS

The Okefenokee Swamp is one of the largest freshwater wetlands in the United States. Situated in Charleton, Clinch, Echols and Ware counties, Georgia, and Baker and Columbia counties, Florida, the Okefenokee watershed includes both swamp (189,000 ha) and surrounding uplands (181,000 ha). It lies within the humid subtropical climatic zone (Trewartha 1968) and is characterized by warm moist springs, hot wet summers, warm dry falls, and cool moist winters. Weather is predominantly influenced by tropical maritime air masses from the Gulf of Mexico and the tropical Atlantic Ocean in spring, summer and fall, but by continental air masses in winter. Annual precipitation averages 100-150 cm (Hunt 1972).

The Okefenokee consists of a variety of vegetational habitat types. Plant specimens are on file at the University of Georgia Herbarium.

a. Two prairie habitat types are identified, comprising approximately 21% of the swamp. (1) Aquatic macrophyte prairies are dominated by emergent, floating-leaved, and submerged hydrophytes such as white water lily, *Nymphaea odorata*; yellow water lily, *Nuphar luteum*; neverwet, *Orontium aquaticum*; floating heart, *Nymphoides aquaticum*; yellow eyed grass, *Xyris smalliana*; pickerel weed, *Pontederia cordata*; redroot, *Lachnanthes caroliniana*; and bladderwort, *Utricularia* spp. (2) Grass-sedge prairies are characterized by various species of sedges, *Carex*; panic grasses, *Panicum*; and beak rush, *Rhynchospora*, as well as broomsedge, *Andropogon virginicus*; giant chain fern, *Woodwardia virginica*; and *Sphagnum* moss.

b. Shrub swamps cover approximately 34% of the swamp and are predominated by hurrah bush, *Lyonia lucida*; fetter bush, *Leucothoe racemosa*; titi, *Cyrilla racemiflora*; sweet spire, *Itea virginica*; pepper bush, *Clethra alnifolia*; and dahoon, *Ilex cassine*.

c. Blackgum forests cover less than 6% of the swamp. Blackgum, *Nyssa sylvatica* var. *biflora*, with a small amount of dahoon and pond cypress, *Taxodium ascendens*, dominates the canopy, with red maple, *Acer rubrum*, and dahoon the predominant understory plants.

d. Bay forests also cover less than 6% of the swamp. Loblolly bay, *Gordonia lasianthus*; red bay, *Persea borbonia*; and sweet bay, *Magnolia virginiana*, are the predominant canopy species although occasional pond cypress, blackgum, and slash pine, *Pinus elliotii*, are seen.

e. Mixed cypress forests are characterized by pond cypress dominated canopy and subcanopy, but loblolly bay, dahoon, and blackgum are frequently scattered in the subcanopy. This and the following habitat make up approximately 23% of the swamp.

f. Pure cypress forests are limited in extent but consist almost entirely of a cypress canopy with a sparse subcanopy or understory.

g. There are approximately 70 islands in the swamp and they account for roughly 12% of the area. Vegetation is dominated by loblolly pine, *Pinus taeda*; slash pine; longleaf pine, *Pinus palustris*; water oak,

*Quercus niger*; and live oak, *Quercus virginiana*.

The uplands surrounding the swamp are intensively managed pine forests. Historically, the area was dominated by longleaf and slash pine with an understory dominated by saw palmetto, *Serenoa repens*; small gallberry, *Ilex glabra*; and various forbs and grasses. Fire was the major factor maintaining successional stages (Monk 1968). Today the uplands are dominated by slash pine plantations with a similiar understory managed by prescribed periodic burns. Remnants of hardwood and mixed hardwood-pine forests are very limited but occur in scattered locations on some islands and at the periphery of the swamp. Management for pine, including prescribed burns, is responsible for the virtual absence of hardwoods in the uplands.

## FISHES

### HISTORICAL FOUNDATIONS

Scientific collections of fishes in the Okefenokee Swamp span 68 years. The earliest significant collections were undertaken in 1912 by A.H. Wright and Francis Harper, both from Cornell University. The account of Palmer and Wright (1920), based primarily on these collections, represents the only published information on fishes of the swamp. Subsequent collections, resulting from various museum expeditions and the activities of Okefenokee National Wildlife Refuge (ONWR) personnel, were made by R.A. Chesser in 1922, R.T. Berryhill in 1924, T. Reichelderfer in 1935, M.S. Verner, Jr. in 1936, B. Cadbury in 1937, C.B. Obrecht and M. Godfrey in 1941, H.A. Carter in 1941-1942, Southern Piedmont and Coastal Plain Survey in 1941, T. Rodenberry in 1941, and R.J. Fleetwood in 1947. Collecting activities ceased in the 1950s and began again in the 1960s (E. Cypert in 1960, 1963; T. Cavender in 1965; and M.W. Bohlke in 1966), and have continued to the present (B.J. Freeman, 1978-1980). Additional studies in the southeastern lower Coastal Plain (Gassaway 1976; Holder and German 1977) contributed much to existing knowledge of swamp ichthyofauna. Voucher specimens of significant collections are deposited in the National Museum of Natural History, Philadelphia Academy of Natural Sciences, Cornell University, University of Georgia Museum of Natural History, and University of Michigan Museum of Zoology.

### COMPARISON WITH REGIONAL FAUNA

The ichthyofauna of Okefenokee Swamp consists of 36 species representing 13 families (Table 1). The most remarkable character of the fauna is the absence of minnows (Cyprinidae). The remaining fish fauna is not substantially different from adjacent southeastern drainages. Average faunal resemblance values (Ramsey 1965) were computed for Okefenokee Swamp and major drainages in the area. Values can range

from 0 to 1, with 0 indicating no species in common and 1 indicating all species in common. The river systems compared were the Suwannee River (from Fargo, Georgia to its junction with the Alapaha River); the Alapaha River (a Suwannee River tributary); the Withlacoochee River (a Suwannee River tributary); the St. Mary's River, and the Satilla River. The values ranged from a minimum of .84 for the Withlacoochee to a maximum of .90 for the St. Mary's. The Alapaha, Suwannee, and Satilla were intermediate, with resemblance values of .86, .86, and .88, respectively. These differences are due entirely to absence from the swamp of minnows, which otherwise are widely distributed in adjacent drainages. Their absence appears to be due to substantially lower pH values in the swamp.

Swamp pH ranges from 3.1 to 4.2; pH values for surrounding streams (where minnows occur) range from 4.8 to 6.9. In a study of Carolina bay lakes in North Carolina, Frey (1951) noted that in two lakes with a pH of 4.3 there were no minnows, while lakes with higher pH values (up to 5.9) had some minnows present. These were *Notropis chrysoleucas*, *N. chalybaeus*, and *N. petersoni* — three of the species that occur near the Okefenokee Swamp. Comparing minnow distributions with pH shows that appearance of minnows in the St. Mary's River coincides with a pH of 4.8 or higher. The pH values for surrounding streams are even higher. Although detailed pH data for these streams are not available (especially for the Suwannee River section) the general pattern suggests that increasing acidity might limit, or at least influence, minnow distributions. This possibility deserves more critical attention.

#### HABITAT DISTRIBUTION OF THE FISHES

The 36 species of fish occurring in the swamp are distributed in a heterogeneous series of aquatic habitats that can be broadly classified as lake, aquatic prairie, and stream.

Lakes are open bodies of water of .25 ha or larger with depths of .5 m or more. The bottom is generally unconsolidated peat, which may have a depth of .3 m to greater than 1 m; some lakes, however, have hard sand bottoms. The margins are heavily vegetated with rooted and floating aquatic plants as well as submergent vegetation. The topography around the lakes grades into aquatic prairie (when the water levels are not low) composed of a variety of rooted aquatic macrophytes, floating vegetation, sedges, and small shrubs. Water depth may range from several cm to over 1 m. Current in these two areas varies from none in the lakes to noticeable in the prairies. Streams generally have noticeable to moderate current, consolidated banks, and sandy bottoms. Some aquatic vegetation and backwater areas are at the water margins.

The streams are located primarily in the northwest part of the swamp and on some of the islands. The prongs of the Suwannee River and the Suwannee Canal also provide stream habitat. Elements of the prairie habitat, i.e. heavily vegetated areas, can be found bordering lakes

and streams as well as in the large, open expanses of the swamp.

Aquatic habitats are not discrete units in the swamp but are graded and sometimes mixed. The distribution of fishes reflects this. The habitat associations of the swamp ichthyofauna indicates the fishes are rather uniformly distributed (Table 1). Comparison of water current preferences among the species does, however, indicate some degree of habitat segregation. *Noturus leptacanthus* and *Percina nigrofasciata* will generally be found in water with noticeable to moderate current. *Umbra pygmaea*, *Fundulus chrysotus*, *Fundulus cingulatus*, *Fundulus lineolatus*, *Leptolucania ommata*, *Heterandria formosa*, *Elassoma evergladei* and *Elassoma okefenokee* generally are found in areas with no current but with abundant aquatic vegetation. The remaining fishes occur in areas with water currents ranging from none to noticeable. This wide range of current tolerances helps explain the overlap observed in fish distributions across obvious physically different habitats.

Table 1. List of fishes of the Okefenokee Swamp. Based on museum records and data from Dahlberg and Scott (1970), Gasaway (1976), Holder and German (1977), and personal observations (B.J. Freeman). Scientific and common names based on Bailey et al. (1970). L = lake, P = prairie, S = stream.

SPECIES	HABITAT PREFERENCE
<b>ORDER SEMIONOTIFORMES</b>	
Family Lepisosteidae	
<i>Lepisosteus platyrhincus</i> , Florida gar	L P S
<b>ORDER AMIIFORMES</b>	
Family Amiidae	
<i>Amia calva</i> , Bowfin	L P S
<b>ORDER ANGUILLIFORMES</b>	
Family Anguillidae	
<i>Anguilla rostrata</i> , American eel	L P S
<b>ORDER OSTEOGLOSSIFORMES</b>	
Family Esocidae	
<i>Esox americanus</i> , Redfin pickerel	L P S
<i>Esox niger</i> , Chain pickerel	L P S
Family Umbridae	
<i>Umbra pygmaea</i> , Mudminnow	L P S
<b>ORDER CYPRINIFORMES</b>	
Family Catostomidae	
<i>Erimyzon sucetta</i> , Lake chubsucker	L P S
<i>Minytrema melanops</i> , Spotted sucker	L S

SPECIES	HABITAT PREFERENCE
ORDER SILURIFORMES	
Family Ictaluridae	
<i>Ictalurus natalis</i> , Yellow bullhead	L P S
<i>Ictalurus nebulosus</i> , Brown bullhead	L P
<i>Ictalurus punctatus</i> , Channel catfish	L S
<i>Noturus gyrinus</i> , Tadpole madtom	L P S
<i>Noturus leptacanthus</i> , Speckled madtom	S
ORDER PERCOPSIFORMES	
Family Aphredoderidae	
<i>Aphredoderus sayanus</i> , Pirate perch	L P S
ORDER ATHERINIFORMES	
Family Cyprinodontidae	
<i>Fundulus chrysotus</i> , Golden topminnow	L P S
<i>Fundulus cingulatus</i> , Banded topminnow	L P S
<i>Fundulus lineolatus</i> , Lined topminnow	L P S
<i>Leptolucania ommata</i> , Pygmy killifish	L P S
Family Poeciliidae	
<i>Gambusia affinis</i> , Mosquitofish	L P S
<i>Heterandria formosa</i> , Least killifish	L P S
Family Atherinidae	
<i>Labidesthes sicculus</i> , Brook silverside	L P S
ORDER PERCIFORMES	
Family Elasmomidae	
<i>Elassoma evergladei</i> , Everglades pygmy sunfish	L P S
<i>Elassoma okefenokee</i> , Okefenokee pygmy sunfish	L P S
Family Centrarchidae	
<i>Acantharcus pomotis</i> , Mud sunfish	L P S
<i>Centrarchus macropterus</i> , Flier	L P S
<i>Enneacanthus chaetodon</i> , Blackbanded sunfish	L P
<i>Enneacanthus gloriosus</i> , Bluespotted sunfish	L P S
<i>Enneacanthus obesus</i> , Banded sunfish	L P S
<i>Lepomis gulosus</i> , Warmouth	L P S
<i>Lepomis macrochirus</i> , Bluegill	L P S
<i>Lepomis marginatus</i> , Dollar sunfish	L P S
<i>Lepomis punctatus</i> , Spotted sunfish	L P S
<i>Micropterus salmoides</i> , Largemouth bass	L P S
<i>Pomoxis nigromaculatus</i> , Black crappie	L S
Family Percidae	
<i>Etheostoma fusiforme</i> , Swamp darter	L P S
<i>Percina nigrofasciata</i> , Blackbanded darter	S

## AMPHIBIANS AND REPTILES

### HISTORICAL FOUNDATIONS

Serious investigations of the herpetofauna of Okefenokee Swamp began in 1912 with the first in a series of surveys conducted by Cornell University. Prior to this only anecdotal accounts of the reptiles and

amphibians are known (Fountain 1901 [cited in Wright and Funkhouser 1915]; Reese 1907). At least three herpetologists participated in the Cornell collections: A.H. Wright, W.D. Funkhouser, and S.C. Bishop. During the same period (and possibly with the same expedition) F. Harper began recording observations on some of the reptiles and amphibians. In two summary publications (Wright and Bishop 1915; Wright and Funkhouser 1915), 9 chelonians, 6 saurians (actually 7, as Wright and Funkhouser had 2 species of *Ophisaurus*), 21 serpents and 1 crocodilian were recorded. This represents less than half the currently known fauna. Harper (1934) discussed aspects of the ecology and behavior of several Okefenokee reptiles and amphibians based on his visits, and numerous short papers on aspects of the biology of Okefenokee species, mostly authored by A.H. Wright, appeared in various scientific journals. Many of the observations on anurans in Wright (1932) and Wright and Wright (1949) were based on Okefenokee studies. Since these early visits to the swamp (up to about 1946), there has only recently been a renewed interest in its herpetofauna. Several southeastern herpetologists made small collections in the area, including W.T. Neill and F.L. Rose, but the collections made by C.H. Wharton and his students at Georgia State University are by far the most extensive. Additional surveys have been conducted by L. Vitt and J. Laerm. Significant collections of Okefenokee material can be found at Cornell University, Florida State Museum, National Museum of Natural History, University of Georgia Museum of Natural History, and University of Michigan Museum of Zoology.

#### COMPARISON WITH REGIONAL FAUNA

The Okefenokee Swamp contains a diverse herpetofauna of 103 species and subspecies including 2 crocodilians, 15 chelonians, 38 serpents, 11 saurians, 16 urodeles, and 21 anurans (Table 2). The present herpetofauna can be considered a typical southeastern Atlantic Coastal Plain fauna (see Conant 1975). There are no species endemic to the swamp. In general species diversity within the swamp and surrounding uplands is greater than in similar sized areas in the adjacent southeastern Atlantic Coastal Plain, primarily because of the high habitat diversity associated with the swamp. However, the high species diversity can also be attributed to the fact that at least 20 species of reptiles and amphibians reach the limit of their natural range in the region of the swamp (see Conant 1975). Thus, the faunal diversity is somewhat greater in the Okefenokee region in comparison to other Atlantic Coastal Plain localities to the immediate north or south.

#### HABITAT DISTRIBUTION OF THE AMPHIBIANS AND REPTILES

Unlike the other vertebrates, most amphibians and reptiles in the Okefenokee are not usually associated with a particular vegetational habitat (blackgum swamps, for example) but rather seem to be associated with structural habitats (water courses, sandy bottoms, etc.) Thus, it

serves little purpose to group species by vegetation habitats recognized by biologists. Ecological distribution of the herpetofauna can, however, be summarized in terms of general habits of the animals. Many species, for example, are entirely aquatic and use most if not all aquatic habitats in the swamp. Other categories also are useful in respect to ecological distribution of the reptiles and amphibians. For descriptive purposes, the herpetofauna is partitioned into six "ecological" groups (Table 2): 1) Entirely aquatic species are those that spend nearly all of their lives in water; 2) Semi-aquatic species are those that spend a major part of their lives in water, but may often be found on land (does not include species entering water only for breeding); 3) Fossorial species are those that spend most of their lives underground (they may become surface active for breeding or limited foraging); 4) Terrestrial species are those most often encountered on the surface and that spend most of their active time there; 5) Terrestrial-arboreal species may spend nearly as much time in arboreal habitats as on the surface; 6) Arboreal species are those that spend nearly all of their lives in vegetation (some of these may enter water to breed, or lay eggs on the ground).

Of the Okefenokee Swamp herpetofauna, 25 (24.3%) species are entirely aquatic, 21 (20.4%) are semiaquatic, 10 (9.7%) are fossorial, 29 (28.2%) are terrestrial, 9 (8.7%) are terrestrial-arboreal, and 9 (8.7%) are arboreal. Most turtles are either aquatic or semiaquatic, most lizards tend to be terrestrial, terrestrial-arboreal or arboreal, most snakes are terrestrial (but there are large numbers of species in other groups), most salamanders are aquatic, semiaquatic or fossorial, and frogs (including toads) tend to be semiaquatic or arboreal (Table 2).

Table 2. List of amphibians and reptiles of the Okefenokee Swamp. Based on museum records and data from Wright and Funkhouser (1915), Wright and Bishop (1915), Wright (1932), Harper (1934), Wright and Wright (1949), and personal observations (L. Vitt, J. Laerm). Most scientific and all common names based on Collins et al. (1978). Aq = aquatic, Ar = arboreal, F = fossorial, Sa = semi-aquatic, T = terrestrial, T-Ar = terrestrial-arboreal.

SPECIES	HABITAT
CLASS AMPHIBIA	
ORDER ANURA	
Family Bufonidae	
<i>Bufo quercicus</i> , Oak Toad	T
<i>Bufo terrestris</i> , Southern Toad	T
Family Hylidae	
<i>Acris gryllus dorsalis</i> , Florida Cricket Frog	Sa
<i>Hyla chrysoscelis</i> , Gray Treefrog	Ar

SPECIES	HABITAT
<i>Hyla cinerea cinerea</i> , Green Treefrog	Ar
<i>Hyla crucifer bartramiana</i> , Southern Spring Peeper	Ar
<i>Hyla femoralis</i> , Pine Woods Treefrog	Ar
<i>Hyla gratiosa</i> , Barking Treefrog	Ar
<i>Hyla squirella</i> , Squirrel Treefrog	Ar
<i>Limnaoedus ocularis</i> , Little Grass Frog	Sa
<i>Pseudacris nigrita nigrita</i> , Southern Chorus Frog	Sa
<i>Pseudacris ornata</i> , Ornate Chorus Frog	Sa
Family Microhylidae	
<i>Gastrophryne carolinensis</i> , Eastern Narrow-mouthed Toad	F, Sa
Family Pelobatidae	
<i>Scaphiopus holbrooki holbrooki</i> , Eastern Spadefoot Toad	F
Family Ranidae	
<i>Rana areolata aesopus</i> , Florida Gopher Frog	F
<i>Rana catesbeiana</i> , Bullfrog	Aq
<i>Rana clamitans clamitans</i> , Bronze Frog	Aq
<i>Rana grylio</i> , Pig Frog	Aq
<i>Rana heckscheri</i> , River Frog	Aq
<i>Rana utricularia</i> , Southern Leopard Frog	Sa
<i>Rana virgatipes</i> , Carpenter Frog	Sa
ORDER CAUDATA	
Family Ambystomatidae	
<i>Ambystoma cingulatum</i> , Flatwoods Salamander	F <sup>1</sup>
<i>Ambystoma opacum</i> , Marbled Salamander	F <sup>1</sup>
<i>Ambystoma talpoideum</i> , Mole Salamander	F <sup>1</sup>
<i>Ambystoma tigrinum</i> , Tiger Salamander	F <sup>1</sup>
Family Amphiumidae	
<i>Amphiuma means</i> , Two-toed Amphiuma	Aq
Family Plethodontidae	
<i>Desmognathus fuscus auriculatus</i> , Southern Dusky Salamander	Sa
<i>Eurycea bislineata cirrigera</i> , Southern Two-lined Salamander	Sa
<i>Eurycea quadridigitata</i> , Dwarf Salamander	T
<i>Plethodon glutinosus glutinosus</i> , Slimy Salamander	T
<i>Pseudotriton montanus floridanus</i> , Gulf Coast Mud Salamander	Sa
<i>Stereochilus marginatus</i> <sup>2</sup> , Many-lined Salamander	Aq
Family Salamandridae	
<i>Notophthalmus perstriatus</i> , Striped Newt	Sa
<i>Notophthalmus viridescens louisianensis</i> , Central Newt	Sa
ORDER TRACHYSTOMATA	
Family Sirenidae	
<i>Pseudobranchius striatus</i> spp. <sup>3</sup> , Dwarf Siren	Aq
<i>Siren intermedia intermedia</i> , Eastern Lesser Siren	Aq
<i>Siren lacertina</i> , Greater Siren	Aq

	SPECIES	HABITAT
CLASS REPTILIA		
ORDER CROCODILIA		
Family Alligatoridae		
	<i>Alligator mississippiensis</i> , American Alligator	Sa
	<i>Caiman sclerops</i> <sup>4</sup> , Spectacled Caiman	Sa
ORDER SQUAMATA		
Family Anguillidae		
	<i>Ophisaurus attenuatus longicaudus</i> , Eastern Slender Glass Lizard	T
	<i>Ophisaurus compressus</i> , Island Glass Lizard	T
	<i>Ophisaurus ventralis</i> , Eastern Glass Lizard	T
Family Iguanidae		
	<i>Anolis carolinensis</i> , Green Anole	Ar
	<i>Sceloporus undulatus undulatus</i> , Southern Fence Lizard	T-Ar
Family Scincidae		
	<i>Eumeces egregius similis</i> , Northern Mole Skink	F
	<i>Eumeces fasciatus</i> , Five-lined Skink	T-Ar
	<i>Eumeces inexpectatus</i> , Southern Five-lined Skink	T-Ar
	<i>Eumeces laticeps</i> , Broad-headed Skink	Ar
	<i>Scincella laterale</i> , Ground Skink	T
Family Teiidae		
	<i>Cnemidophorus sexlineatus sexlineatus</i> , Six-lined Racerunner	T
Family Colubridae		
	<i>Cemophora coccinea copei</i> , Northern Scarlet Snake	F
	<i>Coluber constrictor priapus</i> , Southern Black Racer	T-Ar
	<i>Diadophis punctatus punctatus</i> , Southern Ring-necked Snake	T
	<i>Drymarchon corais couperi</i> , Indigo Snake	T
	<i>Elaphe guttata guttata</i> , Corn Snake	T-Ar
	<i>Elaphe obsoleta quadrivittata</i> , Yellow Rat Snake	T-Ar
	<i>Elaphe obsoleta spiloides</i> , Gray Rat Snake	T-Ar
	<i>Farancia abacura abacura</i> , Eastern Mud Snake	Aq
	<i>Farancia erythrogramma</i> , Rainbow Snake	Aq
	<i>Heterodon platyrhinos</i> , Eastern Hognose Snake	T
	<i>Heterodon simus</i> , Southern Hognose Snake	T
	<i>Lampropeltis calligaster rhombomaculata</i> , Mole Snake	F
	<i>Lampropeltis getulus getulus</i> , Eastern Kingsnake	T
	<i>Lampropeltis getulus getulus x floridana</i> , intergrade kingsnake	T
	<i>Lampropeltis triangulum elapsoides</i> , Scarlet Kingsnake	T-Ar
	<i>Masticophis flagellum flagellum</i> , Eastern Coachwhip	T-Ar
	<i>Nerodia cyclopion floridana</i> , Florida Green Water Snake	Aq
	<i>Nerodia erythrogaster erythrogaster</i> , Red-bellied Water Snake	Sa
	<i>Nerodia fasciata fasciata</i> , Banded Water Snake	Sa
	<i>Nerodia fasciata pictiventris</i> , Florida Water Snake	Sa
	<i>Nerodia taxispilota</i> , Brown Water Snake	Sa
	<i>Opheodrys aestivus</i> , Rough Green Snake	Ar
	<i>Pituophis melanoleucus mugitus</i> , Florida Pine Snake	T
	<i>Regina alleni</i> , Striped Swamp Snake	Aq
	<i>Regina rigida rigida</i> , Eastern Glossy Water Snake	Aq

<i>Rhadinaea flavilata</i> , Pine Woods Snake	T
<i>Seminatrix pygaea pygaea</i> , North Florida Black Swamp Snake	Aq
<i>Storeria dekayi victa</i> , Florida Brown Snake	T
<i>Storeria occipitomaculata obscura</i> , Florida Red-Bellied Snake	T
<i>Thamnophis sauritus sackeni</i> , Eastern Ribbon Snake	T
<i>Thamnophis sirtalis sirtalis</i> , Eastern Garter Snake	T
<i>Virginia striatula</i> , Rough Earth Snake	T
<i>Virginia valeriae valeriae</i> , Eastern Smooth Earth Snake	T
Family Elapidae	
<i>Micrurus fulvius fulvius</i> , Eastern Coral Snake	F
Family Viperidae	
<i>Agkistrodon piscivorus conanti</i> , Florida Cottonmouth	Sa
<i>Crotalus adamanteus</i> , Eastern Diamondback Rattlesnake	T
<i>Crotalus horridus atricaudatus</i> , Canebrake Rattlesnake	T
<i>Sistrurus miliarius barbouri</i> , Dusky Pigmy Rattlesnake	T
ORDER TESTUDINATA	
Family Chelydridae	
<i>Chelydra serpentina serpentina</i> , Common Snapping Turtle	Aq
<i>Macrochelys temmincki</i> , Alligator Snapping Turtle	Aq
Family Emydidae	
<i>Chrysemys nelsoni</i> , Florida Redbelly Turtle	Aq
<i>Deirochelys reticularia reticularia</i> , Eastern Chicken Turtle	Sa
<i>Pseudemys</i> (= <i>Chrysemys</i> ) <i>floridana floridana</i> , Florida Cooter	Aq
<i>Pseudemys</i> (= <i>Chrysemys</i> ) <i>scripta elegans</i> , Red-eared Slider	Aq
<i>Pseudemys</i> (= <i>Chrysemys</i> ) <i>scripta scripta</i> , Yellowbelly Slider	Aq
<i>Terrapene carolina bauri</i> , Florida Box Turtle	T
<i>Terrapene carolina carolina</i> , Eastern Box Turtle	T
Family Kinosternidae	
<i>Kinosternon bauri palmarum</i> , Striped Mud Turtle	Sa
<i>Kinosternon subrubrum subrubrum</i> , Eastern Mud Turtle	Aq
<i>Sternotherus minor minor</i> , Loggerhead Musk Turtle	Aq
<i>Sternotherus odoratus</i> , Stinkpot	Aq
Family Testudinidae	
<i>Gopherus polyphemus</i> , Gopher Tortoise	T
Family Trionychidae	
<i>Trionyx ferox</i> , Florida Softshell	Aq

<sup>1</sup>Larvae aquatic, adults aquatic and/or terrestrial during breeding only.

<sup>2</sup>May occur around the periphery of the swamp.

<sup>3</sup>Three subspecies are recognized in the region (Conant 1975). It is possible that each occurs on different sides of the swamp.

<sup>4</sup>An introduced species. Known from a single specimen. It is not known if a population exists, although populations are apparently established in Florida.

## BIRDS

### HISTORICAL FOUNDATIONS

The earliest observations on birds of the Okefenokee Swamp were made by W. Bartram (1958). There is, however, some doubt that he actually visited the swamp (Harper 1920). In the 1880s C.F. Batchelder and

M. Thompson (see Wright and Harper 1913) recorded observations on birds, but the most significant avian surveys in the swamp were not to begin until 1912 and the Cornell expeditions. Wright and Harper (1913) listed 94 bird species based on the first expedition. Subsequent avian surveys were conducted by Cornell personnel until 1937, but only incidental accounts were published (Wright 1926). Frederick V. Hebard, an amateur ornithologist, accumulated records of birds of the swamp for almost 50 years. Although he published an annotated winter bird checklist (Hebard 1941), the completion of a more comprehensive list was interrupted by his death. Extensive observations of birds compiled by H.A. Carter, E.R. Green, and F.V. Hebard were to be published. This was never realized because of disagreement and communication problems among the authors.

A number of ONWR biologists (especially H.A. Carter, R.J. Fleetwood, E. Cypert, and L. Walker) have made significant contributions to our knowledge of Okefenokee birds. Carter compiled the most extensive and detailed reports from 1940 to 1942. Later, Fleetwood collected bird notes and conducted a series of quantitative breeding censuses (Fleetwood 1947a, 1947b, 1948). Cypert organized the bird records and compiled the current checklists (Anon. 1971, 1974). Recent surveys have been conducted by J. Meyers.

#### COMPARISON WITH REGIONAL FAUNA

The Okefenokee Swamp is an important wintering and breeding area for approximately 232 bird species (Table 3). The coastal region of Georgia, including the swamp, and the Southeast in general have fewer breeding bird species but higher winter bird densities and species richness than the northeastern United States. Approximately 120 bird species are known to breed in the Coastal Plain of Georgia (Burleigh 1958), although fewer breeding birds actually are found in the Okefenokee Swamp. Salt marsh or coastal breeding birds generally are not observed in the swamp but occasionally are recorded during spring and fall migrations and following strong eastern winds (Table 3). Several Coastal Plain breeding species are either absent or unconfirmed from the swamp (Table 4). Absence of some of these species is due to lack of appropriate breeding habitat, but lack of observations for others may be due to their rarity.

The wintering birds of the swamp are similar to those of the surrounding Coastal Plain with only a few exceptions. The most notable one is the large population of Sandhill Cranes, *Grus canadensis pratensis*, occurring on the refuge (Sanderson 1977).

#### HABITAT DISTRIBUTION OF THE BIRDS

Birds, perhaps more than other vertebrates, are habitat specific. The diversity of Okefenokee Swamp habitats, in comparison to the surrounding uplands, at least partly accounts for the large diversity of resident, breeding, and wintering species. While the specified habitat types

(see above) in the swamp have, for the most part, differing avifaunas, quantitative investigation of several of these is not yet complete and others (pure cypress and shrub swamp) have just begun. Despite this it is possible, based on present knowledge, to provide a fairly accurate general picture of the habitat distribution of birds in the swamp by grouping the previously identified habitat types into more general categories: swamp forest, upland forest, and prairie (Table 3). These general categories include all specific habitat types known to occur in the swamp and surrounding uplands.

Swamp forests include bay, cypress, and blackgum forests in various stages of succession as well as a considerable portion of the shrub swamps. Upland forests are dominated by slash and longleaf pine with associated understory. Remnants of hardwood and mixed pine-hardwood forests exist in the upland forests, but prescribed burning has substantially reduced them. Upland forests are found on several swamp islands, but generally occur on the periphery of the swamp. Prairies contain grass-sedge meadows and aquatic macrophytes as described, with treehouses (small floating islands with an overstory) and shrub batteries scattered more or less throughout.

Table 3. List of birds of the Okefenokee Swamp and their status (A = accidental, B = breeding, H = hypothetical, R = permanent resident, S = summer resident, T = transient, W = winter resident). Based on Wright and Harper (1913), Hebard (1941), checklists (Anon. 1971, 1974), ONWR records, and personal observations (J. Meyers). All common names are those standardized and listed with scientific names by the American Ornithologists' Union check-list committee (A.O.U. 1957, 1973, 1976). P = prairie, Sf = swamp forest, Uf = upland forest.

SPECIES	STATUS	HABITAT
ORDER GAVIIFORMES		
Family Gaviidae		
<i>Gavia immer</i> , Common Loon	W	P
ORDER PODICIPEDIFORMES		
Family Podicipedidae		
<i>Podiceps auritus</i> , Horned Grebe	W	P
<i>Podilymbus podiceps</i> , Pied-billed Grebe	R,T	P
ORDER PELICANIFORMES		
Family Pelicanidae		
<i>Pelecanus erythrorhynchos</i> , White Pelican	A	P
Family Phalacrocoracidae		
<i>Phalacrocorax auritus</i> , Double-crested Cormorant	T	P
Family Anhingidae		
<i>Anhinga anhinga</i> , Anhinga	B,R	P

SPECIES	STATUS	HABITAT
ORDER CICONIIFORMES		
Family Ardeidae		
<i>Ardea herodias</i> , Great Blue Heron	B,R	P
<i>Butorides striatus</i> , Green Heron	B,R	P
<i>Florida caerulea</i> , Little Blue Heron	B,R	P
<i>Bubulcus ibis</i> , Cattle Egret	B,S	P,Uf
<i>Casmerodius albus</i> , Great Egret	B,R	P
<i>Egretta thula</i> , Snowy Egret	B,R	P
<i>Hydranassa tricolor</i> , Louisiana Heron	B,R	P
<i>Nycticorax nycticorax</i> , Black-crowned Night Heron	B,R	P,Sf
<i>Nyctanassa violacea</i> , Yellow-crowned Night Heron	R	P,Sf
<i>Ixobrychus exilis</i> , Least Bittern	B,S	P
<i>Botaurus lentiginosus</i> , American Bittern	R,T	P
Family Ciconiidae		
<i>Mycteria americana</i> , Wood Stork	R,B	P,Sf
Family Threskiornithidae		
<i>Plegadis falcinellus</i> , Glossy Ibis	T	P
<i>Eudocimus albus</i> , White Ibis	B,R	P,Sf
<i>Ajaia ajaja</i> , Roseate Spoonbill	A	P
ORDER ANSERIFORMES		
Family Anatidae		
<i>Olor columbianus</i> , Whistling Swan	A	P
<i>Branta canadensis</i> , Canada Goose	W	P
<i>Chen caerulescens</i> , Snow Goose	A	P
<i>Anas platyrhynchos</i> , Mallard	W	P
<i>Anas rubripes</i> , Black Duck	W	P
<i>Anas strepera</i> , Gadwall	W	P
<i>Anas acuta</i> , Pintail	W	P
<i>Anas crecca</i> , Green-winged Teal	W	P
<i>Anas discors</i> , Blue-winged Teal	W	P
<i>Anas penelope</i> , European Wigeon	A	P
<i>Anas americana</i> , American Wigeon	W	P
<i>Anas clypeata</i> , Northern Shoveler	W	P
<i>Aix sponsa</i> , Wood Duck	B,R	P,Sf
<i>Aythya americana</i> , Redhead	W	P
<i>Aythya collaris</i> , Ring-necked Duck	W	P
<i>Aythya valisineria</i> , Canvasback	W	P
<i>Aythya marila</i> , Greater Scaup	W	P
<i>Aythya affinis</i> , Lesser Scaup	W	P
<i>Bucephala clangula</i> , Common Goldeneye	W	P
<i>Bucephala albeola</i> , Bufflehead	W	P
<i>Oxyura jamaicensis</i> , Ruddy Duck	W	P
<i>Lophodytes cucullatus</i> , Hooded Merganser	B,R	P,Sf
<i>Mergus merganser</i> , Common Merganser	A	P
<i>Mergus serrator</i> , Red-breasted Merganser	W	P
ORDER FALCONIFORMES		
Family Cathartidae		
<i>Cathartes aura</i> , Turkey Vulture	B,R	P,Sf,Uf
<i>Coragyps atratus</i> , Black Vulture	B,R	P,Sf,Uf

SPECIES	STATUS	HABITAT
Family Accipitridae		
<i>Elanoides forficatus</i> , Swallow-tailed Kite	S	Sf,Uf
<i>Accipiter striatus</i> , Sharp-shinned Hawk	W	Uf
<i>Accipiter cooperii</i> , Cooper's Hawk	R	Uf
<i>Buteo jamaicensis</i> , Red-tailed Hawk	B,R	P,Uf
<i>Buteo platypterus</i> , Broad-winged Hawk	A	Uf
<i>Buteo lineatus</i> , Red-shouldered Hawk	B,R	P,Sf
<i>Buteo lagopus</i> , Rough-legged Hawk	A	P
<i>Aquila chrysaetos</i> , Golden Eagle	W	P,Uf
<i>Haliaeetus leucocephalus</i> , Bald Eagle	W	P,Uf
<i>Circus cyaneus</i> , Marsh Hawk	W	P
Family Pandionidae		
<i>Pandion haliaetus</i> , Osprey	B,R	P
Family Falconidae		
<i>Falco peregrinus</i> , Peregrine Falcon	T,W	P
<i>Falco columbarius</i> , Merlin	T,W	P,Uf
<i>Falco sparverius</i> , American Kestrel	B,R	P,Uf
ORDER GALLIFORMES		
Family Phasianidae		
<i>Colinus virginianus</i> , Bobwhite	B,R	Uf
Family Meleagrididae		
<i>Meleagris gallopavo</i> , Turkey	B,R	Uf
ORDER GRUIFORMES		
Family Gruidae		
<i>Grus canadensis</i> , Sandhill Crane	B,R,W	P
Family Aramidae		
<i>Aramus guarauna</i> , Limpkin	A	P
Family Rallidae		
<i>Rallus elegans</i> , King Rail	B,R	P
<i>Rallus longirostris</i> , Clapper Rail	A	P
<i>Rallus limicola</i> , Virginia Rail	T	P
<i>Porzana carolina</i> , Sora	A	P
<i>Coturnicops noveboracensis</i> , Yellow Rail	W	P
<i>Porphyryla martinica</i> , Purple Gallinule	B,R	P
<i>Gallinula chloropus</i> , Common Gallinule	B,R	P
<i>Fulica americana</i> , American Coot	W	P
ORDER CHARADRIIFORMES		
Family Charadriidae		
<i>Charadrius semipalmatus</i> , Semipalmated Plover	A	P
<i>Charadrius vociferus</i> , Killdeer	W	P,Uf
Family Scolopacidae		
<i>Philohela minor</i> , American Woodcock	R	Uf
<i>Capella gallinago</i> , Common Snipe	W	P
<i>Numenius phaeopus</i> , Whimbrel	A	P
<i>Actitis macularia</i> , Spotted Sandpiper	T	P
<i>Tringa solitaria</i> , Solitary Sandpiper	T	P
<i>Catoptrophorus semipalmatus</i> , Willet	A	P

SPECIES	STATUS	HABITAT
<i>Tringa melanoleucus</i> , Greater Yellowlegs	T	P
<i>Tringa flavipes</i> , Lesser Yellowlegs	T	P
<i>Calidris alpina</i> , Dunlin	A	P
<i>Limnodromus</i> sp., Dowitcher	A	P
<i>Calidris pusillus</i> , Semipalmated Sandpiper	T	P
<i>Calidris mauri</i> , Western Sandpiper	T	P
<i>Calidris alba</i> , Sanderling	A	P
Family Laridae		
<i>Larus argentatus</i> , Herring Gull	A	P
<i>Larus atricilla</i> , Laughing Gull	A	P
<i>Sterna forsteri</i> , Forster's Tern	A	P
<i>Sterna paradisaea</i> , Arctic Tern	A	P
<i>Chlidonias niger</i> , Black Tern	T	P
ORDER COLUMBIFORMES		
Family Columbidae		
<i>Zenaida macroura</i> , Mourning Dove	B,R	Uf
<i>Columbina passerina</i> , Ground Dove	B,R	Uf
ORDER CUCULIFORMES		
Family Cuculidae		
<i>Coccyzus americanus</i> , Yellow-billed Cuckoo	B,S	Uf
<i>Coccyzus erythrophthalmus</i> , Black-billed Cuckoo	T	Uf
ORDER STRIGIFORMES		
Family Tytonidae		
<i>Tyto alba</i> , Barn Owl	R	Uf
Family Strigidae		
<i>Otus asio</i> , Screech Owl	B,R	Uf
<i>Bubo virginianus</i> , Great Horned Owl	R	Sf,Uf
<i>Strix varia</i> , Barred Owl	B,R	Sf,Uf
ORDER CAPRIMULGIFORMES		
Family Caprimulgidae		
<i>Caprimulgus carolinensis</i> , Chuck-will's-widow	B,S	Uf
<i>Caprimulgus vociferus</i> , Whip-poor-will	T	Uf
<i>Chordeiles minor</i> , Common Nighthawk	B,S	Uf
ORDER APODIFORMES		
Family Apodidae		
<i>Chaetura pelagica</i> , Chimney Swift	S	Pr,Sf,Uf
Family Trochilidae		
<i>Archilochus colubris</i> , Ruby-throated Hummingbird	B,S	Sf,Uf
ORDER CORACIIFORMES		
Family Alcedinidae		
<i>Megaceryle alcyon</i> , Belted Kingfisher	B,R	P
ORDER PICIFORMES		
Family Picidae		
<i>Colaptes auratus</i> , Common Flicker	B,R	Sf,Uf
<i>Dryocopus pileatus</i> , Pileated Woodpecker	B,R	Sf,Uf

SPECIES	STATUS	HABITAT
<i>Melanerpes carolinus</i> , Red-bellied Woodpecker	B,R	Sf,Uf
<i>Melanerpes erythrocephalus</i> , Red-headed Woodpecker	B,R	Uf
<i>Sphyrapicus varius</i> , Yellow-bellied Sapsucker	W	Sf,Uf
<i>Picoides villosus</i> , Hairy Woodpecker	B,R	Uf
<i>Picoides pubescens</i> , Downy Woodpecker	B,R	Sf,Uf
<i>Picoides borealis</i> , Red-cockaded Woodpecker	B,R	Uf
<i>Campephilus principalis</i> <sup>1</sup> , Ivory-billed Woodpecker	B,H,R	Sf
ORDER PASSERIFORMES		
Family Tyrannidae		
<i>Tyrannus tyrannus</i> , Eastern Kingbird	B,S	Uf
<i>Tyrannus dominicensis</i> , Gray Kingbird	A	Uf
<i>Tyrannus verticalis</i> , Western Kingbird	A	Uf
<i>Myiarchus crinitus</i> , Great Crested Flycatcher	B,S	Sf,Uf
<i>Sayornis phoebe</i> , Eastern Phoebe	W	Uf,P
<i>Empidonax virescens</i> , Acadian Flycatcher	B,S	Sf,Uf
<i>Contopus virens</i> , Eastern Wood Pewee	B,S	Uf
<i>Pyrocephalus rubinus</i> , Vermilion Flycatcher	A	Uf
Family Hirundinidae		
<i>Iridoprocne bicolor</i> , Tree Swallow	T	P
<i>Hirundo rustica</i> , Barn Swallow	T	P
<i>Progne subis</i> , Purple Martin	B,S	Uf
Family Corvidae		
<i>Cyanocitta cristata</i> , Blue Jay	B,R	Sf,Uf
<i>Corvus brachyrhynchos</i> , Common Crow	B,R	P,Uf
<i>Corvus ossifragus</i> , Fish Crow	B,R	P,Uf
Family Paridae		
<i>Parus carolinensis</i> , Carolina Chickadee	B,R	Sf,Uf
<i>Parus bicolor</i> , Tufted Titmouse	B,R	Sf,Uf
Family Sittidae		
<i>Sitta carolinensis</i> , White-breasted Nuthatch	R	Sf,Uf
<i>Sitta canadensis</i> , Red-breasted Nuthatch	W	Uf
<i>Sitta pusilla</i> , Brown-headed Nuthatch	B,R	Uf
Family Certhiidae		
<i>Certhia familiaris</i> , Brown Creeper	W	Uf
Family Troglodytidae		
<i>Troglodytes aedon</i> , House Wren	W	P,Uf
<i>Troglodytes troglodytes</i> , Winter Wren	W	P,Uf
<i>Thryomanes bewickii</i> , Bewick's Wren	W	P,Uf
<i>Thryothorus ludovicianus</i> , Carolina Wren	B,R	Sf,Uf
<i>Cistothorus palustris</i> , Long-billed Marsh Wren	T	P
<i>Cistothorus platensis</i> , Short-billed Marsh Wren	W	P,Uf
Family Mimidae		
<i>Mimus polyglottos</i> , Mockingbird	B,R	P,Uf
<i>Dumetella carolinensis</i> , Gray Catbird	B,R	P,Uf
<i>Toxostoma rufum</i> , Brown Thrasher	B,R	Uf
Family Turdidae		
<i>Turdus migratorius</i> , American Robin	W	P,Sf,Uf
<i>Hylocichla mustelina</i> , Wood Thrush	B,S	Sf

SPECIES	STATUS	HABITAT
<i>Catharus guttata</i> , Hermit Thrush	W	Uf
<i>Catharus ustulata</i> , Swainson's Thrush	T	Uf
<i>Catharus minima</i> , Gray-cheeked Thrush	T	Uf
<i>Catharus fuscescens</i> , Veery	T	Uf
<i>Sialia sialis</i> , Eastern Bluebird	B,R	Uf
Family Sylviidae		
<i>Polioptila caerulea</i> , Blue-gray Gnatcatcher	B,S	Uf
<i>Regulus satrapa</i> , Golden-crowned Kinglet	W	Uf
<i>Regulus calendula</i> , Ruby-crowned Kinglet	W	Sf,Uf
Family Montacellidae		
<i>Anthus spinoletta</i> , Water pipet	W	P
Family Bombycillidae		
<i>Bombycilla cedrorum</i> , Cedar Waxwing	W	Uf
Family Laniidae		
<i>Lanius ludovicianus</i> , Loggerhead shrike	B,R	Uf
Family Sturnidae		
<i>Sturnus vulgaris</i> , Starling	B,R	Uf
Family Vireonidae		
<i>Vireo griseus</i> , White-eyed Vireo	B,S	Sf,Uf
<i>Vireo flavifrons</i> , Yellow-throated Vireo	B,S	Uf
<i>Vireo solitarius</i> , Solitary Vireo	W	Uf
<i>Vireo olivaceus</i> , Red-eyed Vireo	B,S	Sf,Uf
Family Parulidae		
<i>Mniotilta varia</i> , Black-and-white Warbler	W	Uf
<i>Protonotaria citrea</i> , Prothonotary Warbler	S,B	Sf
<i>Limnothlypis swainsonii</i> , Swainson's Warbler	S,B	Sf
<i>Helminthos vermivorus</i> , Worm-eating Warbler	T	Uf
<i>Vermivora chrysoptera</i> , Golden-winged Warbler	T	Uf
<i>Vermivora pinus</i> , Blue-winged Warbler	T	Uf
<i>Vermivora bachmanii</i> , Bachman's Warbler	H	Sf
<i>Vermivora celata</i> , Orange-crowned Warbler	W	Uf
<i>Parula americana</i> , Northern Parula	B,S,W	Sf,Uf
<i>Dendroica petechia</i> , Yellow Warbler	T	Uf
<i>Dendroica magnolia</i> , Magnolia Warbler	T	Uf
<i>Dendroica tigrina</i> , Cape May Warbler	T	Uf
<i>Dendroica caerulescens</i> , Black-throated Blue Warbler	T	Uf
<i>Dendroica coronata</i> , Yellow-rumped Warbler	W	P,Sf,Uf
<i>Dendroica virens</i> , Black-throated Green Warbler	T	Uf
<i>Dendroica cerulea</i> , Cerulean Warbler	T	Uf
<i>Dendroica fusca</i> , Blackburnian Warbler	T	Uf
<i>Dendroica dominica</i> , Yellow-throated Warbler	B,S,W	Uf
<i>Dendroica pensylvanica</i> , Chestnut-sided Warbler	T	Uf
<i>Dendroica striata</i> , Blackpoll Warbler	T	Uf
<i>Dendroica pinus</i> , Pine Warbler	B,R	Uf
<i>Dendroica discolor</i> , Prairie Warbler	S	Uf
<i>Dendroica palmarum</i> , Palm Warbler	W	P,Uf
<i>Seiurus aurocapillus</i> , Ovenbird	T	Uf
<i>Seiurus noveboracensis</i> , Northern Waterthrush	T	Sf

SPECIES	STATUS	HABITAT
<i>Seiurus motacilla</i> , Louisiana Waterthrush	S	Sf
<i>Oporornis formosus</i> , Kentucky Warbler	T	Uf
<i>Oporornis agilis</i> , Connecticut Warbler	T	Uf
<i>Geothlypis trichas</i> , Common Yellowthroat	B,R	P,Uf
<i>Icteria virens</i> , Yellow-breasted Chat	T	Uf
<i>Wilsonia citrina</i> , Hooded Warbler	B,S	Sf,Uf
<i>Wilsonia canadensis</i> , Canada Warbler	T	Uf
<i>Setophaga ruticilla</i> , American Redstart	T	Sf,Uf
Family Ploceidae		
<i>Passer domesticus</i> , House Sparrow	B,R	Uf
Family Icteridae		
<i>Dolichonyx oryzivorus</i> , Bobolink	T	P
<i>Sturnella magna</i> , Eastern Meadowlark	B,R	P,Uf
<i>Agelaius phoeniceus</i> , Red-winged Blackbird	B,R	P,Uf
<i>Icterus spurius</i> , Orchard Oriole	B,S	Uf
<i>Icterus galbula</i> , Northern Oriole	T	Uf
<i>Euphagus carolinus</i> , Rusty Blackbird	W	Uf
<i>Euphagus cyanocephalus</i> , Brewer's Blackbird	W	Uf
<i>Quiscalus major</i> , Boat-tailed Grackle	W	Uf
<i>Quiscalus quiscula</i> , Common Grackle	B,R	P,Uf
<i>Molothrus ater</i> , Brown-headed Cowbird	T	Sf,Uf
Family Thraupidae		
<i>Piranga olivacea</i> , Scarlet Tanager	T	Uf
<i>Piranga rubra</i> , Summer Tanager	B,S	Uf
Family Fringillidae		
<i>Cardinalis cardinalis</i> , Cardinal	B,R	Sf,Uf
<i>Pheucticus ludovicianus</i> , Rose-breasted Grosbeak	T	Uf
<i>Guiraca caerulea</i> , Blue Grosbeak	S	Uf
<i>Passerina cyanea</i> , Indigo Bunting	S	Uf
<i>Passerina ciris</i> , Painted Bunting	T	Uf
<i>Carpodacus purpureus</i> , Purple Finch	W	Uf
<i>Carduelis pinus</i> , Pine Siskin	W	Uf
<i>Carduelis tristis</i> , American Goldfinch	W	P,Uf
<i>Pipilo erythrophthalmus</i> , Rufous-sided Towhee	B,R	Uf
<i>Passerculus sandwichensis</i> , Savannah Sparrow	W	P
<i>Ammodramus savannarum</i> , Grasshopper Sparrow	W	Uf
<i>Ammodramus henslowii</i> , Henslow's Sparrow	W	Uf
<i>Ammospiza leconteii</i> , LeConte's Sparrow	W	Uf
<i>Pooecetes gramineus</i> , Vesper Sparrow	W	Uf
<i>Chondestes grammacus</i> , Lark Sparrow	W	Uf
<i>Aimophila aestivalis</i> , Bachman's Sparrow	B,R	Uf
<i>Junco hyemalis</i> , Dark-eyed Junco	W	Uf
<i>Spizella arborea</i> , Tree Sparrow	H	Uf
<i>Spizella passerina</i> , Chipping Sparrow	W	Uf
<i>Spizella pusilla</i> , Field Sparrow	W	Uf
<i>Zonotrichia albicollis</i> , White-throated Sparrow	W	Uf
<i>Passerella iliaca</i> , Fox Sparrow	W	P,Uf
<i>Melospiza georgiana</i> , Swamp Sparrow	W	P,Uf

SPECIES	STATUS	HABITAT
<i>Melospiza melodia</i> , Song Sparrow	W	P,Uf

<sup>1</sup>Last reported in 1948; current status unknown.

Table 4. Georgia Coastal Plain breeding birds that are absent or unknown as breeding birds in the Okefenokee Swamp.

SPECIES	CAUSE
Pied-billed Grebe	rare — undiscovered
Yellow-crowned Night Heron	undiscovered
Swallow-tailed Kite	rare — undiscovered
Cooper's Hawk	rare — undiscovered
Broad-winged Hawk	unknown
Clapper Rail	lack of breeding habitat
American Coot	unknown
American Oystercatcher	lack of breeding habitat
Black-necked Stilt	lack of breeding habitat
Wilson's Plover	lack of breeding habitat
Killdeer	unknown
Willet	lack of breeding habitat
American Woodcock	rare — undiscovered
Gull-billed Tern	lack of breeding habitat
Least Tern	lack of breeding habitat
Royal Tern	lack of breeding habitat
Black Skimmer	lack of breeding habitat
Rock Dove	lack of breeding habitat
Barn Owl	rare — undiscovered
Great Horned Owl	undiscovered
Chimney Swift	undiscovered
Long-billed Marsh Wren	lack of breeding habitat
Prairie Warbler	unknown
Louisiana Waterthrush	unknown
Yellow-breasted Chat	rare — undiscovered
Boat-tailed Grackle	lack of breeding habitat
Brown-headed Cowbird	rare — undiscovered
Blue Grosbeak	unknown
Indigo Bunting	rare — undiscovered
Painted Bunting	unknown
Seaside Sparrow	lack of breeding habitat
Chipping Sparrow	unknown
Field Sparrow	unknown

## MAMMALS

### HISTORICAL FOUNDATIONS

The earliest account of the mammals of the Okefenokee Swamp (Jones 1876), though largely anecdotal, resulted from a joint expedition

sponsored by the State Geological Survey and the *Atlanta Constitution* in 1875. Somewhat more extensive observations resulted from a brief survey by B.T. Gault in 1903 (reported in Harper 1927). The mammals of the swamp, however, are known primarily as a result of the work of F. Harper. Harper's (1927) classic *Mammals of the Okefenokee Swamp*, based on surveys conducted by him, other Cornell personnel, and local hunters, represents the definitive work on the mammals of the region. Subsequent observations and records by Refuge personnel, particularly R.J. Fleetwood, have provided valuable historical data including the first records of *Myotis austroriparius* and *Tadarida brasiliensis*. More recently small mammal surveys have been conducted in the swamp and surrounding uplands by L. Logan and J. Laerm. Significant collections of mammals from the swamp have been deposited in the Philadelphia Academy of Natural Sciences, Cornell University, Florida State Museum, National Museum of Natural History, and University of Georgia Museum of Natural History.

#### COMPARISON WITH REGIONAL FAUNA

The 48 species and subspecies of mammals known to occur in the Okefenokee Swamp and surrounding uplands represent a typical southeastern fauna (Table 5). It is interesting to note that 12 (25%) of the mammals occurring in or around the swamp are at or very near the limits of their ranges. The Okefenokee Swamp region of Georgia and adjacent Florida represents the southern limit of the range of *Condylura cristata* and *Castor canadensis*, and the northern limit of the range of *Neofiber alleni*. The southern limit of the ranges of the subspecies *Cryptotis parva parva*, *Eptesicus fuscus fuscus*, and *Sciurus niger niger* occurs in the region of the swamp and the northern limits of *Geomys pinetis floridanus*, *Ursus americanus floridanus*, and *Procyon lotor elucus* occur also at or near the swamp. In general the subspecific affinities of these mammals is poorly understood and to a large extent suspect. Proper subspecific affiliation must therefore await systematic study.

The composition of the mammalian fauna of the swamp has changed little since Harper's (1927) surveys. There are, however, apparent changes in population level of a number of species.

*Nycticeius humeralis*, once the most common bat in the swamp (Harper 1927) is one of the most uncommon today. Its decrease is probably due to the decrease in man-made structures, common nursery colony sites (Watkins 1972), since the establishment of ONWR. Similarly, populations of *Plecotus rafinesquii*, *Rattus rattus*, and *Mus musculus* have apparently decreased due to the reduction of such structures.

The most striking change in the mammalian fauna of the swamp has been the extirpation of *Canis rufus niger* and probably *Felis concolor coryi*. These two carnivores were becoming rare during Harper's surveys. There have been a few unconfirmed recent reports of *Felis* in the area. *Odocoileus virginianus* was driven nearly to local extinction by hunters

during the first two decades of this century. Harper (1927) reported seeing only a single live individual during his extensive field work from 1912 and 1922. Since that time populations have recovered dramatically due in large part to introductions and the establishment of the ONWR. Today deer are the most common large mammals on the refuge.

*Dasypus novemcinctus*, introduced into Florida after Harper's surveys (Humphrey 1974) has extended its range significantly in recent years. Although it moved into Georgia in the 1950s (Fitch et al. 1952) it was not known from the swamp until 1968. Today it extends well up the Coastal Plain.

#### HABITAT DISTRIBUTION OF THE MAMMALS

The habitat distribution of mammals occurring in the swamp and surrounding uplands, insofar as it is presently known, is shown in Table 5. With few exceptions it is difficult to define a single habitat or assemblage of habitats to which a particular mammal is restricted; the majority may be found in most of them. Nine of the mammals occurring within the swamp and surrounding uplands have been reported from every habitat defined within the swamp. These include *Pipistrellus subflavus*, *Lasiurus seminolus*, *Sylvilagus palustris*, *Sciurus carolinensis*, *Peromyscus gossypinus*, *Ursus americanus*, *Procyon lotor*, *Lynx rufus*, and *Odocoileus virginianus*. Only two species, *Geomys pinetis* and *Neofiber alleni*, are restricted to a single habitat. The former occurs only in well-drained sandy uplands, while the latter is restricted to boggy prairies (Harper 1927; Birkenholz 1972).

Table 5. List of mammals of the Okefenokee Swamp. Based on museum records, Harper (1927), and personal observations (L. Logan, J. Laerm). Scientific and common names based on Jones et al. (1973). U = uplands, I = islands, P = prairies, SS = shrub swamp, BG = blackgum forest, PB = pure bay forest, PC = pure cypress, MC = mixed cypress.

SPECIES	HABITAT
ORDER MARSUPIALIA	
Family Didelphidae	
<i>Didelphis virginiana pigra</i> , Virginia Opossum	U,I,BG,PC
ORDER INSECTIVORA	
Family Soricidae	
<i>Blarina carolinensis</i> , Southern Short-tailed Shrew	U,I
<i>Cryptotis parva parva</i> , Least Shrew	U,I
Family Talpidae	
<i>Scalopus aquaticus australis</i> , Eastern Mole	U,I
<i>Condylura cristata cristata</i> , Star-nosed Mole	PC,MC
ORDER CHIROPTERA	
Family Vespertilionidae	

SPECIES	HABITAT
<i>Myotis austroriparius austroriparius</i> , Southeastern Myotis	I
<i>Pipistrellus subflavus subflavus</i> , Eastern Pipistrelle	U,I,P,SS,BG,PB,PC,MC
<i>Eptesicus fuscus fuscus</i> , Big Brown Bat	U,I,H
<i>Lasiurus borealis borealis</i> , Red Bat	U,I,BG,MC
<i>Lasiurus seminolus</i> , Seminole Bat	U,I,P,SS,BG,PB,PC,MC
<i>Lasiurus cinereus cinereus</i> , Hoary Bat	I
<i>Lasiurus intermedius floridanus</i> , Northern Yellow Bat	U,BG
<i>Nycticeius humeralis humeralis</i> , Evening Bat	U,I,BG,PC
<i>Plecotus rafinesquii</i> , Rafinesque's Big-eared Bat	U,I
Family Molossidae	
<i>Tadarida brasiliensis cynocephala</i> , Brazilian Free-tailed Bat	I
ORDER EDENTATA	
Family Dasypodidae	
<i>Dasypus novemcinctus mexicanus</i> <sup>1</sup> , Nine-banded Armadillo	U,SS,MC
ORDER LAGOMORPHA	
Family Leporidae	
<i>Sylvilagus palustris palustris</i> , Marsh Rabbit	U,I,P,SS,BG,PB,PC,MC
<i>Sylvilagus floridanus mallurus</i> , Eastern Cottontail	U,I,SS
ORDER RODENTIA	
Family Sciuridae	
<i>Sciurus carolinensis carolinensis</i> , Gray Squirrel	U,I,P,SS,BG,PB,PC,MC
<i>Sciurus niger niger</i> , Fox Squirrel	U,I,PC,MC
<i>Glaucomys volans querceti</i> , Southern Flying Squirrel	U,I,BG,MC
Family Geomyidae	
<i>Geomys pinetis pinetis</i> , Southeastern Pocket Gopher	U
<i>Geomys pinetis floridanus</i> , Southeastern Pocket Gopher	U
Family Castoridae	
<i>Castor canadensis carolinensis</i> , Beaver	U,I
Family Cricetidae	
<i>Oryzomys palustris palustris</i> , Marsh Rice Rat	U,I,P,SS,BG,PB,PC,MC
<i>Reithrodontomys humilus humilus</i> , Eastern Harvest Mouse	U
<i>Peromyscus polionotus polionotus</i> , Oldfield Mouse	U,I
<i>Peromyscus gossypinus gossypinus</i> , Cotton Mouse	U,I,P,SS,BG,PB,PC,MC

SPECIES	HABITAT
<i>Ochrotomys nuttalli aureolus</i> , Golden Mouse	U,I,BG,PC,MC
<i>Sigmodon hispidus hispidus</i> , Hispid Cotton Rat	U,I
<i>Neotoma floridana floridana</i> , Eastern Woodrat	U,I,P,SS,BG,MC
<i>Microtus pinetorum parvulus</i> , Woodland Vole	U
<i>Neofiber alleni exoristus</i> , Round-tailed Muskrat	P
Family Muridae	
<i>Rattus rattus rattus</i> <sup>1</sup> , Black Rat	U,I
<i>Rattus rattus alexandrinus</i> <sup>1</sup> , Black Rat	U,I
<i>Mus musculus musculus</i> <sup>1</sup> , House Mouse	U,I
ORDER CARNIVORA	
Family Canidae	
<i>Canis rufus niger</i> , Red Wolf	U,I,MC
<i>Urocyon cinereoargenteus floridanus</i> , Gray Fox	U,I,SS,MC
Family Ursidae	
<i>Ursus americanus floridanus</i> , Florida Black Bear	U,I,P,SS,BG,PB,PC,MC
Family Procyonidae	
<i>Procyon lotor elucus</i> , Raccoon	U,I,P,SS,BG,PB,PC,MC
Family Mustelidae	
<i>Mustela frenata olivacea</i> , Long-tailed Weasel	U,I,PC,MC
<i>Mustela vison mink</i> , Mink	U
<i>Mephitis mephitis elongata</i> , Striped Skunk	U,I
<i>Lontra canadensis vaga</i> , River Otter	U,P,PC,MC
Family Felidae	
<i>Felis concolor coryi</i> , Florida Panther	U,I,P
<i>Lynx rufus floridanus</i> , Bobcat	U,I,P,SS,BG,PB,PC,MC
ORDER ARTIODACTYLA	
Family Suidae	
<i>Sus scrofa</i> <sup>1</sup> , Wild Pig	U,I,SS,BG,MC
Family Cervidae	
<i>Odocoileus virginianus virginianus</i> , White-tailed Deer	U,I,P,SS,BG,PB,PC,MC

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<sup>1</sup>Introduced.

## DISCUSSION

At this time insufficient data are available to accurately assess the patterns of habitat preference for all species or to quantify patterns of species diversity in the various habitat types present in Okefenokee Swamp. However, sufficient data are available to provide an accurate faunal list and to allow some habitat correlation.

A total of 419 vertebrate species or subspecies occurs in Okefenokee Swamp and surrounding uplands. These include 36 fish, 37 amphibians, 66 reptiles, 232 birds, and 48 mammals. The vertebrates represent a fairly typical southeastern Atlantic Coastal Plain fauna. There are no species endemic to the swamp. In general vertebrate diversity in the swamp is greater than in any area of similar size in the adjacent Southeast. This is due primarily to the swamp's habitat diversity, but another factor is the prevalence of heavily managed pine forests throughout much of the adjacent southeastern region.

The role of ONWR in the preservation of the swamp as an ecosystem is crucial, particularly insofar as threatened or endangered wildlife is concerned. Eleven species or subspecies are considered either threatened or endangered under the guidelines of federal and/or state agencies (Table 6). The status of populations of these species in Okefenokee Swamp has not yet been determined.

Table 6. List of Threatened or Endangered species in Okefenokee Swamp. Legal status as of 15 February 1980, defined by United States Fish and Wildlife Service (USFWS), Florida Game and Freshwater Fish Commission (GFWFC), and Georgia Department of Natural Resources (DNR). E = Endangered; T = Threatened.

SPECIES	STATUS		
	USFWS	GFWFC	DNR
<i>Alligator mississippiensis</i> , American Alligator	T	T	E
<i>Drymarchon corais couperi</i> , Eastern Indigo Snake	T	T	T
<i>Mycteria americana</i> , Woodstork		E	
<i>Haliaeetus leucocephalus</i> , Bald Eagle	E	T	E
<i>Falco peregrinus</i> , Peregrine Falcon	E	E	E
<i>Grus canadensis pratensis</i> , Florida Sandhill Crane		T	
<i>Campephilus principalis</i> , Ivory-billed Woodpecker	E	E	E
<i>Picoides borealis</i> , Red-cockaded Woodpecker	E	T	E
<i>Vermivora bachmanii</i> , Bachman's Warbler	E	E	E
<i>Ursus americanus floridanus</i> , Florida Black Bear		T	
<i>Felis concolor coryi</i> , Florida Panther	E	E	E

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# New Records, Distribution and Diagnostic Characters of Virginia Ictalurid Catfishes With An Adnexed Adipose Fin

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**ABSTRACT.**—Recent introductions of *Ictalurus melas* and *Pylodictis olivaris* and the discovery (possible introduction) of *I. brunneus* has raised the number of ictalurids with an adnexed adipose fin to eight species in the Roanoke River drainage. Introduction of *I. furcatus* to other drainages raised the Virginia total to nine. Although most of these species are widely distributed in North America, none is native in all Virginia drainages. Most species have been variously introduced, and *I. brunneus* and *I. platycephalus* exhibit an atypical distributional interrelationship. Key characters for separating these two flathead bullheads from typical bullheads (*I. melas*, *I. natalis*, *I. nebulosus*) are described, and some diagnostic characters different from those generally used are emphasized for distinguishing *I. brunneus* from *I. platycephalus*, and *I. melas* from *I. nebulosus*. These and characters of other ictalurids with an adnexed adipose fin are discussed; a key is provided for the species of Virginia drainages.

## INTRODUCTION

Exceptional or significant new records, occasional recent misidentifications, vexatious old records, and an atypical distributional interrelationship between two Virginia ictalurids led to this report. Although most species have been long known, the ictalurids with an adnexed (free) adipose fin still present at least local problems in identification, and consequently may subvert zoogeographic studies in North America. Problems have extended elsewhere. For example, Banarescu (1968) found that the bullhead widely introduced in Europe was actually *Ictalurus melas* (Rafinesque) instead of *I. nebulosus* (Lesueur). Important external characters are few, and most are variable and widely shared among similar appearing, often sympatric species; no consistently present external character state of juvenile and adult *Ictalurus* appears unique to a single species.

The Roanoke River drainage is now known to harbor eight species of ictalurids with an adnexed adipose fin, a larger complement than occurs in the Mississippi River basin. A total of nine species is now known from Virginia: *I. brunneus* (Jordan), snail bullhead; *I. catus* (Linnaeus), white catfish; *I. furcatus* (Lesueur), blue catfish; *I. melas*, black bullhead;

*I. natalis* (Lesueur), yellow bullhead; *I. nebulosus*, brown bullhead; *I. platycephalus* (Girard), flat bullhead; *I. punctatus* (Rafinesque), channel catfish; *Pylodictis olivaris* (Rafinesque), flathead catfish. Of this assemblage, *I. melas* and *Pylodictis* are considered to be introduced, and *I. brunneus* probably so, to the Roanoke drainage; the same is true for the status of *I. furcatus* and *I. brunneus* in Virginia.

This report discusses the distribution of each species in Virginia and extralimitally where pertinent. Diagnostic characters with the greatest utility and ease in identifying these species within the study area are discussed and employed in a key. Osteological and other differences among *Ictalurus* species are found in Paloumpis (1964), Yerger and Relyea (1968), Smith and Lundberg (1972), and Lundberg (1975).

Concepts of genera, subgenera, and species groups follow Lundberg (1975). However, regarding our discussion of species identification, for practical purposes we artificially group *I. catus* with the "forktail catfishes," *I. furcatus* and *I. punctatus* of the subgenus *Ictalurus*. *Ictalurus catus* actually is placed, in the subgenus *Amiurus*, in the *catus* group with the species we collectively refer to as "flathead bullheads," i.e., *I. brunneus*, *I. platycephalus* and *I. serracanthus* Yerger and Relyea. The other three species, our "typical bullheads," *I. melas*, *I. natalis* and *I. nebulosus*, are referred by Lundberg to the *natalis* group of the subgenus *Amiurus*.

## METHODS AND MATERIALS

Methods of counting and mensuration follow those outlined by Hubbs and Lagler (1958) and Yerger and Relyea (1968), with one difference from the latter study. Removal of the gill arch for gill raker counts was necessary only in the smallest specimens; otherwise a slit at the dorsal and ventral junctions of the operculum, and adduction of the latter, were sufficient to expose gill rakers. All rakers on the right arch including rudiments on lower limb, were counted; fused rakers were counted as one. To count anal rays it was necessary to expose them by slitting the anal fin base and peeling the skin back. All anterior rudimentary rays were counted; the last two rays with a basal conjuncture were counted as one.

Measurements were made using Helios dial calipers for all proportionally expressed characters (as % SL) and for standard length (SL) of smaller specimens; they were recorded to the nearest 0.1 mm. The SLs of large specimens were obtained with a beam compass and a steel rule, and recorded to the nearest 0.5 mm. Counting was aided by the use of a variable magnification stereo dissecting microscope. The counts from one *I. melas*, 33.6 mm SL, were omitted from tabulation due to extreme low counts (rakers incompletely developed).

Complete locality data on specimens examined are on file at Roanoke College. Flathead bullhead localities are depicted in Figure 1 and are listed in sequence from downstream to upstream. Typical bullhead localities are presented by basin or drainage and therein

alphabetically by state and tributary. All specimens were from Virginia drainages, except for *I. melas*, which was supplemented by material from other states. Localities for both sections are followed by institutional abbreviation and catalog number. Roanoke College and Virginia Commonwealth University are followed by collector's initials and field number.

Institution and agency abbreviations used are:

ACE, U.S. Army Corps of Engineers  
 CU, Cornell University  
 DPC, Duke Power Company  
 FWS, U.S. Fish and Wildlife Service  
 LC, Lynchburg College  
 RC, Roanoke College  
 SCS, Soil Conservation Service  
 UMMZ, University of Michigan Museum of Zoology  
 UNC, University of North Carolina at Charlotte  
 USNM, National Museum of Natural History, Smithsonian  
 UT, University of Tennessee at Knoxville  
 VCGIF, Virginia Commission of Game and Inland Fisheries  
 VCU, Virginia Commonwealth University  
 VFU, Virginia Cooperative Fisheries Unit  
 VIMS, Virginia Institute of Marine Science  
 VPI, Virginia Polytechnic Institute and State University

Collections from the following sources are housed at Roanoke College: ACE, FWS, LC, SCS, VCGIF; some of the collections originally at VCU are also at Roanoke College. Numbers that follow these series refer to collection reference numbers used for a data bank concerning the freshwater fishes of Virginia.

### *Ictalurus brunneus*

Dan River system. — VA: Dan R. RC VCGIF 230; RC FWS 8; NC: Country Line Creek RC ACE 15; Rattlesnake Creek RC ACE 18; VA: RC VCGIF 229; NC: Pumpkin Creek RC ACE 16; VA: Dan R. RC EGM Va-23; Fall Creek RC ACE 2; Dan R. RC FWS 6; Dan R. RC FWS 1; NC: Dan R. DPC 50101-09 and -11; DPC 50101-10, 50107-06; DPC 50101-18; DPC 50101-12 and -19; UNC 76-95.

### *Ictalurus platycephalus*

Chowan River system. — VA: Great Creek RC SCS 8; N. Meherrin R. RC HJP 44, VCU HJP 100.

Lower Roanoke River system (below Dan River mouth). — VA: Flat Creek VPI 1029; Miles Creek VPI 1037; NC: Grassy Creek RC REJ 865; VA: Beaver Pond Creek RC REJ 863.

Lower Dan River system (below Smith River mouth). — VA: Banister R. VCU HJP 84; NC: Cascade Creek ACE 89; Dan R. DPC 50107-07.

Smith River and tributaries (Dan River system). — VA: Leatherwood

Creek RC ACE 80; Beaver Creek CU 13921; Town Creek VPI 984; Green Brook RC ACE 134; Smith R. RC HJP 60.

Upper Dan River system (above Smith River mouth). — NC: Buffalo Creek RC ACE 108; Jacob Creek RC ACE 115; Belews Lake DPC 50107-12 and -18.

Upper Roanoke River system (above Dan River mouth). — VA: Difficult Creek RC REJ 856; Twittys Creek VFU 109; Wards Fork USNM 101324; Turnip Creek RC REJ 873; Falling R. RC HJP 59; Little Falling R. RC HJP 75; Seneca Creek VCU HJP 82; trib. Little Otter R. LC 30; Leesville Reservoir RC REJ 333; Pigg R. RC REJ 402; Blackwater R. VPI 989; Maggoodee Creek VPI 990, 974 and CU 43587 (split collection); Ellie Creek VPI 975; Blackwater R. VPI 690; 2187; South Fork Blackwater R. VPI 2188; North Fork Blackwater R. VPI 1755.

### *Ictalurus natalis*

York River drainage. — VA: Pond Creek RC JRR 124; Smoots Pond RC JRS 23; Ta River RC JRR 134.

James River drainage. — VA: Barrows Creek RC TZ 156; Maury R. RC NMB 73; Tuckahoe Creek RC JRR 131.

Roanoke River drainage. — VA: Beaver Pond Creek RC REJ 863; Great Creek RC SCS 8; Lake Jordan RC JRS 22; Little Buffalo Creek RC REJ 869; Roanoke R. RC REJ 781.

Tennessee River drainage. — VA: Clinch R. RC REJ 503; Clinch R. RC REJ 611; North Fork Holston R. RC NMB 153; RC NMB 157.

### *Ictalurus nebulosus*

York River drainage. — VA: Bunch Creek RC SCS 24; Smoots Pond RC JRS 23.

James River drainage. — VA: Herring Creek RC TZ 157; Jordans Branch Creek RC VCU-B-JB-1.

Roanoke River drainage. — NC: Anderson Swamp Creek RC REJ 867; Belews Lake DPC 50106-15; Flat Creek RC REJ 866; VA: Back Creek RC WJM; Ballows Creek RC ACE 34; Banister R. RC HJP 80; Beaver Pond Creek RC REJ 863; Dan R. RC FWS 6; Falling R. RC REJ 815; Grassy Creek RC REJ 860; Green Branch RC ACE 134; Lawsons Creek RC ACE 26; Mason Creek RC REJ 524; Old Woman Creek RC REJ 401; Pigg R. RC REJ 402; RC DLJ 26; RC DLJ 6; Lake Drummond VPI 1218; Lake Jordan RC JRS 22.

New River drainage. — VA: Meadow Creek RC JRR 207.

### *Ictalurus melas*

Roanoke River drainage. — NC: Belews Lake DPC 50105-07; VA: Grassy Creek RC REJ 860; Little Buffalo Creek RC REJ 869.

Peedee River drainage. — NC: trib. Yadkin R. UMMZ 138401.

Tennessee River drainage. — TN: Big Sandy R. UT 48.114; Dry Creek UT 48.202; Duck R. UT 48.294; Sims Spring Branch UT 48.284; VA:

Copper Creek RC REJ 348.

Cumberland River drainage. — TN: East Fork Stones R. UT 48.7.

Green River drainage. — TN: Hurricane Creek RC REJ 560.

Coosa River drainage. — TN: Coahulla Creek UT 48.57; Mill Creek UT 48.56; UT 48.285.

Mississippi River basin. — TN: backwater Mississippi R. UT 48.26.

Hatchie River drainage. — TN: ditch UT 48.109.

Forked Deer River drainage. — TN: Nixon Creek UT 48.249; slough UT 48.250.

Red River drainage. — LA: ditch VPI 2758; Shepherd Bayou VPI 2342.

Sabine River drainage. — LA: Sabine R. VPI 2652.

### DISTRIBUTION

The ictalurids with an adnexed adipose fin generally occur in moderate to large streams and main river channels of all physiographic provinces in Virginia except the Blue Ridge, from which they are essentially absent except for upper New River. Most species readily adapt to reservoir and farm pond habitats, and a few, notably *I. catus*, *I. furcatus* and *I. punctatus*, tolerate estuarine conditions. One species, *I. brunneus*, commonly occurs in moderate currents (Yerger and Relyea 1968; Bryant et al. 1979; D. Cloutman, pers. comm.) as well as sluggish currents and backwaters with soft bottoms (M. Corcoran, pers. comm.), which are typically inhabited by the remaining species. When collected during daylight most of these species are associated with cover such as undercut banks, logs and boulders. The following discussion includes consideration of native or introduced status in the drainages.

*Ictalurus brunneus*. — The snail bullhead is known in the Roanoke drainage only from the Dan River system above Kerr Reservoir, North Carolina and Virginia (Fig. 1). It was first collected from the lower Dan in 1976 just above this reservoir, and was subsequently taken in low numbers from the main channel and a few tributaries. Prior to the Dan records, Yerger and Relyea (1968) reported its northern limits as the upper Cape Fear and Peedee River drainages, North Carolina, both adjacent on the south to the Dan.

The distributional relationship in the Roanoke drainage of *I. brunneus* and *I. platycephalus*, the closest relative of *I. brunneus* (Lundberg 1975), appears unique. Yerger and Relyea (1968) found that, although the species are broadly sympatric and occasionally syntopic in several drainages, *I. brunneus* tends to be more frequently found in, and perhaps differentially favors, higher gradient areas in the upper parts of those drainages. In the Mobile drainage, where only *I. brunneus* occurs, this species was found only in the upper section, in Georgia, over hard bottom in riffles and moderate currents (Bryant et al. 1979). Although both species occupy upper and lower reaches of many streams, this distribution pattern was not regarded as atypical since higher and lower gradient

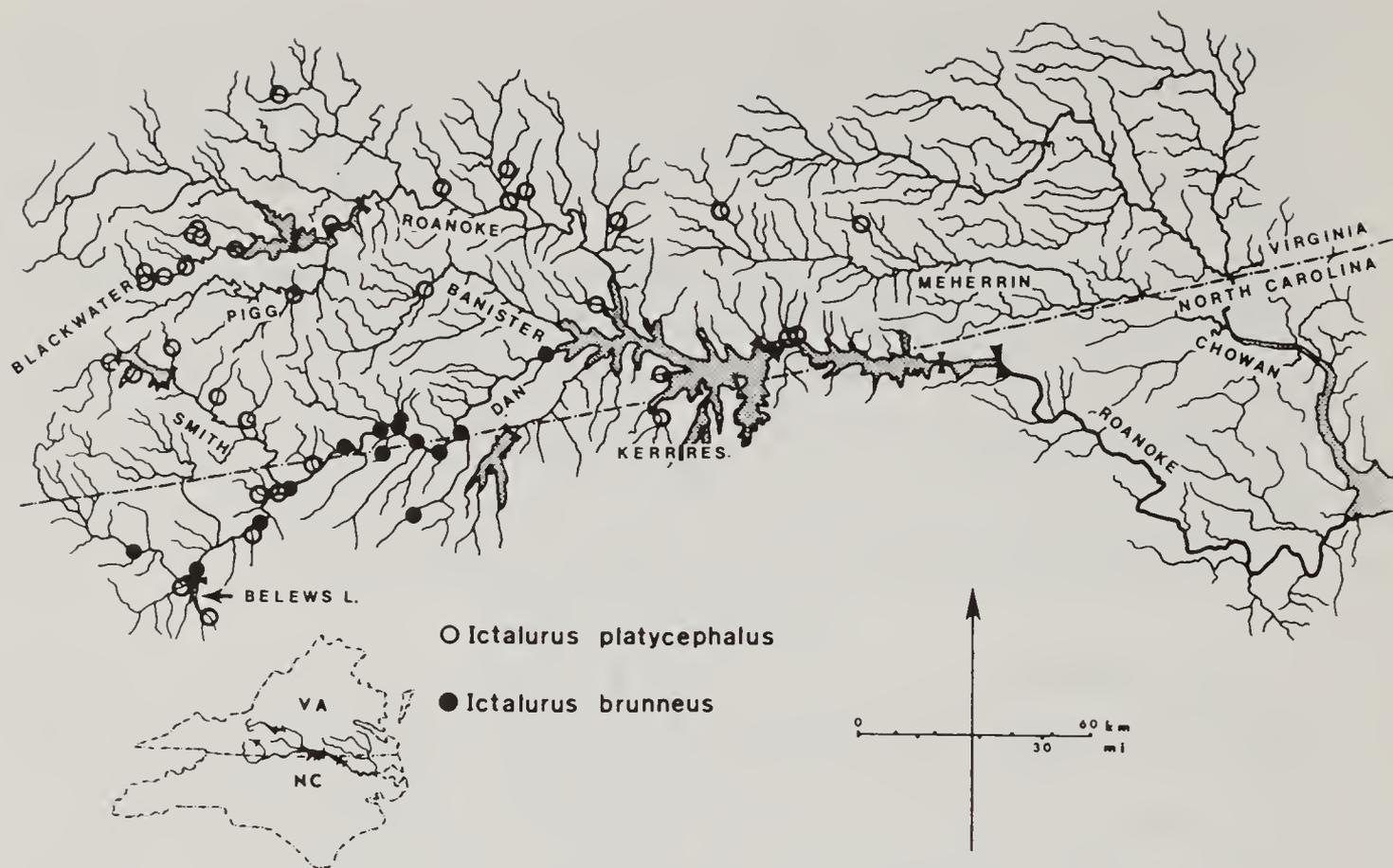


Fig. 1. Distribution of *Ictalurus brunneus* and *I. platycephalus* in the Roanoke River drainage, North Carolina and Virginia.

regimes occur in many parts of these streams (Yerger and Relyea 1968). Extensive surveys of the Neuse drainage for *Ictalurus*, and less extensive surveys of other Carolinian Atlantic Slope drainages, revealed that *I. brunneus* is more abundant, sometimes greatly so, than *I. platycephalus* (M. Corcoran, pers. comm.). Corcoran also determined that, at least in the Neuse, both species are generally absent from the Coastal Plain. Thus, previous concepts of a preference by *I. brunneus* for upper stream sections may partly relate to its numerical abundance over *I. platycephalus*. However, in the Roanoke drainage, only *I. platycephalus* appears to currently occur in the main trunk Roanoke system and the Smith River tributary of the Dan River. In both these systems it extends upstream well through moderate gradients into Blue Ridge foothills.

The apparent absence of *I. brunneus* from most of the Roanoke drainage, including the Chowan system of the lower Roanoke, and the wide geographic and ecological range of *I. platycephalus* therein, suggest that *I. brunneus* was recently introduced to the Dan. Prior absence of *I. brunneus* would have allowed *I. platycephalus* to become widely established. The apparent current exclusion of *I. brunneus* from montane sections of the Dan system thus may relate to former establishment of *I. platycephalus*.

Belews Lake, an upper Dan system impoundment (Fig. 1), was reportedly stocked with *I. melas* by a "concerned citizen" to improve fishing (W. Smith, pers. comm.). These introduced *I. melas* may have

been transferred from the Yadkin system of the Peedee, where both *I. brunneus* and *I. melas* occur. Although *I. brunneus* is not known from the lake (D. Cloutman, pers comm.) it occurs in the immediate area, and the *I. melas* stocking may have included the superficially similar *I. brunneus*. Belews Creek was impounded in 1970 and the lake reached full pool in 1973 (Harrell et al. 1973). If *I. brunneus* dispersed from the Belews Lake area, its mobility would have been similar to that of introduced *Pylodictis olivaris* now spreading in the Cape Fear drainage (M. Corcoran, pers. comm.). However, the Belews Lake area may not have been the point of origin; possibly more than one stocking occurred.

*Ictalurus catus*. — White catfish are native to the major Atlantic slope drainages of Virginia, occurring widely in Piedmont and Coastal Plain parts of large streams and reservoirs. Jordan (1889) reported it from Maury (North) River and elsewhere in the upper James drainage in the Ridge and Valley. It also has been taken in South Fork Shenandoah River (Potomac drainage) in the Ridge and Valley. Clay (1975) noted that *I. catus* introduced to Kentucky were from the James River.

*Ictalurus furcatus*. — The presence in Virginia of the blue catfish, a primarily Mississippi basin and Gulf slope species, has been widely reported, but the species has only recently been verified as introduced. It was stocked in lower Rappahannock (1975 and 1977) and James (1977) rivers by the Virginia Commission of Game and Inland Fisheries (L. Hart, pers. comm.). Juvenile specimens from these stockings have since been collected by Virginia Institute of Marine Science personnel (J. Gourley, pers. comm.; VIMS specimens examined by us). It is not known whether the species is reproducing. *Ictalurus furcatus* is unknown from the Potomac, York, New, Roanoke and Tennessee (in Virginia) River drainages. Records from the Potomac and New River drainages are discussed in detail.

*Ictalurus furcatus* may have been introduced into the Potomac River near Washington, D.C., between 1898 and 1905. The old U.S. Fish Commission rearing and holding ponds in that area were an early active center of fish dispersal. It was not recorded by Smith and Bean (1898), but was reported as introduced (probably with *I. punctatus*) based on 1905 records by Bean and Weed (1911), and by McAtee and Weed (1915) based on two specimens collected in 1912. We located an adult *I. punctatus* (USNM 70281) previously misidentified as *I. furcatus*, apparently one of the specimens on which McAtee and Weed (1915) based their record. Radcliffe and Welsh (1916) reported *I. furcatus* from the Chesapeake and Ohio canal, along the Potomac River, Maryland. The single specimen was reportedly sent to Washington, but it was not found by us at the USNM. It is unknown whether *I. furcatus* was introduced and failed to establish, or if all records are actually of *I. punctatus*. Elser (1950) and Manville (1968) based their records of *I. furcatus* on these early reports. A second body of literature (Wiley 1970;

Jenkins et al. 1972; Lee et al. 1976; Stauffer et al. 1978) reported *I. furcatus* from the Potomac based on records of Schwartz (1961). Frank J. Schwartz (pers. comm.) later felt that these specimens were “odd *I. punctatus*”; no Potomac *I. furcatus* were found in collections of Chesapeake Biological Laboratory, University of North Carolina Institute of Marine Sciences, and Virginia Institute of Marine Science, which house Schwartz’s collection (F. Schwartz, J. Stauffer, J. Gourley, pers. comm.). *Ictalurus furcatus* has not been collected in recent extensive surveys of the Potomac River from Maryland—West Virginia (Energy Impact Associates), along Virginia above Great Falls (E. Enamait, pers. comm.), or from Washington, D.C., downstream (J. Gourley, pers. comm.). If ever introduced into the Potomac River near Washington, D.C., it probably shares extirpated status with *Percopsis omiscomaycus* (Walbaum) and *Percina caprodes* (Rafinesque).

In the New drainage, *I. furcatus* was reported introduced into the West Virginia section (Schwartz in Jenkins et al. 1972), but no specimens were seen. Cope’s (1868) record of *I. “caerulescens”* in the Virginia section was based on *I. punctatus* (Fowler 1945:81). Addair’s (1944) records from West Virginia of *I. “anguilla”* probably are of only *I. punctatus*. His New River, West Virginia, specimens at the UMMZ are *I. punctatus*. Hocutt et al. (1978) listed *I. furcatus* as a hypothetical inclusion to the Greenbrier River fauna based on Addair (1944). Ross (1959) repeated reports by game wardens of “blue catfish” from the New River in three Virginia counties. Also, a single record was reported (specimen discarded) by personnel of the VCGIF from Claytor Lake, New River impoundment. The above two reports of *I. furcatus* are considered to be of *I. punctatus*, based on the absence of *I. furcatus* from extensive New River surveys by Hocutt et al. (1973), Stauffer et al. (1975, 1976) and others, and because nonspotted channel catfish have often been misidentified as blue catfish.

*Ictalurus melas*. — The black bullhead probably is native to Virginia in only the Tennessee and Big Sandy drainages. Until recent collections in the Roanoke drainage, it was thought to be absent from Atlantic slope drainages. Hence, we considered records of collections and literature compilations (Abbott et al. 1977) for *I. melas* to be *I. nebulosus*, a species with which it is sometimes confused. However, recent records from Belews Lake (see *I. brunneus*), from Dan River above Belews Lake, North Carolina (UNC 76-93), from two Virginia tributaries of Kerr Reservoir, and two specimens (UMMZ 138480) taken in 1940 from the North Carolina section of the upper Peedee drainage, prompted us to reconsider records from the Atlantic slope. Collections of *I. nebulosus* from the Roanoke drainage (including Kerr Reservoir preimpoundment collections and the Chowan system) in Virginia were examined, and no *I. melas* were discovered. Also, none were reported from extensive surveys of the North Carolina parts of the Roanoke and Chowan systems (Smith 1963; Carnes 1965). The absence of *I. melas* from earlier collections strongly

suggests that its presence in the Roanoke is the result of single or multiple introductions. Because of difficulties of identification, until specimens are examined we still consider *I. melas* to be absent elsewhere on the Atlantic slope in Virginia. Other species recently introduced into the Roanoke drainage in the North Carolina part of the Dan at Belews Lake are *Notropis lutrensis* (Baird and Girard) and *Pimephales promelas* (Rafinesque) (DPC 30407-04 and 31201-02, respectively).

The occurrence of *I. melas* in the New River drainage is also problematic. It appears to have been introduced but now possibly extirpated. The only extant specimens known are four juveniles from Fries, a town on New River, taken in 1939 by B. Smith (USNM 109467). The only other record of *I. melas* is from Reed Creek at Wytheville based on unretained specimens (Wollitz 1968). Wollitz (pers. comm.) thought the Reed Creek specimens resulted from introduction. *Ictalurus melas* has not been taken in recent extensive New River and tributary surveys in Virginia, or from New River tributaries in West Virginia (Hocutt et al. 1978, 1979). Hocutt et al. (1978) reported *I. melas* as stocked in Sherwood Lake, Greenbrier River system, West Virginia. Like other bullheads, it may be widely introduced in farm ponds.

*Ictalurus natalis*. — The yellow bullhead is native to Virginia, occurring in all drainages except the New. The only record for the latter, from the Gauley River system of the lower New, West Virginia, may represent an introduction (Hocutt et al. 1979).

*Ictalurus nebulosus*. — The brown bullhead is native to the Atlantic slope of Virginia; it occurs in all Atlantic slope drainages as well as being the only ictalurid known from the diminutive freshwater ichthyofauna of the southern part of the Delmarva Peninsula. *Ictalurus nebulosus* is probably introduced to the New drainage. In Virginia it is known from only two collections, both from tributaries entering New River below Claytor Lake: a juvenile (VPI 2039) was rotenoned in 1971 from East River just above its mouth and immediately upstream from the Virginia — West Virginia state line; and two juveniles were collected in 1972 from Meadow Creek, Montgomery County. Hocutt et al. (1979) reported another specimen taken in 1976 from a lower New River tributary system, West Virginia. It may have been stocked in farm ponds in much of the state, but is unknown from the Tennessee River drainage in Virginia.

*Ictalurus platycephalus*. — The flat bullhead occurs only in the Roanoke drainage, including the Meherrin River branch of the Chowan system, in Virginia; this is the northern limit of its distribution (Yerger and Relyea 1968; Fig. 1). The species generally occurs in small to moderate-size streams draining the Piedmont, where it inhabits sluggish waters and is known from reservoirs. In the Roanoke drainage it extends into smaller streams than it is “typically” associated with elsewhere on the Atlantic Slope. The possible historical absence of *I. brunneus* in the

Roanoke drainage may have allowed it to invade smaller stream habitats thought to be typically occupied by only *I. brunneus* when the two species are sympatric. The first life history study of *I. platycephalus* was conducted by Olmstead and Cloutman (1979).

*Ictalurus punctatus*. — The channel catfish is native in the Tennessee and Big Sandy drainages in Virginia and, based on Cope's 1867 record (see *I. furcatus*), probably native in the New River above Kanawha Falls. It has been introduced in all Atlantic slope drainages in the state (Jenkins et al. 1972).

*Pylodictis olivaris*. — The flathead catfish is native to the Tennessee, Big Sandy, and New drainages in Virginia. It has recently been introduced into the James and Roanoke drainages. Introduction into lower James River near Surry accidentally occurred in 1965 when a temporary holding pond at Hog Island Game Refuge washed out during a storm and released about 50 *P. olivaris*. A 20 to 30 pound *P. olivaris* was seen by Dean Estes (Virginia Electric Power Co. biologist) in 1977; it was taken on a trotline near Surry (J. Gourley, pers. comm.). Hart (1978) reported the introduction into Smith Mountain Reservoir (the most upstream reservoir on the Roanoke River, Fig. 1) of one specimen in 1976 and five in 1977. Specimens from 10 inches long to 10 pounds weight, taken from the Roanoke River near Brookneal below Smith Mountain Lake, were observed in 1978-79 by L. Hart (pers. comm.).

### DIAGNOSTIC CHARACTERS

The following account and critique of distinguishing characters includes summaries of our data as well as characters abstracted from the literature. Discussion of diagnostic features is supplemented by frequency distributions of counts for Virginia *Ictalurus* (*Amiurus*) in Tables 1-3, comparison of eye sizes (Fig. 2), and fins (shape and pigmentation), as well as premaxillary teeth configurations (Fig. 3). We emphasize that the following discussion pertains to Virginia *Ictalurus* (except where supplemented; see Methods and Materials), and is limited to characters with known or reputed utility in identifying species. Mention of somatic and fin pigmentation is generally avoided, as many aspects of coloration are variable in all species of *Ictalurus*. Although the Virginia *Ictalurus* fauna is artificially enriched in species, the species are easily distinguished. To reduce redundancy, diagnostic features are discussed by the following groups: the flathead bullheads, the typical bullheads, and the *Ictalurus* with forked tails. Characters of the monotypic genus *Pylodictis* are listed only in the key at the end of this section.

*Flathead bullheads*. — This group is represented in Virginia by *I. brunneus* and *I. platycephalus*. The species were clearly distinguished first by Yerger and Relyea (1968), who recognized the flathead bullheads as a group but did not provide a key character for its separation from the

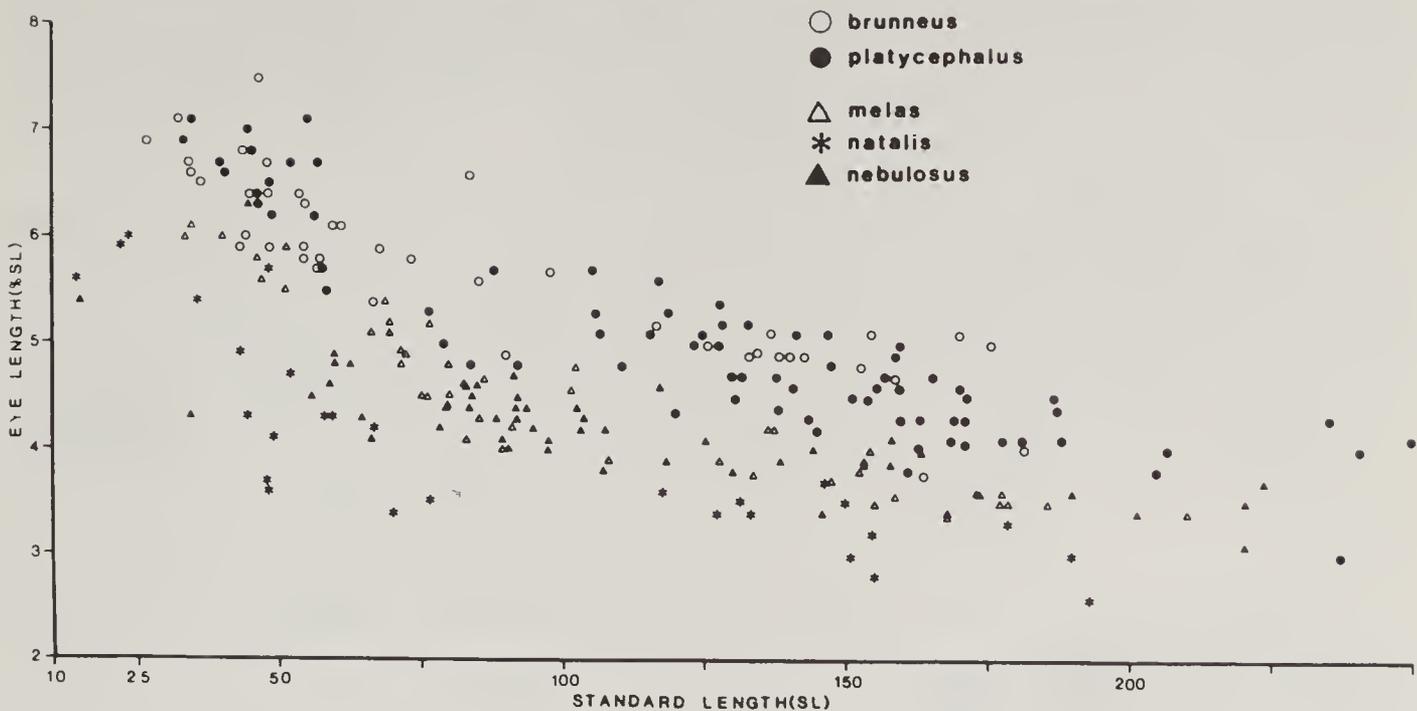


Fig. 2. Relationship of eye length (as % SL) to SL in Virginia *Ictalurus* (*Amiurus*) with emarginate caudal fins.

typical bullheads group. The flathead bullheads are best distinguished from other bullheads by the presence of a large dark basal blotch, its upper edge straight or convexly rounded, in the dorsal fin (Fig. 3D). The blotch was also recognized as a key character and figured for *I. platycephalus* by Eddy (1969), and depicted for *I. brunneus* by Smith-Vaniz (1968). Eye size is secondarily useful in separating the groups, the size being moderate in flatheads and small in typical bullheads. Although size varies allometrically relative to SL, more pronouncedly in small juveniles (Fig. 2), the differences between the groups are generally obvious, with little overlap when comparing specimens of similar lengths. The third member of the flathead bullhead group, *I. serracanthus*, a primarily Floridean species, also has the dorsal blotch and moderate eye size character states (figure and description in Yerger and Relyea 1968). Head shape of flathead and typical bullheads is variable, from essentially flat to slightly convex dorsally in flatheads, versus usually more elevated or markedly convex in typical bullheads. Overlap in head shape and eye size is such that sole reliance on either character for group separation will result in some misidentifications.

*Ictalurus brunneus* and *I. platycephalus* are best distinguished from each other by barbel pigmentation and premaxillary teeth configuration, and secondarily by meristics. Most juveniles and adults of *I. brunneus* examined had profusely dark pigmented mental (chin) barbels, whereas most specimens of *I. platycephalus* had unpigmented or slightly pigmented, pale mental barbels. The absence of profusely developed mental barbel pigment in *I. brunneus* usually occurs in specimens smaller than 100 mm SL. In *I. platycephalus* the presence of slightly pigmented mental barbels occurs mostly in adults, particularly in the lateral pair of barbels; the

medial mental barbels rarely possess melanophores, and then only basally. Additionally, the maxillary barbels of *I. platycephalus* usually appear bicolored (leading edge pale, posterior edge dark), whereas in *I. brunneus* these barbels are uniformly dark.

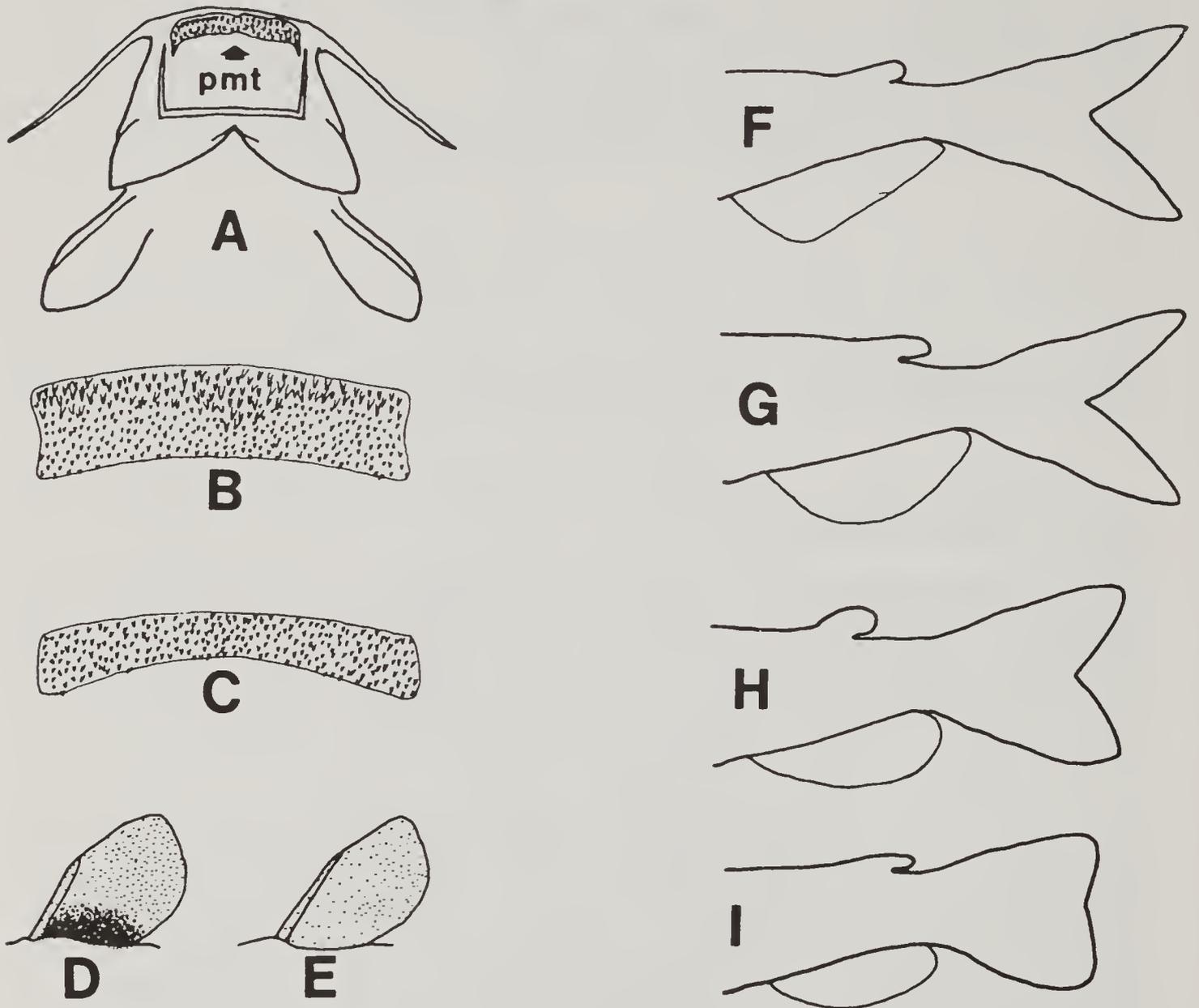


Fig. 3. Diagnostic features of some Virginia ictalurids: A, ventral aspect showing premaxillary tooth patch of *Pylodictis*; B, premaxillary tooth patch of *I. brunneus*; C, premaxillary tooth patch of *I. platycephalus*; D, flathead bullhead dorsal fin with dark basal blotch; E, dorsal fin of typical bullhead; F, fin profiles of *I. furcatus*; G, fin profiles of *I. punctatus*; H, fin profiles of *I. catus*; I, profile of an emarginate caudal fin.

The premaxillary tooth patch of *I. brunneus* differs from *I. platycephalus* in being wider, fairly uniform in width, and usually possessing lateral edentations in the patch (Fig. 3B). The cardiform teeth of *I. brunneus* are more numerous along an anterior-posterior axis (teeth not forming rows) than in *I. platycephalus*, and occur in two distinct sizes. Large cardiform teeth are positioned along the anterior margin of the tooth patch, and are often additionally arranged in a medial, triangular configuration. The tooth patch of *I. platycephalus* usually lacks lateral edentations and is occasionally slightly constricted medially (Fig. 3C).

The cardiform teeth of *I. platycephalus* are small and fairly uniform in size. The premaxillary tooth patch and cardiform teeth size differences are not evident in small specimens. These characters were first recognized by Lundberg (1970).

The greatest meristic differences between *I. brunneus* and *I. platycephalus* are in anal rays and a character index (Tables 2 and 3). Frequency ranges of all counts differed slightly from data of Yerger and Relyea (1968), indicating possible geographic variation. A slightly higher range of character index values exists in Roanoke drainage *I. brunneus* when compared to data of Yerger and Relyea (1968) from some more southerly drainages, and results in greater meristic overlap between the two species in the Roanoke.

The difference in mouth position between the species conformed to Yerger and Relyea's (1968) description; however, we do not advocate general use of the character, as the difference seems to be only an average one and is not as obvious as barbel pigmentation.

*Typical bullheads.* — Three species of typical bullheads (or the *natalis* group of Lundberg 1975) inhabit Virginia waters: *I. natalis*, *I. nebulosus* and *I. melas*. These are best separated from the flathead bullhead group by the absence of a discrete dark blotch at the base of the dorsal fin (Fig. 3E) and by small eye size (Fig. 2).

*Ictalurus natalis* is easily distinguished from the others by its unpigmented mental barbels. The dark blood pigments in vessels of these barbels should not be confused with the presence of melanophores. Preserved blood in mental barbels appears as a dark line. The remaining species, *I. nebulosus* and *I. melas*, have often been reported to be separable by the character of the serrae on the posterior edge of the pectoral spine: moderate serrae in *I. nebulosus*, weak serrae in *I. melas* (Trautman 1957; Blair et al. 1957; Hubbs and Lagler 1958; Pflieger 1975; and others). The posterior pectoral spine serrae in *I. melas* are variable, being absent to moderately developed. Although most often weakly developed in adult *I. melas*, the pectoral serrae are unreliable for consistently distinguishing *I. melas* from *I. nebulosus*. *Ictalurus melas* is best distinguished from *I. nebulosus* by higher (rarely overlapping) gill raker counts (Table 1). The single *I. melas* possessing 15 gill rakers on the right arch had 17 on the left arch.

Fin pigmentation differences have also been reported. Of these characters, only the depigmented "bar" at the caudal base of *I. melas* is consistently present, and then only in larger juveniles and adults. However, it is often evident only when directly compared to specimens of *I. nebulosus*.

*Forked-tail Ictalurus.* — Of the three species in this group, *I. catus* is readily separated by a moderately forked tail (Fig. 3H) and low anal ray counts, usually 22-24, (22-25,  $\bar{x}$  = 23.1). Variation exists in the anal ray count ranges reported for *I. catus*: 19-22 (Jordan and Evermann 1896);

Table 1. Frequency distribution of gill raker counts (total) for subgenus *Amiurus* of Virginia.

Species	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	N	$\bar{x}$	S.D.
<i>I. melas</i>				1	3	6	18	15	3	1	--	1	--	1	48	18.3	1.42	
<i>I. nebulosus</i>			8	28	11	1									48	14.1	0.69	
<i>I. natalis</i>			3	6	7	6	1	2							26	14.3	1.64	
<i>I. platycephalus</i>	4	10	28	29	4	1	2	1							78	12.4	1.14	
<i>I. brunneus</i>		1	3	8	12	5	12	1	1						43	14.4	1.53	

Table 2. Frequency distribution of anal ray counts for subgenus *Amiurus* of Virginia.

Species	17	18	19	20	21	22	23	24	25	26	27	28	N	$\bar{x}$	S.D.
<i>I. melas</i>			2	5	15	7	10	5	3				47	21.7	2.41
<i>I. nebulosus</i>		2		2	8	20	8	8					48	22.1	1.37
<i>I. natalis</i>					4	32	27	14	1			2	25	25.4	1.20
<i>I. platycephalus</i>					4	32	27	14	1				78	22.7	0.91
<i>I. brunneus</i>		8	22	9	3	1							43	19.2	0.92

Table 3. Frequency distribution of character index (anal rays minus gill rakers) for subgenus *Amiurus* of Virginia.

Species	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	N	$\bar{x}$	S.D.
<i>I. melas</i>						8	7	--	1								47	3.6	1.93
<i>I. nebulosus</i>				2	--	3	11	15	10	7							48	8.0	1.41
<i>I. natalis</i>						1	1	--	2	5	3	8	3	2	1		26	11.2	2.07
<i>I. platycephalus</i>						2	1	2	11	29	21	9	3				78	10.3	1.34
<i>I. brunneus</i>		1	4	7	5	12	5	7	1	1							43	4.8	1.83

18-21 (Blair et al. 1957); 18-24 (Trautman 1957); 19-23 (Eddy 1969); 18-22 in key, 19-23 in text (Clay 1975). The larger ranges and lower extremes of these counts may have resulted from failure to count all anterior rudimentary rays in at least some of the material examined by these authors. Smith-Vaniz (1968) reported a count range similar to ours (21-26,  $\bar{x} = 23$ ). The gap in the "bony ridge" between the head and dorsal fin (a disjuncture between the supraoccipital and the anterior process of the first pterygiophore), reported in keys by Hubbs and Lagler (1958) and Clay (1975), was consistently present in *I. catus*. However, a disjuncture also occurs in juveniles of *I. punctatus* and *I. furcatus*.

Until recently, anal ray counts were reported to have little overlap between *I. furcatus* and *I. punctatus* (Trautman 1957; Blair et al. 1957; Pflieger 1975; and others). However, Clay (1975) reported anal ray count ranges to be 27-34 for *I. furcatus* and 23-29 for *I. punctatus* and emphasized the need to consider anal fin shapes (Fig. 3F, G). An obvious character when present are the spots on young to adult *I. punctatus*, but adults often lack them. W. Ralph Taylor (pers. comm.) informed us of a difference in the gas bladders of *I. furcatus* and *I. punctatus*; that of *I. furcatus* has an elongate posterior extension and that of *I. punctatus* does not. The gas bladder difference is illustrated by Pflieger (1975).

#### KEY TO VIRGINIA ICTALURIDS WITH AN ADNEXED ADIPOSE FIN

1. Premaxillary tooth patch with posterolateral extensions (Fig. 3A); upper lobe caudal fin partially depigmented (varies in adults) ..... *Pylodictis olivaris*.  
Premaxillary tooth patch without posterolateral extensions; upper lobe caudal fin not partly depigmented ..... 2.
2. Caudal fin deeply forked (Fig. 3F, G) ..... 3.  
Caudal fin moderately forked to emarginate (Fig. 3H, I) ..... 4.
3. Anal fin margin usually rounded (Fig. 3G); anal rays 23-29; young to small adults often with spots ..... *Ictalurus punctatus*.  
Anal fin margin straight (Fig. 3F); anal rays 27-34; never spotted ..... *I. furcatus*.
4. Caudal fin moderately forked (Fig. 3H); anal rays usually 22-24 (22-25) ..... *I. catus*.  
Caudal fin emarginate (Fig. 3I) ..... 5.
5. Dorsal fin with dark basal blotch (Fig. 3D); eye size moderate (flathead bullheads) ..... 6.  
Dorsal fin without dark basal blotch (Fig. 3E); eye size small (typical bullheads) ..... 7.
6. Mental barbels usually without pigment (pigment may be present in large specimens on lateral barbels, rarely on medial); leading edge of maxillary barbels pale

- (appearing bicolored); premaxillary tooth patch of large juveniles and adults as in Figure 3C; gill rakers usually 10-14 (10-17); anal rays usually 22-24 (21-26) . . . . . *I. platycephalus*. Mental barbels usually profusely pigmented (occasionally pigment only developed basally in small specimens); maxillary barbels uniformly dark; premaxillary tooth patch in large juveniles and adults as in Figure 3B; gill rakers usually 12-16 (11-18); anal rays usually 18-20 (18-22) . . . . . *I. brunneus*.
7. Mental barbels usually pale; anal rays usually 24-27 (24-28); gill rakers usually 12-15 (12-18) . . . . . *I. natalis*. Mental barbels usually profusely pigmented . . . . . 8.
8. Gill rakers usually 17-20 (15-24); a rectangular depigmented area often present at base of caudal fin in adults . . . . . *I. melas*. Gill rakers usually 13-15 (13-16); caudal base with uniform pigmentation . . . . . *I. nebulosus*.

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# Geographic Variation in the Snake *Storeria occipitomaculata* (Storer) (Serpentes: Colubridae) in Southeastern United States

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**ABSTRACT.**—The populations of *Storeria occipitomaculata* occurring in the Gulf Coastal Plain from eastern Texas to the Carolinas differ from the nominate subspecies in nuchal pattern, ventral coloration, relative tail length, and subcaudal number. To accommodate these populations nomenclaturally the concept of *S.o. obscura* Trapido is expanded and redefined.

The Florida red-bellied snake, *Storeria occipitomaculata obscura*, was described by Trapido (1944), who distinguished it from the nominate race on the basis of the former having a black head, the light supralabial spot touching the edge of the lip, a light nuchal collar, fewer ventrals, and more subcaudals. He envisioned the range of *S.o. obscura* as encompassing peninsular Florida and coastal plain Georgia, with intergradation occurring to the north and west of this area. Subsequent authors (Wright and Wright 1957; Cliburn 1959; Mount 1975) reported the occurrence of some of the distinguishing features of *S.o. obscura* in Mississippi and Alabama populations, and we discovered them in Louisiana snakes. These observations, along with the more than fivefold increase in specimens available from the Southeast since the time of Trapido's study, prompted our investigation of variation in the species throughout this region of the country.

## METHODS

We examined 523 specimens of *Storeria occipitomaculata* from southeastern United States (Fig. 1), and for each specimen we recorded sex, ventral and subcaudal numbers, tail length as percent of total length, nuchal pattern, and supralabial light spot condition. To facilitate analysis, data for specimens from geographically proximate and physiographically similar localities were pooled. We also examined living snakes from Wisconsin, Pennsylvania, Georgia, Florida, Alabama, Mississippi, Louisiana, Arkansas, and Oklahoma, and noted various aspects of their color pattern, particularly the ventral coloration.

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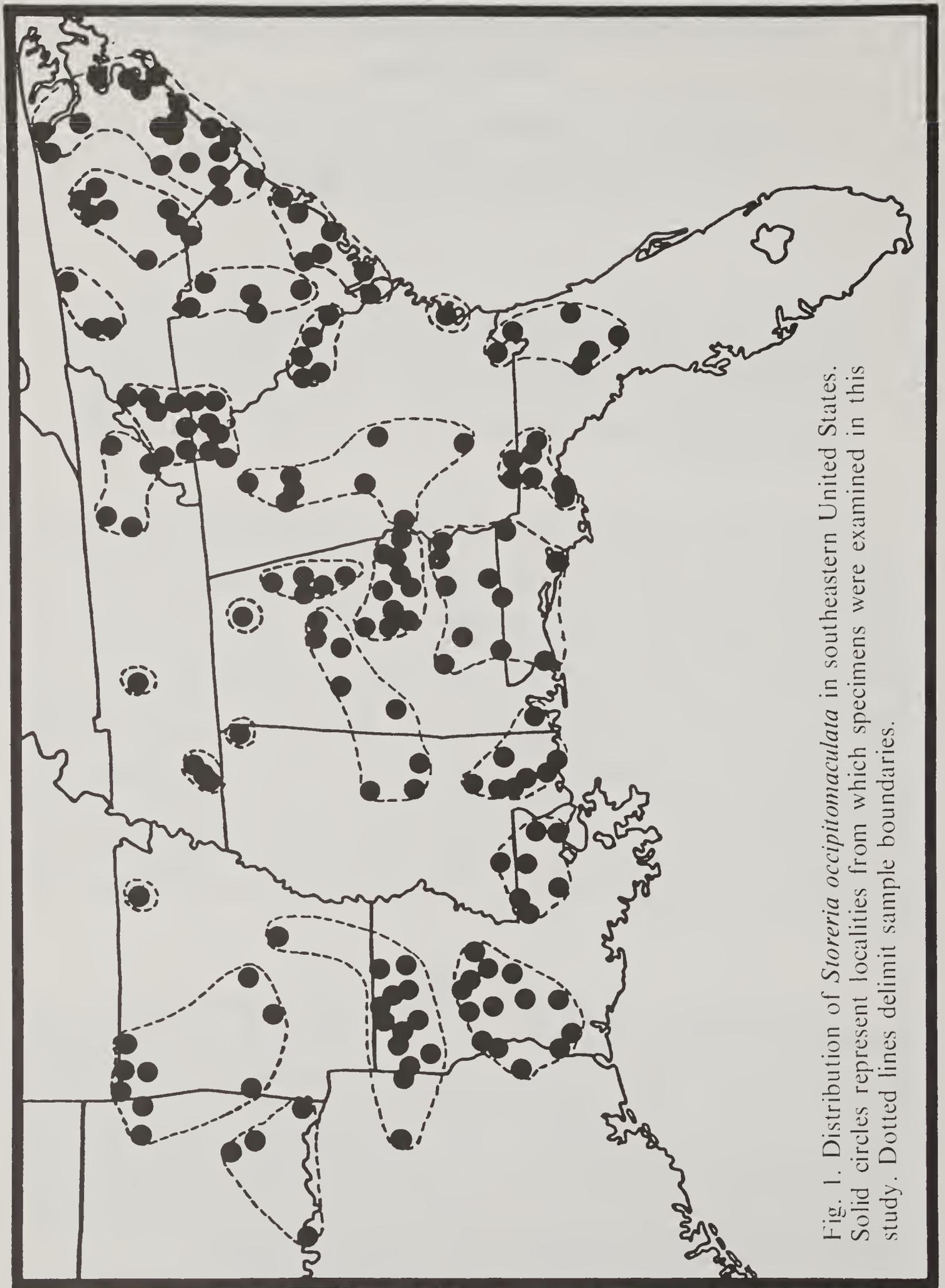


Fig. 1. Distribution of *Storeria occipitomaculata* in southeastern United States. Solid circles represent localities from which specimens were examined in this study. Dotted lines delimit sample boundaries.

## ANALYSIS OF CHARACTERS

*Head Pattern.*—Specimens of *Storeria occipitomaculata* frequently darken if left in formalin for even a few days, so we were not able to determine natural head coloration in many of the individuals we examined. Nevertheless, it is apparent that snakes having a very dark head that contrasts with a lighter dorsum are not confined to the originally described range of *S.o. obscura*, but occur in coastal plain populations from at least South Carolina through Louisiana. Many of these same populations do, however, also contain animals whose head does not contrast markedly with the dorsum, hence we question the taxonomic usefulness of this character.

The presence or absence of a dark bar separating the light supralabial spot from the edge of the lip is virtually impossible to determine in formalin-darkened specimens, and we lack these data for the majority of specimens examined.

*Nuchal Pattern.*—Although *Storeria occipitomaculata obscura* was characterized as having a complete light nuchal collar as opposed to the three light nuchal spots of *S.o. occipitomaculata*, 25% of the specimens we examined (9 of 36) from the described range of *S.o. obscura* have separate spots rather than a complete collar. Moreover, a complete collar occurs fairly frequently in most coastal plain populations (for instance in 10 of 13 animals from the Florida Parishes of Louisiana and 15 of 27 from west-central Louisiana.)

A more consistent character for distinguishing the coastal plain populations from their more northern counterparts is whether or not the light nuchal marks (spots or collar) are in contact with the light coloration of the venter (see Fig. 2). Such contact on both sides of the neck occurs in nearly all specimens examined from Florida, western Georgia, Alabama, Mississippi, Louisiana, eastern Texas, and southern Arkansas. In northern Arkansas, Tennessee, and extreme northern Alabama the frequency of animals having the light nuchal marks separated from the venter on at least one side of the neck ranges from 84 to 100%. Farther east, in northern Georgia and North Carolina, the frequency ranges from 60 to 75%. In the geographically intermediate areas (southeastern Oklahoma, western Tennessee, eastern Georgia, and South Carolina) the light nuchal marks are separated from the venter in 27 to 50% of the animals.

*Ventral Coloration.*—For reasons previously cited we have relatively sparse information about ventral color in living *S. occipitomaculata*. Nonetheless, from our personal observation and from color notes and color transparencies provided by other workers, we can say that the coastal plain snakes rarely have the bloodred or crimson venter typical of the nominate race. Instead, ventral color may range from lemon yellow through pale orange to butterscotch tan.

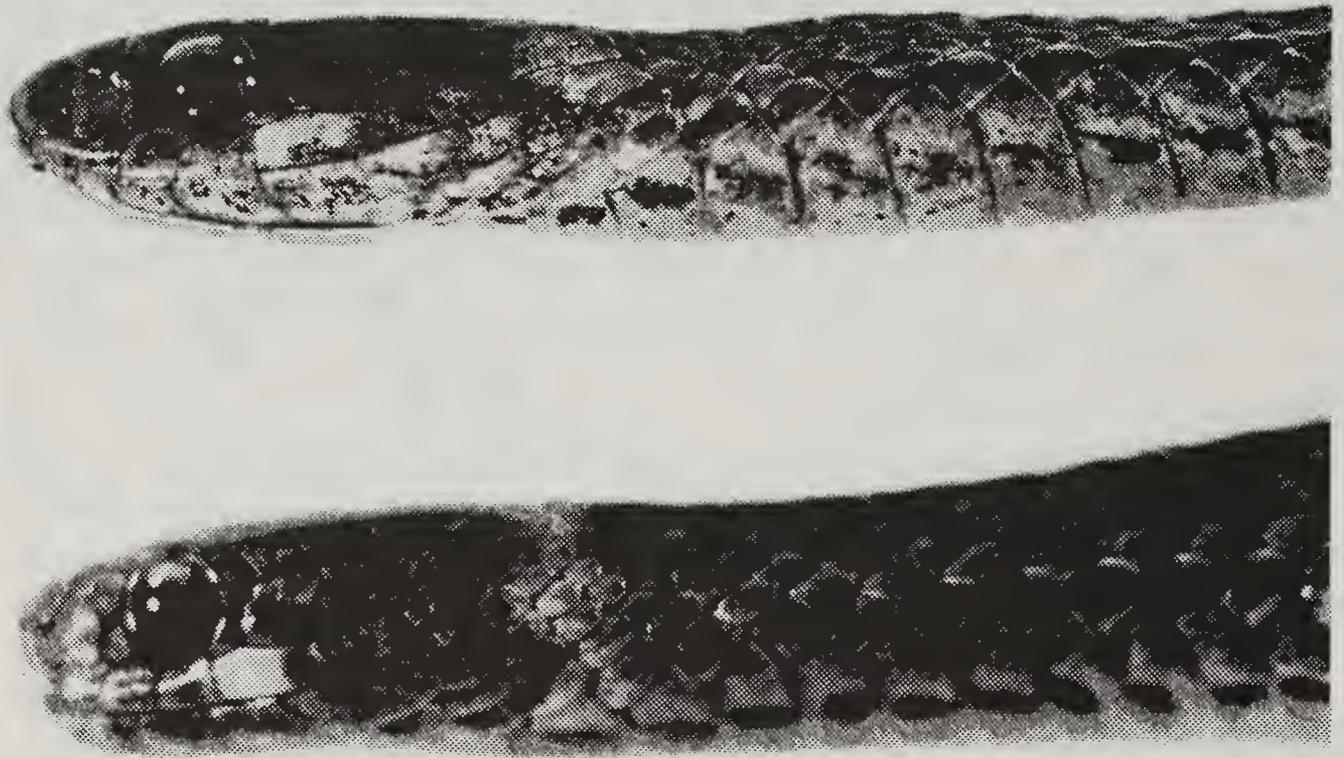


Fig. 2. Lateral view of left side of head and neck in *Storeria occipitomaculata occipitomaculata* (above) and *S.o. obscura* (below) showing the differences in nuchal pattern.

*Relative Tail Length.*—As can be seen from Fig. 3, the tail is proportionally longer in the coastal plain populations than in those farther inland. The longest tail occurs in animals from the Florida Panhandle, southern Alabama, and southern Mississippi.

*Ventrals.*—The number of ventrals exhibits no consistent differences between coastal plain and inland populations (see Fig. 4). Ventral number is markedly higher in Louisiana, southern Arkansas, and eastern Texas, a trend that may reflect the closer geographical proximity of those populations to the Mexican *S.o. hidalgoensis* Taylor, which has even more ventrals and exhibits an increasing north-south cline therein (Trapido 1944; pers. obs.).

*Subcaudals.*—As might be anticipated, geographic variation in subcaudal number (see Fig. 5) parallels that exhibited by relative tail length. In this instance, however, the coastal plain populations from Georgia, South Carolina and North Carolina agree more closely with inland populations than they do with the coastal plain snakes from farther south and west.





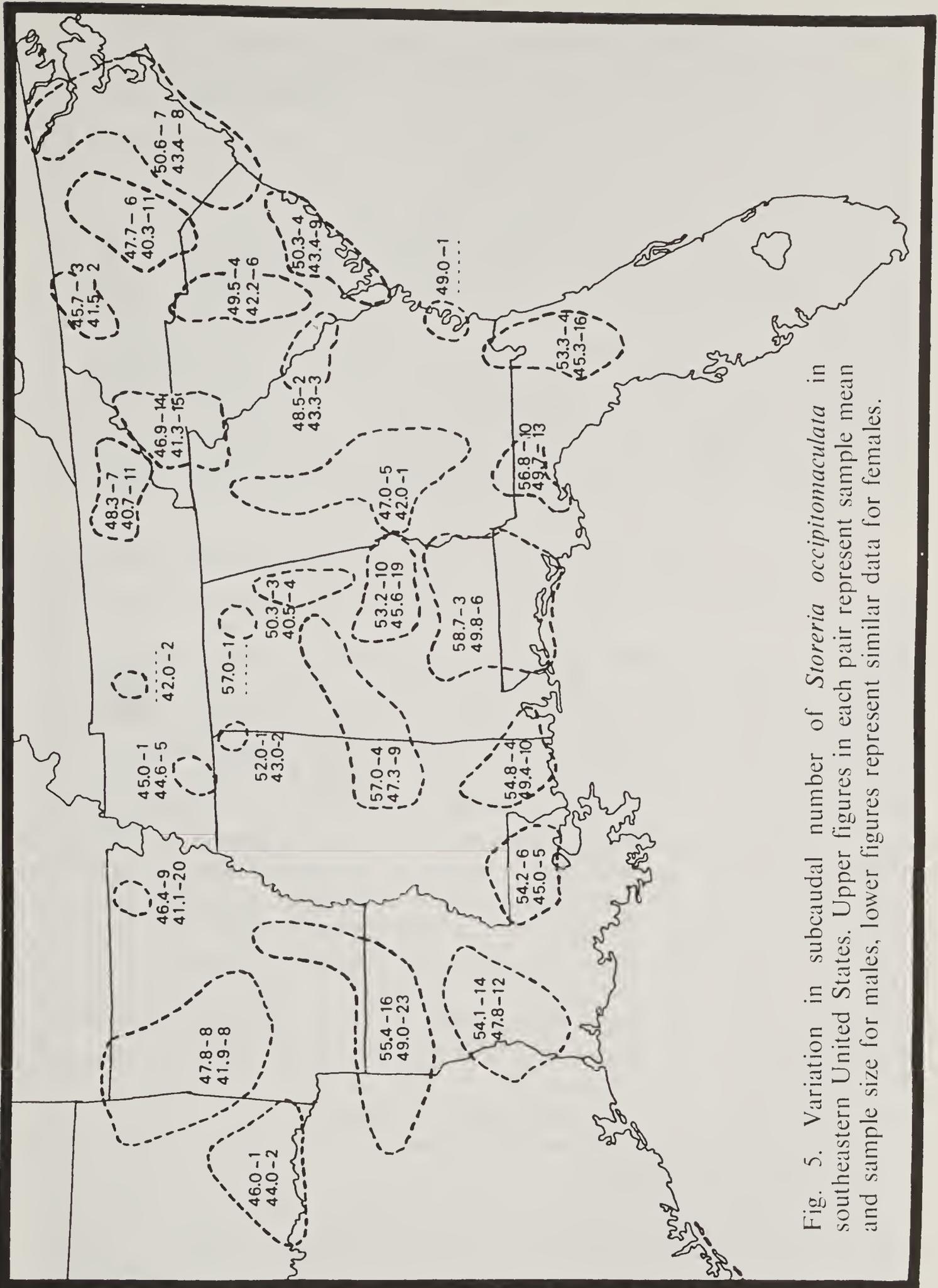


Fig. 5. Variation in subcaudal number of *Storeria occipitomaculata* in southeastern United States. Upper figures in each pair represent sample mean and sample size for males, lower figures represent similar data for females.

### CONCLUSIONS

The general concordance of geographic variation in nuchal pattern, ventral coloration, relative tail length, and subcaudal number suggests

that there is sufficient justification for giving taxonomic recognition to the Gulf Coastal Plain populations of *Storeria occipitomaculata*. This expanded concept of *S.o. obscura* requires, however, that the taxon be redefined. As reconstituted, *S.o. obscura* can be distinguished from the nominate race by having: the light nuchal marks usually contacting the venter (versus usually separated from the venter); the venter yellow, orange, or tan (versus venter some shade of red); the sample means for relative tail length exceeding 25% in males, 22% in females (versus sample means less than 25% in males, 22% in females); the sample means for subcaudal number exceeding 53 in males, 45 in females (versus sample means less than 49 in males, 42 in females). Thus defined, *S.o. obscura* ranges from eastern Texas through southern Arkansas and Louisiana to Florida; it appears to intergrade with *S.o. occipitomaculata* in southeastern Oklahoma, western Tennessee, northern Alabama, Georgia, and the Carolinas (exclusive of the mountains, where the nominate race occurs). Data on ventral coloration in animals from the Carolinas may help to more clearly delimit the zone of intergradation.

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# Effects of Microhabitat Size and Competitor Size on Two Cave Isopods

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**ABSTRACT.**—Two isopods are common in cave streams in northern West Virginia—*Caecidotea cannulus* (Steeves) and *Caecidotea holsingeri* (Steeves). Laboratory experiments using an artificial stream demonstrated that (1) for any given size of isopod, washout rate depended on the size of gravels in the stream bed, i.e., larger isopods had low washout rates in larger gravels and vice versa, and (2) competition (as reflected in washout rate) decreased as size differences among competitors increased. Field evidence provided support for the first result. In particular, there was a concordance between isopod size and gravel size distributions. There was no evidence for character displacement.

Appalachian cave stream communities are relatively simple systems, dominated by one to three isopod and amphipod species (Culver 1976). The limited amount of utilizable habitat is of great importance in structuring these communities. Utilizable habitat is limited to the underside of stream gravels, which provide concentrations of detritus, the major food source, and hiding places from the brunt of the current (Culver 1971, Estes 1978). Dislodgment from a rock often follows the encounter of two individuals and results in significant mortality (Culver 1973). Since washout is density-dependent, competition results, and is important in determining annual population size fluctuations (Culver 1971, Estes 1978), microhabitat separation (Culver 1973), and resistance of communities to invasion by other species (Culver 1976).

In this study we examined the effect of size on competition in two species of isopods found in northern West Virginia caves. We first tested the hypothesis that washout rates of different size isopods and gravel size are correlated. This should result in a "match" between isopod sizes and gravel sizes in cave streams. Second, we tested the hypothesis that interspecific competition is reduced by size divergence of the two species. This should result in a "mismatch" between isopod size and gravel size. Using an artificial stream in the laboratory, we showed that washout rate depends on both gravel and isopod size, and that size differences among isopods reduces competition. Then, using data on the size distribution of isopods and stream gravels in various caves, we assessed the importance of these two factors.

## METHODS AND MATERIALS

The isopods *Caecidotea holsingeri* (Steeves) and *Caecidotea cannulus* comprise the great majority of individuals and biomass of the macroscopic fauna in most cave streams of the Monongahela River drainage in West Virginia. Collections were made in every known location for the species in this drainage. This covers the entire range of *C. cannulus*. *Caecidotea holsingeri* is also known from caves in the New, Greenbrier, Elk, and James River drainages (Holsinger et al. 1976), where it often occurs with a rich amphipod fauna (Culver 1970). For comparative purposes, collections of *C. holsingeri* were taken from Linwood Cave in the Elk River drainage. This is the closest known locality to caves in the Monongahela River drainage. Caves visited are listed in Table 1.

Table 1. List of caves where collections were taken. All collections were made by the authors except for Mill Run, Nelson, and Cave Hollow caves where the collections were made by Dr. J.R. Holsinger. All caves are in the Monongahela River drainage except Linwood Cave, which is in the Elk River drainage. Cave locations and descriptions are in Davies (1965) and Medville and Medville (1972).

Cave	County	<i>C. cannulus</i>	<i>C. holsingeri</i>	Sampling dates
Alpena No. 1	Randolph	X	X	VIII/78
Bazzle	Randolph		X	V/73
Bowden	Randolph	X	X	VII/78, II/79, II/80
Cave Hollow	Tucker	X		III/61, VII/63, V/80
Glady	Randolph	X	X	VII/78, II/79, II/80
Harman	Randolph		X	V/73, II/79, II/80
Harper	Tucker	X	X	II/80
Mill Run	Tucker	X	X <sup>1</sup>	VII/67
Nelson	Randolph		X	VII/67, II/80
Linwood	Pocahontas		X	VII/78, II/79, II/80

<sup>1</sup> Male second pleopods, the critical taxonomic character, were not removed, but the bimodal size distribution is strong presumptive evidence that both species were present.

In four caves (Bowden, Glady, Harman and Linwood) stream gravels were collected from riffles where isopods were found. Gravels were sorted by diameter into 0.3 cm intervals up to 2.5 cm. The larger gravels were divided into those less than and greater than 5 cm in diameter.

For laboratory stream studies the isopods were collected alive and measured using an ocular micrometer on a dissecting microscope. Collections were sorted into two size classes: small (less than 4.5 mm long) and large (greater than 8 mm long). All individuals, including intermediate sizes, were eventually preserved, measured, and identified. All small individuals were *C. holsingeri* and all large individuals were *C. cannulus*.

Two experiments were done in an artificial stream in the laboratory (see Culver 1971 for design of the stream). To measure the effect of gravel size on washout rate, two 10 cm by 10 cm areas of rocks were used in the stream. One consisted of gravels between 0.2 cm and 1 cm in diameter; the other consisted of gravels between 2.2 cm and 3.8 cm in diameter. The washout rate of each size class of isopods was measured for each size class of gravels. Five individuals were used in each run, and each run was repeated at least four times. Animals that washed out were collected at the end of the artificial stream bed. Individuals washing out in the first 30 minutes were placed back in the stream, and then the number washed out after 12 hours was recorded.

The second experiment measured interspecific effects on washout rate, as reflected by size differences of the two species. To measure intrasize washout rates, 10 isopods of a single size class were placed in a 15 cm x 15 cm section of gravels of various sizes, patterned after a cave stream. Each of these runs lasted 24 hours. Intersize class competition was measured by following the procedure outlined above, but using five small isopods and five large isopods. Thus, the total number of isopods present at the beginning of a run was always 10. Each run was repeated five times.

All isopods collected were measured and identified. Identification posed some problems. Species can be separated only on the basis of the second male pleopod. Most males can be identified since the second pleopod sclerotizes at an early age. We found the following two characters to be reliable: the comparative length of the endopodial groove, and the angle between the endopodite tip and the cannula. Since males are usually scarcer than females, and none of the populations are large (we collected less than 50, usually less than 25, in any one cave), it was necessary to try to include females. There is little if any size dimorphism, so we called all females *C. holsingeri* that were smaller than the largest *C. holsingeri* male, and all females *C. cannulus* that were larger than the smallest *C. cannulus* male. Ambiguous cases were randomly assigned to the two species. In practice, such random assignments were only necessary for Glady Cave. We also present size histograms to obviate identification problems.

## RESULTS

Due to the relatively small number of isopods available, it was often necessary to use the same individual for more than one run in the arti-

ficial stream. Since individuals that washed out sometimes died, this introduces a potential bias if there are differences in washout propensity among individuals of the same size class. This would result in higher washout rates in earlier runs of the same experiment. There was no evidence that this happened.

There is a very clear tendency for small *C. holsingeri* to have higher washout rates in large gravels than in small gravels, and for large *C. cannulus* to have higher washout rates in small gravels than in large gravels (Table 2). The washout frequency of *C. holsingeri* is significantly higher ( $P < 0.01$ ) in large gravels ( $\bar{x} = 0.75$ ) than in small gravels ( $\bar{x} = 0.15$ ). Similarly, the washout frequency of *C. cannulus* is significantly higher ( $P < 0.05$ ) in small gravels ( $\bar{x} = 0.55$ ) than in large gravels ( $\bar{x} = 0.24$ ). These data suggest that there should be a "match" between gravel and isopod size distributions in natural streams.

Table 2. Washout rates of small *C. holsingeri* ( $< 4.5$  mm) and large *C. cannulus* ( $> 8$  mm) in small gravels ( $.2$  cm  $<$  diam.  $<$  1 cm) and large gravels ( $2.2$  cm  $<$  diam  $<$  3.8 cm). Statistical analysis used washout frequency transformed to  $\sin^{-1} \sqrt{x}$ , where  $x$  is the washout frequency.

Species	Gravel Size	N	x		$\sin^{-1} \sqrt{x} = y$			
			$\bar{x}$	S.E.	$\bar{y}$	S.E.	t	P
<i>C. holsingeri</i>	small	4	0.15	0.05	20.0	6.7		
<i>C. holsingeri</i>	large	4	0.75	0.05	60.2	3.2		5.46 $<$ 0.01
<i>C. cannulus</i>	small	4	0.55	0.05	47.9	2.4		
<i>C. cannulus</i>	large	5	0.24	0.12	23.3	10.2		2.07 $<$ 0.05

There was also evidence that size differences among isopods reduced the washout rate in an artificial stream with a variety of gravel sizes (Table 3). The washout frequency of large *C. cannulus* is significantly lower when small *C. holsingeri* are present ( $\bar{x} = 0.08$ ) than when the same total density of isopods, all of them large, are present ( $\bar{x} = 0.44$ ). The washout frequency of small isopods was slightly lower when large isopods were present (0.36 compared to 0.42), but the difference was not significant (Table 3).

The difference in washout frequency shown in Table 3 could be due either to size differences *per se* or to species differences *per se*. Washout experiments with intermediate-size isopods (Culver and Ehlinger, in preparation) indicate that size *per se* is more important. In these experiments, five small *C. holsingeri* (or five large *C. cannulus*) were put in the

artificial stream with five intermediate-size *C. holsingeri* or *C. cannulus*. If species differences are important, then total number of isopods washing out when all individuals are the same species should be different than when two species are involved. In fact, total washout of conspecifics ( $\bar{x} = 0.28$ , S.E. = 0.03, N = 6) was nearly identical to total washout of interspecifics ( $\bar{x} = 0.32$ , S.E. = 0.03, N = 4).

Table 3. Fraction of isopods washing out in artificial stream with various sizes of gravel. Statistical analysis used washout frequency (x) transformed to  $\sin^{-1} \sqrt{x}$ . Each run was started with 10 individuals (10 of one size, or 5 each of two sizes).

	N	x		$\sin^{-1} \sqrt{x} = y$			
		$\bar{x}$	S.E.	y	S.E.	t	P
<i>C. holsingeri</i> alone	5	.42	0.04	40.3	2.2	1.08	N.S.
<i>C. holsingeri</i> with <i>C. cannulus</i>	5	.36	0.04	36.7	2.5		
<i>C. cannulus</i> alone	5	.44	0.04	41.5	2.4	4.46	< 0.01
<i>C. cannulus</i> with <i>C. holsingeri</i>	5	.08	0.05	10.6	6.5		

Very limited information is available concerning *Caecidotea* in three of the caves listed in Table 1. Nelson and Bazzle caves have large populations of the amphipod *Gammarus minus*. Only two *C. holsingeri* were found in Bazzle Cave after extensive searching. A situation is similar in Nelson Cave. No isopods could be found in this cave in February 1980. Mill Run Cave has a large isopod population, but is closed by the owner. Specimens in National Museum of Natural History collections were measured, and had a bimodal size distribution. Male second pleopods were not removed for examination, but the bimodal size distribution is strong presumptive evidence that both species were present.

Length measurements for *C. cannulus* and *C. holsingeri* are summarized in Table 4. In all cases of syntopy, *C. cannulus* is at least 1.9 times as large as *C. holsingeri*, all the differences being statistically significant. However, consideration of allotopic populations complicates the issue. The allotopic population of *C. cannulus* in Cave Hollow Cave is slightly smaller ( $\bar{x} = 7.05$  mm) than syntopic populations of the same species ( $\bar{x} = 7.75$  mm, S.E. = 0.25), but the difference is not statistically significant ( $t = -0.83$ ). The allotopic population of *C. holsingeri* in Harman Cave is smaller ( $\bar{x} = 2.8$  mm) than syntopic populations ( $\bar{x} = 3.1$  mm, S.E. = 0.1), but the difference is not statistically significant ( $t = 1.42$ ). On the other hand, the allotopic population of *C. holsingeri* in Linwood Cave (which is in a different drainage basin) is larger ( $\bar{x} = 5.7$  mm) than syntopic populations, and the difference is statistically significant ( $t = 11.34$ ,

$P < 0.01$ ). In summary, there is no clear evidence for divergence in size where the species are syntopic.

Table 4. Length measurements of *Caecidotea holsingeri* and *Caecidotea cannulus*, in mm.

Cave	<i>C. holsingeri</i>			<i>C. cannulus</i>		
	$\bar{x}$	S.E.	N	$\bar{x}$	S.E.	N
Linwood	5.7	0.2	24	—	—	—
Harman	2.8	0.2	21	—	—	—
Bowden	2.5	0.1	23	8.2	0.4	19
Alpena	3.6	0.3	8	8.8	0.4	3
Glady	3.6	0.1	12	7.0	0.4	17
Harper	4.0	0.2	4	7.9	0.6	5
Cave Hollow	—	—	—	7.05	0.3	4

For the four caves where more than 20 individuals were collected, the size distributions of isopods together with the size distributions of the stream gravels are shown in Figure 1. The data given in Table 2 strongly suggest the two distributions should be correlated, although the actual gravel sizes that an isopod of a given size uses are not known. However, there are some striking similarities in the qualitative aspects of the gravel and isopod size distributions for each cave, which are summarized in Table 5. In Bowden Cave, both distributions are strongly bimodal. In Glady Cave, the gravel size distribution is weakly bimodal, while isopod size distribution is apparently unimodal with a broad size range. By contrast, in Harman Cave both gravel and isopod size distributions are strongly unimodal and skewed to the left. In Linwood Cave, gravel sizes are uniformly distributed for small gravels, and skewed to the right overall. Isopod sizes are strongly unimodal, with a narrow size range. There are two discrepancies between isopod and gravel size distributions. First, in Glady Cave, gravel size distributions are weakly bimodal and isopod sizes are not, although they do have the expected broad size range. Second, in Linwood Cave there is a broad size range of gravels and a narrow size range of isopods, and there is little concordance of the two distributions. With these two exceptions, there was a good fit between the two distributions.

## DISCUSSION

There are two interrelated hypotheses about body size of *Caecidotea cannulus* and *C. holsingeri*. The first is that small isopods suffer less washout (and less mortality) in small gravels and large isopods suffer less

washout (and less mortality) in large gravels. Thus, minimization of mortality (whether through natural selection or developmental adjustment of body size) should result in a concordance between body and gravel size distributions. Supporting this, previous work (Culver 1971, 1973) indicated that washout is due to encounters between two individuals, and thus is density-dependent. The second hypothesis is that interspecific competition is size-dependent. If the first hypothesis is true, then the extension to interspecific competition should result in character displacement, and at least a partial discordance between body and gravel size distributions.

Both laboratory and field data strongly support the first hypothesis. The artificial stream experiments (Table 2) clearly show that in the absence of other factors gravel size and isopod size should be correlated. Furthermore, field data support this hypothesis (Fig. 1, Table 5). In Bowden Cave, both distributions are bimodal. In Glady Cave, large gravels are less frequent (Table 3), and *C. cannulus* is smaller than in Bowden Cave. In Harman Cave, small gravels predominate, and *C. holsingeri* is small. The low frequency of large gravels in Harman Cave may be the reason for the absence of *C. cannulus*. Only in Linwood Cave is there a discordance difficult to explain by the first hypothesis (Fig. 1, Table 5). Larger isopods should be present. However, Linwood Cave is separated from the range of *C. cannulus* by a major drainage divide. Thus, the most reasonable explanation for the absence of large *C. cannulus* is historical.

The evidence for the second hypothesis is mostly negative. Artificial stream experiments suggest that size differences reduce interspecific competition (Table 3), at least for the larger species. On the other hand, field evidence provides no support for the character displacement hypothesis. The allotopic population of *C. cannulus* in Cave Hollow Cave is slightly but not significantly smaller than syntopic populations. Unfortunately for the testing of the hypothesis, *C. cannulus* in Cave Hollow Cave does not occur in a gravel-bottom stream area. Only four individuals were collected in three trips to the cave, and all of these were collected on bedrock in the stream (Holsinger, pers. comm.). Gravel-bottom riffles had large populations of the amphipod *Gammarus minus*. The size of *C. cannulus* in water flowing over limestone bedrock may be subject to optimization, but we have no idea what that optimal size is. Thus, even if individuals in Cave Hollow Cave were significantly smaller, its significance would be hard to interpret. *Caecidotea holsingeri* sizes also provide no support for character displacement. One allotopic population (Linwood Cave) is larger than all syntopic populations, and one (Harman Cave) is smaller than most syntopic populations. In addition, gravel size distributions provide no support for character displacement. If character displacement were occurring, then discordances between gravel and isopod distributions should result in greater separation of isopod sizes. But, in the case of Glady Cave, sizes of the two isopod species are unimodal while gravel sizes are bimodal (Fig. 1, Table 5).

Table 5. Qualitative characteristics of isopod and gravel size distributions shown in Figure 1. Quartiles and medians are given for each distribution (in mm for isopods, and diameter in mm for gravels). Frequency (F) of large gravel ( $> 12.3$  mm) is also listed.

Cave	Gravel					Isopods				
	Q <sub>1</sub>	M	Q <sub>3</sub>	Qualitative Features	F	Q <sub>1</sub>	M	Q <sub>3</sub>	Qualitative Features	
Linwood	5.6	11.9	19.1	Uniform for small gravel	0.44	5.0	5.4	6.2	Strongly unimodal, narrow size range, all intermediate in size	
Harman	2.4	5.6	10.3	Unimodal, skewed to small sizes	0.12	1.6	3.1	3.6	Unimodal, narrow size range, all small in size	
Bowden	2.4	11.9	19.1	Strongly bimodal	0.43	2.4	3.3	8.3	Bimodal, broad size range	
Glady	2.4	8.7	19.1	Weakly bimodal	0.27	3.7	5.3	7.6	Unimodal, broad size range, skewed toward small size	

It is worth pointing out that *C. cannulus* is, overall, larger than *C. holsingeri*. The basic question is what determines body size, both in the ultimate and proximate sense. It is unlikely that size differences are due to differences in age structure, since age (or at least size) structure is skewed toward older (or larger) individuals (Culver 1971). However, it is

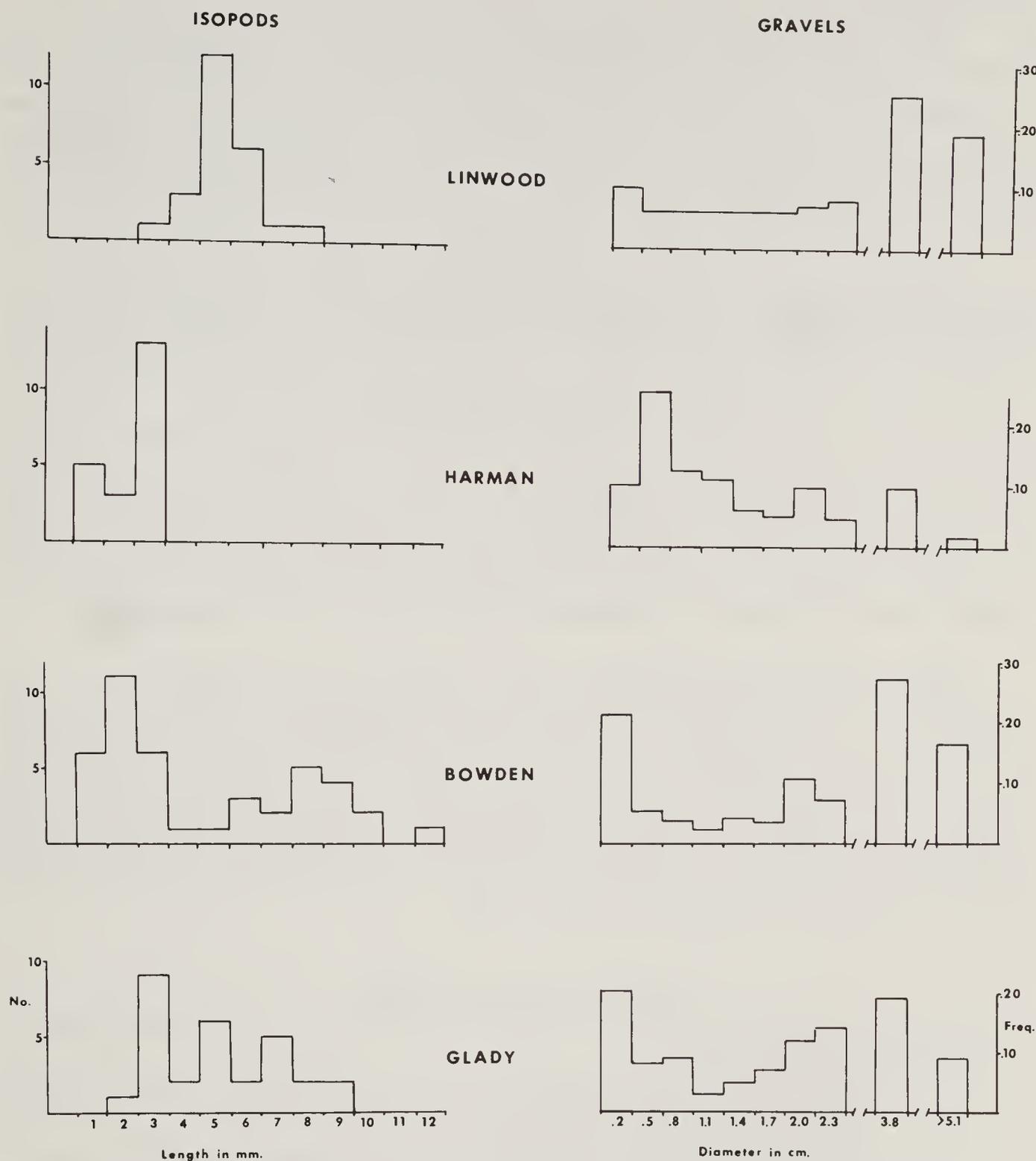


Fig. 1. Gravel and isopod sizes for Harman, Linwood, Bowden, and Glady caves. See Table 5 for description of the distribution.

impossible, with available data, to determine whether size differences are genetically or environmentally determined. Dickson's (1977) finding that drip pool populations of the amphipod *Crangonyx antennatus* had consistently larger size individuals than stream populations, but showed no

genetic differences (Dickson et al. 1979), suggests environmental determination of size. On the other hand, the extensive genetic differentiation of the amphipod *Gammarus minus* in narrow anticlinal valleys similar to those in our study area (Gooch and Golladay, in press) suggests that differences in body size on a small geographic scale may be genetically determined.

Even if *C. cannulus* is genetically larger than *C. holsingeri*, it is not clear that this is the result of past competition. The two species may have descended from a common surface ancestor, and the larger size of *C. cannulus* may be the result of past competition. However, the two species may have descended from separate ancestors that differed in body size. There is no way to determine which of the two scenarios is the correct one.

Finally, elimination of some of the data would result in the conclusion that character displacement is important. In particular, if data for Harman Cave and Glady Cave are eliminated, character displacement would be indicated. Individuals in allotopic populations of *C. holsingeri* are large (Linwood Cave) and individuals of *C. cannulus* in such populations are small (Cave Hollow Cave). In fact, we originally studied these two species because they appeared to show character displacement (see Holsinger et al. 1976). This supports the critique of character displacement by Strong et al. (1979) and shows that sampling should not be ended merely because the "correct" results have been obtained.

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# Life History of the Mottled Sculpin, *Cottus bairdi*, in Northeastern Tennessee (Osteichthyes: Cottidae)

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**ABSTRACT.**—*Cottus bairdi* in northeastern Tennessee spawns for the first time at the end of its second year. Mature males are larger than mature females. Spawning occurs in early April and is completed within a one week period. Comparison with northern and western populations indicates lower fecundity, larger eggs, and larger hatchlings for *C. bairdi* in northeastern Tennessee. Population estimates revealed that immature fish were concentrated in disturbed, exposed habitats, whereas mature fish were evenly distributed between disturbed and undisturbed habitats.

## INTRODUCTION

Several studies reported on the life history and ecology of the mottled sculpin, *Cottus bairdi*, in the northern and western parts of its range (Hann 1927; Koster 1936; Bailey 1952; Zarbock 1952; McCleave 1964; Ludwig and Norden 1969; Patten 1971). This study presents information on the life history of *C. bairdi* in the southeastern part of its range.

## MATERIALS AND METHODS

Specimens of *C. bairdi* (N = 795) were collected from a 2.5 km section of Straight Creek, a tributary to the Nolichucky River, 7.5 km south of Johnson City, Washington County, Tennessee. Stream width in this section ranges from 0.5 to 2.0 m and averages 1.0 m. The stream has a gravel and rubble substrate and is 95% riffle (depth = 5-15 cm) with 5% pool habitat (depth = 0.5-1.0 m). Streamside canopy is either 100% in undisturbed areas or 0% in areas disturbed by road construction 15 years prior to this study. Stream gradient in this section is 39 m km<sup>-1</sup>. Water temperatures were recorded with a mercury thermometer at the time of collection; highest recorded temperature was 19°C on 11 July 1977 and on 5 August 1977.

Collections were made by electrofishing at monthly intervals from March 1977 to April 1978. All specimens were preserved in 10% formalin (buffered with CaCO<sub>3</sub>) within one hour of capture.

A supplementary collection of *C. bairdi* (N = 102) was made from North Indian Creek in Unicoi County, Tennessee on 25 February 1978 to provide comparative information from a larger stream. North Indian Creek at this collection site is 5 to 10 m wide, 0.2 to 0.5 m deep in riffle areas, and 2 to 3 m deep in pools.

Total length (TL) of all specimens was measured to the nearest 1.0 mm and gonads from all specimens greater than 45 mm TL were weighed

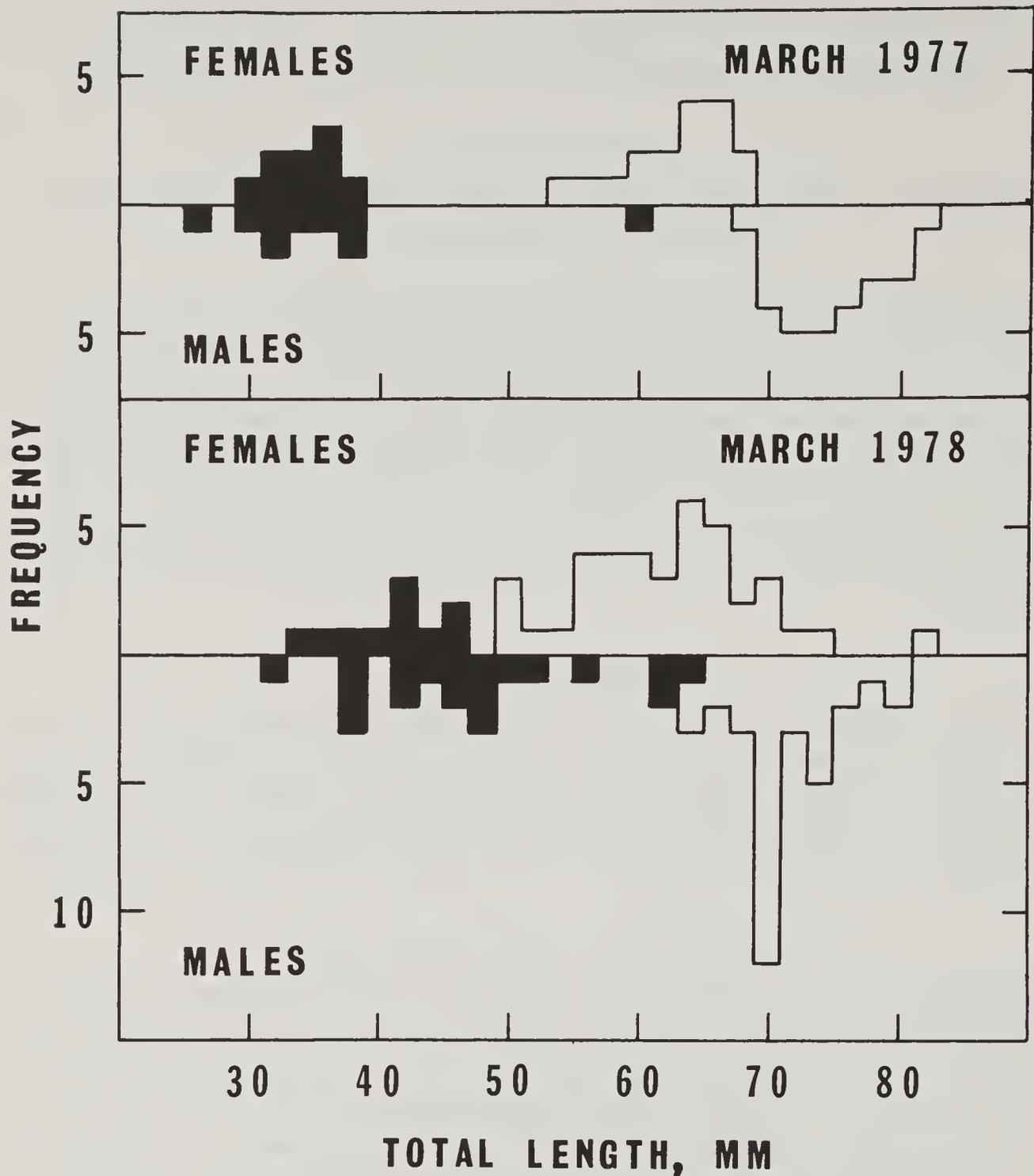


Fig. 1. Frequency distributions of total lengths of all *C. bairdi* collected from Straight Creek, March 1977 and 1978. Each bar represents a 2-mm interval. Solid bars = immatures; open bars = breeding adults.

to the nearest 0.1 mg. Measurements of follicle diameter, egg diameter, and TL of hatchlings were made with an ocular micrometer in a dissecting microscope.

Mark and recapture population estimates were made in April and May 1979 in a 195 m section of Straight Creek. This included a 100 m section (#1) with 100% canopy cover and a 95 m section (#2) with 0% canopy cover. All specimens less than 50 mm TL were marked with a left pelvic clip while specimens over 50 mm TL were tagged with a fingerling tag (Floy Tag and Mfg., Inc., Seattle, Washington 98105) fastened with vinyl thread under the anterior part of the dorsal fin. Some tag loss was noted, but the duration of the study was short enough that tagging wounds were

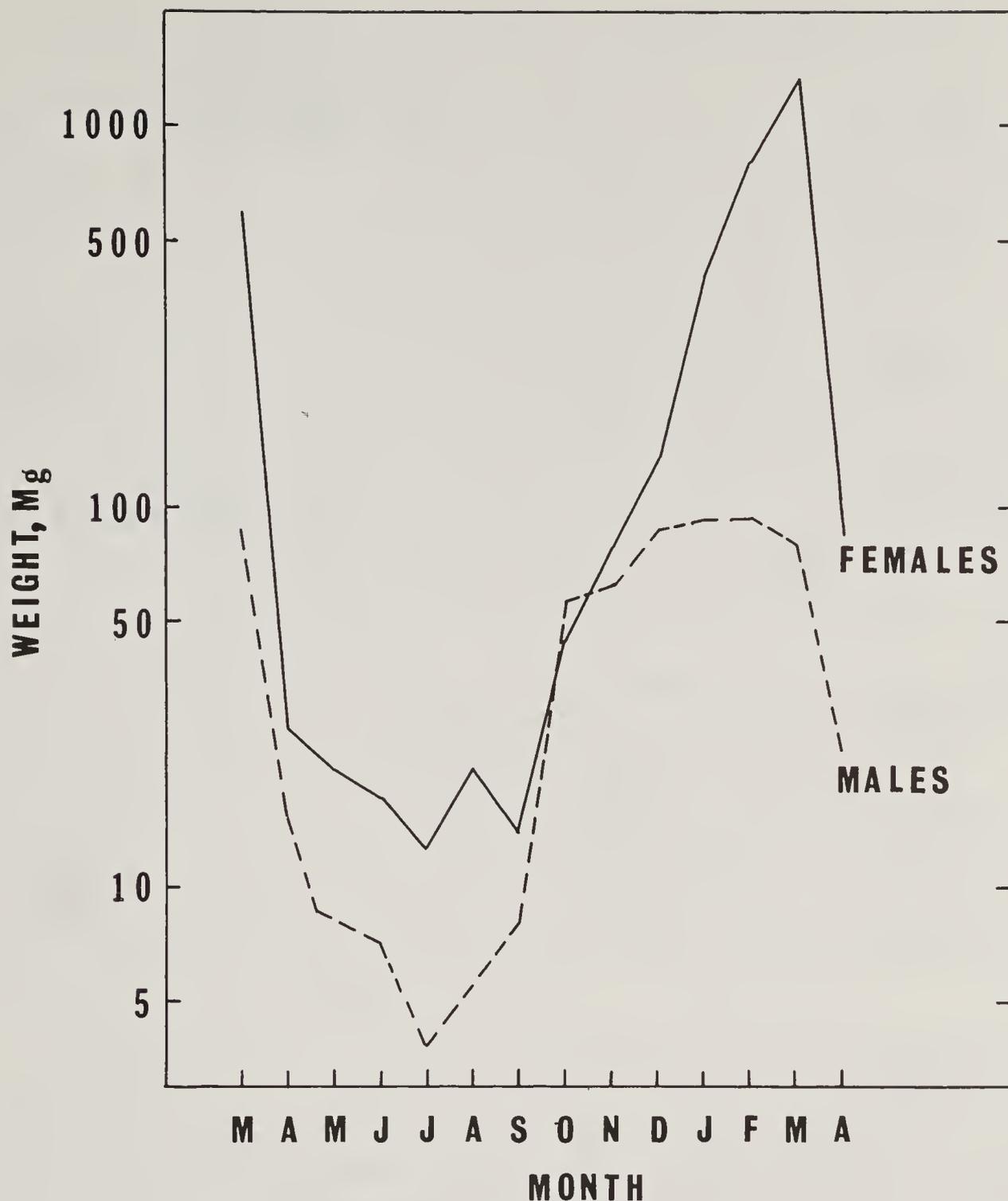


Fig. 2. Mean monthly gonad weights for all *C. bairdi* over 45 mm TL collected from Straight Creek, March 1977 to April 1978.

easily detected and fish with lost tags could be identified for population estimates of this size class.

## RESULTS

*Population structure.*—Length/frequency distributions of all sculpins collected from Straight Creek in March 1977 and March 1978 are presented in Figure 1 and suggest that both males and females reproduce for the first time at the end of their second year. Mature males were distinctly larger than mature females in this population. Comparison of the rather small samples of immatures in the March 1977 and

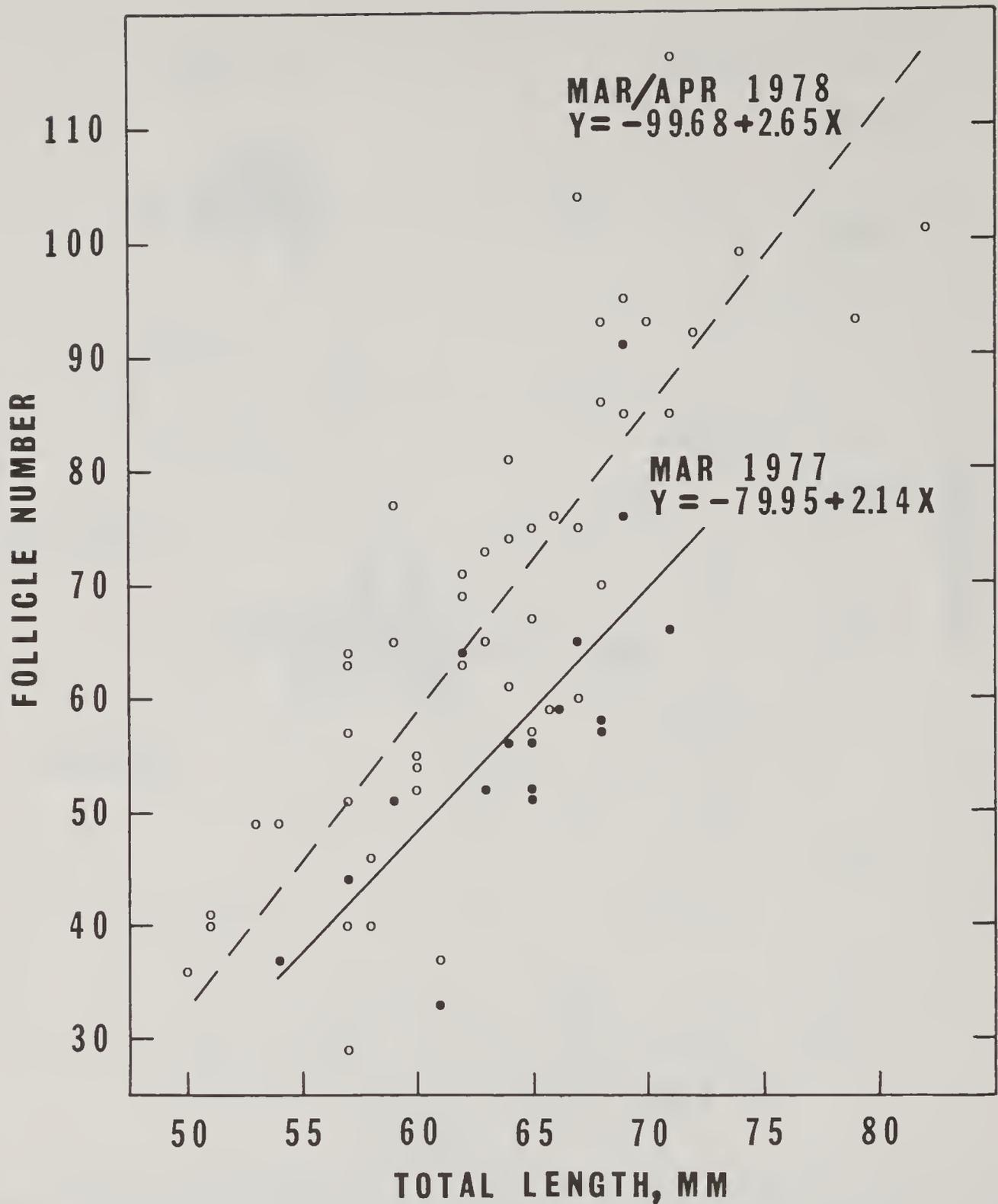


Fig. 3. Number of enlarged follicles related to total length in gravid females from Straight Creek.

March 1978 length/frequency distributions suggests between-year variation in growth rates for the Straight Creek population during this study.

*Reproduction.*—Monthly gonad weights for mature specimens are presented in Figure 2 and indicate that spawning occurred in early April. In 1978, weekly samples were taken during March and April to more precisely indicate the time of spawning. On 4 April all seven mature females were still gravid, but on 11 April all but 1 of 12 mature females were spent. Afternoon water temperatures on these dates were 14°C and 12°C, respectively.

Fecundity estimates were based on gravid females collected just prior to spawning in March 1977 and March/April 1978. Figure 3 presents the relationship between TL and number of mature follicles for 1977 and 1978. Correlation coefficients were 0.69 ( $N = 18$ ,  $P < 0.01$ ) and 0.82 ( $N = 47$ ,  $P < 0.001$ ), respectively. Regression lines were calculated by Bartlett's 3-group method for Model II regression (Sokal and Rohlf 1969); 95% confidence limits for the slopes were 0.85 to 3.43 (1977) and 2.08 to 3.28 (1978). Although the average total lengths for gravid females in 1977 ( $\bar{x} = 63.9$  mm,  $N = 18$ , 95% confidence limits =  $\pm 2.14$  mm) and 1978 ( $\bar{x} = 63.2$  mm,  $N = 47$ , 95% confidence limits =  $\pm 2.00$  mm) were similar, the average number of mature follicles in 1978 ( $\bar{x} = 67.7$ ,  $N = 47$ , 95% confidence limits =  $\pm 5.98$ ) was significantly higher than in 1977 ( $\bar{x} = 56.8$ ,  $N = 18$ , 95% confidence limits =  $\pm 6.34$ ). Gravid females collected from North Indian Creek in February 1978 were similar in TL ( $\bar{x} = 63.2$  mm,  $N = 53$ , 95% confidence limits =  $\pm 1.69$  mm) to the Straight Creek samples and had an average follicle count of 55.5 ( $N = 53$ , 95% confidence limits =  $\pm 3.62$ ).

Average follicle diameter in gravid females collected just prior to spawning in April 1978 was estimated by measuring five follicles each from nine different females. Average diameter was 3.32 mm ( $N = 45$ , 95% confidence limits =  $\pm 0.08$  mm, range = 2.8-3.8 mm). A clutch of eggs collected on 3 May 1978 had an average egg diameter of 3.73 mm ( $N = 10$ , 95% confidence limits =  $\pm 0.05$  mm, range = 3.6-3.8 mm). This clutch was incubated at 15°C and hatched on 8 May 1978. Sac fry at hatching had an average TL of 9.80 mm ( $N = 5$ , 95% confidence limits =  $\pm 0.22$  mm, range = 9.6-10.1 mm).

*Population density.*—Mark and recapture population estimates were calculated from  $N = (M+1)(C+1)/(R+1)$ , where  $N$  = estimated population,  $M$  = number of marked fish,  $R$  = number of marked fish recaptured, and  $C$  = total sample of marked and unmarked fish in recapture sample (Ricker 1975:78, equation 3.7). Calculation of 95% confidence limits was based on the 95% confidence limits of  $R$  (Ricker 1975:78 and Append. II). Population estimates and supporting data are presented in Table 1.

Table 1. Mark and recapture population estimates of *C. bairdi* in Straight Creek, April 1979.

Section	Size Class (TL)	M	C	R	N	95% Confidence Limits (N)
#1	< 50 mm	6	5	2	14.0	5.8-210.0
1	> 50 mm	30	17	9	55.8	32.6-139.5
#2	< 50 mm	145	57	24	338.7	237.9-549.9
2	> 50 mm	33	16	9	57.8	33.8-144.5

At the time of the April/May 1979 population estimates specimens less than 50 mm TL were mainly immature individuals ending their first year, whereas specimens more than 50 mm TL were mature individuals that were two years or older (Fig. 1). Mature specimens were equally abundant in the two sections, whereas the immature size class showed strikingly higher density in the exposed and disturbed habitat of section #2.

## DISCUSSION

In this study one year old fish were all immature and most two year old fish were mature individuals in breeding condition (Fig. 1). This is similar to maturity patterns found by investigations in Michigan (Hann 1927); New York (Koster 1936); Montana (Bailey 1952); Wisconsin (Ludwig and Norden 1969); and Washington (Patten 1971). Koster (1936), however, noted that the lake-dwelling form, *C.b. kumlieni*, appeared to mature at the end of its first year at an average TL of approximately 61 mm (conversion from standard length based on Bailey 1952).

The sexual dimorphism in size found for breeding individuals in this study was noted in other studies (Hann 1927; Koster 1936, for *C.b. bairdi* but not for *C.b. kumlieni*; Simon and Brown 1943; Bailey 1952; Zarbock 1952; Ludwig and Norden 1969).

In this study spawning occurred at water temperature of 12° - 14°C during a one week period in early April. Previous investigations of spawning by *C. bairdi* reported water temperatures ranging from 5° - 18°C and dates from late February to late May (reviewed in Ludwig and Norden 1962). Hann (1927) and Koster (1936) reported brief spawning periods similar to the findings in this study, but Simon and Brown (1943), Bailey (1952), and Ludwig and Norden (1962) reported spawning periods of a month or more.

Several authors presented information on the average number of enlarged follicles in gravid females for western and northern populations of *C. bairdi* (257, Hann 1927; 120 for *C.b. bairdi* and 135 for *C.b. kumlieni*, Koster 1936; 629, Simon and Brown 1943; 203, Bailey 1952; 328, Ludwig and Norden 1969; 95, Patten 1971). Although no particular geographic pattern in this variation is evident in these populations, these estimates are consistently higher than fecundity estimates reported in this study (three separate estimates = 56, 57, and 68) even though the size ranges of gravid females were quite similar in all studies. Correlated with this, average follicle diameter in northeastern Tennessee (3.32 mm) was greater than diameters reported by other authors (2.0-2.5 mm, Hann 1927; 2.2 mm, Simon and Brown 1943; 1.88 mm, Ludwig and Norden 1969). This correlation continues when comparing average egg size (in nest) and average hatchling size. In this study eggs averaged 3.73 mm and sac fry 9.8 mm. Corresponding estimates from other studies are: sac fry — 6.4 mm (Hann 1927); eggs — 2.6 and 2.7 mm, sac fry — 6.9 and 7.9 mm (Koster 1936); 5-day fry — 6.9 mm (Simon and Brown 1943); sac fry

— 8.1 mm (Bailey 1952); sac fry — 5.9 mm (Ludwig and Norden 1969). This striking emphasis on “quality” (larger and fewer eggs) by *C. bairdi* in northeastern Tennessee deserves further investigation in other southern populations to determine whether or not it is a consistent geographic trend.

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# Notes on the Distribution and Ecology of the Black Mountain Dusky Salamander *Desmognathus welteri* Barbour (Amphibia: Plethodontidae) in Tennessee

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**ABSTRACT.**—*Desmognathus welteri* was found at 16 localities in the Cumberland Mountains and the northern half of the Cumberland Plateau. The observed intermittent seasonal nature of most southern Cumberland Plateau small streams, combined with the strong aquatic tendencies of the species, may be responsible for the apparent absence of *D. welteri* in this region. cursory observations indicate that *D. welteri* and *D. monticola* may be competitors, while *D. welteri* and *D. fuscus* probably partition the streamside habitats according to gradient and substrate particle size. Alteration of streams by coal strip mine operations and extensive use of the species for fish bait have resulted in the decline of many local populations. Considering these factors, *D. welteri* should continue to be considered a species “in need of management” in Tennessee.

## INTRODUCTION

*Desmognathus welteri* was originally described from Big Black Mountain, Harlan County, Kentucky, as a subspecies of *D. fuscus* (Barbour 1950). Subsequently, Barbour (1971) believed that sufficient evidence was available to treat it as a distinct species. Recent studies of Caldwell (1977, 1980), Caldwell and Trauth (1979), and Juterbock (1975, 1978) provided substantial morphological evidence that supports this proposal. Barbour (1971) noted the range of *D. welteri* as the eastern third of Kentucky with disjunct populations in east central Alabama and northern West Virginia. Caldwell (1977) stated that *D. welteri* probably does not occur in Alabama and that most reports of the species from the state were based on misidentified *D. monticola*. Juterbock (1975) provided the first Tennessee record of *D. welteri*, from Cumberland Gap National Historic Park, Claiborne County. Caldwell (1977) and Caldwell and Trauth (1979) reported the species from Pickett, Fentress, Cumberland, and Scott counties. Redmond and Jones (1978) noted the Tennessee distribution to include the northern half of the Cumberland Plateau Physiographic Province. Caldwell and Trauth (1979) believed that the distribution of *D. welteri* reached its southern limit in the Crab Orchard Mountains near the northern end of Walden Ridge, Cumberland County, Tennessee.

In 1975, the Tennessee Wildlife Resources Agency included *D. welteri* in a list of species designated as “wildlife in need of management.” This designation includes species that are potential candidates for threatened status, but whose status needs further evaluation in the state

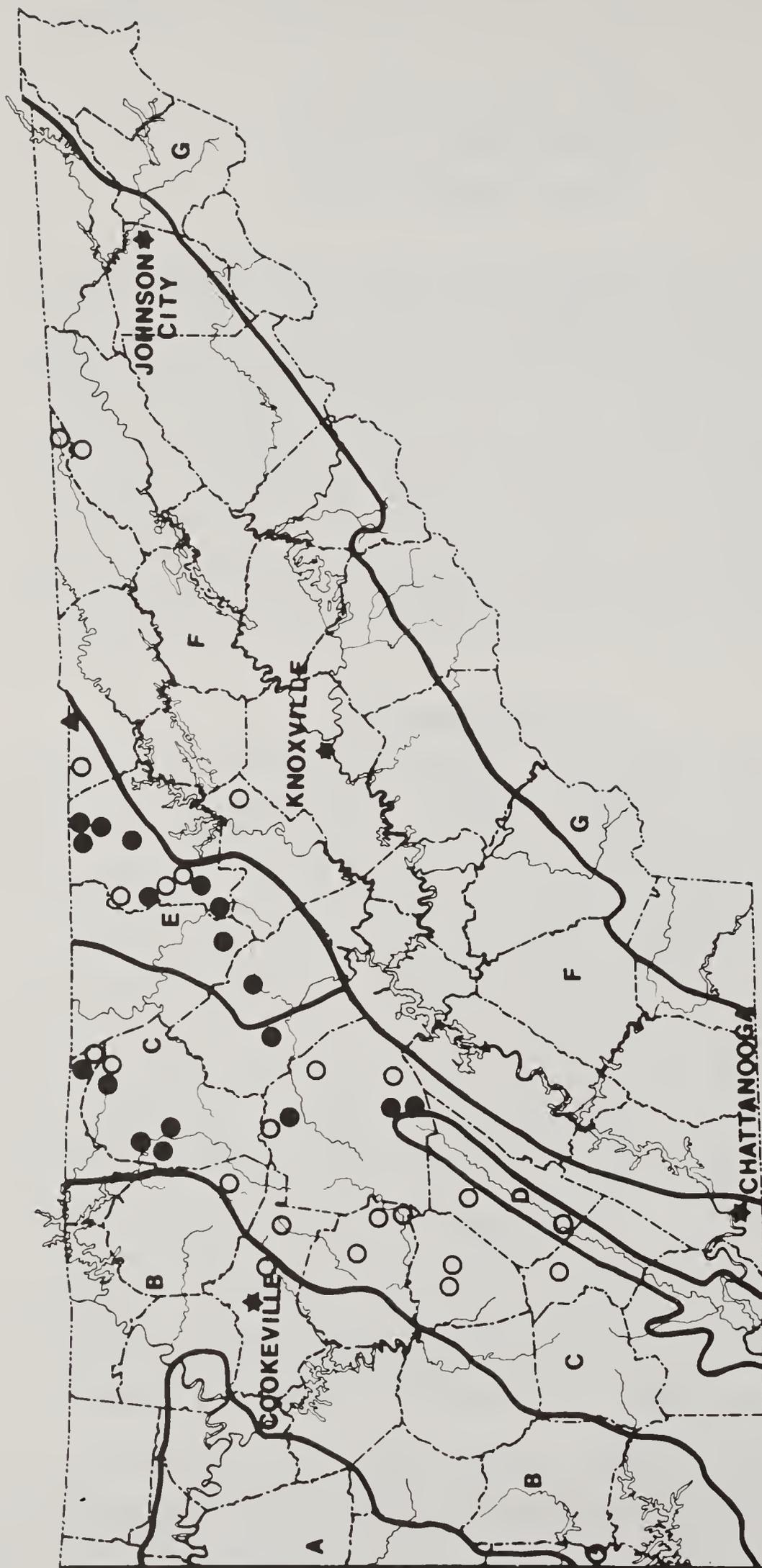


Fig. 1. Map of eastern Tennessee depicting collecting sites. The physiographic features shown were modified from Miller (1974). Solid circles denote localities from which *D. welteri* were examined. Hollow circles denote localities where the species was not found. Solid triangle denotes literature record believed to be valid. Symbols may represent more than one collecting site. Area labeled A denotes Nashville Basin, B denotes Highland Rim, C denotes Cumberland Plateau, D denotes Sequatchie Valley, E denotes Cumberland Mountains, F denotes Ridge and Valley, and G denotes Blue Ridge.

Table 1. Localities from which *D. welteri* were examined, with a list of associated desmognathine species and numbers collected at each locality.

Locality	Associated species (N)
<i>Campbell County</i>	
Bear Branch just off Hwy. 63, 17.4 km NW of Caryville, elev. 500 m; 5 specimens, UTKVZC 01135-39, 20 August 1977.	<i>D. fuscus</i> (7, and 1 egg clutch)
Small trib. to New River, 2.1 km NNW of Shea on gravel road, elev. 463-518 m; 5 specimens, UTKVZC 01144-48, 20 August 1977.	<i>D. monticola</i> (3)
Small trib. to Davids Creek, 0.6 km W of peak Cross Mountain on gravel road, elev. 805 m; 9 specimens, UTKVZC 01156-64, 20 August 1977.	<i>D. fuscus</i> (6)
Small trib. to Clear Fork, 4.3 km E of jct. Hwys. 25W and I-75 on 25W, elev. 305-335 m; 9 specimens, UTKVZC 01337-45, 18 September 1977.	<i>D. fuscus</i> (1) <i>D. monticola</i> (12)
Small trib. to Clear Fork, 6.2 km E of jct. Hwys. 25W and I-75 on 25W, elev. 366-396 m; 1 specimen, UTKVZC 01199, 18 September 1977.	<i>D. fuscus</i> (1)
Small trib. to Hickory Creek, 1.8 km W of jct. Hwys. 25W and 90 on 25W, elev. 366-396 m; 6 specimens, UTKVZC 01219-24, 18 September 1977.	<i>D. fuscus</i> (14) <i>D. monticola</i> (2)
Small trib. to Big Creek, approx. 5.6 km NE of jct. Hwys. 25W and 63 on 25W, elev. 427-442 m; 6 specimens, UTKVZC 01232-37, 18 September 1977.	<i>D. fuscus</i> (1) <i>D. monticola</i> (3)
<i>Cumberland County</i>	
Genesis Creek at Genesis Road, 11.0 km S of Morgan Co. line; 1 specimen, AUM 24602.	unknown*
Small trib. to Renfro Creek, 4.8 km SE of jct. Hwys. 70 and I-40 on 70, elev. 488 m; 1 specimen, UTKVZC 01245, 1 October 1977.	<i>D. ochrophaeus</i> (5)
Small trib. to Renfro Creek, 5.5 km SE of jct. Hwys. 70 and I-40 on 70, elev. 482-488 m; 4 specimens, UTKVZC 01267-70, 1 October 1977.	<i>D. fuscus</i> (7) <i>D. ochrophaeus</i> (7)
Small trib. to Jewett Branch, 4.6 km NW of Cumberland-Bledsoe Co. line on Jewett Road, elev. 634-671 m; 12 specimens, UTKVZC 01298-309, 1 October 1977.	<i>D. fuscus</i> (6) <i>D. ochrophaeus</i> (6)
<i>Fentress County</i>	
Deer Gap, Buffalo Cove, approx. 5.6 km S of Jamestown on Hwy. 127; 25 specimens, AUM 24648-72, 2 September 1975.	unknown*
Northupp Falls; 45 specimens, AUM 24603-47, 1 September 1975.	unknown*
Small trib. to Campbell Hollow Branch, 3.0 km NW of Jamestown on Hwy. 52, elev. 470 m; 2 specimens, UTKVZC 03277-78, 30 April 1978;	none

Locality	Associated species (N)
5 specimens, UTKVZC 02032-36, 9 November 1977. Small trib. to Stuart Creek, 2.4 km (airline) W of Sharp Place, elev. 463-488 m; 2 specimens, UTKVZC 02049-50, 9 November 1977.	<i>D. fuscus</i> (4)
<i>Morgan County</i>	
North Prong of Flat Fork, approx. 6.6 km (airline) WNW of Fork Mountain; 2 specimens, UTKVZC 02704-05, 1976.	none
Catoosa Wildlife Management Area, Pennykin Branch, elev. 494 m; 4 specimens, UTKVZC 01169-72, 28 August 1977.	none
<i>Pickett County</i>	
Small trib. to Rock Creek, 7.7 km (airline) NE of Sharp Place, elev. 408 m; 4 specimens, UTK VZC 02057-60, 9 November 1977.	none
<i>Scott County</i>	
Small trib. to Bill's Branch nr. USGS weather station, elev. 425-460 m; 8 specimens, UTKVZC 02267-74, 2 October 1976.	<i>D. fuscus</i> (24)* <i>D. monticola</i> (1)

\*Localities not collected by the author.

(Tennessee Wildlife Resources Agency 1978). The purpose of this study was to further delineate the range of *D. welteri* and to provide comments concerning its ecology and factors threatening the species in Tennessee.

## METHODS

Field investigations were conducted from July 1976 to May 1979. Forty-one collection sites were visited and two people spent approximately one hour at each site (Fig. 1). Because most published reports indicate that the range of *D. welteri* is predominantly within the Cumberland Plateau and Mountain regions, most field efforts were concentrated in these regions of Tennessee. However, field searches were conducted in the adjacent Highland Rim and Ridge and Valley.

Eighty-five specimens of *D. welteri* from sixteen localities were collected and deposited in The University of Tennessee Vertebrate Zoology Collection, Knoxville (UTKVZC). At each locality, general habitat characteristics were noted, and associated desmognathine species were collected and deposited in UTKVZC (Table 1). General habitat characteristics and desmognathine species present were also noted for collection sites where *D. welteri* was not found (Table 2). Seventy-one specimens of *D. welteri* from three localities were examined from the Auburn University Museum (AUM) (Table 1). Morphological characteristics used to distinguish *D. welteri* from other sympatric desmognathine species were taken from Caldwell (1977, 1980), Caldwell and Trauth (1979), and Conant (1975).

Table 2. Localities where *D. welteri* was not found, with a list of desmognathine species and numbers collected at each locality.

Locality	Desmognathine species (N)
<i>Anderson County</i>	
Spring run, 7.1 km (airline) SE of Norris, elev. 290 m, 21 March 1979.	none
<i>Bledsoe County</i>	
Small stream approx. 1.3 km N of Shoemate Gap on gravel road, elev. 488 m, 2 September 1978.	<i>D. fuscus</i> (1)
McWilliams Creek, 8.3 km (airline) NE of Dunlap, 19 July 1976.	<i>D. fuscus</i> (9)
<i>Campbell County</i>	
Cove Creek, 7.5 km NW of jct. old Hwy. 63 and I-75 on 63, elev. 396 m, 20 August 1977.	<i>D. fuscus</i> (4) <i>D. monticola</i> (1)
Dan Branch, 3.2 km (airline) W of Elk Valley community, elev. 384 m, 18 September 1977.	<i>D. fuscus</i> (1)
Roadside stream, 4.9 km NW of jct. old Hwy. 63 and I-75 on 63, elev. 360 m, 25 March 1978.	<i>D. fuscus</i> (1)
<i>Claiborne County</i>	
Small seepage trib. to Clear Fork, 1.8 km SW of Kentucky-Tennessee state line on Hwy. 90, elev. 390 m, 18 September 1977.	none
<i>Cumberland County</i>	
South Fork of Elmore Creek, Catoosa Wildlife Management Area, 1.8 km NNE of Genesis checking station, elev. 494 m, 28 August 1977.	<i>D. fuscus</i> (16)
Bluffs and seepages along western bank of Yellow Creek, just N of Hebbertsburg Bridge, elev. 463 m, 28 August 1977.	none
Periwinckle Spring, 1.9 km SSE of Grassy Cove community on Hwy. 68, elev. 488-500 m, 1 October 1977.	<i>D. fuscus</i> (14)
<i>Fentress County</i>	
Small seepage area below bluff, 2.1 km (airline) NNE of Sharp Place, elev. 488 m, 9 November 1977.	<i>D. fuscus</i> (4)
<i>Hancock County</i>	
Small southern trib. to Clinch River, 2.4 km (airline) ENE of Horton's Ford, elev. 366 m, 23 March 1978.	<i>D. fuscus</i> (7)
<i>Hawkins County</i>	
Small stream on northern slope of Poor Valley,	<i>D. monticola</i> (4)

Locality	Desmognathine species (N)
10.6 km (airline) NW of Surgoinsville, elev. 469-488 m, 22 March 1978.	
<i>Moore County</i> Small southwestern trib. to Shipman Creek, 0.3 km NW of Ledford's Mill, elev. 305 m, 4 October 1979.	<i>D. fuscus</i> (5)
<i>Overton County</i> Small headwater stream of Big Laurel Creek 0.8 km S of jct Hwys. 85 and 164 on 164, elev. 530-549 m, 12 May 1979.	<i>D. fuscus</i> (12)
<i>Pickett County</i> Small seepage below sandstone bluff at Natural Bridge, 4.9 km (airline) NE of Sharp Place, elev. 494 m, 9 November 1977.	<i>D. fuscus</i> (6)
<i>Putnam County</i> Unnamed Creek and spring run, 1.2 km S of jct. Hwys. 70N and 84 on 84, elev. 518 m, 12 May 1979.	<i>D. fuscus</i> (9)
Eastern trib. to Mill Creek along gravel road, 1.6 km S of Mill Creek Baptist Church, elev. 381 m, 12 May 1979.	<i>D. fuscus</i> (14)
<i>Sequatchie County</i> Reynolds Creek, 9.2 km (airline) NNW of Dunlap, 20 July 1976.	<i>D. fuscus</i> (14)
<i>Van Buren County</i> Small stream, 0.5 km SW of Spencer on Hwy. 30, elev. 533 m, 19 November 1977.	none
Small stream, 3.3 km E of jct. Hwys. 30 and 111 on 30, elev. 488 m, 19 November 1977.	<i>D. fuscus</i> (3)
Small stream, 5.3 km E of jct. Hwys. 30 and 111 on 30, elev. 396 m, 2 September 1978.	<i>D. fuscus</i> (1 with egg clutch)
<i>White County</i> Near jct. of Clifty creek and Millsea Branch, 0.9 km NE of Mobra, elev. 463 m, 19 November 1977.	none
Base of waterfall in upper headwaters of Wildcat Branch, 2.6 km SW of Bon Air, elev. 549 m, 19 November 1977.	none
Virgin Falls and Cave, southern slope of Little Chestnut Mountain, elev. 335 m, 2 September 1978.	<i>D. fuscus</i> (2)

## RESULTS AND DISCUSSION

As determined in this study, the range of *D. welteri* in Tennessee is

shown in Figure 1. The species appears limited to the Cumberland Mountains and northern half of the Cumberland Plateau. The southernmost locality is on the south slope of Brady Mountain at the northern end of the Sequatchie Valley, Cumberland County. This locality is approximately 16 km south of Crab Orchard Mountain, which Caldwell and Trauth (1979) speculated to be the southern distributional limit of the species. In Tennessee, *D. welteri* was commonly found along small- to medium-size streams flowing through mesophytic forests. Inhabited streams were typically permanent, and *D. welteri* usually occurred in areas with steep to moderate gradients and with bedrock to coarse gravel substrates. Specimens were taken from 305 to 805 m elevation.

The factors responsible for the apparent absence of *D. welteri* from the southern half of the Cumberland Plateau are obscure. Seemingly suitable habitats occur in several gorges and along stream courses on the eastern and western escarpments of the region. Caplenor (1979) described these gorge forests and contrasted them with the more xeric forests of the Plateau's tablelands. A general observation made during this study was that most seemingly suitable streams on the southern Plateau were often dry during extended droughts, especially in late summer and fall. *Desmognathus welteri* has been characterized as a semiaquatic species which seldom ventures far from water (Juterbock 1975; Caldwell 1977). Juterbock (1975) noted that, in a given stream, *D. welteri* was found in lower numbers in late summer when streamflow was decreased than during periods of higher flow. The observed seasonal intermittent nature of southern Plateau streams, combined with the strong aquatic tendencies of the species, may be responsible for the apparent absence of *D. welteri* in this region.

Listed in order of abundance, the desmognathine species found closely associated with *D. welteri* were *D. fuscus*, *D. monticola*, and *D. ochrophaeus* (Table 1). Where they were found together, *D. welteri* and *D. fuscus* were seldom in the same habitats. *Desmognathus fuscus* was typically taken along those sections of stream where the gradient was gentle to moderate and where the substrate was silt, sand, or small gravel; it was often found several meters from the stream. *Desmognathus welteri* was most frequently found in areas with steep to moderate gradient where the stream substrate was predominantly large rock, gravel, or bedrock; it was seldom found more than a meter from the stream. In Alabama, Folkerts (1968) described a similar phenomenon involving *D. fuscus* and *D. monticola*, where *D. monticola* was the typical inhabitant of the rocky, swift areas of a stream.

During this study, *D. welteri* and *D. monticola* were taken from remarkably similar areas along the streams surveyed. *Desmognathus welteri* was usually the more abundant in habitats where both species were found. Based on these cursory observations, it appears that *D. monticola* and *D. welteri* may be competitors, with *D. welteri* being the domi-

nant form. However, detailed studies are needed to adequately describe the ecological interactions between these two species. The observed partitioning of streamside habitats in Tennessee by *D. welteri* and *D. fuscus* according to gradient and substrate particle size, and the possible competitive relationship between *D. welteri* and *D. monticola*, are consistent with the findings of Juterbock (1975), Caldwell (1977), and Caldwell and Trauth (1979).

Alteration of streams by coal strip mine operations, and extensive use of the species by bait fishermen, have resulted in the decline of many local populations. *Desmognathus welteri* was never taken from stream habitats where strip mining operations had removed bank vegetation, or from streams with high silt, sand, and heavy metal concentrations. However, because the species can inhabit relatively small streams, it was often found in isolated, unaltered coves adjacent to orphan mine lands. Within its range and in surrounding regions, *D. welteri* was one of the most common "spring lizards" found in bait shops. Its large size makes it a sought after fish bait. Up to 300 individuals were observed in one bait shop holding box in Norris, Anderson County, Tennessee. This collecting pressure is greatest during spring, summer, and early fall, and probably results in the removal of many large, reproductively active females.

Widespread use of *D. welteri* as a live bait may have resulted in numerous introductions and alterations of the natural range of the species in Tennessee. Martof (1953) discussed the distributional and genetic ramifications of the commercial use of salamanders for fish bait. Many *D. welteri* populations studied were found along small rivulets which drained into nearby, often-fished streams. Although the data are inconclusive, this distributional pattern may indicate past introductions by fishermen.

Considering the lack of knowledge concerning factors limiting its distribution, the rapid habitat degradation occurring in the Cumberland Mountains and Plateau, and the widespread use of the species as fish bait, I believe that *D. welteri* should continue to be considered as "in need of management" in Tennessee.

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# Morphological and Habitat Variability in *Gammarus minus* Say (Amphipoda: Gammaridae)

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**ABSTRACT.**—The surface dwelling ecotype of *Gammarus minus* Say in the central Appalachian Mountains varies in morphology partly in conformance to a habitat scale from fully open to borderline hypogean. Characters investigated were eye facet density and relative lengths of eye and three appendages to body length. There also is considerable interdemographic variability not related to habitat scale. This is inferred to be due to isolation of some demes, which have undergone differentiation, and to gene flow among others, which has prevented full ecotypic differentiation.

## INTRODUCTION

Geographical variation in morphology within species of gammarid amphipods is known to occur in *Gammarus minus* (Cole 1970, Minckley and Cole 1963, Holsinger and Culver 1970); *G. bousfieldi* (Minckley and Cole 1963); *G. oceanicus* (Crocker and Gable 1977); *G. pulex* (Pinkster 1971, 1972); and *Crangonyx antennatus* (Dickson 1977). Intraspecific variation in freshwater species has been linked to diet, light, current velocity, substratum, competing and predatory species, and genetic drift.

This study examines interdemographic morphological variation in epigeal populations of *Gammarus minus* Say. This species ranges from the mid-Atlantic piedmont westward through the middle Appalachian Mountains, Interior Low Plateaus, and portions of the Mississippi Valley and Ozarks uplift, reaching peak abundances in caves, springs, and springfed streams underlain by carbonate rocks (Holsinger 1976). Nine populations were examined, seven from Huntingdon and Centre counties in central Pennsylvania, and one outlier population each in Virginia and West Virginia. Our investigation was directed to the question: is morphological variation systematically related to habitat variation? Habitats vary in substratum, velocity, macrofauna, and many other attributes. This study focuses on variation in habitats grading from open surface, i.e. fully epigeal, to cave associated or borderline hypogean. The study by Holsinger and Culver (1970) indicated that the morphology of *Gammarus minus* is particularly sensitive to this habitat spectrum. All future references to Holsinger and Culver will be to this 1970 paper. These authors reported differences in eye shape and size and ratio of appendage to body length in cave and surface dwelling populations in the mid-Appalachians. Shoemaker (1940) earlier recognized a distinct cave form

with reduced eyes and elongate antennae, and Hubricht (1943) further described an intermediate type between the surface and deep cave forms. Holsinger and Culver distinguished three intergradational forms or ecotypes, each associated with a specific habitat. Form I amphipods have considerably reduced eyes, bluish body color, and elongate appendages, and are confined to a few large cave systems in isolated karst areas of Virginia and West Virginia. Form II individuals have slightly reduced eyes, bluish bodies, and slightly lengthened appendages, and occur widely in mid-Appalachian caves. Form III amphipods are brownish and robust, with large eyes and relatively shorter appendages, and are found in surface habitats throughout the species' range. The three forms occur in proximity in the karst areas of southeastern West Virginia. Many populations there are sharply genetically distinct, genetic breaks frequently coinciding with divides between karstic sub-basins (Gooch and Hetrick 1979).

The present study is limited to Form III populations and intergradational Form II, which comprise the great majority of *G. minus* populations. We used, among others, the labile eye and appendage characters of the Holsinger and Culver study. The nine populations occupied habitats which we rank ordered from most open or epigeal to least open (or marginal hypogean). Measurements were taken on each population to determine the degree to which ecotype typifying morphology conformed to the habitat scale. Strong conformance as shown by similar rank order would indicate a predominant influence of environmental factors related to habitat openness. Weak conformance would indicate that other factors such as local adaptation to biotic or physical conditions or the interplay between genetic drift and gene flow strongly influence morphology.

## METHODS AND MATERIALS

Samples of *Gammarus minus* were taken using a Surber sampler and, on highly irregular bottoms, a dip net. From each sample 50 sexually mature individuals, 25 of each sex, were chosen at random. The following measurements were made on one side, indiscriminantly right or left, on each individual:

(1) Packing density and regularity of the eye. The facets bordering the eye may be tightly and regularly packed or loose and irregular, producing, respectively, a border that is smooth or one that is ragged and embayed. Holsinger and Culver treated this character in some detail and depicted eye shape in typical members of the three habitat forms (their Fig. 3). The latitude of regularity was much less in our populations. Eyes were scored on an estimated ordinal scale of high, intermediate, and low density and regularity.

(2) Lobe orientation. The eyes of typical epigeal *G. minus* are short reniform with the lower lobe usually broader than the upper (Cole 1970). In some individuals the lobes are equal or the upper lobe is broader. Eyes

were scored as broad lobe up, equal, or down. This character is not obviously related to habitat but is simply an easily scored trait that may show interdemic variation.

(3) Lobe angle. The reniform eye has a shallow, slightly variable angle opening anteriorly. This angle was not measured but was scored relatively on an ordinal scale from 1 to 3 indicating, respectively, more acute, intermediate, and more obtuse. Like lobe orientation this is not an ecotype differentiating character.

(4) Eye length. The length of the eye is successively less in Form II and Form I amphipods. It was measured (mm) parallel to the long dorsoventral axis of the eye.

(5) Length of antenna 1. Elongate first antennae are particularly striking in cave ecotypes. The first antenna was measured from peduncular base to flagellar tip.

(6) Length of pereopod 7. The seventh pereopod is relatively longer in hypogean habitats. It was measured extended from coxal base to tip of dactyl.

(7) Length of uropod 3. This is a highly variable biramous structure in *G. minus* (Holsinger 1976) and is usually longer in cave forms. The long ramus (exopod) was measured.

Measurements were taken on population samples from sites listed below in inferred rank order, from most nearly hypogean to most open eipigean.

(i) Emma Spring, Huntingdon Co., PA: strongly shaded spring discharging from a subterranean conduit in a limestone rockface.

(ii) Smoke Hole Spring, Giles Co., VA: partially shaded spring pool formed from outflow of Smoke Hole Cave.

(iii) Greenland Gap, Grant Co., WV: partly shaded runoff 4 m downstream from a spring.

(iv) Cunninghams, Huntingdon Co., PA: unshaded runoff 7 m downstream from spring.

(v) Marklesburg, Huntingdon Co., PA: shaded, heavily vegetated first order stream collected 12 m downstream from small spring.

(vi) Church Camp, Centre Co., PA: shaded runoff 15 m downstream from series of large ground seeps.

(vii-viii) Petersburg I and II, Huntingdon Co., PA: large, partly shaded springfed stream; site I is a large, open, impounded pool, site II is runoff about 20 m downstream from the pool.

(ix) James Creek, Huntingdon Co., PA: unshaded site in a second-order stream about 3 km downstream from spring sources.

This rank order is subjectively based on proximity to subterranean water source, likelihood that discharge is from a sizeable cave or conduit, and amount of cover or shade. Emma Spring is very secluded. Smoke Hole Spring receives the immediate discharge of Smoke Hole Cave, which probably contains Form II amphipods as does nearby Tawneys Cave, a site of Holsinger and Culver. These localities would be expected to harbor populations bordering on Form II. The James Creek site is

completely open and relatively remote from hypogean environments, so the Form III morphology should be well developed there. These are the maximally contrasting sites and they define the extremes of the Form III habitat spectrum. Other localities differ less strikingly and are ranked in only an approximate way.

## RESULTS

The ordinal scale scores of eye packing density, broad lobe orientation, and lobe angle of population samples are given by sex in Table 1. Localities are in rank order with the most epigeal at bottom. Packing density is relatively uniform, with most samples distributed in about a 40:60 ratio between high- and intermediate-density scores. Only a few scattered individuals, constituting less than 1% of the total, have the low-density irregular borders indicative of the typical Form II ecotype. There is a shift from intermediate- to high-density eyes in increasingly open populations. James Creek has the highest proportion of regular-eyed individuals, although it does not differ significantly from Emma Spring, using the R x C Chi-square test, with pooling of low and intermediate scores. However, the second to fourth ranked sites have low high-density scores and a 2 x 2 contingency table of the four highest ranking populations with the five lowest, pooled by site and sex, yields a significant difference ( $X^2 = 6.53$ , 1 *df*,  $p < .05$ ). Much of the difference is contributed by Smoke Hole Spring, whose entire sample consists of intermediate density eyes. When sexes pooled over populations are compared by contingency table there is a significantly greater proportion of high-density eyes in females ( $X^2 = 9.83$ , 1 *df*,  $p < .01$ ). We have no hypothesis to account for this difference, but since females are smaller it may be related to size rather than sex.

Table 1 shows little interdemic variation in broad lobe orientation or lobe angle. All pairwise contingency table tests were performed on the sample distributions of both characters, with broad lobe up pooled with equal lobe scores. Of 36 tests none indicated significant differences between localities for lobe orientation. The overall distribution, to which all population samples conform fairly closely, is in the ratio 7:33:60, broad lobe up, equal, and down, respectively. This confirms Cole's (1970) observation that the lower lobe is usually broader in *G. minus*. Although lobe orientation is quite variable within populations, interdemic variation is too low for this character to be useful in geographic studies. Lobe angle is only slightly more variable, with 4 of 36 pairwise tests yielding significant differences between sites. All involve the Petersburg I sample, which has a high proportion (0.49) of individuals with more obtuse angles. The overall ratio is 16:51:33, more acute, intermediate, and more obtuse angle, respectively. This character also appears to have little value in studies of geographical variation.

The characters eye, antenna 1, pereopod 7, and uropod 3 lengths will

Table 1. Scores of eye facet packing density (high, intermediate, low), lobe orientation (broad lobe up, equal, down), and lobe angle (more acute, intermediate, more obtuse). Localities are in rank order, with the most epigeal at bottom.

		Packing density			Broad lobe			Lobe angle		
		High	Inter.	Low	BLU	Equal	BLD	Acute	Inter.	Obtuse
Emma Spring	♂	11	14	0	1	6	18	4	10	11
	♀	7	18	0	1	7	17	2	12	11
Smoke Hole		0	25	0	4	12	9	5	16	4
		0	25	0	4	4	17	3	14	8
Greenland Gap		3	22	0	3	9	13	4	17	4
		8	17	0	2	7	16	2	14	9
Cunninghams		8	17	0	2	9	14	2	13	10
		6	18	1	1	9	15	3	11	11
Marklesburg		7	18	0	3	9	13	10	12	3
		10	15	0	1	11	13	4	11	10
Church Camp		3	22	0	3	9	13	4	13	8
		8	17	0	1	9	15	5	13	7
Petersburg I		4	21	0	0	11	14	4	11	10
		10	13	2	1	7	17	1	10	14
Petersburg II		7	18	0	3	8	14	5	14	6
		9	16	0	3	6	16	2	12	11
James Creek		6	19	0	0	8	17	4	13	8
		18	7	0	0	8	17	7	12	6
Total		49	176	0	19	81	125	42	119	64
Total	♂♂ ♀♀	76	146	3	14	68	143	29	109	87

be treated together. These characters, except for eye length, also were investigated by Holsinger and Culver. They are correlated with body length by the relative growth equation  $Y = aX^b + c$ , in which  $Y$  is any one of the above characters as the dependent variable;  $X$  is the independent variable, body length;  $a$  is the slope of the regression line;  $b$  is the coefficient of allometry; and  $c$  is the intercept of the regression line on the ordinate. If  $b$  is other than 1 there is nonlinear relative growth (allometry) of parts. If  $b = 1$  there is no allometry and the equation simplifies to  $Y = aX + c$ , the linear regression equation. Allometry in populations of differing size distributions would make meaningful comparisons more dif-

Table 2. Linear regression of eye and appendage lengths against body length. Values are for 25 males (upper row) and 25 females (lower row) per locality, averaged over 9 localities. Further explanation in text.

Dependent variable	slope $a$	Y-intercept $c$	$r^2$
Eye length	0.04 $\pm$ 0.02	0.10	.67
	0.01 $\pm$ 0.02	0.27	.12
Antenna 1 length	0.62 $\pm$ 0.16	-0.41	.69
	0.57 $\pm$ 0.17	-0.17	.61
Pereopod 7 length	0.41 $\pm$ 0.12	-0.42	.63
	0.50 $\pm$ 0.09	-0.33	.80
Uropod 3 length	0.23 $\pm$ 0.07	-0.28	.62
	0.20 $\pm$ 0.06	-0.20	.65

ficult. Holsinger and Culver obtained values of  $b$  close to unity and concluded that allometry was not important in the adult growth of antenna 1, pereopod 7, or uropod 3 relative to body length. We also tested for allometry by solving for  $b$  in the equation  $Y = a + b \log X$  (Frazzetta 1975), obtaining the slope  $b$  from plots of sample means of eye and appendages against mean body lengths of males and females separately. Values of  $b$  ranged between 0.78 and 1.15 for appendage growth, none of which was significantly different from unity. For eye length,  $b$  for males was  $1.08 \pm 0.21$  and for females  $0.67 \pm 0.28$ . The latter figure suggests negative allometry, but the large standard error and the anomalously low coefficient of determination for females (0.12) make this estimate of  $b$  meaningless. With qualification for eye length in females, we conclude with Holsinger and Culver that over the range of measurements used in adult *G. minus* allometry is a minor factor in determining length ratios.

Interdemic regression data on sample mean eye and appendage lengths against mean body lengths are presented in Table 2. There are no significant differences in slope between sexes. Excepting female eye length, the coefficients of determination are between 0.61 and 0.80, indicating moderate scatter of locality means and probably reflecting non-uniform slopes and intercepts of growth equations of different populations. The slopes for appendage growth are generally slightly higher than those obtained by Holsinger and Culver for Form III amphipods, but not significantly so.

The ratios of eye and appendage length to body length in rank ordered habitats are given in Table 3. Mean length of males is  $9.28 \pm 0.16$  mm, about 1 mm less than Holsinger and Culver determined for III habitats. Mean female length is  $6.73 \pm 0.14$  or 73% of male length. There is considerable interdemic variation in female/male length ratio, from

Table 3. Body lengths, and ratios of eye and appendage lengths to body length, presented by sex. Localities are rank ordered from most hypogean to most epigean sites.

Locality	Mean length (mm)		Eye/body		Antenna 1 /body		Pereopod 7 /body		Uropod 3 /body	
	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀
Emma Spring	9.67 ± .12	6.96 ± .20	.046	.052	.607	.598	.484	.460	.207	.172
Smoke Hole	8.98 ± .09	6.68 ± .16	.052	.055	.595	.586	.516	.417	.210	.174
Greenland Gap	9.93 ± .13	6.05 ± .09	.050	.059	.549	.514	.472	.438	.199	.161
Cunninghams	8.29 ± .20	7.42 ± .14	.049	.049	.615	.528	.533	.469	.226	.183
Marklesburg	10.37 ± .22	6.59 ± .13	.050	.055	.592	.532	.479	.445	.209	.174
Church Camp	9.48 ± .18	7.08 ± .15	.049	.052	.592	.553	.481	.431	.199	.162
Petersburg I	9.25 ± .14	6.64 ± .09	.053	.060	.572	.530	.464	.428	.194	.153
Petersburg II	9.31 ± .11	7.00 ± .15	.048	.054	.535	.515	.478	.452	.189	.161
James Creek	8.28 ± .22	6.13 ± .17	.053	.054	.529	.561	.442	.462	.172	.179
$\bar{x}$	9.28 ± .16	6.73 ± .14	0.050	0.054	0.576	0.546	0.483	0.451	0.201	0.169

Table 4. Pairwise comparisons of eye/body length ratios vs. antenna 1/body length ratios (top) and uropod 3/body length ratios vs. pereopod 7/body length ratios (bottom) of males of rank ordered localities. Single asterisks indicate significant differences at the 0.05 level, double asterisks at the 0.01 level, using the Mann-Whitney *U* Test.

		Eye/body								
		EM	SH	GR	CU	MK	CC	P-I	P-II	JC
Ant-1/body	EM		**	**	-	**	*	**	**	**
	SH	**		*	**	*	**	-	*	-
	GR	**	*		**	-	-	**	-	*
	CU	-	**	**		**	**	**	**	**
	MK	**	*	-	**		-	**	-	**
	CC	*	**	-	**	-		**	-	**
	P-I	**	-	-	**	*	*		**	-
	P-II	**	*	-	**	-	-	**		**
	JC	**	-	*	**	*	**	-	**	
		Uro-3/body								
		EM	SH	GR	CU	MK	CC	P-I	P-II	JC
Per-7/body	EM		-	*	-	-	-	**	**	**
	SH	**		*	-	-	-	**	**	**
	GR	*	**		-	*	-	-	-	**
	CU	-	**	-		-	-	-	-	**
	MK	**	-	**	**	**	-	**	**	**
	CC	-	**	-	-	**		*	*	**
	P-I	*	**	-	-	**	-		-	**
	P-II	-	**	-	-	**	-	-		**
	JC	**	**	**	**	**	**	**	**	**

0.64 at Marklesburg to 0.90 at Cunninghams. Although Holsinger and Culver found generally larger amphipods in cave populations, there is no evident trend toward larger size in either sex in our less epigeal sites.

The last four columns of Table 3 display length ratios and feature two points of interest: nonsystematic interdemic variation in ratios, and systematic variation associated with rank in the habitat scale. Nonsystematic variation was assessed by testing the ratio arrays of all charac-

Table 5. Pairwise comparisons in females. Captions as in table 4.

		Eye/body								
		EM	SH	GR	CU	MK	CC	P-I	P-II	JC
Ant-1/body	EM		**	**	**	*	-	**	**	-
	SH	-		**	**	-	**	**	-	-
	GR	**	**		**	**	**	-	**	**
	CU	**	**	-		**	**	**	**	**
	MK	**	**	-	-		-	**	-	-
	CC	-	*	*	-	-		**	*	-
	P-I	**	**	-	-	-	-		**	**
	P-II	**	**	-	-	-	-	-		-
	JC	-	**	*	-	-	-	-	-	
		Uro-3/body								
		EM	SH	GR	CU	MK	CC	P-I	P-II	JC
Per-7/body	EM		-	-	*	-	-	*	-	-
	SH	-		-	-	-	-	**	**	-
	GR	**	**		**	-	-	*	*	*
	CU	-	-	**		-	*	**	**	-
	MK	*	**	-	**		-	**	**	-
	CC	*	*	-	*	-		-	-	-
	P-I	**	**	-	**	-	-		-	**
	P-II	-	*	-	*	-	-	*		**
	JC	-	-	**	-	*	-	**	-	

ters in pairwise locality comparisons using the Mann-Whitney  $U$  test. The results for males are shown in Table 4 and for females in Table 5. Interdemic variation in length ratios is extensive. Of 288 pairwise tests, 144 per sex, 166 or 58% show significant ( $p < .05$ ) or very significant ( $p < .01$ ) differences between localities. Variation is greater in males (65% of tests) than females (50%), which may be related to size rather than sex. Among characters with sexes pooled, interdemic differences are greatest in eye length ratio (51 of 72 comparisons, 71%) and are at roughly the same level for appendage ratios (antenna 1, 56%; pereopod 7, 57%; uropod 3, 47%). Some of this variation is due to comparison of samples from strongly contrasting habitats at opposite ends of the ranking. Some

is nonsystematic and unrelated to the epigean-hypogean scale as shown by the fact that many similarly ranked sites differ significantly in ratios. Tables 4 and 5 show this qualitatively: ratio variation due purely to habitat difference would produce a pattern of significant differences (asterisks) in comparisons of widely rank separated sites and non-significant differences (dashes) in comparisons of similar rank. However, asterisks and dashes are so interspersed as to indicate numerous significant differences between like ranked localities.

Systematic variation lies in the association of ratios with habitat rank. If the eye and appendage size differences between ecotypes are also distinguishable within the single Form III ecotype, eye length ratio should increase and appendage length ratios should decrease with increasing (more epigean) rank. The predicted trends are roughly confirmed in Table 3. Some ratios, however, do not conform to expectation for their rank. This is especially so for eye length in both sexes and pereopod 7 length in females, which reveal no discernible trends.

Holsinger and Culver obtained appendage ratios in males of the three ecotypes. Their mean values, followed by ours in parentheses, are: antenna 1, I .720, II .644, III .570, (.576); pereopod 7, I .496, II .463, III .442 (.483); uropod 3, I .211, II .190, III .184 (.169). Our figures approximate the published ones for Form III amphipods except for pereopod 7, which has almost the relative length of Form I. Agreement is good considering the wide range of ratios found in both investigations and the small sample sizes used in the earlier study.

In 24 of 27 comparisons male appendage ratios are higher than female ratios. The sex differences are significant at the 0.05 level by the Mann-Whitney *U* test for all 3 appendages. Ruling out allometry, these data indicate generally greater appendage elongation in males than females. The effect does not extend to eye length, which does not differ significantly between sexes. Curiously, the three instances of higher appendage ratio in females belong to the James Creek population. Unless parasitism or an unusual environmental factor was responsible (neither were evident), this suggests that relative appendage elongation between sexes is genetically labile and occasionally prone to variation in semi-isolated populations.

The findings on all habitat associated characters are summarized in Table 6, which presents each locality rank ordered by its score or ratio, progressing to epigean typical values to the right. For each site there is considerable scatter in rank by both sex and character. Nevertheless the pattern of low rank for borderline type II habitats and high rank for fully open type III habitats does emerge. Emma Spring and Smoke Hole Spring, for example, rank near the hypogean pole for most characters and James Creek and Petersburg I and II usually rank near the epigean. At the foot of Table 6 overall rank order is given and each locality name is provided below in parentheses by its mean rank over all characters. This provides us with two scales of rank order—the habitat scale

Table 6. Rank order of localities for six characters in males and females. Bars between localities indicate rank order ties for that character. Overall rank order is given at bottom, based on the mean rank for characters. Mean rank scores given in parentheses.

Character	Site Rank												
	1	2	3	4	5	6	7	8	9				
Eye density	♂	SH	GR	—	CC	P-I	JC	MK	—	P-II	CU	EM	
	♀	SH	CU	P-I	EM	GR	—	CC	P-II	P-II	MK	JC	
Eye/body		EM	P-II	CC	—	CU	GR	—	MK	SH	P-I	—	JC
		CU	EM	—	CC	P-II	—	JC	SH	—	MK	GR	P-I
Ant-1/body		CU	EM	SH	—	MK	—	CC	P-I	GN	P-II	JC	
		EM	SH	JC	CC	CC	MK	P-I	P-I	CU	P-II	GR	
Per-7/body		CU	SH	EM	CC	CC	MK	P-II	P-II	GN	P-I	JC	
		SH	CU	JC	EM	EM	P-II	MK	GR	GR	CC	P-I	
Uro-3/body		CU	SH	MK	EM	EM	CC	GR	GR	P-I	P-II	JC	
		CU	JC	SH	—	MK	EM	CC	CC	P-II	—	GR	P-I
Overall	CU (2.75)	SM (2.90)	EM (3.55)	CC (4.60)	MK (5.35)	JC (6.20)	P-II (6.25)	GN (6.45)	P-I (6.95)				

previously given and this character scale. A one-to-one conformance of ranks would indicate that interdemic variation in these characters is completely determined by openness of habitats and their proximity to hypogean environments. The scales conform well for six localities, which conform from zero to two rank positions. Three large discrepancies do occur and require explanation: (1) Cunninghams has the highest hypogean character score, very narrowly over Smoke Hole Spring, but ranks as only the fourth most hypogean habitat; (2) Greenland Gap ranks eighth in character scale, third in habitat; (3) James Creek ranks sixth and ninth, respectively. It should be underscored that neither scale is an absolute standard to which the other can be compared. A difference in rank may mean faulty ranking of habitat, i.e. the habitat is less or more epigeal to the amphipods than to the observer, or that factors other than habitat scale affect the characters and their rank. Our discussion can take factors of the second type into account more easily than the first. For example, James Creek is almost certainly the most fully epigeal site, yet its character rank does not reflect this (note, however, that its mean rank is only 0.75 positions higher than that of the ninth ranked locality). Its overall rank is higher due simply to the high appendage ratios of its females, as was mentioned earlier and is apparent from Tables 3 and 6. Presumably slender-limbed females is a genetic characteristic indigenous to the James Creek population and is unrelated to the habitat scale.

The rank discrepancies of Greenland Gap and Cunninghams are at first puzzling. Greenland Gap is about 175 km southwest of seven of the localities and could obey different ecogeographic rules. However, Smoke Hole Spring and most of the localities of Holsinger and Culver are even more distant and they match the Pennsylvania populations quite closely in character trends. One potential influence on ecotype that has not been considered is migration and attendant gene flow. Populations subjected to high migration rates from contrasting habitats would not undergo as marked ecotypic differentiation as isolated demes. This is especially true if the phenotypic expression is largely under genetic control. The Greenland Gap site is only 2 m upstream from North Fork Patterson Creek, which is an open, typical III-habitat harboring a population of *G. minus*. It is probable that gene exchange between the populations has prevented the Greenland Gap population from developing the characters associated with its habitat type. Cunninghams, on the other hand, feeds immediately into Standing Stone Creek, a stream that lacks *G. minus*. We infer that Cunninghams is thus a highly isolated deme that has developed strongly habitat specific characters. No other locality appears to be as exposed to gene flow or as isolated as these two, although this factor has probably influenced character scores everywhere to some extent.

## DISCUSSION AND CONCLUSIONS

A summary analysis of our data falls into three categories. First, a

morphological profile of the common epigean ecotype was done, extending the pioneering work of Holsinger and Culver to additional populations, both sexes, and larger sample sizes. Second, the level of interdemic variability was determined and variability was related to the epigean-hypogean habitat spectrum and to other factors. Last, the overall pattern of interdemic variation was evaluated, which also may be applicable to other freshwater species.

All characters displayed high intrademic variability, and eye density and length ratios of eye and appendages also varied significantly among demes. Lobe orientation and lobe angle scores were distributed quite uniformly over populations and thus have less value in geographical studies in the Appalachians. Growth of appendages was approximately linear on body length in the adult size range, without significant differences in slope between sexes or large differences in intercepts. Growth equations were different enough among populations, however, to give coefficients of determination usually less than 0.70 on locality mean lengths. Female amphipods averaged 73% the length of males, but proportionate size of sexes varied widely. We have no evidence as to genetic or directly environmental causes of size differences. Females also had statistically significant smaller appendage length ratios than males.

Interdemic character variation was both systematic, that is habitat scale related, and nonsystematic. The former is evidenced by the finding that Form III demes in shaded, secluded springs near cave or conduit discharge usually had more irregular eyes and more elongate appendages than more open populations. At Emma Spring and Cunninghams, at least, there are no known Form II populations. This suggests that morphology is an *in situ* adaptation and not the result of genetic mixing with cave ecotypes. These intergradational populations would be expected to possess slightly reduced eyes as well. Although we have included eye length ratio in the composite character scale there is no clear trend toward eye reduction (Table 3). We conclude that ecotypical characters are intergradational among epigean demes and that the characters rank roughly in the same order as habitats scaled from fully epigean to semihypogean.

The conformation of character and habitat rankings is very inexact. Aside from sampling errors and imprecision in assigning habitat rank, there is extensive nonsystematic and statistically significant interdemic variability. Some of this variability may actually be systematic adaptation to habitat variables not apparent to the observer. Minckley and Cole (1963) found variation, mostly of setation patterns, in *G. minus* in two Kentucky streams to be associated with lotic and lentic microenvironments, aquatic vegetation, and the presence of the probable competitor *Gammarus bousfieldi*. Dickson (1977) noted that type and amount of food influenced pigmentation and body and antenna length in the troglobitic species *Crangonyx antennatus*.

A baseline datum in the present study is the existence of extensive

genetic differentiation among demes. This is true of the karst region where the ecotypes were first described (Gooch and Hetrick 1979) and in the central Pennsylvania localities studied here (Gooch and Golladay, in press). The genetic investigations were done on three polymorphic allozyme loci. Genetic patterns have not been found to correspond to habitats or ecotypes and will not be discussed here. They do clearly indicate that the most geographically isolated populations often carry atypical alleles in high frequencies, either due to local adaptation or genetic drift, and that demes linked by likely avenues of migration have not undergone as much genetic differentiation.

James Creek, with its aberrant ratio of female/male appendage lengths, is probably an example of a deme that has evolved morphological characters in partial isolation from other populations. Greenland Gap, on the other hand, apparently has been prevented from acquiring habitat specific characters due to strong gene flow from other habitats. The mid-Appalachian area is an environmental mosaic of epigeal, intermediate, and hypogean habitats. The result in *G. minus* has been the evolution of markedly differentiated ecotypes. Streams and divides, however, provide clear avenues and barriers to migration, leading to highly anisotropic gene flow. Superimposed on ecotypic variation and sometimes discordant with it is the local differentiation of isolated demes. Ecotypic distinctions are further modified by gene flow among demes that are open to migration.

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# Ozarka, A New Subgenus of *Etheostoma* (Pisces: Percidae)

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**ABSTRACT.** — A new subgenus of *Etheostoma* is diagnosed and briefly described. It consists of five species, *Etheostoma punctulatum*, *E. cragini*, *E. pallididorsum*, *E. boschungii*, and *E. trisella*, which have similar breeding colors, tubercle patterns and spawning habitats. The species are distributed from the Arkansas River drainage in Colorado to the upper Coosa River drainage in north Georgia and southeast Tennessee. Distribution, dispersal and relationships of the species are discussed, and a key to the species is presented.

## INTRODUCTION

The nominal darter genera were reduced to four (*Ammocrypta* Jordan, *Etheostoma* Rafinesque, *Hadropterus* Agassiz, and *Percina* Haldeman) by Bailey (1951) and further reduced to three (*Ammocrypta*, *Etheostoma*, and *Percina*) by Bailey (in Bailey et al. 1954). Bailey and Gosline (1955), in a review of the vertebral counts of American percids, placed the 70 species of *Etheostoma* in 12 subgenera (*Boleosoma*, *Ioa*, *Etheostoma*, *Ulocentra*, *Allohistium*, *Nothonotus*, *Oligocephalus*, *Austroperca*, *Psychromaster*, *Catonotus*, *Hololepis*, and *Microperca*). Based primarily on the presence and distribution of breeding tubercles, Collette and Yerger (1962) and Collette (1965) recognized an additional subgenus, *Villora*. The most recent works by Collette and Banareescu (1977) and Page (1977) recognized the additional subgenera *Doration*, *Litocara*, and *Vaillantia*, for a total of sixteen.

The subgenus *Oligocephalus* is the most wide-ranging, large, structurally diverse (Bailey and Richards 1973), complex, and speciose (Ramsley and Suttkus 1965) subgenus of *Etheostoma*. Bailey and Gosline (1955) assigned 19 species and Collette (1965) 21 species to this subgenus. Ramsley and Suttkus (1965) discussed the *E. asprigene* species group within the subgenus *Oligocephalus*.

The purpose of this paper is to remove *E. punctulatum*, *E. cragini*, *E. pallididorsum*, and *E. boschungii* from the subgenus *Oligocephalus*, and *E. trisella* from the subgenus *Psychromaster*, and to erect a subgenus for these closely related species. The close relationship among *E. punctulatum*, *E. cragini*, and *E. pallididorsum* was first recognized by Blair (1964). Wall and Williams (1974) described *E. boschungii* and presented additional data clarifying the relationships among *E. boschungii*, *E. punctulatum*, *E. cragini*, and *E. pallididorsum*.

*Ozarka*, new subgenus

*Type Species*.—*Etheostoma punctulatum* (Agassiz)=*Poecilichthys punctulatus* Agassiz 1854 (original description, type locality Osage River, Missouri).

*Species Included in Ozarka*.—*E. punctulatum*, *E. cragini*, *E. pallidiorum*, *E. boschungii*, and *E. trisella*. *Etheostoma trisella* was originally placed in the subgenus *Psychromaster* by Bailey and Richards (1963) while the other four species have been referred to the subgenus *Oligocephalus* (Bailey and Gosline 1955; Collette 1965; Wall and Williams 1974). The subgenus name *Ozarka* is taken from the Ozark Mountains Physiographic Province, which we believe to have been the center of dispersal for the subgenus.

*Diagnosis*.—A subgenus of the genus *Etheostoma* of moderate to small size, adult males and females ranging from 40-70 mm standard length (SL). Cheeks and opercles usually naked or with embedded scales, except *E. trisella* which has scales on these structures. Lateral line incomplete, except complete in *E. trisella*. Lateral line scale rows 40-80, anterior portion not arched upward. Transverse scale rows 12-24, caudal peduncle scales 20-29. Branchiostegal membranes narrowly joined to overlapping; branchiostegal rays usually 6-6 and unscaled. Frenum present, broad and well developed. Preoperculomandibular canal pores usually 10, infraorbital canal complete with 7 or 8 pores, supratemporal canal complete or interrupted. Preopercle entire. Caudal peduncle deep. Vertebrae 32-39, usually 34-37. Caudal vertebrae usually 18, 19, or 20. First interneural spine between the neural spines of third and fourth or fourth and fifth vertebrae.

Dorsal spines VI-XII usually IX-XI; dorsal rays 10-15, usually 11-14; pectoral rays 9-14, usually 11-13; anal spines 2 except usually 1 in *E. trisella*; anal rays 6-10, usually 7-9. Males with breeding tubercles on scales of belly, around base of anal fin posteriorly to caudal peduncle, and on anal spines and rays and ventral surface of pelvic rays; tubercles absent in females. Sexual dichromatism pronounced in breeding adults, males brightly colored, females not. Breeding males with bold blue-black subocular bar, width one-third to two-thirds diameter of orbit. First dorsal fin of breeding male with black marginal band (usually narrow anteriorly, increasing in width posteriorly), submarginal orange to red-orange band, and blue-green to blue-black basal band. Submarginal and basal bands approximately equal in width. Second dorsal of breeding males without bright colors. Venter from pectoral and pelvic fin insertions to caudal peduncle suffused with varying concentrations of orange to red-orange pigment. Branchiostegal and gular region orange except in *E. trisella*. Genital papilla tubular in females, not long and tubular in males. Anus not surrounded by fleshy villi.

*Additional Characters.*—Body slender to moderately stout; snout moderately to slightly decurved; mouth terminal, slightly oblique; premaxillary frenum present, generally broad and well developed. Head moderately large; eye breaking dorsal contour of head in lateral view; caudal fin slightly rounded; branchiostegal membranes separate to narrowly joined, rays 6-6; preopercle entire; pectoral fin length usually shorter than head length. Lateral line complete or incomplete, arching gently anteriorly; lateral line scales 40-80; vertebrae 32-39, usually 34-37. Transverse scale rows 12-24; caudal peduncle scales 20-29. Dorsal fin spines VI-XII, usually IX-XI; dorsal fin soft rays 10-15, usually 11-14; anal spines II, except in *E. trisella* which usually has I anal spine; anal fin soft rays 6-10, usually 7-9; branched caudal fin rays 12-17; pectoral fin rays 9-14. Supratemporal canal complete or interrupted; lateral canal complete with 5 pores; single coronal pore; postorbital, interorbital, posterior nasal and anterior nasal pores present; preoperculo-mandibular canal complete with 10 pores; infraorbital canal complete with 7 or 8 pores. Nape scaly with exposed or embedded ctenoid scales. Cheeks and opercles naked or scaly; prepectoral region generally naked or with a few scales; anterior portion of belly naked to fully scaly; breast naked or with a few embedded scales. Nuptial tubercles present in males only; tubercles on scales around base of anal fin, anal spines and rays and ventral surfaces of pelvic rays. Breeding tubercles absent in females. Genital papilla sexually dimorphic.

Body generally olivaceous to grayish brown. Well developed humeral spot present in all species except *E. trisella* where it may be indistinct. Bold, dark subocular bar present. Lateral blotches variable; discontinuous or fused into irregular lateral band in *E. cragini*. Dorsal saddles 3-9, conspicuous, and dark. Sexual dichromatism pronounced in all species. Well developed orange to red-orange in breeding males located on the venter from pelvic fins posteriorly to caudal fin. Spinous dorsal fin with black marginal band (may be absent in some individuals), usually narrow anteriorly, increasing in width posteriorly. Submarginal orange to red-orange band below the dark marginal band and followed by blue-green to blue-black basal band of equal width. All species lack bright breeding colors in soft dorsal fin. Soft dorsal fin with six to eight indistinct horizontal bands formed by dark spots of pigment on rays, and darker pigment on fin membranes giving a barred appearance to fins. Caudal fin with spots confined to rays, arranged in four to six irregular vertical rows. Spots on pectoral and pelvic fins aligned in irregular vertical rows. Pelvic fins typically dusky to gray-black; pigment usually restricted to rays or proximal membranes of fin. Anal fin with scattered spots on rays and membranes. Gular and branchiostegal regions orange.

Females with generally olivaceous or brownish-gray bodies. Bright orange coloration not observed in females. Spinous dorsal fins, while occasionally tinged with orange or yellow pigment, never brightly banded as in males. Soft dorsal fin without bright colors; some irregular spotting of rays occurs.

*Distribution.*—The geographic range of the five species of the subgenus *Ozarka* is centered in the Ozark Mountains Physiographic Region. The species are found from eastern Colorado (*E. cragini*) to southeastern Tennessee and northwestern Georgia (*E. trisella*). They are allopatric except for *E. punctulatum* and *E. cragini*, which are sympatric in southwestern Missouri and northeastern Oklahoma. *Etheostoma punctulatum*, *E. cragini*, and *E. pallididorsum* are found west of the Mississippi Embayment, and *E. boschungii* and *E. trisella* east of the Embayment. None of the species is known from the Coastal Plain Province.

The stippled darter, *Etheostoma punctulatum*, is known from the Arkansas River drainage in northwestern Arkansas (Buchanan 1973), northeastern Oklahoma (Miller and Robison 1973), extreme southeastern Kansas (Cross 1967), and southern Missouri (Pflieger 1975). It also occurs in the Missouri River drainage in central Missouri and the Castor River system, tributary to the Mississippi River, in southeastern Missouri (Pflieger 1975) as well as in the White River drainage of southern Missouri and northern Arkansas (Buchanan 1973; Pflieger 1975). Distribution of the Arkansas darter, *E. cragini*, is in the Arkansas River drainage from eastern Colorado (Ellis 1914; Ellis and Jaffa 1918), southern Kansas (Cross 1967), northeastern Oklahoma (Miller and Robison 1973), and extreme southwestern Missouri (Pflieger 1975). In the original description, *E. pallididorsum* was reported from the Caddo River of the Ouachita River drainage in western Arkansas (Distler and Metcalf 1962). Robison (1974a) reported an additional population from the upper Ouachita River drainage.

East of the Mississippi Embayment, *Etheostoma boschungii* is known from widely separate tributaries of the Tennessee River in western Tennessee and northern Alabama (Wall and Williams 1974). *Etheostoma trisella* is known from isolated localities in the Coosa River drainage in northeastern Alabama (Bailey and Richards 1963; Ramsey 1976), northwest Georgia (Howell and Caldwell 1967), and southeastern Tennessee (Etnier 1970). Based on available distributional data, *E. trisella* has the most limited distribution of the species in the subgenus. The only extant population known is in the Conasauga River near the Tennessee-Georgia border.

*Habitat.*—Members of the subgenus *Ozarka* typically inhabit gentle riffles and slackwater areas of small to medium-size shallow, upland tributary streams. *Etheostoma punctulatum* is generally restricted to small, clear, moderate to high gradient permanent streams or spring branches with substrates of gravel or rubble (Blair 1959; Miller and Robison 1973; Pflieger 1971, 1975). It is frequently found in vegetation or in detritus in quiet side pools and backwaters away from the main current (Branson 1967). Moore and Paden (1950) reported that this form was taken principally in heavily vegetated springs with slight gradient and in small leaf-filled indentations along the shore.

*Etheostoma cragini* prefers quiet pools of the smallest spring branches. It also occurs in spring-fed creeks where it is most often found along the shallow margins of pools and riffles in thick growths of water-cress, *Nasturtium officinale* (Ellis and Jaffa 1918; Blair 1959; Branson 1967; Cross 1967; Pflieger 1971, 1975; Miller and Robison 1973). Moore and Cross (1950) collected *E. cragini* in small clear streams of moderate current over mud, gravel, and sand substrates in quiet pools in which aquatic vegetation flourished (*Ranunculus*, *Potamogeton*, *Myriophyllum*, *Callitriche*, and *Radicula*).

*Etheostoma pallididorsum* inhabits small, spring-fed brooks, 0.6 m in average width and 5 cm in depth over mud, gravel and/or rubble bottoms (Distler and Metcalf 1962). The species typically prefers shallow (15-30 cm) backwater pool areas with leaf-litter and small gravel-rubble bottoms when found in larger streams (Robison 1974a, b; Hambrick and Robison 1979).

*Etheostoma boschungi* inhabits clear, medium-current, second and third order streams ranging in width from 3 to 6 m, and ranging in depth from less than 15 cm to 1.7 m (Wall and Williams 1974). Boschung (1976) collected this species over gravel infiltrated by silt, and over silt and mud, but never over clean gravel. Individuals seemed to prefer accumulations of detritus in areas of relatively low water velocity.

*Etheostoma trisella* was hypothesized by Bailey and Richards (1963) to live in springs, although the holotype was collected from a small, sluggish pasture stream with a bottom of silt mixed with sand and gravel and heavily overgrown with emergent *Diathera*. Etnier (1970) reported that *E. trisella* appears to inhabit riffles and almost stagnant quiet backwaters of small, low-gradient streams.

Breeding habits and habitats of all species except *E. punctulatum* have been examined to some degree (Ellis and Jaffa 1918; Distler 1972; Boschung 1976; M. Ryon, pers. comm.; and HWR and JDW, pers. observ.). Although no actual observations of spawning of *E. punctulatum* have been made, field data from several workers attest to the presence of nuptial males during the spring (W. Pflieger, pers. comm.; L. Knapp, pers. comm.; and HWR, pers. observ.).

The unique spawning habitat of the species of *Ozarka* affirms their close phylogenetic relationship. All typically live in or enter small tributary streams during later winter and spawn during early spring (March-April). *Etheostoma pallididorsum*, *E. boschungi*, and *E. trisella* enter and spawn in tiny spring-fed rivulets or seepage water in open fields that drain into nearby streams. More specific life history information linking these three species is available to us and will be published later by HWR (*E. pallididorsum*), H. T. Boschung (*E. boschungi*), and M. Ryon (*E. trisella*). A detailed analysis of the systematics of the five species of *Ozarka* will be forthcoming from the authors and B. R. Wall.

Key to Species of the Subgenus *Ozarka*

1. Anal spines one; lateral line complete with 44-52 scales; three distinct dorsal blotches . . . . . *Etheostoma trisella*.  
(Coosa River system in Alabama and Georgia, Conasauga River system in Tennessee.)  
Anal spines two; lateral line incomplete with 5-59 pored scales; dorsal blotches variable . . . . . 2
2. Lateral line with more than 30 pored scales . . . . . 3  
Lateral line with 5-25 pored scales . . . . . 4
3. Lateral line scales 58-80; soft dorsal fin usually 14 or 15 rays . . . . .  
. . . . . *Etheostoma punctulatum*.  
(Arkansas River drainage in Arkansas, Oklahoma, Kansas and Missouri, White River drainage in Arkansas and Missouri, and Missouri River drainage and Castor River system of Missouri.)  
Lateral line scales 43-58 (usually 34-38 pored); soft dorsal fin usually 11 or 12 rays . . . . . *Etheostoma boschungii*.  
(Tennessee River drainage in northern Alabama and southcentral Tennessee.)
4. Prominent pale mid-dorsal stripe present; venter behind pelvics naked; prepectoral areas naked . . . . . *Etheostoma pallididorsum*.  
(Upper part of Caddo River system and Hallmans Creek in upper Ouachita River system, Arkansas.)  
No prominent pale mid-dorsal stripe; venter behind pelvics fully scaly; prepectoral areas with few scales . . . . . *Etheostoma cragini*.  
(Arkansas River drainage in Colorado, Kansas, Oklahoma, and Missouri.)

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# Stomach Contents of Some Snakes from Eastern and Central North Carolina

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**ABSTRACT.** — Stomach contents of eight species of snakes from the Coastal Plain and Piedmont Plateau regions of North Carolina were identified. The majority of the snakes were of the genus *Nerodia*: *N. sipedon sipedon* contained primarily amphibians; *N. taxispilota* contained fishes; and single specimens of *N. erythrogaster erythrogaster* and *N. fasciata fasciata* contained frogs. *Agkistrodon piscivorus piscivorus* was omnivorous, and *A. contortrix contortrix* contained a frog and a small mammal.

Food habits of snakes from various localities in the United States have been noted by a number of authors (see Brown 1979). That author also provided food records for a number of snakes in North and South Carolina. In addition to those studies cited by Brown, several other authors furnished pertinent information on snake food habits. Mushinsky and Hebrard (1977) and Oliver (1970) gave records for *Nerodia* spp. and *Elaphe obsoleta*, respectively. Stomach contents of 17 *Agkistrodon piscivorus leucostoma* were noted by Collins and Carpenter (1970) and of 4 *A. p. piscivorus* by Goodman (1958). The food items of 93 individuals of the latter subspecies were provided by Wharton (1969). He studied snakes from Sea Horse Key, Florida, and also listed the findings of a number of other authors. Kofron (1978) studied several species of *Nerodia* as well as *A. p. leucostoma* from a variety of habitats. Although the subspecies were different from those in my study, their food habits appeared to be similar in terms of species designations. However, the small number of *Nerodia* spp. examined in both studies precludes any definite conclusions.

Arthropods are not common foods of most colubrids or crotalids. However, as Brown noted, it is probably erroneous to assume that some species do not take arthropods under certain conditions. Of the species I examined, only a single specimen of *Elaphe o. obsoleta* contained arthropod material, a larva of *Phengodes* sp. (glowworm). This snake was a mature female that did not contain any other food remains. Brown did not report arthropods from 39 specimens of this snake. However, arthropod remains (primarily lepidopteran larvae) were noted by him in 9 *Agkistrodon contortrix*. I found a small mammal and a *Rana catesbeii*-

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Table 1. Stomach contents of snakes from eastern and central North Carolina

Species	No. examined	No. with food	Food items
Colubridae:			
<i>Elaphe obsoleta obsoleta</i>	2	1	coleopteran larvae
<i>Elaphe obsoleta quadrivittata</i>	2	1	small mammal
<i>Nerodia erythrogaster erythrogaster</i>	6	1	frog
<i>Nerodia fasciata fasciata</i>	10	1	<i>Rana palustris</i>
<i>Nerodia sipedon sipedon</i>	21	1	fish (Centrarchidae)
		1	salamander
		1	<i>Notophthalmus viridescens</i>
		4	frog
		2	<i>Rana catesbeiana</i> (tadpole)
		2	<i>Bufo woodhousei fowleri</i>
<i>Nerodia taxispilota</i>	16	3	fish (Centrarchidae)
		1	<i>Ictalurus</i> sp.
Crotalidae:			
<i>Agkistrodon contortrix contortrix</i>	2	1	<i>Rana catesbeiana</i>
		1	small mammal
<i>Agkistrodon piscivorus piscivorus</i>	16	1	<i>Micropterus</i> sp.
		1	<i>Ictalurus</i> sp.
		1	frog
		1	<i>Chelydra serpentina</i> (hatchling)
		2	small mammal

*ana* in the two individuals in my study. Amphibians were not found in any of the 35 *A. contortrix* examined by Brown.

The *Nerodia* species examined in my study comprise the majority of individuals examined. There are no major differences between the classes of food items found by Brown and by me. However, some additional species were seen. Amphibians were the major food of *N. s. sipedon*. In addition to the items listed by Brown, one individual contained an adult *Notophthalmus viridescens*. This snake was captured in a farm pond. A *N. f. fasciata* contained a *Rana palustris*, an item not found by Brown in 12 snakes of this species. This snake was captured in a swamp near the Northeast Cape Fear River in Duplin County. *Natrix taxispilota* was not studied by Brown. As noted above, this species is primarily riverine in eastern North Carolina. Unlike the other species of *Nerodia* studied, which apparently feed mainly on amphibians, its primary food source probably is fish. This was also noted by Laughlin (1959) for this species from a lacustrine habitat in Oklahoma.

*Agkistrodon p. piscivorus* exhibited a more varied diet than any of the other snakes examined. These data, along with those of Hamilton and

Pollack (1955), Goodman (1958), Laughlin (1959), Wharton (1969), Collins and Carpenter (1970), Kofron (1978), and Brown, show that this species will feed on certain members of every class of vertebrates. In addition, Collins and Carpenter (1970) reported insects in the stomach contents of two snakes.

Only three individuals contained mixed categories of food items: a *Nerodia s. sipedon* contained four toads and a fish; an *Agkistrodon p. piscivorus* contained a small mammal and a bass; and an *A. c. contortrix* contained a *Rana catesbeiana* and a small mammal. None of the other snakes contained more than a single class of food item. The total number of snakes containing any food items was therefore 24, including the three individuals mentioned above.

Whether certain snake species can be characterized as "opportunists" in terms of food items consumed is conjectural. Of the species examined, *Agkistrodon piscivorus* most readily can be characterized this way, but some species of *Nerodia* also may be opportunists. Brown mentioned observing *N. f. fasciata* eating road-killed anurans; I have seen *N. erythrogaster transversa* eating chunks of fresh fish. Snakes generally are considered to be predators, but these kinds of observations indicate that under certain circumstances some species can adopt other feeding habits.

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# Mandibular Dental Anomaly in White-tailed Deer

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**ABSTRACT.** — Agenesis of the second mandibular premolar in four White-tailed deer from Dorchester County, Maryland, was considered to be of genetic origin. The body condition of anomalous animals apparently was not affected.

The dentition of most mammalian species has been well studied because of its importance in systematics and evolution, and in estimation of individual age. As a result, associated dental anomalies have been described for a variety of species encompassing many mammalian orders (Choate 1968; Colyer 1936; Lavelle and Moore 1972; Pavlinov 1975; Sheppe 1963). This paper describes a dental anomaly found in 4 of 24 yearling and adult White-tailed deer, *Odocoileus virginianus*, obtained during the 1976 through 1978 hunting seasons in southern Dorchester County, Maryland. The skull and dentary bone were collected from each animal. Skulls were solicited and obtained from hunters at two deer check stations. No samples were examined prior to solicitation and all hunters entering the stations were approached. Thus, the sample was considered to be random.

Bilateral agenesis of the second premolar ( $p_2$ ) (Fig. 1) was found in two female and one male yearlings, all in which the permanent dentition had erupted. A unilateral  $p_2$  agenesis occurred in an adult female. In all four occurrences, the anomaly was considered to be genetic in origin because: 1) there was no evidence of previous traumatic injury; 2) no alveoli were present at the  $p_2$  position; and 3) X-rays of the dentary revealed no vestigial or impacted teeth in the underlying bone tissue at the  $p_2$  positions. The mean total length of the mandibular tooth row for animals with the anomaly was significantly less than that of animals with a normal complement of mandibular cheek teeth ( $t=4.80$ ;  $p < 0.001$ ). However, all the anomalous animals had a normal complement of maxillary cheek teeth, exhibited normal occlusion and showed no unusual wear.

Benson (1957) attributed a missing second premolar in two White-tailed deer to traumatic injury. No sample size was given and only a single mandible was available from each animal. A unilateral absence of  $p_2$  in a Mule deer, *Odocoileus hemionus*, similarly was attributed to injury (Short and Short 1964). Apparent genetic agenesis of the second premolar involv-

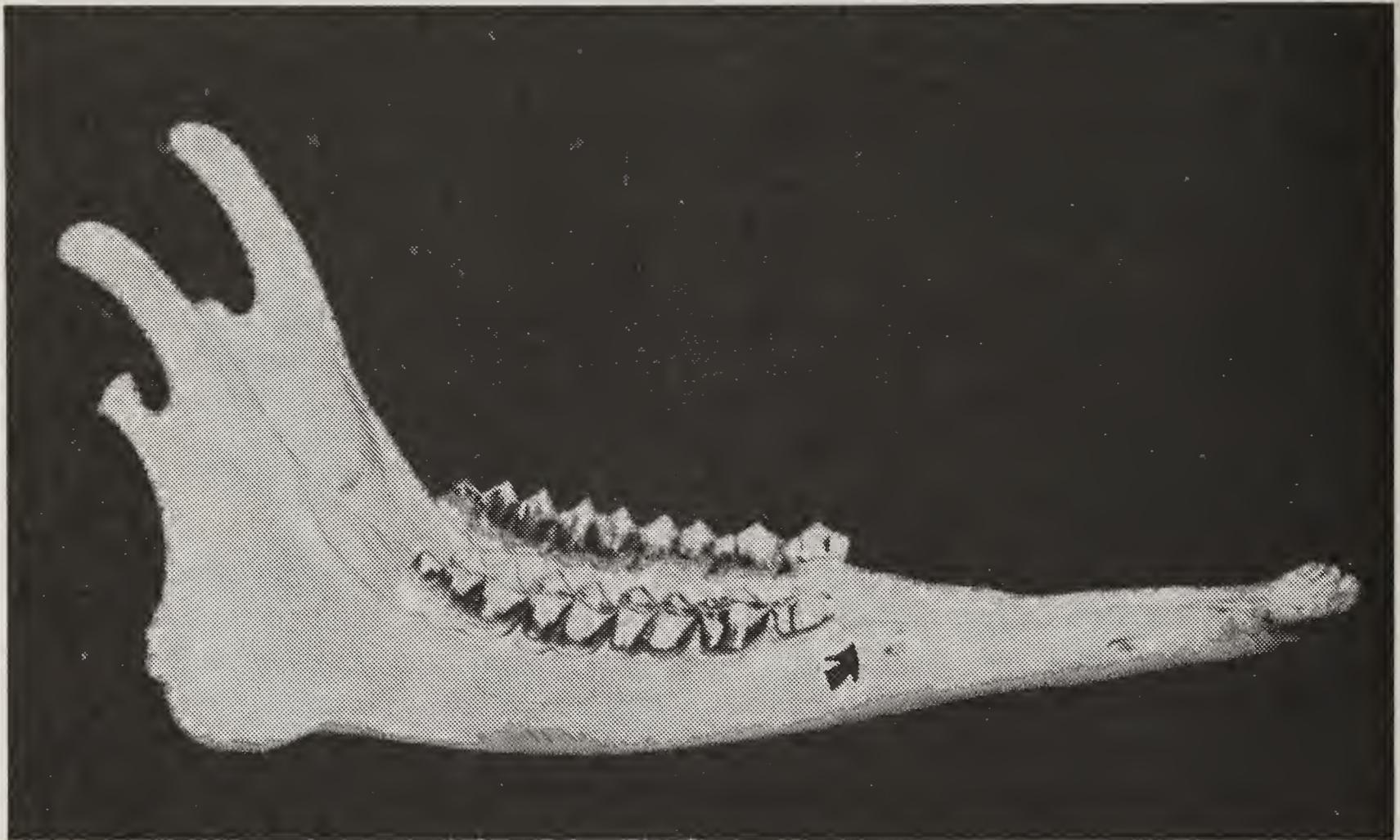


Fig. 1. Representative bilateral agenesis of second premolar ( $p_2$ ) in a White-tailed deer (AEL #1103) from Dorchester County, Maryland.

ing one or both mandibles was noted in only 5 of 422 (1.2%) White-tailed deer from New York (Free et al. 1972), and 8 of 401 (2.0%) White-tails from northern Minnesota (Mech et al. 1970). This anomaly also has been described in Roe deer, *Capreolus capreolus*, by Meyer (1977). It is interesting that this anomaly apparently did not occur among 33,337 White-tailed deer examined over a 3-year period in Michigan (Ryel 1963). Although from a limited sample, the occurrence of this characteristic in 16.7 percent of the White-tailed deer examined from Dorchester County suggests the trait may be well established in this population.

Missing second premolars probably were not detrimental to the overall condition or survival of the individual deer (Pekelharing 1968). Body weights and standard measurements from two anomalous animals from the 1978 sample were comparable to those animals with normal dentition. Weights and measurements of the remaining three anomalous animals were not available. This lends support to the suggestion of previous investigators (Manville 1963, Smith et al. 1977) that dental anomalies, although of intrinsic interest, probably are of little significance to the total dynamics of the population.

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## ERRATUM

The following error appeared in *Brimleyana* No. 3:

Page 95, line 1 — insert “± S.E.” between 3.5 and 0.3 mm.

## JOURNAL RECEIVES STC INTERNATIONAL AWARD

The Society for Technical Communications bestowed an Award for Merit on *Brimleyana* in its Eleventh Annual International Technical Communications Competition for 1980. The journal was entered in the Complete Periodicals category of the competition, through STC's Carolina Chapter. STC is the world's largest professional society devoted to technical communications, and has more than 65 chapters in the United States and abroad.

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