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SOUTHEASTERN U. S. COASTAL PLAIN HABITATS OF THE PLETHODONTIDAE: THE IMPORTANCE OF RELIEF, RAVINES, AND SEEPAGE

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1. INTRODUCTION

Because the Coastal Plain is geologically and biologically a very distinct region of the southeastern United States -- the southern portion having a nearly subtropical climate -- the life cycles, ecology, and evolutionary relationships of its plethodontid salamanders may be significantly different from plethodontids in the Appalachians and Piedmont. Little attention has been paid, however, to Coastal Plain plethodontids. For instance, of the 133 scientific papers and posters presented at the four plethodontid salamander conferences held in Highlands, North Carolina, since 1972, only three (2%) dealt with Coastal Plain plethodontids. And yet, while it possesses fewer total species than the Appalachians and Piedmont, the Coastal Plain boasts of slightly more plethodontid diversity at the generic level. The genera *Phaeognathus*, *Haideotriton*, and *Stereochilus* are Coastal Plain endemics, whereas in the Appalachians and Piedmont *Gyrinophilus* is the only endemic genus unless one accepts *Leurognathus* apart from *Desmognathus*. In addition, *Aneides* is found in the Appalachians and not the Coastal Plain, but the genus also occurs in the western U. S. All the rest of the plethodontid genera east of the Mississippi River are shared by the Coastal Plain with the Appalachians and Piedmont.

Geographically, the Coastal Plain includes Long Island in New York, and stretches south from the New Jersey Pine Barrens to include all of Florida, then west to Texas (Fig. 1). Hugging the coast, it is a band of land of varying width, averaging about 200 km deep along the Atlantic coast and extending 900 km up the Mississippi Embayment, reaching inland from the seashore to a physical limit called the Fall Line. The Fall Line marks the position upstream on Coastal Plain rivers where bedrock is first encountered, or the coastward limit of waterfalls going downstream from the Appalachians and Piedmont. The Appalachians and Piedmont are underlain by crystalline rocks and their streams usually have bedrock, boulders, cobbles, and coarse gravel in their beds. In contrast, because the Coastal Plain is entirely a sedimentary region, the substrates of habitats occupied by Coastal Plain salamanders are quite different. They are composed exclusively of sand, clay, some occasional small pea-sized gravel, limestone, peat, muck, or a combination of these. Few rocky substrates exist.

Fig. 1.--Physiographic map showing the Coastal Plain (shaded) in comparison with Appalachian uplands (stippled).

Dunn (1926, 1928) commented extensively on the habitats of plethodontid salamanders, but his main observations were focused on mountain brook habitats of montane areas, especially the southern Appalachians. For 38 years I have conducted most of my own plethodontid salamander research in Coastal Plain habitats, and I have come to believe that fruitful insights into the systematic diversity and overall evolutionary history of the Plethodontidae are being overlooked by the lack of research focus on Coastal Plain species. In this chapter I discuss the principal Coastal Plain habitats in which plethodontids are found. Then, based upon my own insights gained on plethodontid ecology in the Coastal Plain, I offer a new hypothesis on the geographical and ecological settings in which plethodontid salamanders may have evolved.

2. COASTAL PLAIN PLETHODONTID HABITATS

All Coastal Plain habitats can be categorized as either upland, wetland, or aquatic. Wetlands are habitats in which water resides on a site long enough during the year so that (1) only plants that can tolerate saturated soils or inundation live there, and (2) the soil has >30% organic content (Mitsch and Gosselink, 1993). Near their upland boundary, wetlands may have saturated soils only for a few weeks in the year, such as in wet flats and some seepage bogs; near their aquatic boundary wetlands may be permanently inundated such as in a marsh or at the margins of a pond or swampy lake. Upland habitats, therefore, are all the dry land environments upslope from wetlands. In the Coastal Plain these can be generally categorized as flatwoods, clayhills, or sandhills. Aquatic habitats are all those permanently inundated situations without emergent plants, such as the flowing waters contained in the low water channels of streams and rivers and the open water portions of lakes.

Having small bodies and moist skin, plethodontids are restricted to habitats with nearly perennial moisture or at least constant high humidity. Coastal Plain uplands, therefore, are unsuitable habitats for plethodontids because they are hot and dry. About 60% of the presettlement Coastal Plain landscape from Virginia to east Texas was occupied by upland longleaf pine forests (Ware et al., 1993), which are characterized by open canopies, abundant sunlight reaching the ground, and frequent (1-3 years), lightning-set wildfires (Means, 1996a). A prominent early Coastal Plain botanist, musing about how harsh longleaf pine habitats were for plants, called the wiregrass sandhills "deserts in the rain" (Wells, 1932). No plethodontids live in longleaf pine forests, except that *Eurycea quadridigitata* breeds in flatwoods and sandhills ponds and lives around the margins of such ponds as adults (personal observation). How far *E. quadridigitata* ranges into the longleaf pine uplands is unknown.

The second most abundant native upland vegetation in the Coastal Plain is the southern temperate hardwood forest (Platt and Schwartz, 1990) that is confined to steep slopes, bottomlands, and other places naturally protected from fire. These forests are dominated by evergreen and deciduous hardwood trees having a closed canopy under which high humidity is maintained during the growing season. It is in southern temperate hardwood forests where the only upland-inhabiting Coastal Plain plethodontids live. These are species of *Plethodon* (*grobmani, chlorobryonis, variolatus, ocmulgee, mississippi, albagula, kisatchie,* and *websteri*), and they are generally confined to forested ravines or hillsides where the salamanders seek refuge in moist leaf litter and decomposing logs during the heat of the day (Conant and Collins, 1998). The Red Hills Salamander, *Phaeognathus hubrichti*, should be considered an upland species by the above definitions, but it alone of all the Coastal Plain salamanders is highly specialized for burrowing (Dodd, 1991). Interestingly, plethodontids have not invaded the ruderal forests of mixed hardwoods and pine or pine plantations that have largely replaced longleaf forests (e.g., Ware et al., 1993).

Only two species of Coastal Plain plethodontids are truly aquatic. One of these, *Haideotriton wallacei*, is a paedomorphic troglobite (Carr, 1939) that lives in the ground water of the Floridan Aquifer under the Marianna Lowlands/Dougherty Plain, a small (50 x 150 km) physiographic region (Fig. 1) in southwest Georgia and part of the Florida panhandle. The second Coastal Plain aquatic species is *Stereochilus marginatus*, which comes as close to being as totally aquatic as *Desmognathus marmoratus* of the southern Appalachians. It lives its entire larval and metamorphosed life in shallow, acid waters of lower Coastal Plain swampy streams, coming onto land only occasionally. In fact, however, its habitats are usually choked with sphagnum and other emergent plants, so by habitat criteria *S. marginatus* is technically a wetland species.

The remaining Coastal Plain plethodontids are found in various types of wetlands. It is these habitats and the plethodontids that inhabit them that I wish to discuss in depth in this paper. For each of the wetland localities in which I have personally collected one or more of 11 species of Coastal Plain plethodontids, I qualified the habitat relationships of its plethodontids by characterizing its wetland nature (Table 1). Lentic habitats were either small isolated water bodies (temporary or ephemeral ponds), lakes, or standing water sloughs in river floodplains. For lotic habitats I assigned a Strahler (1964) stream order by locating each locality on a USGS 7 1/2-minute quadrangle map and estimating the Strahler stream order for each.

TABLE 1.--Habitat characterization of 715 occurrences of 11 species of plethodontid salamanders from Coastal Plain wetland habitats in the 5-year period, 1969-1974. Types of habitats, from most lentic to most lotic: pond = all standing water; >3, 3, 2, 1 = streams of respective Strahler orders. 1 = ravines heads only, but 2, 3 = swampy flatwoods streams for Assemblage 1, and ravines for Assemblage 2. See Means (1975) for application of Strahler (1964) stream order to plethodontid habitat analyses.

Inspection of Table 1 reveals two habitat assemblages of plethodontids in the Coastal Plain. One is all the plethodontids that live in low, swampy habitats such as pond margins, creek swamps, and river floodplains. These species are all syntopic in various parts of the Coastal Plain. For instance, I have collected *Hemidactylium scutatum, Eurycea quadridigitata*, *E. guttolineata, Pseudotriton montanus,* and *Desmognathus auriculatus* together in the Ochlockonee River and Alaqua Creek floodplains in Florida. Up the Atlantic coast, I have taken *Stereochilus marginatus* with *P. montanus, E. quadridigitata,* and *D. auriculatus*. Some members of this assemblage are more restricted in habitat, such as *E. guttolineata* which breeds only in large creek and river floodplains, but others such as *Eurycea quadridigitata* and *D. auriculatus* are wide-ranging across all the swampy lentic and lotic habitats.

In the discussion of wetland habitats that follows, I move topically up-gradient from standing water habitats to swampy streams and the backwaters of river floodplains with relatively short hydroperiods to the more permanent seepage habitats found in ravines. This sequence represents a natural gradient of Coastal Plain wetland habitats, from low-lying, standing-water wetlands in unrelieved terrain that are preferred by the larvae of ambystomatids, salamandrids, amphiumids, and sirenids to the gently flowing, cooler, more permanent seepage waters of ravines that are utilized exclusively by the larvae of plethodontids.

Lentic habitats in the Coastal Plain consist of small, isolated water bodies (Moler and Franz, 1988), lakes, or standing water in river and creek floodplain swamps. Lentic habitats are primarily utilized for breeding sites by ambystomatid, salamandrid, sirenid, and sometimes amphiumid (about which more later) species, whose larvae require ponds for development, and all of which have short larval periods. Except for the larger lakes, most Coastal Plain lentic habitats are ephemeral, having hydroperiods of much less than one year. This is especially true of temporary ponds and standing water in floodplains where annual droughts cause the complete drying of small, isolated water bodies. Even the larger lakes are subject to drying on temporal scales of a decade to century. In the case of river and creek floodplain swamps, they may go dry during low water stages and droughts, but they are also subject to periodic inundation during high water stages of their associated streams.

Lakes and temporary ponds are distributed in varying densities in the Coastal Plain depending on local geology. In southern Alabama, Mississippi, and northern panhandle Florida there are hundreds of Citronelle ponds (Folkerts, 1997). Eastward and south from the eastern panhandle of Florida lie literally thousands of limesink depressions and lakes (Atlas of Florida, 1996). The Coastal Plain of the Carolinas is famous for its hundreds of pocosins, or Carolina Bays (Savage, 1983). Generally, few plethodontid species occupy these lakes and temporary ponds, but *Eurycea quadridigitata* is an exception. It breeds in small, isolated water bodies, especially acidic cypress ponds. Adults may live in the moist emergent plant zones surrounding the edges of such ponds. In a four-year study of one such pond surrounded by a 300-m drift fence, few metamorposed *E. quadridigitata* fell into drop buckets 60 m upslope from pond and none were taken from other drift fences 120 and 180 m further upslope, but I could dipnet individuals from the shallow water at the pond margins at will (personal observation). Most of the major lakes in north Florida support thriving populations of *Eurycea quadridigitata* larvae and metamorphosed individuals in the shallow waters (0-2 cm) of their edges.

The brief larval life of *Eurycea quadridigitata*, like that of newts and ambystomatids, is probably an adaptation to the unpredictable and short hydroperiods of temporary ponds. *Eurycea quadridigitata*, however, is not restricted to temporary ponds and lake margins. It is also found in river and creek swamps. Creek swamps are extensive throughout the Coastal Plain landscape, especially close to the coastline in flatwoods where water spreads out over the landscape in wide, mucky floodplains. Wherever creeks and larger streams meander over the gently inclined landscapes of the Coastal Plain, *Eurycea quadridigitata* is common.

Creek swamps are the least understood of all wetland habitats in the Coastal Plain. A swamp is any forested wetland. Under this general definition, creek swamps range from the shrub-dominated wetlands at the bottoms of the extremely gently-sloped valleys draining the flatwoods of low coastal terraces of the Coastal Plain, to the extensive hardwood-dominated floodplains of the larger rivers that have a regular high-water cycle in which water spills out of the low-water channel banks and flows broadly through a forested wetland of ridges and swales. The low-gradient flatwoods streams usually have peaty soils which are created by shallow, surficial aquifers from which groundwater seeps laterally out of adjacent sandy soils toward the open-water channel; these are always blackwater streams. The larger streams with extensive floodplains originate further inland in soils with a heavy clay content, so that the waters of the stream are turbid with clay and silt, and the floodplains are a mosaic of clay-bottomed swales, sandy ridges (ancient levees), and occasional oxbow lakes and backwater sloughs.

It is tempting to categorize the blackwater creek swamps separately from those of the alluvial streams having more extensive floodplains, except that Coastal Plain plethodontids appear not to recognize the differences. In addition to *Eurycea quadridigitata*, the principal plethodontid species inhabiting creek swamps are *Pseudotriton montanus* and *Desmognathus auriculatus*. These three species are the only plethodontids found in small blackwater streams of the Gulf Coastal Plain. To the north on the Atlantic seaboard, *Stereochilus marginatus* is found in blackwater streams in syntopy with all three species. Blackwater streams, in comparison with alluvial and aquifer-spring-fed streams, have the highest fluctuations between high and low water stages, often pulsing annually through three or four orders of magnitude of flow (Wolfe et al., 1988).

The four plethodontids most commonly associated with blackwater streams are the most aquatic of all Coastal Plain plethodontids. *Pseudotriton montanus* and *Desmognathus auriculatus* are often raked from just under the surface of the water in pockets of decomposing organic litter as is, occasionally, *Eurycea quadridigitata* (personal observation). *Stereochilus marginatus* is largely aquatic throughout its life cycle, even after it metamorphoses (Bruce, 1971). These four species are often found with *Eurycea guttolineata*, which breeds in the backwaters of the floodplains of larger creeks (>Strahler order 3) and large alluvial rivers such as the Leaf, Apalachicola, and Savannah. This large species has the habit of wandering quite far upstream from its breeding sites, and the adults are often found in ravine habitats if these happen to confluence with the larger streams through the escarpments of the valley sidewalls of the larger streams. In the Coastal Plain where the physical relief is great (along certain reaches of the Alabama, Escambia/Conecuh, Choctawhatchee, Apalachicola/Chattahoochee rivers and in the Alabama Red Hills, for instance), it is not uncommon for first- and second-order headwater ravines (discussed below) to confluence with third-, fourth-, and greater order blackwater or alluvial streams. In the vicinity of the confluence, the low-order ravine-inhabiting plethodontids are sometimes syntopic with those of the higher-order creek swamps. These sites, therefore, have the highest species richness of plethodontids in the Coastal Plain.

The headwaters of creeks in flatwoods are swampy, shrub-dominated areas with lots of black, wet peat created by high water tables and seepage (Wolfe et al., 1988). Very often the transition zone going upslope into longleaf pine uplands is a gently-sloped, relatively treeless, herb-dominated seepage bog (Folkerts, 1982; Means, 1996a). Such low-elevation terrains, however, are not nearly as abundant in the Coastal Plain as are higher-elevation landforms with elevations ranging from 50-200 m. The headwaters of streams in the high-elevation landforms are typically ravines with steep valley sidewalls vegetated with closed canopy hardwood forest. These ravines contain the second plethodontid assemblage in the Coastal Plain (Table 1), but the ravines may be formed by two very different geological processes. I discuss the geological processes first and the second plethodontid assemblage next.

Generally, unless trapped in basins with no outflow, rainwater that neither percolates into the ground nor evaporates nor transpires, runs off to the sea first by means of sheet flow, then gathers into small creeks, larger streams, and rivers. Moving water is strongly influenced by topographic relief, of course, so that where relief is greatest, ravines are formed by the gullying action of runoff water from the high to the low points on the landscape. If the distances between high and low points are short, gullying action forms impressively deep, V-shaped valleys wherever the soil is relatively impervious to water. In the Coastal Plain this condition is met where soils with a heavy clay content exist next to an escarpment, such as along the valley walls of the larger streams and rivers. Most of the major Coastal Plain rivers from the Mississippi eastward have deep valleys with relatively high sidewalls along at least one side of their drainage basin. Thus, deep ravines are common along the valley walls of the Mississippi, Mobile/Alabama, Escambia, Choctawhatchee, Apalachicola, Chattahoochee, Savannah, and other rivers, providing highly shaded, humid habitats that are especially favorable for plethodontids.

Another type of ravine exists in the Coastal Plain, but until the past couple of decades has been altogether unknown to biologists. Such ravines are called "steepheads" because of the peculiar geomorphology of their valley heads, which are impressive amphitheaters up to 35 m deep (Means, 1985; Sellards and Gunter, 1918; Sharp, 1938). Steepheads and the downstream ravines they form have a geological provenience entirely different from that of gully-eroded ravines (Fig. 2). Steepheads are actively migrating heads of valleys that are formed in large, deep sand deposits of the lower Coastal Plain. The sand bodies appear to be ancient, usually Plio-Pleistocene, barrier island complexes (Gremillion et al., 1964; Means, 1975) with little clay or silt, and sands so porous that rainwater rapidly percolates downward to some confining layer, usually a silty marl or limestone, and resides there as a surficial aquifer.

Fig. 2.--Valley geomorphology: typical gully-eroded valley versus steephead configuration. Gully-eroded valleys are formed by scouring action of the creek, downward into the landform. Steephead valleys are formed by headward migration of the steephead into deep sands, through the sapping action of seepage water emerging from the toe of the steephead slope.

Wherever local relief permits, such as where a large river has cut through the sand deposit to the level of the confining layer, the surficial aquifer saps or bleeds laterally from the escarpment or valley sidewall of the river. The sapping groundwater carries away the sand grain by grain until the escarpment slumps due to the undercutting. Because the slumped sand is porous, the groundwater continues to sap through it, carrying the sand away until the escarpment is steep again, whereupon the cycle is repeated. In time, amphitheater-shaped nicks in the escarpment are formed by this sapping action, each of which migrates headward into the sand body. The nicks are the steepheads where active slumping takes place. Some steepheads have progressed more than 5 km into the sand body away from the original escarpment. While deep U-shaped valleys are being formed by steephead action, new steepheads may develop along the valleys and migrate in different directions from the principal steephead. Usually, the surficial aquifer bleeds along the toe of the valley sidewalls into the stream valley formed by migrating steepheads along the entire length of the valley, but the sheer volume of water sapping from the aquifer is only strong enough to undercut the valley sidewall at just the steepheads.

Steepheads and the seepage pockets along the sidewalls of steephead-formed valleys are special havens for plethodontid salamanders. There are strong physical differences between steepheads and the heads of gully-eroded valleys, but they may be more of degree than kind, as far as plethodontids are concerned. The "streamside microhabitats" or moist seepage wetlands of steepheads, for example, begin abruptly at the base of a steep-walled valley head that is deeply incised into the landscape. Around the toe of the amphitheater are tens to hundreds of square meters of moist substrate fed by spring seepage, covered with decomposing hardwood litter, shaded by a closed hardwood canopy, and highly suitable for plethodontids. The volume of spring water is so great that only five to ten meters downstream from the initial seepages, especially where several seepages flow together, creeks form that have one to three cubic feet per second (cfs) of flow, and often have small cyprinid and poeciliid fishes in them. The larger steepheads may form creeks with flows of 5-10 cfs 50-100 m downstream from the valley headwall. Steephead-formed valleys usually have a U-shaped cross-section because of the broad nature of the migrating amphitheater, and because a small amount of lateral sapping causes the valley sidewalls to retreat from the center of the valley.

By contrast, a typical Coastal Plain gully-eroded ravine begins as a gently-sloped depression scooped out by sheet flow that has water only for a few minutes during and following rains. The ravine head begins gently at the top of the landscape, and gradually becomes deeper and more incised into the landform as one progresses downhill. After several hundred meters, the scouring action of water has incised a narrow gully that gradually becomes deeper, the valley having a V-shaped cross-section. Eventually, depending upon slope and soil conditions, a small creek begins to flow, often going underground and re-emerging several times before forming a permanently open channel. Plethodontids abound along the streamlet where water first flows and for several hundred meters downstream where the fall of the creek is so steep that only erosion takes place. Thereafter, where the stream-gradient lessens and alluviation begins (the filling of the valley with sediments), the physical habitat becomes affected by the dual processes of deposition and erosion, and the plethodontid assemblage changes to that of the swampy creeks.

Steepheads are similar enough in quality to the headwaters of gully-eroded ravines that the same assemblage of plethodontids (assemblage 2, see Table 1) occurs in both: *Eurycea cirrigera*, *Pseudotriton ruber*, and either *Desmognathus apalachicolae* or *D. fuscus conanti* (Means, 1974, 1975; Means and Karlin, 1989). Downstream, both types of streams eventually become sluggish, have a well developed floodplain that is periodically overwashed by high waters, and generally become attractive to plethodontid species of assemblage 1: *Pseudotriton montanus, Desmognathus auriculatus*, *Eurycea guttolineata*, and the *Eurycea quadridigitata* complex.

Where the deep steephead ravine systems are close to the coast, as on Eglin Air Force Base in the Florida panhandle, they may have served as "evolutionary engines" during sea level changes. For instance, ravines on the northwest side of Eglin Air Force Base (Fig. 3) may contain a new species of *Desmognathus*. These same ravines form the principal geographic distribution of the bog frog, *Rana okaloosa* (Moler, 1985). A slight increase in sea level (2-5 m) would have isolated ancestral populations of *Desmognathus* and *Rana* in these deep steephead valleys having huge volumes of permanent seepage outflow, allowing them the time and isolation to diverge from ancestral stocks. In another drainage system only about 50 km to the east, *D. apalachicolae* may have evolved from similarly isolated stocks of the *D. ochrophaeus* complex in the Apalachicola ravines during a higher sea level stand in the early Pleistocene (Means and Karlin, 1989). Similar barrier island sand bodies have occurred during the 65-million year period of the formation of the Coastal Plain, such as Trail Ridge on the eastern margin of Okefenokee Swamp in southeastern Georgia and northeastern Florida, and the Fall Line Sand Hills that stretch from the Chattahoochee River in midwest Georgia to the Cape Fear River in southeastern North Carolina.

Fig. 3.--Topographic map of the approximate 200,000-ha Eglin Air Force Base in the Florida panhandle; contour interval = 10 m. Steepheads, up to 35-m deep, have migrated into the deep sands of the western two-thirds of Eglin; on the eastern one-third of the Base, classic gully erosion has etched many deep ravines into the landform. The highest

elevations are over 65 m, only 3 km from the Gulf of Mexico. A sea-level rise of only 5 m would cause freshwater animals in many northwest steephead valleys to be isolated by salt water at the valley mouths. This may have been the isolating mechanism enabling *Rana okaloosae* to evolve from *R. clamitans*, and a possible new species of *Desmognathus* to evolve from *D. fuscus conanti*.

3. SEEPAGE: THE TRANSITION FROM POND- TO LAND-BREEDING

The evolutionary origin of the family Plethodontidae was long thought to have been centered on the Appalachians because lunglessness, a diagnostic character of the family, was hypothesized to be an adaptation for reducing larval buoyancy in mountain streams (Beachy and Bruce, 1992; Bruce et al., 1994; Wilder and Dunn, 1920). Recently, however, Ruben and Boucot (1989) argued that lunglessness could not have evolved as a response to mountain brook habitats because the Appalachians were a flat peneplane during the time of the first plethodontids (late Cretaceous to early Cenozoic). They advanced a new hypothesis suggesting that lunglessness was the result of cephalic narrowing which lead to decreased pulmonary efficiency and greater reliance on cutaneous respiration; cephalic narrowing was brought about by some unknown ecological or biomechanical factors in either semi-aquatic or terrestrial ancestors (Ruben and Boucot, 1989; Ruben et al., 1993). While the two hypotheses are in disagreement over the habitat of ancestral plethodontids, their other components are not mutually exclusive. Below I examine aspects of the biology of Coastal Plain plethodontids for fresh insights about the ecological setting in which plethodontid salamanders, and lunglessness, may have evolved. Then I propose a third hypothesis that combines the strengths of the two previous theories with the new insights.

I believe that the ecology of primitive living plethodontids -- hemidactyliines with lengthy larval periods, for example, *Gyrinophilus porphyriticus*, *Pseudotriton ruber*, *Pseudotriton montanus*, and *Stereochilus marginatus* (Beachy and Bruce, 1992) -- has much to tell us about the origin of the Plethodontidae.

In the Coastal Plain, both larval and adult *Pseudotriton montanus* inhabit wet pockets of organic matter along swampy creeks and in mucky depressions and seeps in the floodplains of streams of Strahler order 3 or greater. Its common name, mud salamander, derives from its habit of being submerged in muck -- partially decomposed organic matter -- not inorganic mud (i.e., clay and silt). The mud salamander occurs primarily in lowland environments in the southeastern U. S., where it inhabits mucky springs and streams, and swampy pools and ponds, often occurring in burrows in peat or muck (Bruce,1975). Occasionally I have found metamorphosed individuals under logs where their bodies were entirely in the air, but far more often I have raked adults of this species from underwater in pockets of muck or leaf litter in swampy streams. This tendency to be submerged may explain why *P. montanus* is difficult to find (Means, 1986; Mount, 1975). In the Coastal Plain, the wet pockets are always choked with stick and leaf litter, roots, and as often as not, are full of liquid muck of the type preferred by *Amphiuma pholeter*, with which *P. montanus* is occasionally found (Means, 1977, and unpublished data). Muck and peat deposits require relatively constant water in which to form, otherwise they will decompose quickly. The peat and muck deposits of swampy creeks result mostly from the permanent seepage waters that continually issue from small adjacent sand aquifers (personal observation), but in river floodplains, the water is supplied by periodic and often regular high runoff events. A common associate of *P. montanus* in swampy creek habitats is *Desmognathus auriculatus*, which is found under wet debris at the edges of mucky, floodplain sloughs, swampy lakes, and other sites of decomposing muck associated with blackwater or spring-fed streams (Means, 1974).

In the Coastal Plain, *Pseudotriton ruber* and *P. montanus* are rarely syntopic, in spite of the fact that larvae of both live submerged in peaty/mucky sites in the same drainages. *Pseudotriton montanus* is found far downstream from ravine heads in swampy portions of drainages, while *P. ruber* lives at the very heads of drainages, in ravines. In those drainages not having ravines, however, *P. montanus* lives all the way to the swampy source (personal observation). In ravines, *P. ruber* larvae are found in peaty or mucky seepage pools and seepage slopes full of decomposing organic matter. A good way to collect them is to scrape the top couple of centimeters of muck aside with one's boot and watch for larvae wriggling furiously to burrow back down into the muck. Metamorphosed adults of *P. ruber* are often bathed in water that seeps from the wet sandy sidewalls of steepheads, partly or wholly immersed in decomposing organic matter. In gully-eroded ravines, the species is usually associated with leaf packs bathed in cascading or flowing water. I have also dug them from the flooded tunnels of burrowing crayfish.

In the Atlantic Coastal Plain, the many-lined salamander, *Stereochilus marginatus,* has a lifestyle very similar to that of *Pseudotriton montanus* and *Desmognathus auriculatus,* with which it is closely associated. Of its habitat Brimley (1909) said, "apparently an aquatic mud-burrower, ...obtained by merely scraping away the covering of semi-decayed vegetable matter around the edges of the pools...." The species is usually aquatic but is occasionally found beneath sphagnum or under logs in damp situations; it is most abundant in pools and slow streams in swampy woods (Bishop, 1943; Bruce, 1971). Of the four primitive living species under consideration, only *S. marginatus* is not found in Appalachia, probably because *Stereochilus* never gave rise to a species that lives in first-order ravines.

Of the four species, *Gyrinophilus porphyriticus* is not found in the Coastal Plain, but its habitats are very much like seepages in Coastal Plain ravines. Based upon locations in the Carolinas, Bruce (1972) described its habitat preferences as springs, seeps, and small streams.

Within-drainage syntopy of the two species of *Pseudotriton* illustrates that low-elevation Coastal Plain habitats are sufficiently diverse that the primitive genus *Pseudotriton* has been able to exploit physical differences within drainages. The ancestral plethodontids could also have made the transition from lowland, swampy habitats and seepages of high-order streams such as *P. montanus* inhabits, to the more aereated waters upstream in low-order ravines where *P. ruber* is found. It is not necessary, therefore, to posit mountainous terrain as the ecological theater in which plethodontids first evolved. Coastal Plain ravines, or those developed in the peneplane or other low-elevation terrains of the late Cretaceous and early Cenozoic, are ecologically similar to mountain cove habitats in the southern Appalachians. As the Appalachians were uplifted in the Cenozoic, primitive plethodontids were pre-adapted and already available to invade developing mountain brook habitats.

For many years plethodontids were thought to be most closely related to ambystomatid salamanders (Hecht and Edwards, 1977), most of which have pond-inhabiting larvae (Petranka, 1998). The hypothesis of mountain brooks as the ecological setting of plethodontid origins (Beachy and Bruce, 1992; Bruce et al., 1994; Wilder and Dunn, 1920) does not explain how early plethodontid larvae made the transition from ponds to mountain brooks. This problem is obviated if one accepts the proposal of Larson and Dimmick (1993) that the Amphiumidae is the sister family of the Plethodontidae. Amphiumas are entirely Coastal Plain in geographic distribution (Conant and Collins, 1998) and it is reasonable to expect that Cretaceous amphiumids lived in low-lying terrains much as they do today. The three species in the small family occupy nearly all the aquatic and wetland habitats of the Coastal Plain. *Amphiuma means* and *A. tridactylum* live in swamps, cypress bays, ditches, temporary ponds, sloughs, and sluggish streams (Petranka, 1998). And *A. pholeter* is a strong habitat associate of assemblage 1 Coastal Plain plethodontids which includes *Pseudotriton montanus* (Means, 1974, 1996b).

The fully aquatic modern amphiumas are quite derived morphologically, and no doubt are quite different from the common ancestor that gave rise to plethodontids and amphiumids. Unlike the primitive living plethodontids, *Amphiuma means* and *A. tridactylum* have short larval periods of only a few weeks (Petranka, 1998). Larvae of the muck-inhabiting *A. pholeter* have never been found in spite of intensive searching (Means, 1996b). Amphiumas, however, have egg-brooding behavior like plethodontids and unlike ambystomatids (Petranka, 1998).

The common ancestor of the Amphiumidae and Plethodontidae probably had a complex life cycle like that of many pond-breeding salamanders. It probably bred in ponds, swampy lakes, and slack waters in large river floodplains (overflow ponds), had a flexible larval life (normally short but possessing the prospect of neoteny when the annual hydroperiod was long), and a terrestrial adult stage. As the lineage leading to modern amphiumids diverged from that of the plethodontids, amphiumas evolved a fully aquatic mode of life, large body size, and have nearly lost the gilled larval stage. In contrast, other features of ancient habitats invited the lengthening of the larval life of early plethodontids. Ephemeral wetland habitats, such as temporary ponds and overflow ponds of river floodplains, whose hydrology is driven by rainfall and stormwater runoff, would not have been conducive to lengthened larval life. Wetlands whose hydrology is driven by groundwater seepage, however, are usually permanent as well as buffered thermally and chemically by aquifer water. Seepage water is also quite cool, maintaining a temperature that is approximately the same as the annual average air temperature, locally. Seepage habitats, therefore, presented a vast adaptive zone awaiting colonization and exploitation. And, as noted above, all of the more primitive living plethodontids, plus some others, occupy this adaptive zone.

I propose that the ancestral plethodontids invaded seepage habitats like those occupied by *Pseudotriton ruber, P. montanus,* and *Gyrinophilus porphyriticus* today. Larval life lengthened because seepage keeps larval habitats wet year-round. Seepage and its associated organic deposits are rich in aquatic invertebrate life, including insect larvae (Ephemeroptera, Diptera, Coleoptera, Odonata, etc.), earthworms (e.g., Sparganophilidae), and even tiny molluscs (Sphaeriidae). And the organic matter in seeps and springs provides protection from visually orienting predators that live in the air column. Selection that favored increased larval life in seepages probably also favored the retention of the larval habitat in the life of the metamorphosed adult.

Mucky seepages, as the ancestral habitat of the Plethodontidae, fulfill the requirement of Ruben and Boucot (1989) that ecological or biomechanical factors favored cephalic narrowness in plethodontid ancestors. A biomechanical advantage would obviously accrue to organisms that swam in water as the modern amphiumas do, but cephalic narrowness would confer an even greater advantage in the viscous fluid medium of wet leaf litter in varying stages of decomposition, as I propose happened in the earliest plethodontids. The ecological factor was muck and pockets of particulate organic matter in seepages; the biomechanical factor was streamlining to reduce friction during locomotion in the viscous habitat.

Presumably, the reproductive biology of the first plethodontid was like that of living amphiumids and all other salamanders: courtship and the deposition of spermatophores took place underwater. Because of severely reduced visibility and the resistance to locomotion that would be encountered by salamanders trying to breed in muck and wet peat, courtship and spermatophore deposition probably would have been very difficult to accomplish in seepage habitats. All plethodontids court and deposit spermatophores in the air column on land, however. The evolutionary exploitation of seepage habitats by larvae as well as adults, therefore, may have facilitated the evolution of terrestrial mating (Reagan and Verrell, 1991). In summary, the hydrostatic function of lungs, which is valuable to larvae in the open water column, was not necessary in muck and wet peat. Cephalic narrowing, which was necessary for locomotion in the viscous medium of muck and wet peat, made pulmonary respiration less efficient. The loss of lungs was compensated by increased cutaneous respiration in cool seepage waters. Terrestrial mating evolved in the earliest plethodontids because of the mechanical impediments caused by particulate organic matter to vision and to the complex movements required by courtship and spermatophore deposition.

Irrespective of whether the Appalachians were available for colonization by ancestral plethodontids (see controversy in Ruben and Boucot, 1989, and Ruben et al., 1993, versus Beachy and Bruce, 1992, and Bruce et al., 1994), some or much of the environment of eastern North America in the Late Cretaceous and early Cenozoic, during the period when the Plethodontidae probably originated (the sister family, Amphiumidae, is known from Late Cretaceous fossils, Holman, 1995), was a low-lying, slightly hilly landscape with low-gradient, swampy streams, but also with scattered ravines probably much like the present-day Coastal Plain. Just as in Coastal Plain steepheads and ravines today, and all along the valley sidewalls of rivers and streams, seepage habitats were abundant. While montane environments have come and gone as tectonism and peneplanation have waxed and waned, lowlands with seepage habitats in streams, rivers, and ravines -- that even today are inhabited by basal plethodontids -- have always been present. They are probably occupied today much the same as they were when the ancestral plethodontids first invaded seepages, lost their lungs, and evolved terrestrial mating behavior.

4. SUMMARY

All the types of habitats utilized by Coastal Plain plethodontids are briefly discussed, with special emphasis on wetlands ranging from lentic habitats and swampy streams and backwaters of river floodplains to the cooler, more permanent seepage habitats in ravines. Aside from *Plethodon* spp., few Coastal Plain plethodontids are strictly terrestrial or aquatic. Eleven species of wetland-inhabiting plethodontids fall into one of two habitat assemblages: those breeding in ponds or swampy habitats of large streams and rivers and those that breed and live in ravines. I hypothesize that the basal

plethodontids, much like the primitive living plethodontids that inhabit seepage habitats today, evolved lengthened larval life and lunglessness as adaptations for existance in the wet peat and muck of seepage habitats.

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Table 1.

	Type of habitats				
Species	pond	>3	3	2	1
Assemblage 1					
Eurycea quadridigitata complex	25	24	7	3	6
Desmognathus auriculatus	8	60	19	4	27
Pseudotriton montanus	1	25	15	-	2
Stereochilus marginatus	-	2	-	-	-
Hemidactylium scutatum	-	2	-	-	-
Eurycea guttolineata	-	26	10	5	27

<u>Assemblage 2</u>

Pseudotriton ruber	-	2	3	4	85
Eurycea cirrigera	-	24	15	11	123
Desmognathus apalachicolae	-	4	3	2	67
Desmognathus fuscus	-	2	2	4	56
Desmognathus monticola	-	-	-	1	9