TECHNICAL DRAFT RECOVERY PLAN

for

Cumberland Elktoe (*Alasmidonta atropurpurea*), Oyster Mussel (*Epioblasma capsaeformis*), Cumberlandian Combshell (*Epioblasma brevidens*), Purple Bean (*Villosa perpurpurea*), and Rough Rabbitsfoot (*Quadrula cylindrica strigillata*)

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A third group within the lampsilines expel superconglutinates (Haag et al. 1995). The superconglutinate is tethered by a secreted transparent mucilaginous strand that may reach 8 feet in length; it resembles a fish, complete with stripes and an eyespot. None of the lampsiline species addressed in this recovery plan utilizes superconglutinates as a host fish attractant.

As few as 1 to as many as 25 fish species are known to serve as suitable hosts for particular species of mussels (Fuller 1974, Gordon and Layzer 1989). Relative host specificity appears to be common in mussels (Neves 1993), with most species utilizing a few host fishes. Research on these five species seems to corroborate this assertion (see "Reproductive Biology of the Five Species").

Glochidial parasitism serves as a means of dispersal for this relatively sedentary group (Neves 1993). Expelled glochidia can survive only a few days without infesting a proper host fish (Neves and Widlak 1988). Attempts to parasitize nonhost fish will result in rejection and glochidial death by the host's immune system (Neves et al. 1985). The parasitic stage generally lasts 2 to 3 weeks (Gordon and Layzer 1989), but may last much longer (Yeager and Saylor 1995, Haag and Warren 1997), and is temperature dependent (Watters and O'Dee 1997). After dropping from fish hosts, newly metamorphosed juveniles passively drift with currents and ultimately settle in depositional areas with other suspended solids (Neves and Widlak 1987, Yeager et al. 1994). Juveniles must, however, come into contact with suitable habitat to begin their free-living existence (Gordon and Layzer 1989).

Reproductive Biology of the Five Species

Cumberland elktoe

Gordon and Layzer (1993) summarized the reproductive biology and identified fish hosts of the Cumberland elktoe. This bradytictic anodontine species was found gravid from October through May, but they observed no fish infested with its glochidia until March. They found Cumberland elktoe glochidia to develop equally well on both fin and gill surfaces. Five fish species collected from the wild were parasitized by Cumberland elktoe glochidia--whitetail shiner (*Cyprinella galactura*), northern hogsucker (*Hypentelium nigricans*), rock bass (*Ambloplites rupestris*), longear sunfish (*Lepomis megalotis*), and rainbow darter (*Etheostoma caeruleum*). However, under laboratory conditions, juvenile specimens transformed only on the northern hogsucker (Gordon and Layzer 1993). The period of glochidial encystment (i.e., until transformation into free-living juveniles) took 24 days, at 66.2 ± 5.4°F.

Oyster mussel

The lampsiline oyster mussel appears to be bradytictic. Spawning probably occurs in late summer, as glochidia have been observed in the marsupia during May, June, and July (Gordon and Layzer 1989). In the Powell River, Yeager and Saylor (1995) found that 58 percent of the females were gravid, but specimens were gravid only in May at a water temperature from 59.0 to 64.0°F. The age of gravid females, using the external growth ring method (Chamberlain 1931, Crowley 1957), was estimated at 7 to 10 years. The glochidia are likely released in early summer (Gordon and Layzer 1989). Four fish species have been identified as hosts--the wounded darter (*Etheostoma vulneratum*), redline darter (*E. rufilineatum*), dusky darter (*Percina sciera*), and banded sculpin (*Cottus carolinae*) (Yeager and Saylor 1995). Transformation took from 19 to 34 days, at 60.4 to 62.4°F.

Cumberlandian combshell

Spawning in the bradytictic lampsiline Cumberlandian combshell probably occurs in late summer with the glochidia being held over winter and released in late spring (Gordon 1991). Ahlstedt (1991a) reported observing gravid individuals in May and June. Gravid females were reported from early May (but probably occurred earlier) to early June at a temperature of 59.0 to 64.0°F by Yeager and Saylor (1995). Estimated age (see Chamberlain 1931, Crowley 1957) of gravid females was 8 to 13 years. Six host fish species have been identified: wounded darter, redline darter, Tennessee snubnose darter (*E. simoterum*), greenside darter (*E. blennioides*), logperch (*Percina caprodes*), and banded sculpin (Yeager and Saylor 1995). Transformation took from 16 to 48 days, at 60.4 to 62.4°F.

Purple bean

The purple bean, another lampsiline species, appears to be bradytictic, as gravid females have been observed in January (Ahlstedt 1991a). Three host fish species have been identified--the fantail darter (*Etheostoma flabellare*), greenside darter, and mottled sculpin (*Cottus bairdi*) and/or banded sculpin (Watson and Neves 1996). Transformation took from 11 to 25 days, at 70.7 to 76.1°F.

Rough rabbitsfoot

Yeager and Neves (1986) summarized the reproductive biology and identified fish hosts of the amblemine rough rabbitsfoot. This tachytictic species spawned from May (when water temperature reached 68.0 to 71.6°F) through June. Fertilization success was high (>95 percent) through late June, but by July only unfertilized ova were found. Unlike most amblemines, 65 percent of 82 gravid females examined utilized only the outer demibranchs as marsupia. They estimated gravidity rates of from 30 to 60 percent, peaking in late May, then gradually declining. Females release lanceolate-shaped whitish to reddish brown conglutinates (0.4 inches long) that contain 375 to 505 semicircular-shaped glochidia. Fecundity was estimated at 115,000 embryos per female. Estimated age (see Chamberlain 1931, Crowley 1957) of the females studied was 10 to 22 years. Three cyprinid host fish species have been identified--the whitetail shiner, spotfin shiner (*C. spiloptera*), and bigeye chub (*Hybopsis amblops*). Infestation rates ranged from as few as 5 to 10 glochidia on individual fishes. Transformation took from 13 to 23 days, at 68.9 to 71.4°F.

REASONS FOR DECLINE

Past and Present Threats

The collapse of the mussel fauna outlined in the "Background" section of this plan is primarily the result of habitat loss and degradation (Williams et al. 1992a, Neves 1993) caused by impoundments, siltation, channelization, and water pollution that have altered or eliminated those habitats that are essential to the long-term viability of many riverine mussel populations. Neves et al. (1997) summarized these major categories of impacts, while Richter et al. (1997) identified specific stressors that threatened imperiled mussels and other aquatic species. The mussel fauna of the Cumberlandian Region is no exception to this long-standing and general status trend (Neves 1991). From observations made at the turn of the century, Adams (1915) commented on mine waste, industrial contamination, deforestation, and resulting sedimentation in the upper Tennessee River system. Coupled with the increased susceptibility that certain species have to environmental perturbations, particularly members of the genus *Epioblasma* (Dennis 1987, Neves et al. 1997), it is not difficult to realize the plight of mussels stemming from major habitat alterations.

Ortmann (1909) may have been the first biologist to correctly assess, but significantly underestimate, the impact of dams on the aquatic biota (Stansbery 1970). Impoundments have significantly altered riverine ecosystems (Ellis 1942, Baxter 1977, Baxter and Glaude 1980, Williams et al. 1992b, Allan and Flecker 1993, Ligon et al. 1995, Sparks 1995) and have been a major factor in the high extinction rate of freshwater mollusks (Johnson 1978, Lydeard and Mayden 1995).

Impoundments result in the dramatic modification of riffle and shoal habitats and the resulting loss of mussel resources, especially in larger rivers (Ortmann 1925, Scruggs 1960, Bates 1962, Neel 1963, Isom 1969, 1971, Stansbery 1973b, Fuller 1974, Schmidt et al. 1989, Williams et al. 1992b, Parmalee and Hughes 1993, Lydeard and Mayden 1995, Sickel and Chandler 1996, Neves et al. 1997). Impoundment impacts are most profound in riffle and shoal areas, which harbor the largest assemblages of mussel species (Stansbery 1970, Layzer et al. 1993).

Dams interrupt most of a river's ecological processes by modifying flood pulses, controlling impounded water elevations, and altering water flow, sediment, nutrients, energy input and output, and the riverine biota (Ligon et al. 1995, Sparks 1995) and also by increasing depth, decreasing habitat heterogeneity, and causing the loss of bottom stability due to subsequent sedimentation (Williams et al. 1992b). The reproductive process of riverine mussels is generally disrupted by impoundments (Fuller 1974). Most Cumberlandian Region species (including these five species) are unable to successfully reproduce and recruit under reservoir conditions (Neves et al. 1997).

In addition, dams can seriously alter downstream water quality and riverine habitat (Allan and Flecker 1993, Ligon et al. 1995, Collier et al. 1996) and negatively impact tailwater mussel populations (Cahn 1936, Hickman 1937, Ahlstedt 1983, Layzer et al. 1993, McMurray 1994).

These changes include thermal alterations immediately below dams (Neves 1993), and channel characteristics, habitat availability, and flow regime are also profoundly affected, all having drastic effects on the stream biota (Allan and Flecker 1993). Altered effects also include fish community shifts (Brim 1991) and the resultant colonization by fewer native species and more nonindigenous species (Williams and Neves 1992). Daily discharge fluctuations, high silt loads, and altered host fish distribution contributed to limited recruitment and skewed demographics of the mussel fauna on the lower Cumberland River below Barkley Reservoir (Sickel 1982). Coldwater releases from large nonnavigational dams and scouring of the river bed from highly fluctuating, turbulent tailwater flows have also been implicated in the demise of mussel faunas (Miller et al. 1984, Layzer et al. 1993).

Population losses due to impoundments have probably contributed more to the decline of these five species and other Cumberlandian Region mussels than has any other single factor. A significant percentage of the main stems of the Tennessee and Cumberland Rivers and many of their largest tributaries are now impounded. For example, over 2,300 river miles (about 20 percent) of the Tennessee River and its tributaries with drainage areas of 25 square miles or greater were impounded by the TVA by 1971 (TVA 1971). The subsequent completion of additional major impoundments on tributary streams (e.g., Duck River in 1976 and Little Tennessee River in 1979) significantly increased the total miles impounded behind the 36 major dams in the Tennessee River system (Neves et al. 1997).

Approximately 90 percent of the 562-mile length of the Cumberland River downstream of Cumberland Falls is either impounded (three locks and dams and Wolf Creek Dam) or otherwise adversely impacted by cold water discharges from Wolf Creek Dam. Miller et al. (1984) located only two mussel specimens in a survey below Wolf Creek Dam covering 68 miles of river that formerly harbored 39 species (Neel and Allen 1964). Other major U.S. Army Corps of Engineers impoundments on Cumberland River tributaries (e.g., Laurel River, Obey River, Caney Fork, Stones River) have inundated over 125 miles of potential riverine habitat for the Appalachian elktoe, oyster mussel, and Cumberlandian combshell.

Heavy metal-rich drainage from coal mining and associated sedimentation have adversely impacted many stream reaches (Barnhisel and Massey 1969, Ahmad 1973, Curry and Fowler 1978), destroying mussel beds and preventing natural recolonization (Simmons and Reed 1973, McCann and Neves 1992). Impacts associated with coal mining activities have particularly altered upper Cumberland River system streams with diverse historical mussel faunas (Stansbery 1969, Blankenship 1971, Blankenship and Crockett 1972, Starnes and Starnes 1980, Anderson 1989, Schuster et al. 1989, Anderson et al. 1991) and have been implicated in the decline of *Epioblasma* species, especially in the Big South Fork (Neel and Allen 1964). Strip mining continues to threaten mussels in coal field drainages of the Cumberland Plateau (Anderson 1989), including Cumberland elktoe, oyster mussel, and Cumberlandian combshell populations. The low pH commonly associated with mine run-off can lead to an inability of glochidia to clamp their valves on host tissues thus preventing proper encystment (Huebner and Pynnönen 1992). Acid mine run-off may thus be having local impacts on recruitment of, particularly, the

Cumberland elktoe, since most of its range is within watersheds where coal mining is still occurring. The Marsh Creek population of the Cumberland elktoe has also been adversely affected and is still threatened by potential spills from oil exploration activities. Circumstantial evidence indicates that salinity, a by-product of oil exploration activities, is lethal to some glochidia (Liquori and Insler 1985).

The role that coal mining has played in the decline of the Powell River mussel fauna in Virginia was prophesied by Ortmann (1918) and has been briefly summarized by Wolcott and Neves (1991, 1994). Mine discharge from the 1996 blowout of a large tailings pond on the upper Powell River in Virginia resulted in a major fish kill (Koch, pers. comm., 1996). Research by Kitchel et al. (1981) indicates that Powell River mussel populations were inversely correlated with coal fines in the substrate. When coal fines were present, decreased filtration times and increased movements were noted in laboratory-held mussels (Kitchel et al. 1981). In a quantitative study in the Powell River, Ahlstedt and Tuberville (1997) attributed a 15-year decline of the oyster mussel, Cumberlandian combshell, and rough rabbitsfoot and the long-term decrease in species composition (from 30 in 1979 to 21 in 1994) to general stream degradation due primarily to coal mining activities in the headwaters. Mining activities also likely contributed to the extirpation of the purple bean from the Powell River several decades ago.

In-stream gravel mining, which is a localized threat to some of these species, has been implicated in the destruction of mussel populations (Stansbery 1970, Yokley and Gooch 1976, Grace and Buchanan 1981, Schuster et al. 1989, Hartfield 1993). Negative impacts associated with gravel mining include stream channel modifications (e.g., altered habitat, disrupted flow patterns, sediment transport), water quality modifications (e.g., increased turbidity, reduced light penetration, increased temperature), macroinvertebrate population changes (e.g., elimination, habitat disruption, increased sedimentation), and changes in fish populations (e.g., impacts to spawning and nursery habitat, food web disruptions) (Kanehl and Lyons 1992). Once mussels have been eliminated, a decade or more may pass before recolonization occurs (Stansbery 1970, Grace and Buchanan 1981). Substrate disturbance and siltation impacts can also be realized for considerable distances downstream (Stansbery 1970). Gravel mining activities threaten the Cumberlandian combshell and oyster mussel populations in Buck Creek, one of only two remaining populations of these two species in the entire Cumberland River system.

The effects of heavy metals and other contaminants on freshwater mussels was reviewed by Havlik and Marking (1987) and Naimo (1995). Contaminants contained in point and nonpoint discharges can degrade water and substrate quality and adversely impact, if not destroy, mussel populations (Neves and Zale 1982, Havlik and Marking 1987, McCann and Neves 1992). The effects are especially profound on juvenile mussels (Robison et al. 1996), as they can readily ingest contaminants adsorbed to silt particles during normal feeding activities (see "Food Habits"), and on glochidia, which appear to be very sensitive to some toxicants, such as ammonia (Goudreau et al. 1993). Of the many organisms used in toxicological tests, mussels appear to be among the most intolerant of heavy metals (Keller and Zam 1991). Although the adults of some species may tolerate short-term exposure (Keller 1993), Huebner and Pynnönen (1992) indicated that low levels of certain heavy metals may inhibit glochidial attachment to fish hosts. Sediment from the upper Clinch River, where several of these species occur, was found to be toxic to juvenile mussels (Robison et al. 1996, Ahlstedt and Tuberville 1997). Ahlstedt and Tuberville (1997) speculated that the presence of toxins in the Clinch River may explain the decline and lack of mussel recruitment at some sites in the Virginia portion of that stream.

Numerous streams have experienced mussel kills from toxic chemical spills and other causes (Cairns et al. 1971, Crossman et al. 1973, Neves 1986, Wolcott and Neves 1994). The dramatic impact the chlor-alkali chemical plant in Saltville, Virginia, has had on the aquatic fauna in the North Fork Holston River is well documented (Adams 1915, Cairns et al. 1971, Stansbery and Clench 1974, Hill et al. 1975, Ahlstedt 1980, 1991c, Neves and Zale 1982, Sheehan et al. 1989). Since its opening in 1893, mercury and various salts from this site have polluted the river and decimated the entire molluscan fauna 80 miles to its mouth (Ahlstedt 1991c), including populations of the oyster mussel, Cumberlandian combshell, purple bean, rough rabbitsfoot, and 34 other mussel species (Neves and Zale 1982). The long-term kill was so thorough that only one mussel species was reported by Hill et al. (1975). The closing of the plant in 1972 brought about the possible opportunity for mussel recolonization, either naturally (Stansbery and Clench 1974) or artificially (Ahlstedt 1980). Sheehan et al. (1989) considered habitat in the North Fork Holston River below Saltville to be suitable for mussels once again, although natural recolonization had not occurred by 1990 (Ahlstedt 1991c).

An alkaline fly ash pond spill in 1967 and a sulfuric acid spill in 1970 on the Clinch River at Carbo, Virginia, caused a massive mussel kill for up to 12 miles downstream from a power plant site (Cairns et al. 1971, Crossman et al. 1973, Stansbery 1986, Sheehan et al. 1989). Populations of the oyster mussel, Cumberlandian combshell, rough rabbitsfoot, and purple bean that may have resided in the affected river reach were undoubtably impacted by these spill events. Natural recolonization has not occurred in the impacted river reach (Stansbery 1986, Ahlstedt 1991a), and an experimental reintroduction of nonlisted mussels in 1981 and 1984 has largely failed (Sheehan et al. 1989).

Siltation and sedimentation run-off has been implicated as the primary factor in water quality impairment in the United States (Neves et al 1997) and has contributed to the decline of mussel populations (Ellis 1931, 1936, Imlay 1972, Coon et al. 1977, Marking and Bills 1979, Wilber 1983, Dennis 1985, Schuster et al. 1989, Wolcott and Neves 1991, Houp 1993, Richter et al. 1997). Sources of siltation and sedimentation include poorly designed and executed timber-harvesting operations and associated activities; complete clearing of riparian vegetation for agricultural, silvicultural, or other purposes; and those construction, mining, and other practices that allow exposed earth to enter streams. Specific impacts on mussels from sediment include clogged gills, which reduces their feeding and respiratory efficiency, disrupts metabolic processes, reduces growth rates, contributes to substrata instability and the physical smothering of mussels under a blanket of silt (Ellis 1936, Stansbery 1971, Marking and Bills 1979, Kat 1982, Aldridge et al. 1987).

Predation upon rare freshwater mussels by muskrats (*Ondatra zibethicus*) has been shown to be potentially detrimental to the recovery of mussel species (Neves and Odom 1989). Muskrat predation appears to continue to be a significant problem in localized stream reaches in at least the upper Tennessee River system (Koch, pers. comm. 1997).

The invasion of the nonnative zebra mussel (*Dreissena polymorpha* [Pallas 1773]), poses a potential new threat to the mussel fauna of the Tennessee and Cumberland River basins. Although zebra mussels are now in the Tennessee and Cumberland River systems, the extent to which they will impact native mussels is unknown. However, zebra mussels in the Great Lakes have attached, in large numbers (up to 10,000 per unionid), to the shells of live and fresh dead native mussels (Schlosser and Kovalak 1991), and they have been implicated in the loss of mussel beds (Hunter and Bailey 1992, Masteller et al. 1993, Schlosser and Nalepa 1995).

The information presented in this section and in the "Distributional History and Relative Abundance" section indicates that current populations of these five mussels are isolated from one another by impoundments, unsuitable habitat, or other impediments to migration. Natural repopulation of many of the sites with extirpated populations is impossible without human intervention. Many extant populations are restricted to short river reaches, making them very vulnerable to extirpation from a single stochastic event, such as a toxic chemical spill (Havlik and Marking 1987).

Patterns of Imperilment

Mussels become jeopardized when their population size is diminished by any factor that reduces glochidial or juvenile survivability, adult spawning stocks, and host fish abundance (Neves 1993). Furthermore, any perturbation that limits fertilization rates and survivability of the glochidia, decreases host fish abundance, decreases fish community composition, and/or alters density, aggregation, or size distribution of mussel populations is detrimental to population viability and, ultimately, the species as a whole (Downing et al. 1993, Neves 1993, Neves et al. 1997).

The complex life cycle of mussels increases the probability that weak links in their life history will preclude successful reproduction and recruitment (Neves 1993). Egg formation and fertilization are critical phases in the life history, as many mussels fail to form eggs (Downing et al. 1989), or fertilization is incomplete (Matteson 1948). Fertilization success has been shown to be strongly correlated with spatial aggregation, and either influences the rate of egg formation, or improves fertilization rates of individuals, or both (Downing et al. 1993).

A study on the eastern elliptio, *Elliptio complanata* (Lightfoot 1786), in a Canadian lake (Downing et al. 1993) offers interesting insights on various aspects of reproductive biology. Complete fertilization failure occurred at densities of <0.9 mussels per square foot. Not until densities reached 3.7 per square foot were fertilization rates 100 percent. Thus, fertilization success of sparse populations is extremely low. Population viability is therefore questionable in

mussel beds with low densities, and where fertilization does occur, recruits may be more homozygous than those in denser populations. Populations with cohort dominance skewed toward only old, large mussels will have limited reproductive success due to senescence. The occurrence of large numbers of gonad-destroying trematode parasites in old individuals of some mussel species (Zale and Neves 1982) might indicate senescence is partially a result of gonadal infestation.

The fluvial nature of riverine ecosystems would likely indicate that mussel beds would not need to be as aggregated for successful reproduction, as stream flow patterns would potentially disperse sperm over long linear distances. Where very low densities occur, however, reproductive success would probably be minimal. There is some evidence that hermaphroditism in certain mussel species may allow even minuscule populations to enjoy a level of reproductive viability (R. J. Neves, USGS, pers. comm., 1996). Hermaphroditism has not been investigated in these five species.

The apparently inefficient reproductive cycle involving obligate fish hosts would appear to be a weak link in population recruitment (Bogan 1993). Despite the high number of glochidia produced, contact between glochidia and host fishes is a low-probability event (Neves et al. 1997), promoted by the respiratory and feeding behavior of fishes (Dartnall and Walkey 1979, Neves et al. 1985) and the behavioral characteristics of some mussel species (Davenport and Warmuth 1965, Kraemer 1970). Infestation rates are therefore generally low for riverine mussels (Neves and Widlak 1988, Bruenderman and Neves 1993). Although glochidia may initially

attach to many fish species, immune system incompatibility results in unsuitable fish hosts quickly sloughing off the parasites (Zale and Neves 1982).

Despite the dearth of available quantitative information, the evidence is overwhelming that individual and combined stressors resulting from anthropogenic forces have been responsible for the demise of mussel faunas (Havlik and Marking 1987, Neves et al. 1997). Gradual reductions in recruitment and survival of vulnerable mussel species occur when anthropogenic factors act insidiously in altering sediment and water quality (Fleming et al. 1995). Susceptibility of glochidia and host fish to altered and degraded habitats, coupled with the chance encounter between glochidia and host, can contribute to periodic recruitment failures (Zale and Neves 1982) and relic populations dominated by cohorts of older adults (Neves 1993, Stansbery 1995). Unfortunately, many mussel populations are indeed characterized by large, old, and spatially separated individuals that are commonly on their way towards extirpation (Stansbery 1995).

Mussel recolonization of impacted river reaches is achieved by dispersal of newly metamorphosed juveniles via infested host fish, passive adult movement downstream (Neves 1993), and active migration or passive movement downstream of small individuals (Kat 1982). Due to slow growth and relative immobility, however, the establishment of self-sustaining populations requires decades of immigration and recruitment, even where suitable habitat exists for common species that may occur in high densities (Neves 1993). Mussel recruitment is typically low and sporadic, with population stability and viability being maintained by numerous slow-growing cohorts and occasionally good year classes (Neves and Widlak 1987). Only when a significant number of viable populations have been verified should that species be considered stable (A. E. Bogan, North Carolina State Museum of Natural Sciences, in litt., 1995).

Due to their extreme longevity, direct effects of some anthropogenic factors on mussels may not be evident for years and, in some cases, not until the species has disappeared or experienced significant range reduction (Bogan, in litt., 1995). Studies suggest that although individual impacts may be minor, cumulative effects may become lethal over time (Bogan 1993).

Determination of the relative rarity of species has been divided by Rabinowitz et al. (1986) into the following three factors: (1) geographic range, (2) habitat specificity, and (3) population abundance. Based on the fact that these five species are highly restricted in range, are habitat specialists, and generally occur in small populations, their imperilment is made more acute.

Principles of population genetics give valuable insight into the heightened imperilment of rare species. Neves (1997) presents a thorough summary of genetic considerations in freshwater mussel conservation. Many of the populations of these five mussel species are extremely small and geographically isolated so that the natural interchange of genetic material between populations is prohibited. Such isolation can eventually lead to inbreeding depression, which can be a major detriment to a species' recovery (Frankham 1995). Inbreeding may result in decreased fitness of multiple life stages, and the loss of genetic heterozygosity results in significantly increased risk of extinction in localized natural populations (Saccheri et al. 1998). The effect of heterozygosity on extinction risk is most noticeable in small, isolated populations.

However, even in populations exhibiting more intermediate levels of isolation, extinction risk increases dramatically with decreasing heterozygosity in the smallest populations (Saccheri et al. 1998).

The fragmentation of populations is of paramount importance when considering the likelihood of long-term survival of narrowly distributed species (Burkhead 1993). Population genetics has emphasized the profound negative effects the loss of genomic heterogeneity has on overall population viability of species with restricted ranges (Chesser 1983, Gilpin and Soulé 1986). It is likely that some of the populations of these five mussel species may be below the level required to maintain long-term genetic viability (see further discussion in Recovery Task 1.3.6 in the "Narrative Outline"). Many, if not all, of the factors addressed in this section have probably played, and some may continue to play, roles in the demise of the five mussels addressed in this recovery plan.

CONSERVATION MEASURES

A National Native Mussel Conservation Committee has been formed to conserve this highly imperiled fauna. This committee has drafted a national strategy to address mussel conservation (Biggins et al. 1995). Its goals are to conserve native species; ensure their continued survival; and maintain their ecological, economic, and scientific values to our society (Neves 1997). Neves (1997) presents a summary of the national mussel strategy and outlines actions needed to implement mussel conservation and recovery on a global scale.

Ecosystem management is the most effective method of protecting the greatest number of species (Doppelt et al. 1993, Shute et al. 1997). The Service has implemented ecosystem management in conserving, restoring, and recovering Federal trust species and their habitats nationwide. This holistic approach to the management of biotic resources has been deemed much more effective than managing single species in a complex natural and political environment. Shute et al. (1997) summarized the ecosystem approach to the management of imperiled aquatic resources, provided a literature review on the subject, and recommended a series of steps for developing and implementing an ecosystem management program. These include prioritizing ecosystems in need of protection, identifying and partnering with all potential agencies and organizations with watershed interests, prioritizing ecosystem threats, identifying strategies to minimize or eliminate threats, and educating ecosystem inhabitants and other stakeholders.

A number of conservation measures are available for federally listed and other species pursuant to Federal regulations and other Federal and State activities. Conservation actions by Federal, State, and private organizations, groups, and individuals are facilitated once a species has been listed under the Act. The Act requires that recovery actions be conducted for listed species; provides for possible land acquisition in cooperation with the States (Section 5); through cooperation with the States, provides funding to effect recovery activities (Section 6); requires Federal agencies to evaluate their actions with respect to any listed species (Section 7); and protects listed species from illegal taking (Sections 9, 10, and 11).

The Clean Water Act (CWA), administered by the Environmental Protection Agency (EPA), has taken great strides in reducing point discharge pollutants into streams (Neves et al. 1997). Municipalities and industries have improved wastewater treatment facilities with grants and aid from the EPA and State environmental protection departments. Nonpoint source pollution is dealt with in a number of ways under the CWA, including providing funds through its Section 319 program to improve water quality and reduce nutrient loading, sedimentation, and the likelihood of other pollutants entering the streams. In addition, the EPA and USGS have assessed and monitored water quality in streams throughout much of the Southeastern United States. Programs under the U.S. Department of Agriculture, particularly those administered by the Natural Resources Conservation Service (e.g., Conservation Reserve Program, Environmental Quality Improvement Program, Wetlands Reserve Program, Wildlife Habitat Improvement Program), are increasingly addressing impaired streams with imperiled species.

Numerous stakeholders have realized that wise stream management, which involves restoring and protecting riparian habitat, improves water quality (Osbourne and Kovacic 1993), and is crucial for mussels (Neves et al. 1997). Water and stream habitat quality improvements have made it possible for mussel populations to expand in some river reaches and to explore the possibility of establishing once depleted or extirpated mussel populations in other streams. Such improvements in habitat conditions have come to fruition through the concerted efforts of the TVA, EPA, and other Federal agencies; State water resources and natural resources agencies; industry; municipalities; conservation organizations; and concerned citizens. For instance, the

TVA has modified water releases from several of its dams to improve water quality conditions in the tailwaters.

The Service's Asheville Field Office has partnered with other field offices and a legion of stakeholders to initiate several watershed-based riparian habitat restoration projects on streams having diverse mussel faunas within the Cumberlandian Region. Seed money provided by the Service's Partners for Fish and Wildlife Program, which aids private landowners in restoring habitat, has been particularly instrumental in getting the restoration program started and leveraging up to a 20:1 increase in funding for on-the-ground projects. Projects include the Clinch and Paint Rock Rivers in the Tennessee River system and Buck Creek in the Cumberland River system. All three projects are aiding in the recovery of the oyster mussel and Cumberlandian combshell, while the Clinch River project also benefits the purple bean and rough rabbitsfoot. Other streams with populations of these species are being considered for future restoration efforts.

Activities that have helped improve riverine habitat include reducing erosion by stabilizing stream banks and using no-till agricultural methods, controlling nutrient enrichment by carefully planning heavy livestock use areas, establishing buffer zones by erecting fencing and revegetating riparian areas, developing alternative water supplies for livestock, and implementing voluntary best management practices to control run-off for a variety of agricultural and construction activities. Perhaps the greatest accomplishment of all is that riparian landowners and other stakeholders are proving that they can be good stewards of the land by taking increased interest and pride in aquatic resources.

The Nature Conservancy (TNC) has played a pivotal role in establishing and coordinating watershed-based restoration projects in the Cumberlandian Region. Demonstrating a strong commitment to imperiled aquatic resources, they have established bioreserves and other community-based projects on high-diversity streams, such as the upper Clinch River in Tennessee and Virginia and Horse Lick Creek in Kentucky. The upper Clinch River, which has more at-risk mussel and fish species than any other small watershed, has also been selected by TNC as one of eight priority watersheds nationwide critical for protecting aquatic biodiversity (Master et al. 1998). Field representatives work closely with landowners and other stakeholders to effect riparian and aquatic habitat restoration. Recently, TNC established the Southern Appalachian Rivers Initiative in Chattanooga, Tennessee, to oversee existing watershed restoration projects in Tennessee and Georgia and to determine focus streams for future efforts in a multi-State area. Partnering with State and Federal agencies and the coal industry, TNC is also working on the coal re-mining initiative, which addresses the complex issue of abandoned mine land (Master et al. 1998).

Public outreach and environmental education play a major role in Asheville's recovery and restoration programs. Working with various other Federal agencies through a private company, an imperiled streams exhibit featuring mussels was recently installed in the Tennessee Aquarium in Chattanooga. A large series of brochures, posters, and videos on mussels and fishes and other materials have been developed for public dissemination. Other projects being planned include *Russell the Mussel*, a storybook for children relating the plight of mussels; aquatic trunks that will enable secondary school educators to teach students about how the public benefits from aquatic ecosystems, while stressing the need for their protection and restoration; and a video on stream restoration techniques for private landowners.

State and Federal agencies and the scientific community have cooperatively developed mussel propagation and reintroduction techniques and conducted associated research that has facilitated the reintroduction of mussels into historical habitats. A major reintroduction project is being planned for the Tennessee River at Muscle Shoals, Alabama, a site that was historically the most diverse of all known mussel beds worldwide (Ortmann 1924b, 1925, Stansbery 1964). A proposed rule is currently being drafted that would allow for the reintroduction of 16 federally listed mussel species and 1 aquatic snail to the remaining habitat of the site below Wilson Dam. Studies are underway to better understand and eliminate threats to mussels from contaminants and other environmental perturbations.

Certain Cumberlandian Region streams, some of which harbor populations of these five species, receive a level of State protection by being designated as outstanding resource waters. Some streams have been protected by the National Park Service. Much of the Big South Fork system, with populations of the Cumberland elktoe, oyster mussel, and Cumberlandian combshell, is protected as the Big South Fork National River and Recreation Area in northern Tennessee, as is a population of the purple bean in the Obed Wild and Scenic River in east-central Tennessee.

PART II

RECOVERY

A. Recovery Objectives

The ultimate goal of this recovery plan is to restore viable populations[1] of the Cumberland elktoe (*Alasmidonta atropurpurea*), oyster mussel (*Epioblasma capsaeformis*), Cumberlandian combshell (*Epioblasma brevidens*), purple bean (*Villosa perpurpurea*), and rough rabbitsfoot (*Quadrula cylindrica strigillata*) within a significant portion of their historical ranges, eliminate threats to their continued existence, and remove them from the Federal List of Endangered and Threatened Wildlife and Plants.

Criteria for downlisting to threatened status:

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot will be considered for reclassification to threatened status when the likelihood of

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[1]Viable population: A wild, naturally reproducing population that is large enough to maintain sufficient genetic variation to enable the species to evolve and respond to natural habitat changes without further intervention. The number of individuals needed and the amount and quality of habitat required to meet this criterion will be determined for these species as one of the recovery tasks.

their becoming extinct in the foreseeable future has been eliminated by achieving the following criteria:

1. Through protection of existing populations, reestablishment of historical populations, and/or discovery of currently unknown populations, there exists:

    a. At least three distinct viable Cumberland elktoe populations in the upper Cumberland River system.

    b. At least five distinct viable oyster mussel populations--two in the upper Cumberland River system and three in the Tennessee River system.

    c. At least five distinct viable Cumberlandian combshell populations--two in the upper Cumberland River system and three in the Tennessee River system.

    d. At least three distinct viable purple bean populations in the upper Tennessee River system.

    e. At least three distinct viable rough rabbitsfoot populations in the upper Tennessee River system.

2. One distinct naturally reproduced year class exists within each of a species' viable populations. The year class must have been produced within 5 years prior to the time the species is reclassified from endangered to threatened. Within 1 year of the downlisting date, gravid females of the mussel and its host fish must be present in each viable population.

3. Studies of the mussels' biological and ecological requirements have been completed and any required recovery measures developed and implemented from these studies are beginning to be successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited by the species.

4. No foreseeable threats exist that would likely impact the survival of the species over a significant portion of their ranges.

Criteria for removing the species from the Federal List of Endangered and Threatened Wildlife and Plants:

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot will be considered for removal from Federal List of Endangered and Threatened Wildlife and Plants when the likelihood of their becoming endangered in the foreseeable future has been eliminated by achieving the following criteria:

1. Through protection of existing populations, reestablishment of historical populations, and/or discovery of currently unknown populations, there exists:

   a. At least four distinct viable Cumberland elktoe populations in the upper Cumberland River system.

   b. At least seven distinct viable oyster mussel populations--two in the Cumberland River system; three in the Tennessee River system above Knoxville, Tennessee; one in the Tennessee River system from the Sequatchie River, Tennessee, downstream to Muscle Shoals, Alabama; and one in the Duck River system, Tennessee.

   c. At least seven distinct viable Cumberland combshell populations--two in the Cumberland River system; three in the Tennessee River system above Knoxville, Tennessee; one in the Tennessee River system from the Sequatchie River, Tennessee, downstream to Muscle Shoals, Alabama; and one in the Duck River system, Tennessee.

   d. At least four distinct viable purple bean populations in the upper Tennessee River system.

   e. At least four distinct viable rough rabbitsfoot populations in the upper Tennessee River system.

2. Two distinct naturally reproduced year classes exist within each of the viable populations. Both year classes must have been produced within 10 years, and 1 year class within 5 years of the recovery date. Within 1 year of the recovery date, gravid females of the mussel and its host fish must be present in each viable population.

3. Studies of the mussels' biological and ecological requirements have been completed and recovery measures developed and implemented from these studies have been successful, as evidenced by an increase in population density and/or an increase in the length of the river reach inhabited in each of the viable populations.

4. No foreseeable threats exist that would likely threaten the survival of any of the viable populations.

5. The viable populations of a species are separated to the extent that it is unlikely that a single event would eliminate or significantly reduce more than one of the populations.

B. Narrative Outline

1. **Preserve extant populations and currently inhabited habitats.** Since only a small number of populations of these five species exist, it is essential that they all be protected.

   1.1 **Continue to use existing legislation and regulations (the Act, CWA, Fish and Wildlife Coordination Act, Federal and State surface mining laws, wetland and water quality regulations, stream alteration regulations, Federal Energy Regulatory Commission relicensing, etc.) to protect the species and their habitats.** Prior to and during implementation of this recovery plan, it is critical to the species' survival that Federal and State agencies continue to protect the existing populations with those laws and regulations that address protection and conservation of the species and their habitats.

   1.2 **Solicit help in protecting the species and their essential habitats through the development of cooperative partnerships (local watershed projects) with Federal and State agencies, local governments, agricultural groups, mining interests, conservation organizations, local landowners, and other stakeholders.** Section 7 consultation under the Act, the Fish and Wildlife Coordination Act, and other laws and regulations can assist in the protection of species when Federal programs are involved, but implementation of these programs alone cannot recover the species. The assistance of various stakeholders will be essential. More importantly, the support of the local community, including farming and mining interests and local individuals and landowners, will be essential in order to meet these recovery goals. Without a partnership with the people who live and work in these watersheds and who have an influence on habitat quality, recovery efforts will be doomed.

1.2.1 **Meet with local government officials and regional and local planners to inform them of our plans to attempt recovery for these species and request their support.** This recovery criterion is particularly important in high-growth metropolitan areas in the Cumberlandian Region.

1.2.2 **Meet with agricultural, silvicultural, construction, and mining interests and try to elicit their support in implementing protective actions.** The support of these groups is essential. They should be informed of current, but strictly voluntary, best management practices that could be implemented to minimize the impact of their activities on aquatic resources and should be encouraged to promote the safe mixing, application, storage, and disposal of pesticides and herbicides and to comply with current water quality regulations.

1.2.3 **Develop cooperative ventures with private landowners to restore riparian habitat through programs like the Service's Partners for Fish and Wildlife and those administered by Natural Resources Conservation Service.** Federal and State natural resource agencies and conservation organizations, in cooperation with willing landowners, have begun to implement programs to restore riparian and aquatic habitat (see "Conservation Measures"). These programs, which are designed to benefit both the landowner and our natural resources, should be pursued with willing landowners to help minimize soil erosion and toxic run-off and enhance habitat for these five mussels.

1.2.4 **Develop an educational/outreach program to promote a watershed management approach to managing water and aquatic habitat quality in the Cumberlandian Region.** The use of tools and activities (e.g., slide/tape presentations, workshops, volunteer workdays, brochures) to achieve this task should be championed among government agencies, schools, agricultural groups, civic and youth groups, churches, and other watershed stakeholders. Educational materials and activities that further recovery goals, with emphasis on the ecological and human benefits to be derived from maintaining and upgrading water and aquatic habitat quality, is essential for gaining public support for this recovery program and fostering pride in and the wise stewardship of these natural resources.

1.3 **Determine threats to the species, conduct research necessary for the species' management and recovery, and implement management actions where needed.**

1.3.1 **Conduct life history research on the species to include such factors as reproduction, food habits, age and growth, and demography.** Some limited information is available with regard to the life history of these species (see "Ecology and Life History" and "Reproduction of the Five Species"). However, much additional life history information will be needed in order to successfully implement the recovery tasks.

1.3.2 **Characterize the species' habitats (e.g., relevant physical, biological, and chemical components) for all life history stages.** These species have been able to withstand some degree of habitat degradation. However, much of their habitat has been so severely altered that the species have been extirpated from numerous stream reaches (see "Distributional History and Relative Abundance"). Knowledge of species-specific microhabitat requirements and ecological associations is needed in order to focus management and recovery efforts on explicit habitat problems.

1.3.3 **Determine present and foreseeable threats to the species.** Siltation and toxic run-off from certain agricultural, silvicultural, construction, and mining practices have contributed, and may continue to contribute, to substrate and water quality degradation. The mechanisms by which the species and their habitats are impacted by these factors are poorly understood, and the extent to which the species can withstand these impacts is unknown.

1.3.4 **Determine contaminant sensitivity for each life history stage.** Sensitivity of mussel glochidia, juveniles, and adults to contaminants may vary significantly (see "Reasons for Decline"). The technology and methodology to determine sublethal and lethal levels of common contaminants (e.g., pesticides, herbicides, chemical discharges) on these species or their surrogates should be developed.

1.3.5 **Based on the biological data and threat analyses, investigate the need for management, including habitat improvement.** Management actions, if needed, should be implemented in order to secure viable populations. Specific components of the species' habitats may be lacking, limiting the species' potential expansion, or certain activities in the watersheds may be adversely impacting the species. Habitat improvement programs may be needed as a prerequisite for reintroduction in order to increase host fish abundance, spawning success for both mussels and host fishes, and overall survivability. Cooperative projects with willing landowners for the purpose of providing alternative water sources may be needed to help minimize the impacts of water withdrawal and livestock access to the streams. Such efforts will be needed to overcome some of the threats identified in Task 1.3.3 (also see Task 1.2.3).

1.3.6 **Determine the number of individuals required to maintain a long-term viable population.** Inbreeding depression can be a major obstacle to a species' recovery, especially if the remaining population size is small and/or it has gone through some type of genetic bottleneck. The actual number of individuals in a population is not necessarily a good indication of a population's genetic viability; rather, the effective population size (EPS) is important (Neves 1997). The EPS is the size of an "ideal" population in which genetic drift takes place at the same rate as in the actual population (Chambers 1983).

Franklin (1980) suggested that the inbreeding coefficient should be limited to no more than 1 percent per generation, a figure which implies that maintenance EPS, in the short term, should be no fewer than 50 individuals (Frankel and Soulé 1981, Franklin 1980, Soulé 1980). Because the EPS is typically only one-third to one-fourth the actual population size (being affected by sex ratio, overlapping generations, generally nonrandom distribution of offspring, and nonrandom mating) (Soulé 1980), a population of 150 to 200 individuals is needed for short-term population maintenance. Soulé (1980) further suggests that for long-term viability, an EPS of 500 individuals is necessary, translating into a population size of 1,500 to 2,000 individuals.

The EPS for all five species needs to be determined in order to calculate whether their remaining populations are capable of long-term self-maintenance or whether propagation programs should be initiated. Some of these factors can be addressed under Task 1.3.3, while others will be addressed as needed.

Allozyme and/or mitochondrial DNA studies should also be considered in order to assess genetic variability in the remaining populations of the five species.

1.3.7 **Conduct detailed anatomical and molecular genetic analyses of the five species throughout their ranges.** Researchers in the Southeastern United States recognize that the taxonomic identity for many mussel taxa has probably not been determined (Butler 1989, Mulvey et al. 1997). There is evidence that the oyster mussel may represent a species complex (see "Species Descriptions"). If true, the taxa that comprise this complex are more endangered than the oyster mussel. Accordingly, there would be major implications for the recovery and management of the multiple entities comprising the species complex. Research on molecular genetics, soft anatomy, life history, and ecology should be undertaken to determine if the oyster mussel or any populations of the other four species is a distinct genetic entity that may warrant specific conservation and management consideration. Genetic information on various populations of these species would also be useful in determining which genetic stocks should be used in particular translocation efforts (see Task 3).

2. **Search for additional populations of the species.** It is possible that some currently unknown populations of these five species may exist. An effort should be made to search

unsurveyed river reaches and to resurvey river reaches from which the species are thought to have disappeared.

3. **Determine, through research, the feasibility of augmenting extant populations and reintroducing the species into historical habitat.** Severe range restriction and overall population declines characterize the status of these species (see "Distributional History and Relative Abundance"). Their recovery is not possible without augmenting some existing populations and/or reintroducing populations into habitat within their historical ranges.

3.1 **Refine techniques and methodologies for propagating and translocating individuals as a prelude to potential augmentation and reintroduction efforts.** Sufficient specimens of most listed mussels are not presently available to allow for the translocation of enough adults to augment or reintroduce populations. The development of propagation and translocation techniques is an advancing, but on-going, research endeavor (see Neves 1997 for a summary of captive propagation and mussel translocations and Watters 1994 for an annotated bibliography of mussel propagation). These methodologies will need to be tested on a variety of species in order to increase production levels and improve survival rates of captive-propagated and translocated animals.

3.2 Determine the need, appropriateness, and feasibility of augmenting and expanding certain existing populations. Many extant populations may be characterized by a size or demographic composition that is insufficient to maintain long-term genetic viability (see Task 1.3.6). These populations may be able to expand naturally if environmental conditions are improved. However, some populations may be too small and may need to be augmented to reach a sustained level of viability.

3.2.1 In coordination with partners, survey efforts should be undertaken to identify and prioritize extant populations suitable for augmentation activities based on biological, ecological and habitat characterization criteria. A set of biological, ecological, and habitat parameters will need to be developed to determine if an existing population will be suitable for species augmentation. Prioritized populations for this task will be selected based on present population size, demographic composition, population trend data, potential site threats, habitat suitability, and any other limiting factors that might decrease the likelihood of long-term benefits from population augmentation efforts.

3.3 Determine the need, appropriateness, and feasibility of reintroducing the species into prioritized stream reaches within their historical ranges. Numerous populations of these five species have been lost from streams and stream reaches within their historical ranges. Habitat and water quality improvements have recently been documented in some stream reaches where these species once occurred (see "Conservation Measures"). However, since extant populations are isolated by impoundment or otherwise long stretches of inappropriate habitat, natural repopulation of now suitable but unoccupied historical habitat is impossible. This task will explore the possibility or reintroducing populations into unoccupied historical habitat.

3.3.1 **In coordination with partners, survey efforts should be undertaken to identify and prioritize sites within the species' historical ranges based on ecological and habitat characterization criteria as a prerequisite for reintroduction activities.** A set of ecological and habitat parameters will need to be developed to determine if a site will be suitable for species reintroduction. These will include habitat suitability, substrate stability, presence of host fishes, potential site threats, and any other limiting factors that might decrease the likelihood for long-term benefits from population reintroduction efforts.

3.4 **Identify and prioritize those streams, stream reaches, and watersheds most in need of protection from further threats.** Streams, stream reaches, and watersheds should be prioritized for protection based on a variety of factors. These include high endemicity; high diversity of imperiled species; biogeographic history of rare species; highly fragmented habitats; cost effectiveness and ease of preservation, management, recovery, and restoration; landowner complexity; watershed size; existing land use patterns; public accessability; likelihood for success; and those systems exhibiting low resilience to disturbance (Angermeier et al. 1993, Carroll and Meffe 1994, Shute et al. 1997). Furthermore, augmentation and reintroduction activities should not be conducted at totally unprotected sites or at sites with significant uncontrollable threats.

3.5 **Augment existing populations and/or reintroduce populations into their historical ranges, and evaluate and monitor the success of these efforts.** Using techniques developed under Task 3.1, augment and/or reintroduce populations of the five species. Stream reaches with augmented and/or reintroduced populations should be monitored annually for at least 5 years to evaluate the success of these activities.

3.6 **Implement protective measures for reintroduced populations.** Although reintroduced populations will undoubtably be designated nonessential experimental populations and not receive the full protection of Sections 7 and 10 of the Act, other laws and regulations can provide protection for these populations.

4. **Develop and implement a program to monitor population levels and habitat conditions and assess the long-term viability of currently existing, newly discovered, augmented, and reintroduced populations.** During and after the implementation of recovery actions, the status of the species and their habitats must be monitored to assess

progress toward recovery. Information gathered from this task and Task 3.5 will aid in refining techniques and methodologies that are critical aspects of the recovery program for these species. This task should be conducted on a biennial schedule.

5. **Develop and implement cryogenic techniques to preserve the species' genetic material until such time as conditions are suitable for reintroduction.** Cryogenic preservation of the species could maintain genetic material (much like seed banks for endangered plants) from all extant populations. If a population were lost to a catastrophic event, such as a toxic chemical spill, cryogenic preservation could allow for the eventual reestablishment of the population using the genetic material preserved from that population.

6. **Annually assess the overall success of the recovery program and recommend action (e.g., changes in recovery objectives, delist, implement new measures, conduct additional studies).** The recovery plan must be evaluated periodically to determine if it is on track and to recommend future actions. As more is learned about these species, the recovery objectives may need to be modified.

C. Literature Cited

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Recovery plans delineate reasonable actions that are believed to be required to recover and/or protect listed species. Plans published by the U.S. Fish and Wildlife Service are sometimes prepared with the assistance of recovery teams, contractors, State agencies, and other affected and interested parties. Plans are reviewed by the public and submitted to additional peer review before they are adopted by the Service. Objectives of the plan will be attained and any necessary funds made available subject to budgetary and other constraints affecting the parties involved, as well as the need to address other priorities. Recovery plans do not obligate other parties to undertake specific tasks and may not represent the views nor the official positions or approval of any individuals or agencies involved in developing the plan, other than the U.S. Fish and Wildlife Service. Recovery plans represent the official position of the U.S. Fish and Wildlife Service **only** after they have been signed by the Director or Regional Director as **approved.** Approved recovery plans are subject to modification as dictated by new findings, changes in species status, and the completion of recovery tasks.

By approving this recovery plan, the Regional Director certifies that the data used in its development represent the best scientific and commercial data available at the time it was written. Copies of all documents reviewed in the development of this plan are available in the administrative record located at the Asheville, North Carolina, Field Office.

Literature citations for this document should read as follows:

U.S. Fish and Wildlife Service. 1998. Technical Draft Recovery Plan for Cumberland Elktoe, Oyster Mussel, Cumberlandian Combshell, Purple Bean, and Rough Rabbitsfoot. Atlanta, GA. 119 pp.

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Fees for recovery plans vary, depending on the number of pages.

EXECUTIVE SUMMARY

Current Status: The Cumberland elktoe (*Alasmidonta atropurpurea*), oyster mussel (*Epioblasma capsaeformis*), Cumberlandian combshell (*Epioblasma brevidens*), purple bean (*Villosa perpurpurea*), and rough rabbitsfoot (*Quadrula cylindrica strigillata*) were listed as endangered species under the Endangered Species Act of 1973, as amended, on January 10, 1997. All five species have undergone significant reductions in total range and population density. They once existed over hundreds of river miles and now survive in only a few relatively small, isolated populations. The Cumberland elktoe still exists in eight mostly small tributaries to the upper Cumberland River in Kentucky and Tennessee. The oyster mussel survives in nine tributaries of the Tennessee and Cumberland River systems in Kentucky, Tennessee, and Virginia. The Cumberlandian combshell persists in eight tributaries of the Cumberland and Tennessee River systems in Alabama, Kentucky, Tennessee, Virginia, and possibly Mississippi. The purple bean is extant in five tributaries and the rough rabbitsfoot is extant in three tributaries of the upper Tennessee River system in Tennessee and Virginia.

Habitat Requirements and Limiting Factors: These species, which are adapted to live in gravel shoals of free-flowing rivers and streams, were eliminated from much of their historical ranges by impoundments, other significant modifications to their riverine environments, sedimentation, and pollution. The species and their habitats are being impacted by deteriorated water and substratum quality (primarily resulting from poor land use practices); contaminants;

completed and any required recovery measures developed and implemented from these studies have been successful; (4) no foreseeable threats exist that would likely threaten the survival of any of the viable populations; and (5) the viable populations of a species are separated to the extent that it is unlikely that a single event would eliminate or significantly reduce more than one of the populations.

Actions Needed:

1. Utilize existing legislation/regulations to protect the current populations.
2. Determine threats and alleviate those which threaten the species.
3. Determine the species' life history requirements.
4. Solicit the assistance of local landowners and communities and initiate projects to improve habitat quality and populations.
5. Develop and utilize an information/education program.
6. Through augmentation or reintroduction establish viable populations.
7. Search for additional populations.

Date of Recovery: The downlisting and delisting dates cannot be estimated at this time. A time period of at least 10 years is needed to document the long-term viability of mussel populations.

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PART I

INTRODUCTION

The U.S. Fish and Wildlife Service (Service) determined endangered species status for the Cumberland elktoe (*Alasmidonta atropurpurea* [Rafinesque 1831]), oyster mussel (*Epioblasma capsaeformis* [Lea 1834]), Cumberlandian combshell (*Epioblasma brevidens* [Lea 1831]), purple bean (*Villosa perpurpurea* [Lea 1861]), and rough rabbitsfoot (*Quadrula cylindrica strigillata* [Wright 1898]), under the Endangered Species Act of 1973, as amended (Act), on January 10, 1997 (Service 1997). All five species have undergone significant reductions in total range and population density. They once existed over hundreds of river miles and now survive in only a few relatively small, isolated populations. The Cumberland elktoe still exists in eight mostly small tributaries to the upper Cumberland River in Kentucky and Tennessee. The oyster mussel survives in nine tributaries of the Tennessee and Cumberland River systems in Kentucky, Tennessee, and Virginia. The Cumberlandian combshell persists in eight tributaries of the Cumberland and Tennessee River systems in Alabama, Kentucky, Tennessee, Virginia, and possibly Mississippi. The purple bean is extant in five tributaries and the rough rabbitsfoot is extant in three tributaries of the upper Tennessee River system in Tennessee and Virginia. These species were eliminated from much of their historical ranges by impoundments, other significant modifications to their riverine environments, sedimentation, and pollution. The species and their habitats are being impacted by deteriorated water and substratum quality (primarily resulting from poor land use practices); contaminants; and, potentially, the invasion of the nonnative zebra mussel (*Dreissena polymorpha*). Their restricted ranges and low population levels also increase their vulnerability to toxic chemical spills and possible genetic bottlenecks. This recovery plan outlines the recovery objectives for the Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot and the tasks needed to conserve and recover the species so they no longer require the protection afforded by the Act.

BACKGROUND

The North American mussel fauna is comprised of 297 taxa (Turgeon et al. 1988), of which 91 percent inhabit the Southeastern United States (Neves et al. 1997). The Cumberlandian Region, with 37 percent of the fauna, is the primary center for North American freshwater mussel biodiversity (Ortmann 1918, 1925), and is one of six regional faunas on the continent (van der Schalie and van der Schalie 1950). The Cumberlandian Region is defined as the Cumberland River and its tributaries downstream to the vicinity of Clarksville, Montgomery County, Tennessee; the Tennessee River and its tributaries downstream to the vicinity of Muscle Shoals, Colbert and Lauderdale Counties, Alabama; and the Duck River (Tennessee River system) downstream to just below Columbia, Maury County, Tennessee (Ortmann 1924a). Historical records of Cumberlandian mussel species (e.g., oyster mussel) are known, in some cases, from throughout the length of the Buffalo River, the largest tributary of the Duck River (van der Schalie 1973). The confluence of the Buffalo River is very near the Tennessee River (approximately Duck River mile 15) and about 115 river miles downstream of Columbia. This zoogeographical information indicates that the Buffalo River should also be considered a part of the Cumberlandian Region when defining its boundaries.

Historically, 95 mussel taxa (including 4 endemic and 25 Cumberlandian endemic) were found in the Cumberland River system (Gordon and Layzer 1989, Gordon 1995), while the Tennessee River system harbored 104 taxa (including 9 endemic and 31 Cumberlandian endemic) (Starnes and Bogan 1988, Cicerello et al. 1991). Collectively, 111 taxa historically inhabited the two river systems, and 35 taxa are endemic to the region (Starnes and Bogan 1988, Gordon and Layzer 1989, Cicerello et al. 1991, Gordon 1995).

There is evidence that mussel populations throughout the Central and Eastern United States remained relatively unchanged for centuries prior to European settlement (Parmalee et al. 1982). However, as modern civilization began to significantly alter aquatic habitats in the late 1800s and early 1900s, the collapse of our native mussel populations began (Lewis 1868, Ortmann 1909, 1918, 1924b, 1925, van der Schalie 1973).

No other wide-ranging faunal group in North America has experienced, or is undergoing, as profound a degree of imperilment during this century as are the freshwater mussels. An assessment of the continent's entire mussel fauna recommended conservation status for 67 percent (Stein and Flack 1997) to 72 percent (Williams et al. 1992a) of the taxa. Thirty-six taxa (13 percent) are presumed extinct (Neves et al. 1997), and 69 taxa (21 percent) are classified as federally endangered or threatened species. Over one-third of the continents's mussel fauna either became extinct or was federally listed during the past century.

Experts have reluctantly resigned themselves to the fact that numerous other taxa are functionally extinct and/or are expected to become extinct in the foreseeable future (Neves 1993, 1997; Shannon et al. 1993). Nott et al. (1995) noted that North American mussels and fishes have suffered recent extinction rates in the "kilo-death" range, or three orders of magnitude higher than the rates that have been estimated for species over geological time. A major increase in the global extinction rate is expected in the near future for freshwater mussels and other mollusks as compared with the past global extinction rate (Nott et al. 1995).

The level of imperilment in the Southeastern mussel fauna--75 percent--exceeds that of the continent as a whole (Neves et al. 1997). Further focus of the Southeastern faunal imperilment indicates Tennessee River system mussels appear to have been the most severely impacted (Neves et al. 1997). There are far more species-at-risk mussels and fishes (104) in the Cumberland and Tennessee River systems (including six of the top seven ranked small watershed areas) than in any other region in the country (Master et al. 1998).

SPECIES DESCRIPTIONS

Cumberland elktoe

The Cumberland elktoe has a thin, but not fragile, shell. The outside surface of the shell (periostracum) is smooth, somewhat shiny, and covered with greenish rays. Young specimens have a yellowish brown periostracum, while that of the adults is generally black. The inside surface of the shell (nacre) is shiny with a white, bluish white, or sometimes peach or salmon color. See Clarke (1981) for a more complete description of the species.

Gordon (1991) presents the following diagnostic characters to separate the Cumberland elktoe from the elktoe (*Alasmidonta marginata* [Say 1818]):

> This species is quite similar to *Alasmidonta marginata*, but tends to differ from the latter by its darker color, less pronounced corrugations on the posterior slope, and the less acutely angular development of the posterior ridge. In older individuals of *A. atropurpurea*, the posterior ridge may be rather high and the resulting slope may be quite steep, but the posterior ridge retains a rounded character. The two species may occur in adjacent stream systems but do not appear to be sympatric at any locality.

Oyster mussel

The oyster mussel has a dull to sub-shiny yellowish to green colored periostracum with numerous narrow dark green rays. The shells of females are slightly inflated and quite thin and fragile toward the shell's posterior margin. The nacre is whitish to bluish white in color. See Johnson (1978) for a more complete description of the species.

Gordon (1991) provides the following diagnostic characters:

> The pronounced development of the posterior-ventral region in females distinguishes *Epioblasma* from similarly shaped species. [*Epioblasma*] *capsaeformis* is recognized by the typically dark coloration and fragility of the marsupial expansion and the lack of development of the posterior ridge (e.g., not angular, no knobs). Males in comparison to similar *Epioblasma* tend to be more elliptical, have a moderately developed posterior ridge and accompanying sulcus, and have a regularly curved ventral margin. The ventral margin in species such as *E. florentina* (Lea 1857) and *E. turgidula* (Lea 1858) often exhibit an emargination of the ventrum just anterior to the terminus of the posterior ridge. Yellowish specimens of *E. capsaeformis* have been mistaken for *E. walkeri* (Wilson and Clarke 1914) (including records in Johnson [1978: as *E. florentina*]). Males of *E. walkeri* tend to be broader and have a rounded posterior ridge; females lack the distinctive darkening of the marsupial expansion.

Ortmann (1924a) was the first to note color differences in female oyster mussel mantle pads, which is presumably a host fish attractant. The mantle color appears to be bluish or greenish white in the Clinch River, greyish to blackish in the Duck River, and nearly white in Big South Fork population (Ortmann 1924a, S. A. Ahlstedt and J. B. Layzer, U.S. Geological Survey [USGS], personal communication [pers. comm.], 1997). Varying mantle coloration may be an indication that *Epioblasma capsaeformis* is a species complex (see Recovery Task 1.3.7 in the "Narrative Outline").

Cumberlandian combshell

The Cumberlandian combshell has a thick solid shell with a smooth to clothlike periostracum, which is yellow to tawny brown in color with narrow green broken rays. The nacre is white. The shells of females are inflated, with serrated teethlike structures along a portion of the shell margin. See Johnson (1978) for a more complete description of the species.

Gordon (1991) provides the following diagnostic characters:

> The broad, yellowish shell with broken rays and the distinctive marsupial expansion of the female distinguish this species from most other mussels in the range except *Pychobranchus fasciolaris* [(Rafinesque 1820)] and *Epioblasma lenoir* (Lea 1842). Male *E. brevidens* are broader than *P. fasciolaris* and the females of the latter species do not exhibit the marsupial development of the former. Raying patterns on *P. fasciolaris* usually are not developed. *Epioblasma lenoir* is a considerably smaller species, has a much lighter shell, tends to be greenish, does not have as developed a marsupial expansion, and probably is extinct.

Purple bean

The purple bean has a small to medium-sized shell. The periostracum is usually dark brown to black with numerous closely spaced fine green rays. The nacre is purple, but the purple may fade to white in dead specimens. See Bogan and Parmalee (1983) for a more complete description of the species.

Gordon (1991) provides the following diagnostic characters:

> *Villosa perpurpurea* most closely resembles *V. trabalis* [(Conrad 1834)]. The most obvious difference is the purple nacre of the former in comparison to the white nacre of the latter. However, this character is somewhat variable as noted by Ortmann (1925) and the purple color may fade rapidly in dead specimens. With regards to other shell characters, [*V.*] *perpurpurea* tends to be more compressed, thinner, slightly broader, the beak is less developed, and the emargination of the ventral margin in female shells is not as pronounced. The base color of the periostracum in [*V.*] *trabalis* is greenish. Simpson (1914) noted that *perpurpurea* was "less exaggerated in its particular characters than [*V.*] *trabalis*." The glochidia of the two species are also shaped differently (Hoggarth, 1988). *Villosa vanuxemii* [=*V. v. vanuxemensis*] (Lea 1838) may be sympatric with *perpurpurea* but it tends to be a bit larger. Its [*V. vanuxemii*] nacre is shiny purple but tends to be reddish or brownish in the area of the beak cavity and may be lighter around the periphery of the shell, the base color of the periostracum is brown, and raying is rather obscure. Female shells are strongly truncated, often with a distinct notch just ventral to the terminus of the posterior ridge which runs approximately parallel to the dorsal margin.

Rough rabbitsfoot

The rough rabbitsfoot has an elongated, heavy, highly pustulate shell. Some specimens may have low knobs on the posterior slope. The periostracum is yellowish to greenish in color and is covered with green rays, blotches, and chevron patterns. The nacre is silvery to white with an iridescence in the posterior area of the shell. See Bogan and Parmalee (1983) for a more complete description of the species.

Gordon (1991) provides the following diagnostic characters:

The tendency for the shell to be compressed, highly pustulate, and have low to no knobs on the posterior ridge distinguishes this morph from *Quadrula cylindrica* s.s. [i.e., *Q. c. cylindrica* (Say 1817)]. It is not easily confused with any other sympatric species . . . .

DISTRIBUTIONAL HISTORY AND RELATIVE ABUNDANCE

The Cumberland elktoe, oyster mussel, Cumberlandian combshell, purple bean, and rough rabbitsfoot are all endemic to either the Cumberland River system (Cumberland elktoe), the Tennessee River system (purple bean and rough rabbitsfoot), or to both these river systems (oyster mussel and Cumberlandian combshell). These species are restricted in range to the Cumberlandian Region, with minor exceptions noted in the species accounts for the oyster mussel and Cumberlandian combshell.

The downstream extent of the Cumberlandian Region approximately coincides with the westernmost portion of the Highland Rim Physiographic Province, near the Coastal Plain Physiographic Province (Mississippi Embayment). The gradient of the Cumberland and Tennessee Rivers downstream of this area decreases to the extent that the shoal habitat upon which Cumberlandian mussel species depend was historically extremely scarce or nonexistent. Most of the larger river reaches at the western edge of the Highland Rim are now permanently impounded by the Barkley (Cumberland River) and Kentucky (Tennessee River) Reservoirs.

The mussel fauna of the Cumberlandian Region has been the subject of numerous zoogeographic studies since the work of Lewis (1870) on the Tennessee River at Knoxville. Extensive survey information has become available since 1960 (see Gordon and Layzer [1989] and Winston and Neves [1997] for stream-specific survey citations). These faunal studies form the basis upon which the distributional history of the species addressed in this recovery plan are outlined (Tables 1 through 5). Personal communications with researchers active in the Cumberlandian Region have served to update more recent records of these species long before publication of such data is possible.

Cumberland elktoe

The Cumberland elktoe is limited in distribution to the upper Cumberland River system in southeast Kentucky and north-central Tennessee, occupying streams both above and below Cumberland Falls (Table 1). The original type locality was simply "river Cumberland," according to Clarke (1981), who, upon ascertaining that the type specimen was lost, designated a neotype from the Clear Fork River, a tributary to the Big South Fork, in Fentress County, Tennessee (see Table 1, footnote 2). All verified sites of occurrence are in the Cumberland Plateau Physiographic Province, giving it one of the most restrictive ranges of any Cumberlandian species. The literature, based on museum records, has perpetuated the confusion associated with the historical distribution of this species and a congener--the elktoe (*Alasmidonta marginata*)--in the upper Cumberland River system. Museum and literature records of *A. marginata* in streams draining the Cumberland Plateau should be verified as they may actually represent the Cumberland elktoe (see note for Table 1).

Table 1. *Alasmidonta atropurpurea* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.		
Stream, County, State	**Authority**	**Date**
Cumberland River System		
Laurel Fork, Whitley County, KY	R. R. Cicerello (Kentucky State Nature Preserves Commission, personal communication [pers. comm.], 1997)	1996, 1993
Cumberland River, McCreary and Whitley Counties, KY	Schuster (1988) Clarke (1981)	1935 ?
Laurel River, Laurel County, KY[1]	Cicerello (pers. comm., 1997)	1948
Lynn Camp Creek, Whitley County, KY	Clarke (1981)	?
Marsh Creek, Whitley County, KY	Cicerello (1995) Call and Parmalee (1982)	1994 1979-80
Big South Fork, Pulaski County, KY	Clarke (1981)	?
Big South Fork, McCreary County, KY	Bakaletz (1991)	1986
Rock Creek, McCreary County, KY	Cicerello (1996) Call and Parmalee (1982)	1995 1979
Big South Fork, Scott County, TN	P. W. Shute (Tennessee Valley Authority, pers. comm., 1998) Bakaletz (1991) Hatcher and Ahlstedt (1982)	1996 1986 1980
Clear Fork, Scott County, TN	Bakaletz (1991) Hatcher and Ahlstedt (1982)	1986 1980
Clear Fork, Fentress and Morgan Counties, TN[2,3]	Gordon and Layzer (1993) Bakaletz (1991) Call and Parmalee (1982) Clarke (1981)	1989 1985-86 1980 <1897[4]
North Prong Clear Fork, Fentress County, TN	Ohio State University Museum of Zoology	1988
White Oak Creek, Morgan County, TN	Call and Parmalee (1982)	1980
Bone Camp Creek, Morgan County, TN	R. M. Anderson (U.S. Geological Survey, pers. comm., 1998)	~1988
White Oak Creek, Scott County, TN	Bakaletz (1991)	1986

[1]This museum record for *Strophitus rugosus* (=*Strophitus undulatus* [Say 1817]) by Neel and Allen (1964) actually represents, in part, *Alasmidonta atropurpurea*.

[2]Clarke (1981:71) in his "Remarks" section of the *Alasmidonta atropurpurea* species account designated a neotype (U.S. National Museum of Natural History [USNM] 150522) for this species (Rafinesque's type material is lost), giving the locality as "South Fork, Cumberland River, Fentress Co., Tennessee collected by B. H. Wright." The South Fork does not flow through Fentress County, but a tributary, Clear Fork, does (forming the Fentress/Morgan County line), which better coincides with a locality Clarke (1981:71) presented in his "Geographical Records": "South Fork Cumberland River, Armathwaite, Fentress County, Tenn." (despite naming "J. Lewis! [Museum of Comparative Zoology (MCZ)]" and not "B. H. Wright! [USNM]" as the alleged collector and the museum of deposition, respectively, for this record). As further evidence on the clarification of this matter, Wright (1898) mentions a collection from "A branch of the South Fork of the Cumberland River at Armathwaite, Fentress Co., Tenn." of *Margaritana raveneliana* (=*Alasmidonta raveneliana* [Lea 1834]), actually *Alasmidonta atropurpurea*. In reality, this collection was made by Mr. E. F. Hassler, not Wright. This collection undoubtably refers to the Clear Fork site and represents the material upon which Clarke (1981) designated the neotype for *Alasmidonta atropurpurea*. The correct type locality should therefore read "Clear Fork, near Armathwaite and Rugby, Fentress/Morgan Counties, Tennessee," probably in the vicinity of the Tennessee Highway 52 crossing (see footnote 3 below).

[3]In the *Alasmidonta marginata* account's "Geographical Records," under "Clinch River Drainage," Clarke (1981:66) reports "Clear Fork Creek, Rugby, Morgan Co. Tenn. (MCZ)." This record is probably for *A. atropurpurea* and presumably refers to the Clear Fork site in the Big South Fork system from which he designated the neotype for *A. atropurpurea* (see footnote 2 above). Rugby (Morgan County) is approximately 5 miles from Armathwaite (Fentress County) on Tennessee Highway 52, with the Clear Fork crossing approximately halfway between the two towns.

[4]Clarke (1981:71) mentions that this collection of four specimens attributed to B. H. Wright (and from which the neotype was selected; see footnote 2 above) was originally cataloged as USNM 783317 in January 1897.

NOTE: Records are presumed to be for live or fresh dead individual(s) unless otherwise stated. Compilation studies (e.g., Schuster 1988) are given only when no primary authority can be identified or no significant additional dates of collection can be verified. The Schuster (1988) record is housed in the University of Michigan Museum of Zoology (UMMZ). Other erroneous localities (see footnote 2 above) are given for *Alasmidonta atropurpurea* by Clarke (1981): (1) the "North Fork Cumberland River (B. H. Wright! [USNM])" record given under "Geographical Records" is presumed to be from the main stem of the Cumberland River in Kentucky, as there is no North Fork Cumberland River; (2) his caption for the neotype (USNM 150522) illustrated in Figure 22 (p. 69) as being from the "Cumberland River, Tennessee," is actually the same locality for the neotype (Clear Fork) as stated under his "Remarks" section (p. 71; see footnote 2 above); and (3) the locality given in Table 15, "South Fork, Cumberland River, Fentress County, Tennessee (UMMZ 11190)" also represents the Clear Fork type locality (see footnote 2 above). A record from Horse Lick Creek, Jackson County, Kentucky (Ahlstedt 1986), ". . . could represent a misidentification" of *A. marginata* (Cicerello et al. 1991). A 1978 *Alasmidonta atropurpurea* record for Collins River, Grundy County, Tennessee, given by Call and Parmalee (1982) was considered a misidentification of *Alasmidonta marginata* by Gordon (1995) or possibly represents an undescribed taxon (Anderson, pers. comm., 1998). The New River (Big South Fork system in Tennessee) record given by Gordon (1991) needs substantiation.

The Cumberland elktoe has apparently been extirpated from the main stem of the Cumberland River, Laurel River, and its tributary Lynn Camp Creek. Based on post-1985 records, populations of the Cumberland elktoe persist in eight tributaries--Laurel Fork and Marsh Creek, both Whitley County, Kentucky; Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky; Rock Creek, McCreary County, Kentucky; Clear Fork, Fentress, Morgan, and Scott Counties, Tennessee; North Prong Clear Fork, Fentress County, Tennessee; White Oak Creek, Scott County, Tennessee; and Bone Camp Creek, Morgan County, Tennessee (Table 1). The latter five streams, which comprise the Big South Fork system, may represent a single metapopulation of the Cumberland elktoe; there may be suitable habitat for the species and/or its fish hosts in intervening stream reaches, potentially allowing for natural genetic interchange to occur.

Considered a "rare species" by Clarke (1981), few sites continue to harbor the Cumberland elktoe, although relatively large populations are currently known. Marsh Creek harbors the largest population known in Kentucky (Cicerello 1995, R. McCance, Kentucky State Nature Preserves Commission, in litt., 1994), although populations in Rock Creek are also sizable (Cicerello 1996). In both streams the Cumberland elktoe represented the second most abundant unionid species sampled (Cicerello 1995, 1996). Bakaletz (1991) reported that the largest population in the Big South Fork system in Tennessee was located in the headwaters of Clear Fork, where several hundred specimens were secured from muskrat middens in the late 1980s (Layzer, pers. comm., 1998). Several age classes of the Cumberland elktoe were represented in samples taken from throughout the larger tributaries of the Big South Fork system in Tennessee during a 1985-86 survey (Bakaletz 1991).

Oyster mussel

The oyster mussel was described from the Cumberland River (probably in Tennessee) and historically was one of the most widely distributed Cumberlandian mussel species (Table 2). Its range historically included four physiographic provinces (i.e., Interior Low Plateau, Cumberland Plateau, Ridge and Valley, Blue Ridge) and six States (i.e., Alabama, Georgia, Kentucky, North Carolina, Tennessee, Virginia). In the Cumberland River it occurred from the base of Cumberland Falls, McCreary and Whitley Counties, Kentucky, downstream to Stewart County, Tennessee. In the Tennessee River it occurred throughout the main stem downstream to Colbert and Lauderdale Counties, Alabama. Dozens of tributaries in the Cumberland and Tennessee River systems also harbored this species. The downstreammost site known from the Cumberland River represents an archeological record (P. W. Parmalee, McClung Museum, University of Tennessee, pers. comm., 1997), indicating that at least in premodern times this species occurred further downstream from the area strictly defined as the Cumberlandian Region.

Many streams no longer harbor populations of the oyster mussel. Populations have been totally eliminated from both main stems of the Cumberland and Tennessee Rivers (Table 2). In addition, populations have apparently been extirpated from several tributaries in the Cumberland River system (e.g., Rockcastle River, Beaver Creek, Obey River, Caney Fork, Harpeth River)

Table 2. *Epioblasma capsaeformis* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.

Stream, County, State	Authority	Date
Cumberland River System		
Cumberland River, McCreary and Whitley Counties, KY	Neel and Allen (1964)	1947-49
Rockcastle River, Laurel and Pulaski Counties, KY	Neel and Allen (1964)	1948
Cumberland River, Pulaski County, KY	R. R. Cicerello (Kentucky State Nature Preserves Commission, personal communication [pers. comm.], 1997)	?
Buck Creek, Pulaski County, KY	Ahlstedt (1986) Schuster et al. (1989) Gordon (1991) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1985 1984, 1982 1980-81, 1974-75, 1971 1959
Big South Fork, Scott County, TN	Bakaletz (1991)	1986
Big South Fork, McCreary County, KY	Gordon (1991) Bakaletz (1991) Schuster (1988) Harker et al. (1980)	~1990 1986 1986 1979
Big South Fork, Pulaski and Wayne Counties, KY	Neel and Allen (1964) Wilson and Clark (1914)	1948 1910-12
Cumberland River, Wayne County, KY	Wilson and Clark (1914)	1910-12
Cumberland River, Russell County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947 1910-12
Beaver Creek, Russell County, KY	Neel and Allen (1964)	1947-48
Cumberland River, Clinton County, KY	Wilson and Clark (1914)	1911
Cumberland River, Cumberland County, KY	Neel and Allen (1964)	1947
Obey River, Pickett County, TN	Gordon (1991) Johnson (1978)	1911 ?
Cumberland River, Smith County, TN	Parmalee et al. (1980)	A

Caney Fork, Smith County, TN	Layzer et al. (1993) Gordon (1991) Johnson (1978)	~1990 R 1981 R, <1954[1] 1911-12
Cumberland River, Davidson County, TN	Ortmann (1924a)	1800s?
Harpeth River, Williamson County, TN	Athearn (pers. comm., 1997) Johnson (1978)	1964 ?
Harpeth River, Davidson County, TN	Pilsbry and Rhoads (1896) Johnson (1978)	1895 ?
Cumberland River, Stewart County, TN	P. W. Parmalee (University of Tennessee, pers. comm., 1997)	A
Tennessee River System		
Clinch River, Tazewell County, VA	Church (1991) Gordon (1991) Goodrich (1913) Ortmann (1918)	1989-90 1965 1913 1912-13
Clinch River, Russell County, VA	Gordon (1991) P. W. Shute (Tennessee Valley Authority, pers. comm., 1998) Athearn (pers. comm., 1997) Goodrich (1913) Ortmann (1918)	1985, 1963 1980 1967 1913 1913, 1899
Clinch River, Wise County, VA	Gordon (1991) Goodrich (1913) Ortmann (1918)	1965, 1963 1913 1912-13, 1899
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service [Service], pers. comm., 1997) Ahlstedt and Tuberville (1997) Gordon (1991) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997) Ortmann (1918) Boepple and Coker (1912)	1997 1994, 1983, 1979 1990, 1970, 1963 1944 1978-83 1973-75 1968-69, 1955, 1953 1913, 1899 1909
Little River, Scott County, VA	Shute (pers. comm., 1998)	1989 R
Copper Creek, Scott County, VA	S. A. Ahlstedt (U.S. Geological Survey, pers. comm., 1997) Barr et al. (1993-1994) Ahlstedt (1982) Gordon (1991)	1995, 1991 1981 1980 1970, 1965

Clinch River, Hancock County, TN	R. G. Biggins (Service, personal observation) Ahlstedt and Tuberville (1997) Barr et al. (1993-1994) Ahlstedt (1991a) Dennis (1985) Gordon (1991) Ortmann (1918)	1997 1994, 1988, 1979 1981 1978-83 1973-75 1967 1899
Clinch River, Claiborne and Grainger Counties, TN	Gordon (1991) Athearn (pers. comm., 1997) Ortmann (1918) Boepple and Coker (1912)	1968, 1965 1956, 1949 1915, 1913 1909
Clinch River, Union County, TN	Ortmann (1918) Boepple and Coker (1912)	1915, 1899 1909
Clinch River, Anderson County, TN	Hickman (1937) Cahn (1936) Ortmann (1918)	1935-37 1936 1914-15
Powell River, Lee County, VA	Wolcott and Neves (1991) Wolcott and Neves (1994) Ahlstedt (pers. comm. 1997)[2] Barr et al. (1993-1994) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997)	1989 1988-89 1983, 1979 1981 1979 1975-78 1973-78 1951
Wallen Creek, Lee County, VA[3]	Gordon (1991)	?
Powell River, Hancock County, TN	Barr et al. (1993-1994) Ahlstedt (1991b) Ahlstedt and Tuberville (1997) Ahlstedt and Brown (1980) Dennis (1981)	1981 1979 1979 1975-78 1973-78
Powell River, Claiborne County, TN	Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1979 1979 1975-78 1973-78 1964 1915, 1913, 1899
Powell River, Campbell and Union Counties, TN	Ortmann (1918)	1899
Clinch River, Anderson and Knox Counties, TN	Ortmann (1918) Parmalee and Bogan (1986)	1914 A
Poplar Creek, Roane County?, TN	Gordon (1991)	?

North Fork Holston River, Washington County, VA	Ahlstedt (1980) Ortmann (1918)	1975 T 1900
North Fork Holston River, Scott County, VA	Neves (1995) Ahlstedt (1980) Ortmann (1918) Boepple and Coker (1912)	1991-95 R 1978, 1976 T 1913, 1901 1909
North Fork Holston River, Hawkins and Sullivan Counties, TN	Gordon (1991) Ortmann (1918)	1950 1913
Big Moccasin Creek, Scott County, VA	Atheam (pers. comm., 1997) Ortmann (1918)	1963 1915, 1913
Middle Fork Holston River, Smyth County, VA[4]	Gordon (1991)	1914?
Middle Fork Holston River, Washington County, VA[5]	Gordon (1991)	~1900
South Fork Holston River, Washington County, VA[6]	Gordon (1991)	1901
South Fork Holston River, Sullivan County, TN	Ortmann (1918)	1914
Holston River, Hawkins County, TN	Ortmann (1918)	1914
Holston River, Hamblen County, TN	Boepple and Coker (1912) Gordon (1991)	1909 ~1900
Holston River, Grainger County, TN	Ortmann (1918)	1913-14
Holston River, Jefferson and Knox Counties, TN	Gordon (1991) Ortmann (1918)	<1954[1] 1913-15
French Broad River, Buncombe County, NC	Ortmann (1918)	<1913
French Broad River, ?County, TN	Gordon (1991)	?
Nolichucky River, Greene County, TN	Gordon (1991) Atheam (pers. comm., 1997)	1968 1964
Nolichucky River, Cocke and Hamblen Counties, TN	Ahlstedt (pers. comm., 1997) Ahlstedt (1991a) Gordon (1991) Ortmann (1918)	1997 1980 1969 1913
Little Pigeon River, Sevier County, TN	Gordon (1991) Parmalee (1988) Ortmann (1918)	1988 1985-87 1914
West Prong Little Pigeon River, Sevier County, TN	Parmalee (1988)	1985-87, A

Tennessee River, Knox County, TN	Ortmann (1918) Lewis (1870)	<1918 <1870
Little River, Blount County, TN	Hatcher and Ahlstedt (1982)	1981
Little Tennessee River, Monroe County, TN	Bogan (1990)	A
Little Tennessee River, Loudon County, TN	Ortmann (1918)	<1918
Tennessee River, Meigs and Rhea Counties, TN	Parmalee et al. (1982)	A
Hiwassee River, ?County, TN[7]	Parmalee and Hughes (1994)	A
South Chickamauga Creek, Catoosa County, GA	Athearn (pers. comm., 1997)	1961, 1958
South Chickamauga Creek, Hamilton County, TN	Athearn (pers. comm., 1997)	1964
Lookout Creek, Dade County, GA	Athearn (pers. comm., 1997)	1970
Sequatchie River, Sequatchie County, TN	Hatcher and Ahlstedt (1982) Athearn (pers. comm., 1997) Gordon (1991)	1980 1955 ~1900
Sequatchie River, Marion County, TN	Athearn (pers. comm., 1997)	1958
Tennessee River, Jackson County, AL	Bogan (1990)	A
Paint Rock River, Jackson County, AL	Ahlstedt (1991b) Gordon (1991) Isom and Yokley (1973) Athearn (pers. comm., 1997) Ortmann (1925)	1980 1976, 1973, ~1925 1965, 1967 1957 <1920[8]
Estill Fork, Jackson County, AL	Gordon (1991)	1976, 1973, 1966
Larkin Fork, Jackson County, AL	Gordon (1991) Athearn (pers. comm., 1997)	1976 1966
Hurricane Creek, Jackson County, AL	Ahlstedt (1991b) Gordon (1991)	1980 <1920[8]
Flint River, Madison County, AL	Gordon (1991)	<1920[8]
Limestone Creek, Limestone County, AL	Ortmann (1925)	<1925
Elk River, Franklin County, TN	Isom et al. (1973) Bogan (1990)	1965-67 A
Elk River, Lincoln County, TN	Gordon (1991) Isom et al. (1973) Ortmann (1925)	1966, 1957, 1953 1965 <1920[8]
Richland Creek, Giles County, TN	Ortmann (1925)	1923

Tennessee River, Colbert and Lauderdale Counties, AL	Ortmann (1925) Athearn (pers. comm., 1997) Morrison (1942)[9]	<1920[8] 1900 A
Shoal Creek, Lauderdale County, AL	Ortmann (1925) Athearn (pers. comm., 1997) Gordon (1991)	<1920[8] 1914 1909
Bear Creek, Franklin County, AL	Ortmann (1925)	<1920[8]
Duck River, Bedford County, TN	Isom and Yokley (1968) Bogan (1990)	1965 A
Duck River, Marshall County, TN	J. T. Garner (Alabama Department of Conservation and Natural Resources, pers. comm., 1997) Shute (pers. comm., 1998) Gordon (1991) Barr et al. (1993-94) Ahlstedt (1991b) Ahlstedt (1981) Isom and Yokley (1968) Athearn (pers. comm., 1997) van der Schalie (1973) Ortmann (1924a)	1997, 1993-95 1991 1988, 1982 1981 1979 1976-78 1965 1956 1931 1923
Duck River, Maury County, TN	Isom and Yokley (1968) Gordon (1991) Ortmann (1924a) Athearn (pers. comm., 1997)	1965 1937, 1891 1921-23 <1900
Buffalo River, Perry County, TN	van der Schalie (1973)	1931

[1]This record is based on a collection by C. Goodrich who died in 1954.

[2]These records represent data from Ahlstedt and Tuberville (1997) that was inadvertently omitted during publishing.

[3]Gordon (1991) presents a record from "Virginia, Lee County, Waldens Creek" (U.S. National Museum of Natural History [USNM] 133474) and another record as "Wallens Creek, Virginia" (University of Michigan Museum of Zoology [UMMZ] 90708). These both presumably refer to Wallen Creek, a stream from which several species are recorded by Ortmann (1918).

[4]Gordon (1991) presents this Ortmann (1918) collection record (from Chilhowie, Smyth County) as UMMZ 90700. Ortmann (1918) gives the exact same locality for *Epioblasma walkeri*, a species easily confused with, but that he distinguished from, *E. capsaeformis*. This locality record for *E. capsaeformis* needs verification, as the two species rarely occur together, and no other records for *E. capsaeformis* are available for the Middle Fork.

[5]Gordon's (1991) Washington County record is based on an Adams collection that Ortmann (1918) omitted (missed?), as Ortmann's only Middle Fork records were from Smyth County, Virginia. This locality record for *E. capsaeformis* also needs verification (see footnote 4 above).

[6]Gordon (1991) presents this record as "Holston River, Virginia, Wyeth [Wythe] Co., Barren Spring, coll. C. C. Adams" (UMMZ 90699). Ortmann (1918) listed a site where he reported *Epioblasma*

walkeri, but not *E. capsaeformis*, that both he (in 1913) and Adams (in 1901) collected labeled simply as "Barron" on the South Fork in Washington County. Stansbery and Clench (1978) gave Ortmann's locality as "Alvarado (Barron Station)," reiterating that both Ortmann and Adams collected at this site in 1913 and 1901, respectively. This locality therefore probably refers to the South Fork, Washington County. This *E. capsaeformis* record should also be verified (see footnote 4 above), despite the fact that Ortmann (1918) reported it from the South Fork in Sullivan County, Tennessee.

[7]Parmalee and Hughes (1994) present this record as *Epioblasma* cf. *capsaeformis*.

[8]This record is based on a collection by H. H. Smith who died in 1920.

[9]Morrison's (1942) archeological site is located near the Mississippi border, a considerable distance downstream of Ortmann's (1925) Muscle Shoals locality.

NOTE: Records are presumed to be for live or fresh dead individuals unless otherwise stated. Compilation studies (e.g., Johnson 1978, Schuster 1988, Gordon 1991) are given only when no primary authority can be identified or no significant additional dates of collection can be verified. Schuster (1988) and Gordon (1991) records were compiled from the following museums: Academy of Natural Sciences, Philadelphia; Carnegie Museum; Ohio State University Museum of Zoology; UMMZ; and USNM; while Schuster (1988) also reported records from the Museum of Comparative Zoology. General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee); (2) Dennis (1985) represents 1972-1976 collections from Duck River Mile 15-180 (Marshall to Humphreys Counties, Tennessee); (3) Dennis (1985) represents 1978 collections from North Fork Holston River (Scott County, Virginia, to Hawkins County, Tennessee); and (4) Stansbery (1973a) represents 1963-1971 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: A = Archeological record; R = Relic shells only; and T = Translocated specimens.

and the Tennessee River system (e.g., Little River [in Virginia], Powell River, Wallen Creek, Poplar Creek, North Fork Holston River, Big Moccasin Creek, South Fork Holston River, Holston River, French Broad River, Little River [in Tennessee], Little Tennessee River, Hiwassee River, South Chickamauga Creek, Lookout Creek, Sequatchie River, Paint Rock River, Estill Fork, Larkin Fork, Hurricane Creek, Flint River, Limestone Creek, Elk River, Richland Creek, Shoal Creek, Bear Creek, Buffalo River). The oyster mussel has also been extirpated from large portions of additional Cumberlandian streams (e.g., Clinch and Duck Rivers), from the entire Blue Ridge Physiographic Province, and is apparently no longer found in the States of Alabama, Georgia, and North Carolina (Table 2).

In the Cumberland River system, post-1985 oyster mussel populations remain in isolated stretches of Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky, and possibly Buck Creek, Pulaski County, Kentucky. Tennessee River system records since 1985 include the Clinch River, Russell and Scott Counties, Virginia, and Hancock County, Tennessee; Powell River, Lee County, Virginia; North Fork Holston River, Scott County, Virginia (reintroduced population); Nolichucky River, Cocke and Hamblen Counties, Tennessee; Little Pigeon River, Sevier County, Tennessee; West Prong Little Pigeon River, Sevier County, Tennessee; and Duck River, Marshall County, Tennessee (Table 2).

Based on museum collections, the oyster mussel ". . . must have been abundant, especially in the Tennessee River system" (Johnson 1978). Wilson and Clark (1914) stated that it was "fairly common" in the Big South Fork, but that it was found "sparingly" in the main stem of the

Cumberland River. Neel and Allen (1964) found it to be rare to abundant in the main stem of the Cumberland River, albeit at few localities. It was reported as being abundant throughout the Tennessee River system, particularly in the upper portion (Ortmann 1918, 1925).

A quantitative study by Ahlstedt and Tuberville (1997) in the Powell and Clinch Rivers in Tennessee and Virginia provides valuable insight into recent oyster mussel densities in the upper Tennessee River system. Sampling at 14 to 16 sites (varied by year) in the Powell River revealed the oyster mussel to "occur in extremely low densities," and it was found during only the first 2 of the 4 years of sampling effort. Taking at least 432 quadrats (2.7 square feet) per year, they were found at densities of 0.76 and 0.22 per square foot in 1979 and 1983, respectively, but they were absent from the 1988 and 1994 samples. Similar sampling at 11 to 14 sites in the Clinch River revealed the oyster mussel at considerably higher densities than in the Powell River in 2 of the 3 years represented (Ahlstedt and Tuberville 1997). Sampling at least 345 quadrats per year, they found densities of 3.24, 0.11, and 2.92 per square foot in 1979, 1988, and 1994, respectively. According to Ahlstedt and Tuberville (1997), a prolonged drought between 1983 and 1988 probably accounted for the low numbers during the sampling efforts expended in 1988 (see comments on coal mining in "Past and Present Threats"). Limited quantitative sampling for the oyster mussel in the Powell River in Virginia by Wolcott and Neves (1994) during 1988 and 1989 revealed no specimens.

Neves (1991) considered the oyster mussel to be "extremely rare" throughout the upper Tennessee River system, an observation based partially on the work of Dennis (1987) that documented the recent decline of this once abundant species in the Clinch River. During 1996 and 1997, however, biologists documented significant adult population size and strong evidence of recent recruitment of the oyster mussel from muskrat middens at certain localities in the Clinch River in both Virginia (L. M. Koch, Service, pers. comm., 1997) and Tennessee (Ahlstedt, pers. comm., 1997). The Duck River also apparently harbors a fairly healthy population of this species (J. T. Garner, Alabama Department of Conservation and Natural Resources, pers. comm., 1997). The Big South Fork oyster mussel population, which may represent the only viable population in the entire Cumberland River system, is small (Bakaletz 1991) compared to those extant populations in the Clinch and Duck Rivers.

Cumberlandian combshell

The Cumberlandian combshell was described from the Cumberland River in Tennessee. Historically, it ranged throughout the Cumberlandian Region (Table 3), occurring in three physiographic provinces (i.e., Interior Low Plateau, Cumberland Plateau, Ridge and Valley) and five states (i.e., Alabama, Kentucky, Mississippi, Tennessee, Virginia). In the Cumberland River it occurred from the base of Cumberland Falls, McCreary and Whitley Counties, Kentucky, downstream to Stewart County, Tennessee. In the Tennessee River, it occurred throughout the main stem downstream to Decatur County, Tennessee. The Cumberlandian combshell also occurred in numerous tributaries in the Cumberland and Tennessee River systems. The downstreammost records in both rivers are from archeological sites (Parmalee, pers. comm.,

Table 3. *Epioblasma brevidens* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.

Stream, County, State	Authority	Date
Cumberland River System		
Rockcastle River, Laurel, Pulaski, and Rockcastle Counties, KY	Schuster (1988) Neel and Allen (1964)	1973, 1968, 1963 1948
Cumberland River, Pulaski County, KY	Schuster (1988)	1902
Buck Creek, Pulaski County, KY	G. A. Schuster (Eastern Kentucky University, personal communication [pers .comm.], 1997) Gordon (1991) Schuster et al. (1989) H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1997 1985, 1971 1975-84 1959
Big South Fork, Scott County, TN	R. S. Butler (U.S. Fish and Wildlife Service [Service], personal observation [pers. obs.]) Bakaletz (1991)	1998 1985-86
Big South Fork, McCreary County, KY	Gordon (1991) Bakaletz (1991) Harker et al. (1980)	~1990 1986 1979
Big South Fork, Pulaski County, KY	Wilson and Clark (1914)	1910
Cumberland River, Wayne County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947 1910
Cumberland River, Russell County, KY	Schuster (1988) Neel and Allen (1964) Wilson and Clark (1914)	1982 R 1947 1910
Beaver Creek, Russell County, KY	Neel and Allen (1964) Wilson and Clark (1914)	1947-48 1910-12
Cumberland River, Cumberland County, KY	Neel and Allen (1964)	1947
Cumberland River, Jackson County, TN	Wilson and Clark (1914) Bogan (1990)	1910-12 A
Obey River, Clay and Pickett Counties, TN	Gordon (1991)	?
Cumberland River, Smith County, TN	Parmalee et al. (1980)	1977-79, A

Cumberland River, Trousdale and Wilson Counties, TN	Parmalee et al. (1980)	1977-79
Caney Fork, Dekalb County, TN	Athearn (pers. comm., 1997)	1961 R
Caney Fork, Smith County?, TN	Layzer et al. (1993) Gordon (1991)	~1990 R 1981 R
Caney Fork, Putnam County, TN	Wilson and Clark (1914)	1910-12
Stones River, Davidson and Rutherford Counties, TN	Schmidt et al. (1989) Gordon (1991) Johnson (1978)	1965-68 1964-65 ?
Cumberland River, Davidson County, TN	Ortmann (1924a) Johnson (1978)	~1830[1] ?
Red River, Robertson County, TN	Gordon (1991)	1966
Red River, Montgomery County, TN	Athearn (pers. comm., 1997)	1967
Cumberland River, Stewart County, TN	P. W. Parmalee (University of Tennessee, pers. comm., 1997)	A
Tennessee River System		
Clinch River, Scott County, VA	L. M. Koch (Service, pers. comm., 1997) Gordon (1991) Ahlstedt and Tuberville (1997) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997) Ortmann (1918)	1997 1990, 1929 1988, 1979 1978-83 1973-75 1968, 1965, 1953 1913, 1899
Clinch River, Hancock County, TN	R. G. Biggins (Service, pers. obs.) Ahlstedt and Tuberville (1997) Barr et al. (1993-1994) Ahlstedt (1991a) Dennis (1985) Athearn (pers. comm., 1997)	1997 1994, 1988, 1979 1981 1978-83 1973-75 1968
Clinch River, Claiborne and Grainger Counties, TN	Ortmann (1918) Boepple and Coker (1912)	1915, 1913 1909
Clinch River, Union County, TN	Ortmann (1918)	1915, 1899
Clinch River, Anderson County, TN	Hickman (1937) Cahn (1936) Ortmann (1918)	1935-37 1936 1914-15

Powell River, Lee County, VA	S. A. Ahlstedt (U.S. Geological Survey, pers. comm., 1997) Ahlstedt (pers. comm.,1997)[2] Gordon (1991) Wolcott and Neves (1994) Barr et al. (1993-1994) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Ortmann (1918)	1997 1994, 1988, 1983, 1979 1990, 1983, 1932 1988-89 1981 1979 1975-78 1973-78 1901
Station Creek, Lee County, VA[3]	Johnson (1978)	?
Wallen Creek, Lee County, VA[4]	Gordon (1991)	?
Powell River, Hancock County, TN	B. T. Watson (Virginia Polytechnic Institute and State University, pers. comm., 1998) Ahlstedt (pers. comm., 1997) Gordon (1991) Ahlstedt and Tuberville (1997) Barr et al. (1993-1994) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981)	1997 1994 1990, 1983, 1980 1988, 1983, 1979 1981 1979 1975-78 1973-78
Powell River, Claiborne County, TN	Ahlstedt (pers. comm., 1997) Ahlstedt and Tuberville (1997) Gordon (1991) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1988 1983, 1979 1983, 1967 1979 1975-78 1973-78 1964 1915, 1913, 1899
Powell River, Union County, TN	Ortmann (1918)	1899
Powell River, Campbell County, TN	Bogan and Parmalee (1983) Johnson (1978)	??
Clinch River, Roane County, TN	Gordon (1991) Parmalee and Bogan (1986)	<1954[5] A
North Fork Holston River, Scott County, VA	Neves (1995) Gordon (1991) Athearn (pers. comm., 1997) Ortmann (1918)	1991-95 R 1977 1950 1913, 1901
North Fork Holston River, Hawkins and Sullivan Counties, TN	Athearn (pers. comm., 1997) Ortmann (1918)	1950 1913
Holston River, Grainger, Hamblen, and Hawkins Counties, TN	Ortmann (1918) Boepple and Coker (1912)	1913-14 1909

Holston River, Jefferson and Knox Counties, TN	Ortmann (1918)	1913-1915
Nolichucky River, ?County, TN	Johnson (1978)	?
West Prong Little Pigeon River, Sevier County, TN	Parmalee (1988)	A
Tennessee River, Knox County, TN	Gordon (1991) Lewis (1870)	<1920[6] <1870
Little Tennessee River, Monroe County, TN	Bogan (1990)	A
Tennessee River, Meigs and Rhea Counties, TN	Parmalee et al. (1982)	A
Tennessee River, Jackson County, AL	Gordon (1991) Bogan (1990)	? A
Paint Rock River, Jackson County, AL	Ahlstedt (pers. comm., 1997) Ortmann (1925)[7]	1976 <1914
Tennessee River, Colbert and Lauderdale Counties, AL[8]	Ortmann (1925) Morrison (1942)	<1920[6] A
Elk River, Lincoln County, TN	Gordon (1991) Athearn (pers. comm., 1997) Johnson (1978)	1966 1957 ?
Elk River, Limestone County, AL[9]	Ortmann (1925)	1833
Bear Creek, Colbert County, AL	McGregor and Garner (1997)	1997
Bear Creek, Tishomingo County, MS	Isom and Yokley (1968)	1965
Little Bear Creek, Franklin County, AL	P. W. Shute (Tennessee Valley Authority, pers. comm., 1998)	1978
Cedar Creek, Franklin County, AL	J. T. Garner (Alabama Department of Conservation and Natural Resources, pers. comm., 1997) Isom and Yokley (1968)	1988 1965
Cedar Creek, Tishomingo County, MS	Isom and Yokley (1968)	1965
Tennessee River, Hardin County, TN	Athearn (pers. comm., 1997)	<1900?
Tennessee River, Decatur and Perry Counties, TN	Parmalee (pers. comm., 1997)	A
Tennessee River, Benton County, TN	A. E. Bogan (North Carolina State Museum of Natural Sciences, pers. comm., 1998)	A

Duck River, Marshall County, TN	Shute (pers. comm., 1998) Ahlstedt (pers. comm., 1997) Ahlstedt (1981) Gordon (1991) Athearn (pers. comm., 1997) Ortmann (1924a)	1991 1988 1976-78 1973, 1964 1956, 1953 1923
Duck River, Maury County, TN	L. J. Levine (Cumberland Science Museum, pers. comm., 1997) van der Schalie (1973) Ortmann (1924a)[10] Hinkley and Marsh (1885)	1997 R 1931 1921-22 <1885

[1]Ortmann (1924a) mentions that Conrad, who was actively studying unionids in the 1830s, reported *Epioblasma brevidens* from the Cumberland River at Nashville (Davidson County).

[2]These records represent data from Ahlstedt and Tuberville (1997) that was inadvertently omitted by the publisher.

[3]Johnson (1978) includes Station Creek, Lee County, Virginia, as a tributary of Clinch River, but it is actually a tributary of the upper Powell River.

[4]Gordon (1991) presents a record from "Virginia, Lee County, Waldens Creek" (U.S. National Museum of Natural History [USNM] 133471). This presumably refers to Wallen Creek, a stream from which several species are recorded by Ortmann (1918).

[5]This record is based on a collection by C. Goodrich who died in 1954.

[6]This record is based on a collection by H. H. Smith who died in 1920.

[7]Ortmann (1925) stated that Simpson (1914) reported *Epioblasma metastriata* (Conrad 1840) from "Woodville, Alabama," which is on the Paint Rock River. As *E. metastriata* appears to be the Mobile Basin sister taxon to *E. brevidens*, this record probably represents *E. brevidens*, whose occurrence in the Paint Rock River was verified in 1976 by Ahlstedt (pers. comm., 1997).

[8]Morrison's (1942) archeological site is located near the Mississippi border, a considerable distance downstream of Ortmann's (1925) Muscle Shoals locality.

[9]Ortmann (1925) reported this species as having been collected by Conrad from the lower Elk River. The only visit Conrad made to the Elk River was in 1833 (Wheeler 1935).

[10]Ortmann (1924a) reported on central Tennessee mussel collections made by Hinkley and Marsh (1885), "[a] number of [them] from Duck River at Columbia, Maury Co., Tenn." This record probably came from this locality.

NOTE: Records are presumed to be for live or fresh dead individuals unless otherwise stated. Compilation studies (e.g., Johnson 1978, Bogan and Parmalee 1983, Schuster 1988, Gordon 1991) are given only when no primary authority can be identified or no significant additional dates of collection can be verified. Schuster (1988) and Gordon (1991) records were compiled from the following museums: Academy of Natural Sciences, Philadelphia; Carnegie Museum; Ohio State University Museum of Zoology; University of Michigan Museum of Zoology; and USNM; while Schuster (1988) also reported records from the Museum of Comparative Zoology. General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee); (2) Dennis (1985) represents 1972-1976 collections from Duck River Mile 15-180 (Marshall to Humphreys Counties, Tennessee); (3) Dennis (1985) represents 1976-1983 collections from Cumberland

Cumberland River, Tennessee (counties unknown); and (4) Stansbery (1973a) represents 1963-1971 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: A = Archeological record; and R = Relic shells only.

1997), indicating that at least in premodern times this species occurred further downstream from the area strictly defined as the Cumberlandian Region.

The Cumberlandian combshell has been extirpated from a large percentage of its former range (Table 3). Main-stem Tennessee River populations are no longer found. If extant, only senescent individuals comprise the Cumberland River main-stem population known circa 1980 from the Tennessee portion of that river (Parmalee et al. 1980, Gordon 1991). This species has apparently also been eliminated from numerous tributaries in the Cumberland (e.g., Rockcastle River, Beaver Creek, Obey River, Caney Fork, Stones River, Red River) and Tennessee (e.g., Station Creek, Wallen Creek, Holston River, Nolichucky River, West Prong Little Pigeon River, Little Tennessee River, Paint Rock River, Elk River, Little Bear Creek) River systems (Table 3). The Cumberlandian combshell has also been extirpated from large portions of additional tributaries in the Cumberlandian Region (e.g., Clinch River, Powell River, North Fork Holston River, Bear Creek).

Extant (post-1985) Cumberland River system populations occur in Buck Creek, Pulaski County, Kentucky; and Big South Fork, Scott County, Tennessee, and McCreary County, Kentucky (Table 3). In the Tennessee River system, populations are thought to remain in the Powell River, Lee County, Virginia, and Claiborne and Hancock Counties, Tennessee; Clinch River, Scott County, Virginia, and Hancock County, Tennessee; North Fork Holston River, Scott County, Virginia (reintroduced population); Bear Creek, Colbert County, Alabama; Cedar Creek, Franklin County, Alabama; and Duck River, Marshall County, Tennessee (Table 3).

The Cumberlandian combshell "... must once have been relatively abundant" based on museum collections studied by Johnson (1978). Neel and Allen (1964) reported it as being "very common" in the upper Cumberland River below the Falls. Paradoxically, Wilson and Clark (1914), who reported only dead specimens, failed to find the Cumberlandian combshell live anywhere in the main stem of the Cumberland River. They stated that this species was "most abundant" in the Big South Fork (relatively speaking, among the three sites where it was found), where it became extirpated by the late 1940s according to Neel and Allen (1964) (see Table 3). Ortmann (1924a, 1925) reported it as relatively abundant in the upper Tennessee River system but rare in the lower Tennessee and Cumberland River systems.

Recent density information is available for the Cumberlandian combshell in the headwaters of the Tennessee River system. Ahlstedt and Tuberville (1997) quantitatively assessed populations since 1979 in the Powell and Clinch Rivers, Tennessee and Virginia. Sampling at 14 to 16 sites (varied by year) in the Powell River revealed the Cumberlandian combshell to be "rare" over the course of the 15-year study. Taking at least 432 quadrats (2.7 square feet) per year, they recorded a steady decline in densities of 0.97, 0.54, 0.32, and 0.11 per square foot in 1979, 1983, 1988, and 1994, respectively. Similar sampling at 11 to 14 sites in the Clinch River revealed a gradual increase in Cumberlandian combshell densities of 0.32, 0.65, and 0.76 per square foot in 1979, 1988, and 1994, respectively, from the minimum of 345 quadrats taken each year (Ahlstedt and Tuberville 1997). They attributed the decline in Powell River populations of this species to general stream degradation (see comments on coal mining in "Past and Present Threats"). Wolcott and Neves (1994) conducted both qualitative and limited quantitative sampling for mussels in the Powell River in Virginia during 1988 and 1989. Two of the five sites that qualitatively yielded Cumberlandian combshell specimens had densities of 0.03 and 0.01 per square foot, respectively.

The Cumberlandian combshell was considered "extremely rare" by the 1980s throughout its range, and its numbers were declining in the upper Tennessee River system, particularly in Virginia (Neves 1991, Dennis 1987). Currently, the largest extant population of the Cumberlandian combshell probably occurs in the Clinch River in Virginia and Tennessee (Ahlstedt, pers. comm., 1998). Biologists have recently documented the presence of significant numbers of adults and verified recent recruitment with the presence of juvenile specimens from muskrat middens in the Clinch River (Ahlstedt and Koch, pers. comm., 1997). Populations in other stream reaches are small (e.g., Buck Creek, Big South Fork, Powell River, Duck River) (Bakaletz 1991, Wolcott and Neves 1994, Ahlstedt, pers. comm., 1997). The Bear Creek population appears to be highly tenuous, as only three fresh dead specimens have been collected in recent years (S. W. McGregor, Alabama Geological Survey, in litt., 1998; Garner, pers. comm., 1997).

Purple bean

The purple bean is endemic to the upper Tennessee River system above its confluence with the Clinch River (Table 4). Its type locality was stated simply as "Tennessee." Primarily a species

Table 4. *Villosa perpurpurea* occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.

Stream, County, State	Authority	Date
Tennessee River System		
Clinch River, Tazewell County, VA	R. J. Neves (U.S. Geological Survey [USGS], personal communication [pers. comm.], 1998)	1996
	Winston and Neves (1997)	1995-96 R
	Ahlstedt and Tuberville (1997)	1994
	Church (1991)	1989-90
	Ortmann (1918)	1912-13
Indian Creek, Tazewell County, VA	Watson and Neves (1998)	1996-97
	Winston and Neves (1997)	1995-96 R
Clinch River, Russell County, VA	Stansbery (1986)	1985-86, 1965
	Ahlstedt (1991a)	1978-83
	Ortmann (1918)	1913, 1899
Clinch River, Wise County, VA	Ortmann (1918)	1913
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service, pers. comm., 1997)	1997
	S. A. Ahlstedt (USGS, pers. comm., 1997)	1988, 1979
	Ahlstedt (1991a)	1978-83
	Ortmann (1918)	1913
Copper Creek, Scott County, VA	Ahlstedt (pers. comm., 1997)	1997, 1991
	Barr et al. (1993-1994)	1981
	Ahlstedt (1982)	1980
Clinch River, Hancock County, TN	Ahlstedt (pers. comm., 1997)	1997 R
	Ahlstedt (1991a)	1978-83
	H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1950 R
	Ortmann (1918)	1913
Powell River, Lee County, VA	Ortmann (1918)	1899
Emory River, Morgan County, TN	R. M. Anderson (USGS, pers. comm., 1998)	~1987 R
Emory River, Roane County, TN	Ortmann (1918)	1915
Obed River, Morgan County, TN	Athearn (pers. comm., 1997)	1967
	Gordon (1991)	?

Obed River, Cumberland County, TN	Ahlstedt (pers. comm., 1997) Gordon (1991)	1996 ?
North Fork Holston River, Washington County, VA	Ortmann (1918)	1913
North Fork Holston River, Scott County, VA	Ortmann (1918)	1913
North Fork Holston River, Hawkins and Sullivan Counties, TN	Ortmann (1918)	1913
Beech Creek, Hawkins County, TN	Ahlstedt (pers. comm., 1997) Ahlstedt (1982)	1996 <1982

NOTE: Records are presumed to be for live or fresh dead individuals unless otherwise stated. Compilation studies (e.g., Gordon 1991) are given only when no primary authority can be identified or no significant additional dates of collection can be verified. General drainage records where specific localities were not given: Stansbery (1973a) represents 1963-1971 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: R = Relic shells only.

of the Ridge and Valley, it also occurs at the eastern edge of the Cumberland Plateau. The entire range of the purple bean occurs in northeastern Tennessee and southwestern Virginia.

The purple bean has apparently been extirpated from the Powell River, North Fork Holston River, a portion of the upper Clinch River in Tennessee and Virginia, and the Emory River (Table 4). Extant populations (post-1985) are located in the Clinch River, Tazewell, Russell, and Scott Counties, Virginia; Indian Creek, Tazewell County, Virginia; Copper Creek, Scott County, Virginia; Obed River, Cumberland County, Tennessee; and Beech Creek, Hawkins County, Tennessee (Table 4).

Ortmann (1918) considered the purple bean as being "not rare" in the Virginia portion of the Clinch River. A recent quantitative study by Ahlstedt and Tuberville (1997) in the Clinch River in Tennessee and Virginia revealed this species to be "rare" over the 15-year sampling period. Sampling of at least 345 quadrats from 11 to 14 sites in the Clinch revealed densities of 0.11 per square foot in both 1979 and 1988, but no specimens were taken during 1994. Neves (1991) reported that it was uncommon to rare throughout its range and that populations were declining. Currently, population sizes are all generally small. The largest population probably occurs in the upper Clinch River/Indian Creek (Ahlstedt, pers. comm., 1997). The Copper Creek population was considered to be the largest population by Neves (1991), but that was before the discovery of the Indian Creek population in 1995 (Table 4). In Beech Creek, the only extant population of the purple bean in the entire Holston River system is declining (Ahlstedt, pers. comm., 1997). The status of the Emory River system population is unknown.

Rough rabbitsfoot

The rough rabbitsfoot was described as a subspecies of the wide-ranging rabbitsfoot, *Quadrula c. cylindrica*, from the upper Clinch River in Virginia (the type locality was erroneously given as "Clinch River, Lee Co., VA."; Ortmann 1918). This taxon is restricted to the upper Tennessee River system of northeastern Tennessee and southwestern Virginia, wholly within the Ridge and Valley, making it one of the more narrowly distributed species endemic to the Cumberlandian Region (Table 5).

Ortmann (1918) reported the presence of intergrades of the rough rabbitsfoot with the typical form--*Quadrula c. cylindrica*--in the general vicinity of the Tennessee/Virginia border. Due to the permanent impounding (e.g., lower portions of the Clinch, Powell, and Holston Rivers) or protracted pollution history (e.g., lower North Fork Holston River) of several large upper Tennessee River system tributaries, it is now impossible to precisely delineate the historical range of the rough rabbitsfoot. However, in a later paper, Ortmann (1924a) noted that the range of the rough rabbitsfoot was ". . . [the] headwaters of Powell, Clinch, and Holston [Rivers] only," with a footnote stating "I do not believe it is found elsewhere, as recently reported." No mention was made of the source of these other reports. With the occurrence of several impoundments that effectively and permanently isolate populations in the Ridge and Valley portion of the upper Tennessee River system and other localized habitat perturbations, its present pattern of distribution is further restricted, if not well understood. The chance for the natural interchange of

Table 5. ***Quadrula cylindrica strigillata*** **occurrences by stream (working downstream), county, and state; authority; and chronology of occurrence for primary literature and other records.**

Stream, County, State	Authority	Date
Tennessee River System		
Clinch River, Tazewell County, VA	P. W. Shute (Tennessee Valley Authority, personal communication [pers. comm.], 1998)	1995 R
	Church (1991)	1989-90
	Ortmann (1918)	1912-13
Indian Creek, Tazewell County, VA	Watson and Neves (1998)	1996
Clinch River, Russell County, VA	Ahlstedt and Tuberville (1997)	1994
	Church (1991)	1989-90
	Ahlstedt (1991a)	1978-83
	H. D. Athearn (Museum of Fluviatile Mollusks, pers. comm., 1997)	1967
	Ortmann (1918)	1913
Clinch River, Scott County, VA	L. M. Koch (U.S. Fish and Wildlife Service, pers. comm., 1997)	1997
	Ahlstedt and Tuberville (1997)	1994, 1979
	Yeager and Neves (1986)	1982-83
	Ahlstedt (1991a)	1978-83
	Dennis (1985)	1973-75
	Athearn (pers. comm., 1997)	1969
	Ortmann (1918)	1913
Copper Creek, Scott County, VA	S. A. Ahlstedt (U.S. Geological Survey [USGS], pers. comm., 1997)	1991
	Shute (pers. comm., 1998)	1987-89
	Ahlstedt (1982)	1980
	Athearn (pers. comm., 1997)	1961, 1955
Clinch River, Hancock County, TN	J. T. Garner (Alabama Department of Conservation and Natural Resources, pers. comm., 1997)	1997, 1993
	Barr et al. (1993-1994)	1981
	Ahlstedt and Tuberville (1997)	1979
	Ahlstedt (1991a)	1978-83
	Dennis (1985)	1973-75
	Athearn (pers. comm., 1997)	1968, 1956, 1950-51

Powell River, Lee County, VA	Koch (pers. comm., 1997) Shute (pers. comm., 1998) Wolcott and Neves (1994) Barr et al. (1993-1994) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997) Ortmann (1918)	1997 1994, 1989, 1987 1988-89 1981 1979 1975-78 1973-78 1951 1899
Powell River, Hancock County, TN	R. J. Neves (USGS, pers. comm., 1998) Yeager and Neves (1986) Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Athearn (pers. comm., 1997)	1997 1982-83 1979 1979 1975-78 1973-78 1964
Powell River, Claiborne County, TN	Ahlstedt and Tuberville (1997) Ahlstedt (1991b) Ahlstedt and Brown (1980) Dennis (1981) Ortmann (1918)	1988 1979 1975-78 1973-78 1899
Clinch River, Claiborne County, TN	Ahlstedt (1991a)	1978-83
North Fork Holston River, Washington County, VA	Ahlstedt (1980) Ortmann (1918)	1975 T 1913
North Fork Holston River, Scott County, VA	Ahlstedt (1980) Ortmann (1918)	1975-78 T 1913, 1901
Big Moccasin Creek, Scott County, VA	Athearn (pers. comm., 1997) Ortmann (1918)	1963 1915, 1913
Possum Creek, Scott County, VA	Winston and Neves (1997)	1995-96 R
North Fork Holston River, Hawkins and Sullivan Counties, TN	Ortmann (1918)	1913
South Fork Holston River, Sullivan County, TN	Ortmann (1918)	1914

NOTE: Records are presumed to be for live or fresh dead individuals unless otherwise stated. The historical distribution of this taxon is generally considered to be above Norris Reservoir (Powell and Clinch rivers) and in the forks of the Holston River. Downstream (main stem of the Tennessee River and larger tributaries) the typical form (*Quadrula c. cylindrica*) is presumed to have occurred. General drainage records where specific localities were not given: (1) Bates and Dennis (1978) represents 1972 collections from Clinch River Mile 190-280 (Russell County, Virginia, to Hancock County, Tennessee);

and (2) Stansbery (1973a) represents 1963-1971 collections from the Clinch River system above Norris Reservoir (Tazewell County, Virginia, to Claiborne County, Tennessee).

CODES: R = Relic specimens only; and T = Translocated specimens.

genetic material between *Q. c. cylindrica* and *Q. c. strigillata* has therefore been totally eliminated.

The entire Holston River system population of the rough rabbitsfoot has been extirpated (e.g., North and South Fork Holston Rivers, Big Moccasin Creek, Possum Creek) (Table 5). Populations of this species remain, based on post-1985 records, in the Clinch River, Russell and Scott Counties, Virginia, and Hancock County, Tennessee; Indian Creek, Tazewell County, Virginia; Copper Creek, Scott County, Virginia; and Powell River, Lee County, Virginia, and Hancock and Claiborne Counties, Tennessee (Table 5).

Recent quantitative population density information is available for the rough rabbitsfoot in the Powell and Clinch Rivers in Tennessee and Virginia. Sampling by Ahlstedt and Tuberville (1997) revealed "extremely low densities" of the rough rabbitsfoot in the Powell, and a decline in the Clinch, over the course of the 15-year study. Taking at least 432 quadrats (2.7 square feet) at 14 to 16 sites per year, they found Powell River densities of 0.11 per square foot in both 1979 and 1988 but none in 1983 and 1994 samples. Similar sampling of at least 345 quadrats from 11 to 14 sites in the Clinch River revealed densities of 1.84 and 0.32 per square foot in 1979 and 1994, respectively. According to Ahlstedt and Tuberville (1997), a prolonged drought between 1983 and 1988 at least partially accounted for the low numbers detected during 1988 sampling efforts (see comments on coal mining in "Past and Present Threats"). Limited quantitative sampling in the Powell River in Virginia by Wolcott and Neves (1994) during 1988 and 1989 revealed no specimens of the rough rabbitsfoot.

Preimpoundment historical abundance of this species was not recorded by Ortmann (1918) or any other investigator. Current population size of the rough rabbitsfoot is largest in the Clinch River in general, but particularly in the Scott County, Virginia, portion of the Clinch, where it may be locally abundant (Yeager and Neves 1986, Ahlstedt 1991a). Its population status elsewhere appears to be much more tenuous. Efforts by the Tennessee Valley Authority (TVA) to transplant specimens into the North Fork Holston River during the mid-1970s (Ahlstedt 1980) have apparently failed (Ahlstedt, pers. comm., 1997).

HABITAT

Cumberland elktoe

This species inhabits medium-sized rivers and may extend into headwater streams where it is often the only mussel present (Gordon and Layzer 1989, Gordon 1991). Gordon and Layzer (1989) reported that the species appears to be most abundant in flats, which were described by Gordon (1991) as shallow pool areas lacking the bottom contour development of typical pools, with sand and scattered cobble/boulder material, relatively shallow depths, and slow (almost imperceptible) currents. They also report the species from swifter currents and in areas with mud, sand, and gravel substratum.

Oyster mussel

This species inhabits small to medium-sized rivers (Dennis 1985), and sometimes large rivers, in areas with coarse sand to boulder substrata (rarely in mud) and moderate to swift currents (Gordon 1991). It is sometimes found associated with water-willow (*Justicia americana*) beds (Ortmann 1924a, Gordon and Layzer 1989) and in pockets of gravel between bedrock ledges in areas of swift current (Neves 1991). Gordon (1991) reports that this species, like other freshwater mussels, can bury itself below the substratum surface, but females have been observed to lie on top of the substratum while displaying and releasing glochidia.

Cumberlandian combshell

This species inhabits medium-sized streams to large rivers on shoals and riffles in coarse sand, gravel, cobble, and boulders (Dennis 1985, Gordon 1991). It is not associated with small stream habitats (Dennis 1985) and tends not to extend as far upstream in tributaries. In general, it occurs in larger tributaries than does its congener the oyster mussel. Gordon (1991) states that the species prefers depths less than 3 feet, but it appears to persist in the deep-water areas of Old Hickory Reservoir on the Cumberland River, where there is still fairly strong flow from the Cordell Hull and Center Hill Reservoirs (Gordon and Layzer 1989).

Purple bean

This species inhabits small headwater streams (Neves 1991) to medium-sized rivers (Gordon 1991). It is found in moderate to fast-flowing riffles with sand, gravel, and cobble substrata (Neves 1991) and rarely occurs in pools or slack water (Ahlstedt 1991a). It is sometimes found out of the main current adjacent to water-willow beds and under flat rocks (Ahlstedt 1991a, Gordon 1991)

Rough rabbitsfoot

This species inhabits medium-sized to large rivers in moderate to swift current but often exists in areas close to, but not in, the swiftest current (Gordon 1991). It is reported to live in silt, sand, gravel, or cobble in eddies at the edge of midstream currents and may be associated with macrophyte beds (Yeager and Neves 1986, Gordon 1991).

LIFE HISTORY

Food Habits

Adult freshwater mussels are filter feeders, orienting themselves in substrata to facilitate siphoning of the water column for oxygen and food (Kraemer 1979). Specific food habits of all five species are unknown, but they likely ingest food items similar to those consumed by other freshwater mussels. Mussels are known to consume detritus, diatoms, phytoplankton, zooplankton, and other microorganisms (Coker et al. 1921, Churchill and Lewis 1924, Fuller 1974). According to Ukeles (1971), phytoplankton is the principal food of bivalves. However, other food sources (e.g., bacteria, organic detritus, assimilated organic material, phagotrophic protozoans) may also play an important role (Neves et al. 1996).

According to Baldwin and Newell (1991), bivalves feed on an entire array of naturally available particles (e.g., heterotrophic bacteria, phagotrophic protozoans, phytoplankton). Based on the findings of studies such as Baldwin and Newell (1991), Neves et al. (1996) suggests that an omnivorous opportunistic diet would allow mussels to take advantage of whatever food type happens to be abundant. Churchill (1916) concluded that mussels could absorb fat, protein, and starch dissolved in the water. Gordon (1991) suggests that detritus may be an important food source for the Cumberland elktoe, which inhabits small headwater streams with little available plankton.

Juvenile mussels employ foot (pedal) feeding, and are thus suspension feeders (Yeager et al. 1994). Video observations of the rainbow (*Villosa iris* [Lea 1829]) by Yeager et al. (1994) revealed juveniles to occupy the top 0.4 inch of sediment and to employ the following two types of feeding mechanisms: (1) collecting organic and inorganic particles that adhere to the foot and conveying them to the pedal gape with either posterior to anterior or anterior to posterior sweeping motions and (2) extending the foot anteriorly, pulling themselves along while picking up organic and inorganic particles on the foot. These methods of suspension feeding have been termed pedal sweep feeding and pedal locomotory feeding, respectively (Reid et al. 1992). The juvenile diet (up to two weeks of age) includes bacteria, algae, and diatoms with amounts of detrital and inorganic colloidal particles (Yeager et al. 1994). In juvenile freshwater mussel feeding experiments, Neves et al. (1996) found that algae was a suitable food but that a tri-algal diet high in oils resulted in better growth. Silt provided some nutritional value (also observed by Hudson and Isòm 1984), but bacteria in riverine sediments was not essential to growth and survival (Neves et al. 1996).

Growth and Longevity

Growth rates for freshwater mussels tend to be relatively rapid for the first few years (Scruggs 1960, Negus 1966) then slows appreciably to approximately 0.04 inches per year (Bruenderman and Neves 1993, Hove and Neves 1994), apparently at sexual maturity. The relatively abrupt decline in growth rate is probably due to the fact that energy is being diverted from growth to gamete production. The rate of growth may also fluctuate with habitat conditions. Riverine populations of particularly heavy-shelled species grow slowly relative to thin-shelled species (Coon et al. 1977, Hove and Neves 1994). Growth was deemed greater under conditions of high water velocities in river shallows that facilitated increased oxygen and food availability per unit time (Bruenderman and Neves 1993).

As a group, mussels are extremely long-lived, with life spans of 100 to 200 years for certain species (Neves and Moyer 1988, Bauer 1992, Mutvei et al. 1994). Heavy-shelled species, which includes many riverine forms, tend to reach higher maximum ages (Stansbery 1961). No age-specific information is available for these five species. However, considering the longevity of thick-shelled species (Stansbery 1961), which characterizes the Cumberlandian combshell and rough rabbitsfoot, it would seem probable that at least these two species have fairly long life spans.

General Reproductive Biology of Mussels

Following is a summary of freshwater mussel reproduction (see Watters [1994] for an annotated bibliography of mussel reproduction). Freshwater mussels generally have separate sexes. Males expel clouds of sperm into the water column, although some species expel spermatozeugmata (sperm balls), which are comprised of thousands of sperm (Barnhart and Roberts 1997). Females draw in sperm with the incurrent water flow (Gordon and Layzer 1989). Fertilization takes place in their suprabranchial chambers, and the resulting zygotes develop into specialized veliger larvae, termed "glochidia," in water tubes of the gills. Depending on the three subfamilies within the family Unionidae, all four gills (Ambleminae)--the entire outer pair of gills (Anodontinae, some Ambleminae) or discreet portions of the outer pair of gills (Lampsilinae)--are used as marsupia or brood chambers for glochidia (Gordon and Layzer 1989). Spawning appears to be temperature dependent (Zale and Neves 1982, Bruenderman and Neves 1993) but may also be influenced by stream discharge (Hove and Neves 1994). Fertilization rates are dependent on spatial aggregation of reproductive adults (Downing et al. 1993). The age of sexual maturity for mussels is variable (Gordon and Layzer 1989), usually requiring from 3 years (Zale and Neves 1982) to 9 years (Smith 1979), and may be dependent upon gender (Smith 1979).

Mussels are generally categorized as either short-term summer brooders (tachytictic) or long-term winter brooders (bradytictic) (Neves and Widlak 1988). Tachytictic species have a spring fertilization period; the glochidia are then incubated for a few months and are expelled during the summer or early fall. Bradytictic species have a late summer or early fall fertilization period, with the glochidia incubating over winter, and are expelled the following spring or early summer.

After a variable incubation period, mature glochidia, which may number in the tens of thousands to several million (Neves et al. 1997), are expelled into the water column and must come into contact with specific fish species, whose gills and fins they temporarily parasitize (Gordon and Layzer 1989). Glochidia are released individually in a mucous matrix that entangles fishes (Haag and Warren 1997) or as discreet packets, termed "conglutinates," which represent all the glochidial contents of a single water tube packaged in a mucilaginous capsule (Ortmann 1911). A newly described method, termed a "superconglutinate," involves the expulsion of the sum of the conglutinates from discreet portions of both outer gills that are packaged in a single glochidial mass (Haag et al. 1995).

Each of the three basic methods of glochidial expulsion has been adapted to attract specific host fishes. These methods of glochidial expulsion and the two reproductive strategies of mussels (tachytictic and bradytictic) are generally subfamily specific (Gordon and Layzer 1989). Mussels in the subfamily Anodontinae are generally bradytictic and are thought to broadcast masses of hooked glochidia that generally parasitize the fins of fishes (Gordon and Layzer 1993, Haag and Warren 1997). Members of the Ambleminae are generally tachytictic and package their glochidia in conglutinates, which oftentimes resemble colorful fish prey items (e.g., worms, insect larvae, fish fry) (Ortmann 1911, Chamberlain 1934, Haag and Warren 1997), and are expelled out of the excurrent aperture (Neves and Widlak 1988). Researchers have demonstrated that conglutinates are actively foraged by fishes (Ortmann 1911, Neves and Widlak 1988) and that amblemine glochidia are hooked and parasitize fish gills (Neves et al. 1985).

Members of the Lampsilinae are generally bradytictic and utilize only discreet portions of the outer pair of gills as marsupia (Gordon and Layzer 1989). Some lampsilines expel conglutinates out of the excurrent aperture, while others expel large masses of individual glochidia out pores in the ends of the marsupialized water tubes (Neves and Widlak 1988). Lampsilines that expel masses of glochidia usually have some sort of mantle modifications with bright colors, rhythmic movements, or actual mimicry of fish prey items (e.g., worms, insect larvae, fishes) that serve to attract host fishes (Ortmann 1911, Chamberlain 1934, Kraemer 1970, Zale and Neves 1982). The brilliant mantle in displaying oyster mussels is well known to the field researcher in the Cumberlandian Region. The swollen marsupialized portion of the gills often extrudes past the edge of the shell margins and between the modified mantle tissues (Kraemer and Swanson 1985). When the mantle "lure" is hit by a fish, a cloud of hookless glochidia is released into the fish's buccal cavity, thus facilitating gill infestation.