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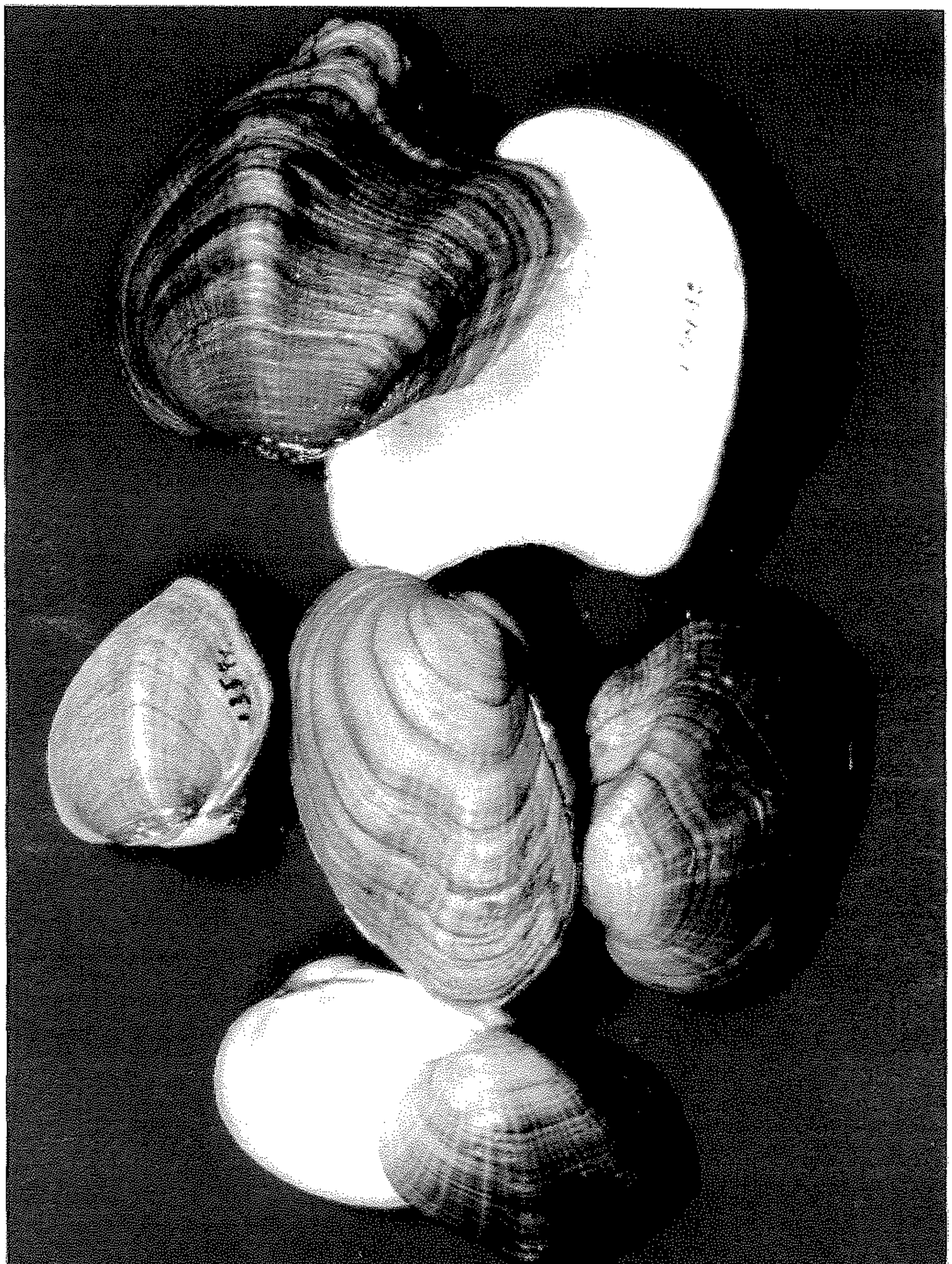

The Silent Extinction

by Arthur E. Bogan

Extinction is a concept familiar to both paleontologists and vertebrate biologists, but is a topic relatively new to invertebrate biologists -- those scientists who study the most common animals on Earth. Today the scientific and conservation journals are replete with articles on biodiversity and its loss worldwide. Although most of this attention is directed toward large land-living vertebrates (e.g., Eldredge, 1992; but see Emberton [1996] for a recent discussion of the problem of conservation of soil invertebrates and their lack of protection in Madagascar), today we are experiencing a major wave of extinctions among more humble creatures -- bivalved mollusks (unionoids) -- in the rivers and streams of our own backyard, eastern North America. This extinction, although less widely known than those affecting larger, more "charismatic" species such as tigers and marmosets, has profound implications for both the health of our ecosystems and our understanding of nature and its history.

Before any discussion of extinction may proceed, several definitions are necessary to clear up some common misconceptions. *Extinction* of a species occurs with the loss of the last remaining individual of that species throughout the total range of the species. *Extirpation* occurs when a local population of a species is completely eliminated, but other populations of the same species continue to exist in other areas within the total range of that species. Another term is useful in the discussion of extirpation and exinction in freshwater bivalves: *functionally extinct*. Functionally extinct refers to a species in which females continue to produce larvae (glochidia) but due to habitat loss and destruction and host fish loss, there is no metamorphosis from glochidia to juveniles on the gills of the host fish. There are thus only a few relict, senescent individuals remaining of the species. Such a species is effectively or functionally extinct; there are still a few animals extant but reproduction has ceased and the species will become extinct when the last remaining individual of this species dies.

Unionoid freshwater bivalves are unique in the Class Bivalvia in requiring a parasitic stage for its young on the gills of a host fish, or in one case the gills of the mudpuppy salamander. At the present time, we know the host fish(es) for only about 25 percent of the unionoid species in North America. The information for the host fish of unionoid species for the rest of the world's unionoid species is even more meager (see Watters, 1994).

Prior to modern times, the freshwater unionoid bivalves in North America (families Margaritiferidae and Unionidae) were the most diverse in the world, with approximately 300 species (Turgeon et al., 1988; Bogan, 1993). The two river systems with the most diverse freshwater molluscan fauna were the Mobile Bay and the Tennessee River basins (Bogan, 1993).

The fossil record of the freshwater bivalves in eastern United States is long but incomplete. It begins with unionoid specimens from the Upper Jurassic of Connecticut, followed by Miocene fossils from western Louisiana. Pliocene unionoid evidence is limited to some isolated specimens from Florida. The earliest Pleistocene unionoid fauna is from the southwest coast of Florida (1-1.6 million years old; Bogan and Portell, 1994). The next oldest unionoid faunas are reported from eastern West Virginia (ca. 800,000 years before present [ybp]; Bogan and Grady, 1991) and from New Jersey (ca. 125,000 ybp; Bogan et al., 1992). Fossil evidence of the freshwater molluscan fauna becomes more abundant in the latter part of the Pleistocene, especially beginning about 35,000 ybp (Bogan and Grady, 1991). The Pleistocene freshwater fossil record of the eastern United States, although limited, does not contain any evidence of extinct unionoid species; all known Pleistocene fossils are referable to living species.

The Holocene or Recent period is represented by a variety of archaeological assemblages (Bogan, 1990). The archaeological record for the Mississippi River Basin, including the Cumberland, Ohio, Tennessee, and Mississippi River drainages, contains no evidence of any species which became extinct before 1800 AD. A single extinct, undescribed species has been identified from late prehistoric archaeological sites on the Apalachicola River, Florida and the Chattahoochee River in Alabama/Georgia, which is unknown in modern unionoid collections (J. D. Williams, pers. comm., 1997).

The recognition that the freshwater mollusks of North America are disappearing is not a new concept. Higgins (1858) decried the decline of the rich molluscan fauna in Ohio and blamed the phenomenon on land clearing. Rhoads (1899) noted the loss of the freshwater mussel fauna from the Monongahela River at and above Pittsburgh and blamed damming and pollution. Ortmann (1909) reported on the destruction of the freshwater fauna in Western Pennsylvania due to pollution and the detrimental effects of acid mine drainage, and in 1918 he reported the destruction of the freshwater bivalve fauna of the Pigeon River in East Tennessee due to the effluents of a paper mill. These were all local events, however, resulting in the extirpation of local populations. Van der Schalie (1938) pointed out the deleterious effect of silty waters on unionoid bivalves and lamented the construction of dams on the Tennessee River by Tennessee Valley Authority and the impending loss of diversity in the river.

The first serious attempt to assess the status of freshwater bivalves in America began in 1970 and 1971; at that time 11 bivalve species or subspecies were presumed extinct and 120 were generally considered rare or endangered (Stansbery, 1970, 1971). In 1973, the Endangered Species Act was passed and the U. S. Fish and Wildlife Service began evaluating the status of species and listed some as threatened or endangered. Because of increased interest and the federal listing, various states began listing freshwater bivalves as locally extirpated, threatened or endangered. The American Fisheries Society, in its *Common and Scientific Names of Aquatic Invertebrates from the United States and Canada: Mollusks* (Turgeon et al., 1988) listed 13 bivalve species or subspecies as extinct and 30 as federally endangered. Today at least 30 kinds of freshwater bivalves are presumed extinct, 56 endangered, 6 threatened at the federal level, and an additional 70 listed as candidates for either threatened or endangered status. At this time 12% of this fauna is presumed extinct, 42% is listed or to be listed, and an additional 25% of the taxa is declining. Less than 25% of present freshwater bivalves appear to be maintaining stable populations today (Williams et al., 1993).

Knowledge of the status of the freshwater snail (gastropod) fauna is even more limited than that of the unionoid bivalves. Of about 601 freshwater gastropod species in North America, 42 have become extinct, 38 in the Mobile Bay Basin (Bogan et al., 1995). This includes the extinction of four genera of aquatic gastropods: *Clappia* [2 species, Hydrobiidae]; *Gyrotoma* [6 species, Pleuroceridae]; *Neoplanorbis* [4 species] and *Amphigyra* [1 species, Planorbidae] (Bogan et al., 1995). All of these genera were restricted to the Coosa River in the Mobile Bay Basin. These species were lost when their habitat of shoals in large rivers was impounded and covered with deep, standing water and silt. A number of other pleurocerid gastropod species are only persisting on the clean-swept shoal areas below the dams on the Tennessee River.

The central cause of this decline and decimation of the freshwater molluscan fauna is the modification and destruction of their aquatic habitat, with sedimentation as a leading major factor. Sources of sedimentation include poor agricultural and timbering practices. Damming of major rivers has also had a dramatic impact on this fauna with the loss of unionoid obligate host fish due to changes in local water quality and loss of habitat. In-stream gravel mining, dredging, and channelization have further eliminated stable aquatic mollusk habitat. Acidic mine drainage and various point and non-point pollution sources also continue to decimate local aquatic mollusk populations.

A new threat to the continued survival of unionoid and pleurocerid gastropod taxa is the introduction in the mid-1980's of the zebra mussel (*Dreissena polymorpha*). These small bivalves colonize an area and attach to any hard bottom by means of tough threads called a byssus; if they land on another bivalve they can cover and smother it. This is what is happening to the native unionoids in areas infested by zebra mussels; pleurocerids gastropods can be completely encased by zebra mussels.

This is a rather dark picture of the state of freshwater mollusks especially in the eastern United States. It shows us that a highly diverse, thriving fauna can be decimated in a relatively short time by environmental change. There are, however, occasional bright spots, like the Ohio River below Pittsburgh where six species of unionoids have recolonized a stretch of river which was previously devoid of mussels. Such instances suggest that with very active conservation efforts -- such as stabilization of stream banks, curtailing of poor farming practices and improvement of water quality -- this wave of extinctions might be slowed or even stopped.

References Cited

Bogan, A.E. 1990. Stability of Recent unionoid (Mollusca: Bivalvia) communities over the past 6,000 years. *In* Paleocommunity temporal dynamics: the long-term development of multispecies assemblies. William Miller III, ed. The Paleontological Society Special Publication No. 5, pp. 112-136.

Bogan, A.E. 1993. Freshwater bivalve extinctions: search for a cause. American Zoologist, 33:599-609.

Bogan, A.E., and F.V.Grady. 1991. Two Pleistocene Molluscan faunas from Eastern West Virginia. *In* Beamers, bobwhites and blue-points: tributes to the career of Paul W. Parmalee. J.R. Purdue, W.E. Klippel, and B.W. Styles, eds., Illinois State Museum Scientific Papers, Vol. 23, Springfield and The University of Tennessee, Department of Anthropology Reports of Investigations No. 52, Knoxville, pp. 189-213.

Bogan, A.E., J. M. Pierson, and P. Hartfield. 1995. Decline in the freshwater gastropod fauna in the Mobile Bay Basin. *In* Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals, and ecosystems. LaRoe, E.T., G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, (eds). U.S. Department of the Interior, Biological Service, Washington, D.C. pp. 249-252.

Bogan, A.E. and R.W. Portell. 1995. Freshwater bivalves (Bivalvia: Unionidae) from the Early Pleistocene Leisey Shell Pits, Hillsbough County, Florida. Bulletin Florida State Museum Natural History, Biological Sciences 37 (Pt.1) (6):171-182.

Bogan, A.E., E.E. Spamer, G.C. Manville, W.B. Gallagher, and A.J. Cain. 1989. Preliminary reexamination of the Fish House Local Fauna and Flora (Pleistocene), Pennsauken, Camden County, New Jersey. Mosasaur 4:111-126.

Eldredge, N., ed. 1992. Systematics, ecology and the biodiversity crisis. Columbia University Press, New York. 220 pp.

Emberton, K.C. 1996. Conservation priorities for forest-floor invertebrates of the southeastern half of Madagascar: evidence from two land-snail clades. Biodiversity and Conservation 5:729-741.

Higgins, F. 1858. A catalogue of the shell-bearing species, inhabiting the vicinity of Columbus, Ohio, with some remarks thereon. Twelfth Annual Report, Ohio State Board of Agriculture for 1857, pp. 548-555.

Ortmann, A.E. 1909. The destruction of the fresh-water fauna in western Pennsylvania. Procedings of the American Philosophical Society 48(191): 90-110.

Ortmann, A.E. 1918. The nayades (freshwater mussels) of the Upper Tennessee drainage. With notes on synonymy and distribution. Proceedings of the American Philosophical Society 57:521-626.

Rhoads, S.N. 1899. On a recent collection of Pennsylvanian mollusks from the Ohio river system below Pittsburgh. The Nautilus 12(12):133-138.

Stansbery, D.H. 1970. Eastern freshwater mollusca. (I.) The Mississippi and St. Lawrence River systems. American Malacological Union Symposium on Rare and Endangered Mollusks. Malacologia 10(1): 9-22.

Stansbery, D.H. 1971. Rare and endangered freshwater mollusks in eastern United States. *In* Proceedings of a symposium on rare and endangered mollusks (naiads) of the U.S. Region 3, Bureau of Sport Fisheries and Wildlife, U.S. Fish Wildlife Service. S.E. Jorgensen and R.E. Sharp, eds. Twin Cities, Minnesota. pp. 5-18.

Turgeon, D.D., A.E. Bogan, E.V. Coan, W.K. Emerson, W.G. Lyons, W.L. Pratt. C.F.E. Roper, A. Scheltema, F.G. Thompson, and J.D. Williams. 1988. Common and scientific names of aquatic invertebrates from the United States and Canada: Mollusks. American Fisheries Society, Special Publication 16, 277 pp.

van der Schalle, H. 1938. Contributing factors in the depletion of naiades in eastern United States. Basteria 3(4): 51-57.

Watters, G.T. 1994. An annotated bibliography of the reproduction and propagation of the Unionoidea (Primarily of North America). Ohio Biological Survey Miscellaneous Contributions No. 1, 158 pp.

Williams, J.D., M.L. Warren Jr., K.S. Cummings, J.L. Harris, and R.J. Neves. 1993. Conservation status of the freshwater mussels of the United States and Canada. Fisheries 18(9):6-22.

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DODSON ON DINOSAURS

by Peter Dodson

Did Dinosaurs Fly?

I have noticed a surprisingly widespread aesthetic revulsion to the principle of evolution by natural selection among otherwise educated, even erudite, people. To those of us who have dealt with evolution all of our professional lives, this realization comes as a bit of a surprise. I tell my friends that, like Puritans who are mortified at having been born naked in bed with a woman, they simply have to deal with it -- we live in an evolving world. Similarly, whether the reasons be understood or not, there exists among many biologists a revulsion to cladistics -- the method of reconstructing life's history by rigorous analysis of "shared-derived" versus "shared-primitive" characteristics; the former indicate evolutionary relationship, the latter do not. The cladistics wars, fought with great heat and light over a decade and a half beginning in the late '60s, have been chronicled in David Hull's (1988) masterful book, *Science as a Process*. Cladistics now reigns triumphant, only in part because of the inherent strength of its tenets, as the prevailing paradigm for interpreting relationships among taxa. An entire generation of young systematists has come of age without witnessing a cogent challenge to the hegemony of cladistics.

This tranquil state of affairs has been challenged by Alan Feduccia of the University of North Carolina at Chapel Hill, who has published a splendid, provocative, beautifully illustrated new book, *The Origin and Evolution of Birds* (Yale University Press, autumn, 1996). The author's modest goal is to dismantle the damnable link between dinosaurs and birds, the forging of which has been one of the crowning achievements of cladistics during the past 20 years. I myself have never been a great enthusiast of cladistics, but I accept that it is a useful tool. To my admittedly dino-centric mind, one of the most constructive things that the method has achieved is to demonstrate the monophyly of the Dinosauria, including birds, rendering secondary the division into Saurischia and Ornithischia. When something as fundamental as the link between dinosaurs and birds is challenged, I take notice.

Feduccia is an ornithologist with wide-ranging knowledge. He draws on anatomy, embryology, physiology, paleontology, and systematics to make his case. Deconstructing the link between small theropods and birds seems a daunting, uphill battle, but he goes straight to the source, examining closely Thomas Henry Huxley's statements on *Archaeopteryx*. In 1870, Huxley stated "if the whole hind limb quarters from the ilium to the toes, of a half-hatched chicken could be suddenly enlarged, ossified, and fossilized as they are, they would furnish us with the last step of the transition between Birds and Reptiles; for there would be nothing in their characters to prevent us from referring them to the Dinosauria" (quoted from Feduccia, p. 67). Feduccia draws two inferences from this remarkable statement. One is the mischief caused by selecting a chicken, a highly specialized ground bird, which he characterizes as "rather atypical of the class Aves as a whole," (ibid.) as the prototype for comparisons of birds and dinosaurs. The other is the observation that similarities of hind limbs noted result from convergence due to the similarity of lifestyles of dinosaurs, especially small dinosaurs, and birds. Some of the greatest minds in paleontology, from Louis Dollo to Henry Fairfield Osborn to G.G. Simpson to A.S. Romer have regarded the similarities between dinosaurs and birds as parallelisms and convergences, not as evidence for phylogenetic relationship.

Indeed, for Feduccia, one of the greatest problems of cladistics is that the method assumes that convergence is relatively rare and that most characters evolved only once, whereas in fact convergence turns out to be a pervasive attribute of nature. He analyzes several examples where cladistic analysis of skeletal morphology seems to give incorrect results due to convergence. Two of these are ornithological examples that are apparently falsified by DNA-DNA hybridization studies. In 1982, Joel Cracraft inferred that loons, grebes and Cretaceous hesperornithiforms, all foot-propelled diving birds with hypertrophied crests on the tibiotarsus, formed a single clade. Charles Sibley and Jon Ahlquist showed in DNA hybridization that grebes are without modern relatives. Again, Cracraft attempted to demonstrate that hawks (Falconiformes) and owls (Strigiformes) formed a monophyletic clade, even though those two groups have been held by ornithologists throughout the 20th century to be distinct orders. Sibley and Ahlquist again falsified the Cracraft position, and maintain the separateness of the two orders, a position that is widely supported among ornithologists (e.g., Gill, 1995).

I have no vested interest in the outcome of quarrels in