

SEMIONOTID FISHES FROM THE MESOZOIC GREAT LAKES OF NORTH AMERICA

AMY REED McCUNE, KEITH STEWART THOMSON, and PAUL ERIC OLSEN

INTRODUCTION

Fishes of the "holostean" family Semionotidae have been found throughout the Mesozoic in both freshwater and marine sediments, although generally the nature and extent of their diversity has not been recognized (McCune 1982; Olsen et al. 1982). We will show that, like African cichlids, American semionotids were extremely diverse, dominating a system of large, deep, stratified, rift valley lakes, the geological record of which forms part of the Newark Supergroup of eastern North America (Olsen 1978). While the historical record of African cichlids is fragmentary at best (Van Couvering 1982), the fossil record of the semionotid species complex in Newark lake deposits is exceptional. In Newark sediments, semionotids are extremely abundant, often whole, and fully articulated. Also, because of the cyclic nature of the sedimentary record, we are able to sample the fishes from a temporal succession of discrete lakes within a given lake basin. Within a portion of each lake history the stratigraphic resolution is in yearly intervals, not thousands or tens of thousands of years—within the range of a genetical-historical time scale (Stebbins 1982), and far superior to the usual resolution in the "best" stratigraphic sequences (Williamson 1981; Schindel 1982; Dingus, Sadler 1982).

This unusual combination of paleobiological and sedimentological circumstances offers a unique opportunity to examine the historical development of an "adaptive radiation" of fishes. Owing to the high diversity of both cichlid and semionotid fishes and the similarities of their respective physical and environmental settings, study of these two unrelated groups may be reciprocally illuminating. Most biological information of the kind

available for living cichlids will always be lacking for semionotid fishes. For that kind of information, we are limited to inference and analogy based on living fishes. On the other hand, direct historical studies of semionotids may be more informative about possible long term factors in the evolution of lake species than inferences based on living cichlids.

Various questions have been asked about the conditions that allow or initiate "explosive" radiation (e.g., Greenwood 1981; Fryer, Iles 1972). In general these conditions fall in two categories: those intrinsic to the organism, and those that are environmental. What are the initial conditions for "explosive" radiation, and what sort of interplay is necessary between evolutionary potentials of the organism and environmental opportunities? In semionotids, the overall patterns of variation that we have charted point to an intrinsic but not obviously adaptive component to diversification. Beyond that, long term environmental cyclicality—the geological evanescence of Newark lakes—may have repeatedly provided these fishes new ecological opportunities.

GEOLOGICAL BACKGROUND

The Late Triassic to Early Jurassic Newark Supergroup includes the lacustrine sediments deposited in ten major and several minor basins in eastern North America (Figure 1). These basins are part of a rift valley system, much like the rift valleys in Africa today, formed during the tectonic prelude to the opening of the Atlantic Ocean (Manspeizer et al. 1978). Intermittently, for about 45 million years during the Late Triassic and Early Jurassic, these basins were filled by very large deep lakes, some of which may have been as large as modern lakes Tanganyika, Malawi, and Baikal (Olsen 1980b). For simplicity, we give a

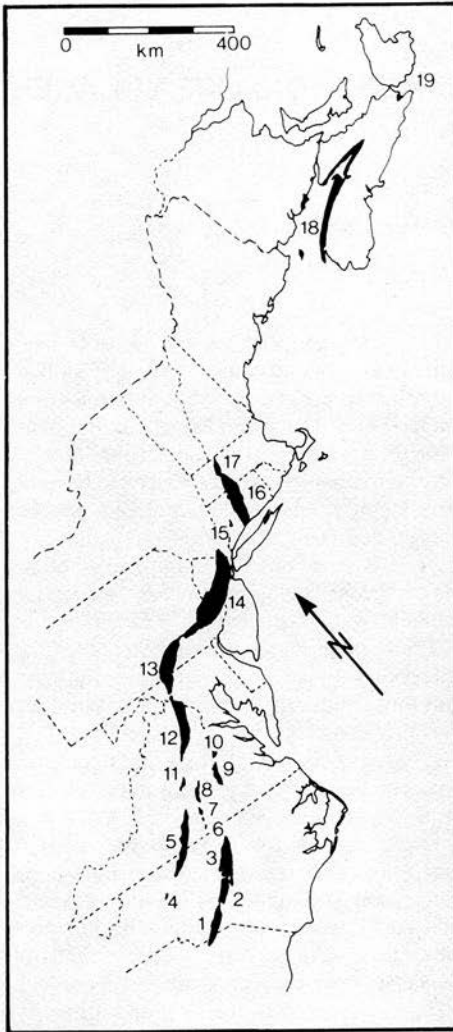


Figure 1. Exposures of the Newark Supergroup in eastern North America. 1. Wadesboro Basin (Chatham Group). 2. Sanford Basin (Chatham Group). 3. Durham Basin (Chatham Group). 4. Davie County Basin. 5. Dan River Basin. 6. Scottsburg Basin. 7. Basins south of Farmville Basin. 8. Farmville Basin. 9. Richmond Basin. 10. Taylorsville Basin. 11. Scottsville Basin. 12. Culpeper Basin. 13. Gettysburg Basin. 14. Newark Basin. 15. Pomperaug Basin. 16. Hartford Basin and Cherry Brook Outlier. 17. Deerfield Basin. 18. Fundy Basin (Fundy Group). 19. Chedabucto Basin (Olsen et al. 1982)

generalized picture of Newark paleolimnology, taken mainly from Olsen et al. (1978) and Olsen (1980b).

Newark lake sediments are cyclic with a

regularly repeating sequence of physically different sediments. These different sedimentary features, produced by sedimentation in different depths of water, reflect cyclic changes in lake level. Thus, understanding the deposition of these sedimentary cycles provides significant insight into the environmental context of semionotid evolution. Each sedimentary cycle records the history of one manifestation of a lake in the basin concerned. As lakes formed and reformed in the same basin through time, new cycles of sediment were laid down. A cycle or lake history can be divided into three units which represent 1) the expansion of a shallow lake over swamps and dry land, 2) a period of maximum lake transgression when the lake was large, deep, and stratified, and 3) the contraction and eventual evaporation of the lake (Figure 2).

The lower unit (Division 1) deposited during lake transgression is poorly bedded and may contain mudcracks, current bedding, and fossils such as plants (including roots), pollen, spores, dinosaur footprints and stromatolites. This basal unit grades upward into rock that is very finely bedded or microlaminated (Division 2). These microlaminated sediments, deposited in very large deep stratified lakes, contain fully articulated fish, reptiles and invertebrates—sometimes even insects. At this stage of maximum lake transgression, the lakes in some basins were in excess of 8000 square kilometers in area and more than 100 meters deep. The uppermost unit (Division 3) is defined by the breakdown of the microlaminated structure of the sediments. As in Division 1, the sediments of Division 3 were deposited in shallow water, but they reflect a contracting, not expanding lake. Here we find current bedding, salt casts from evaporation, mudcracks, in situ roots, and dinosaur footprints (Figure 2). Although there are fossils throughout the cycles, they are preserved best in the middle microlaminated sediments laid down in deep stratified lakes. The hypolimnion of these stratified lakes was anoxic, and thus hostile to bioturbating organisms and scavengers, allowing preservation of both fine sedimentary structures and articulated fossils like those pictured in Figure 3.

The microlaminated sediments in Division 2 comprise alternating layers of organic-rich silt and carbonate-rich silt analogous to the

GENERALIZED NEWARK SEDIMENTARY CYCLE

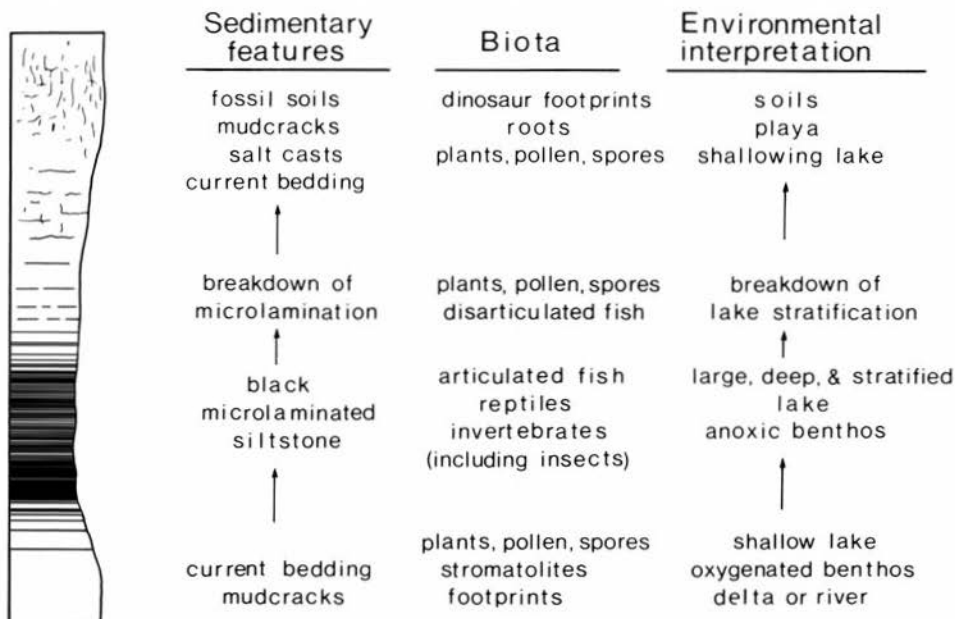


Figure 2. Generalized Newark sedimentary cycle. A schematic stratigraphic section of a single Newark sedimentary cycle is pictured at left. The corresponding progression of certain sedimentary features characteristic of a cycle is listed in the first column. Characteristic fossils and their state of preservation at corresponding positions are in the "biota" column. Together, the sedimentary features and character of the biota form the basis for the environmental interpretation of the stages of lake development (3rd column). One sedimentary cycle corresponds to the formation and evaporation of a single lake.

annual varves (each couplet = one year of deposition) deposited in modern perennially stratified lakes (Olsen 1980b; Davies, Ludlam 1973; Livingstone 1965). The analogy is important because it means that within the microlaminated portion of a given cycle, we can place individual fish in a year-by-year chronology.

As remarkable as it may seem, these great deep lakes periodically evaporated completely, as shown by the presence of salt casts, mudcracks, reptile footprints, in situ roots, and fossil soils in the upper divisions of cycles. Periodicity of lake formation and evaporation was first estimated at about 21,000 years by varve counts (Van Houten 1969; Olsen 1980b) and corroborated by an independent estimate based on radiometric dates and a stratigraphic correlation derived from vertebrate, palynological and paleomagnetic data (Olsen 1983). This periodicity has been linked to the climatic changes induced by the precession

cycle of the equinox and the cycle of eccentricity of the earth's orbit (Olsen 1983; Van Houten 1969).

SEMIONOTID FISHES

Semionotid fishes were first reported in North America early in the 19th century (Hitchcock 1819; Agassiz 1833-44). Since then, many thousand individuals have been collected from over 200 fish localities in Newark Supergroup sediments (McDonald 1983). It may seem remarkable that "species flocks" could go unrecognized for more than 160 years in such a well-collected fauna. Certainly early workers, recognizing that *Semionotus* was both abundant and diverse, described numerous species, although their descriptions were rarely diagnostic. Also, much variability remained hidden by poor preservation or lack of preparation. Confusion in early descriptions led most 20th century workers to believe that these Newark semionotids were much more

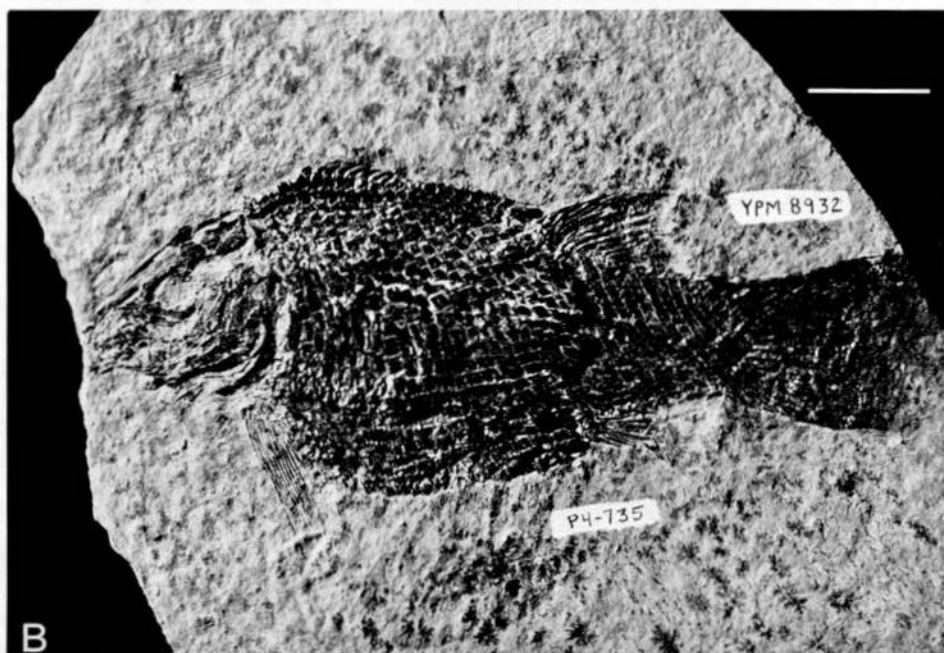
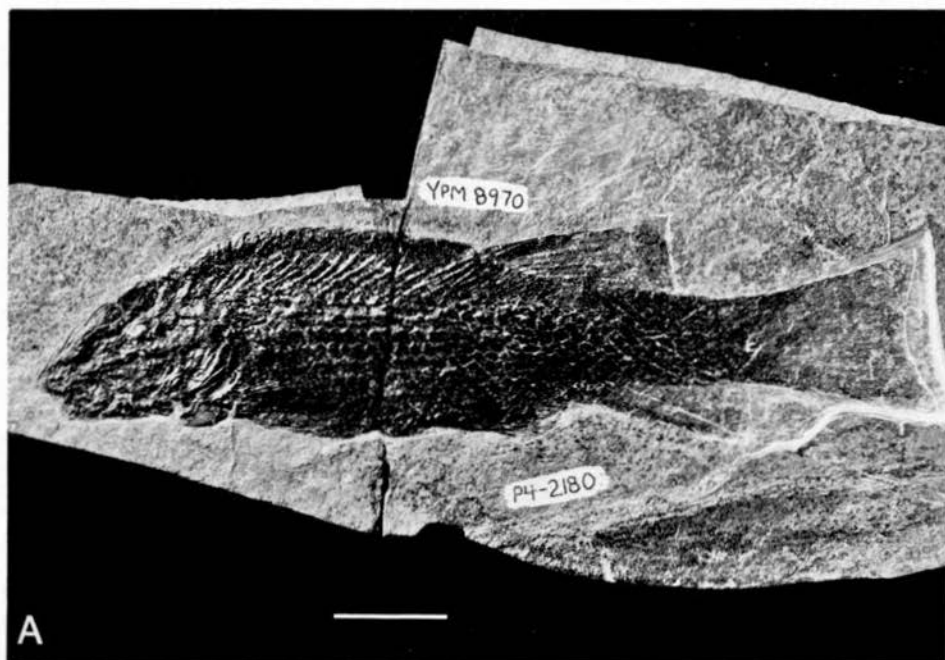


Figure 3. Exemplars of two semionotid species showing the preservational quality of fishes in microlaminated sediments. (Descriptions in McCune 1982). Both specimens are from cycle P4 (division 2) of the early Jurassic Towaco Formation of the Newark Basin. A: Member of species "p" in Figures 6, 7. B: Member of species "r" in Figures 6, 7. Scale bars = 2 cm.

diverse in name than in reality (eg., Schaeffer 1967).

Our revised assessment of semionotid diversity in Newark lakes is based on the many thousands of specimens that we collected from several large excavations in New Jersey and Connecticut, as well as by extensive prospecting throughout a broad range of other Newark Supergroup deposits (Olsen et al. 1982). To collect complete fish, and preserve the most detailed stratigraphic data possible, we removed sheets of rock 1-2 cm thick, collected the fish in each layer, and recorded the microgeographic positions of individual fish (McCune 1982). In addition to the advantages afforded by the resulting large samples of complete specimens, application of relatively recent advances in fossil preparation (e.g., negative acid preparation and high resolution casting compounds; see Rixon 1976) has enabled us to see and characterize variation in a way earlier workers could not.

Variation, Diversity, Distribution

Semionotus, *Lepidotes*, and two undescribed American genera form a monophyletic group, the Semionotidae, defined by 1) the presence of dorsal ridge scales, 2) a large posteriorly directed process on the epiotic, 3) premaxillae with prominent rostral processes sutured to the frontals, and 4) serially subdivided lacrymals (Olsen, McCune ms; McCune 1982). Semionotids, exemplified by the Newark semionotid illustrated in Figure 4, exhibit a suite of primitive characters such as hemiheterocercal tail, rhomboid shaped scales covered with ganoine, fins comprised of lepidotrichia and fringed by paired fulcra, a vertical suspensorium, a small mouth, and ordinary conical teeth. Most of the observed morphological diversity among Newark semionotids is confined to two complexes of characters—the modified scales along the dorsal midline (dorsal ridge scales) and the overall form of the body. There seems to be little diversity in the morphology of feeding structures. A few meristic characters are useful to define particular species.

Dorsal ridge scales are convex with posteriorly directed spines in the primitive state for semionotids (Figure 5a; Olsen et al. 1982). Deviations from this design are almost unknown in semionotids outside the Newark system (for exceptions see McCune 1982,

Olsen et al. 1982), but Newark semionotids exhibit an impressive array of morphological diversity (Figure 5). The dorsal ridge scales may be concave, often decorated by small tubercles anteriorly (Figure 5g) as described for the "*S. elegans* group" (Olsen et al. 1982). They may be laterally undercut and only partially covered by ganoine (Figure 5d). The spines may be abbreviated and the size of the scales reduced relative to the body (Figure 5c) as described for the "small scale group" (Olsen et al. 1982), or they may be dorsoventrally enlarged in the anterior region (Figure 5e,f), the more angular variety corresponding to scales described for the "*S. tenuiceps* group" (Olsen et al. 1982). There is a gradient of modification of scale structure according to position along the anterior-posterior axis of the series. In all cases, the anterior scales in the series are the most distinctive. Differences between types of dorsal ridge scales cannot be explained as ontogenetic stages. Even the most extreme forms of dorsal ridge scale types are found in both very small and very large individuals.

The adaptive significance of the dorsal ridge scale series is difficult to assess. Mate recognition is an unlikely adaptive explanation, as groups of species share the same dorsal ridge scale morphology. While there might also have been different locomotor consequences for different morphologies, there is no association of a particular body form with a particular dorsal ridge scale morphology.

Diversity of body form is the most prominent aspect of variability among Newark semionotids. Different shapes have been recognized by an iteration of pairwise geometrical comparisons of individuals, standardized by size. These groups were then described by bivariate plots and by a discriminant analysis of 13 measurements (McCune 1982). A sample of the variation in body shape for semionotids from a single lake cycle sharing the primitive dorsal ridge scale type is illustrated (Figure 6C a-g).

Because variation in dorsal ridge morphology and body shape is not concordant, the diversity of distinguishable forms is very high. For example, not all deep-bodied fish have robust scales, and both slender and deep-bodied fish may have robust scales. Though there are obvious difficulties in using

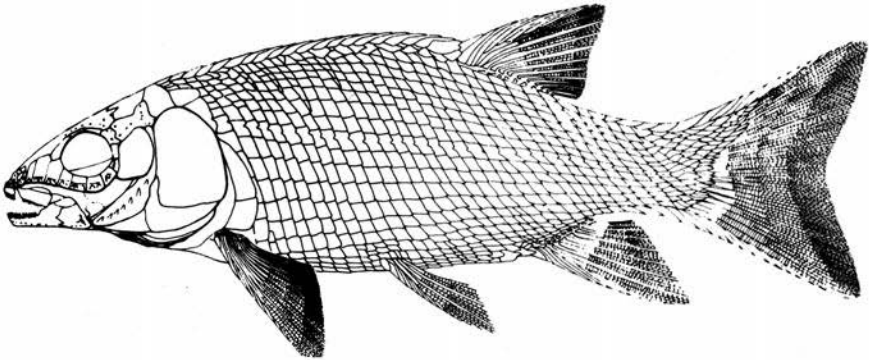


Figure 4. Reconstruction of semionotid fish from the Early Jurassic Boonton Formation of the Newark Basin. The figure is based on camera lucida drawings of a complete fish, both part and counterpart (YPM 6567) and taken from Olsen and McCune (ms).

only morphology to define species (e.g., Kornfield et al. 1982, Wake 1981), this practice at least communicates the diversity of form when information about reproductive behavior and genetics is lacking. Here, the inference may be partly justified because initial results seem to show that different "species" of semionotids, like different species of *Lepisosteus* exhibit distinct patterns of scale growth (Thomson, McCune 1983). Species of semionotids have been determined in this manner for only one Newark lake, lake cycle P4. The principal result was the description of 21 species of semionotids, 20 of them new (McCune 1982). In Figure 6C, each of these species is represented by an outline drawing and grouped with other species having the same dorsal ridge scale morphology.

In different lake cycles of the Newark Basin and in other basins of the Newark Supergroup different assemblages of fishes have been found (Olsen et al. 1982).

Semionotids are known from 8 basins of the Newark Supergroup, including the Fundy Basin in Nova Scotia, Deerfield Basin in Massachusetts, Hartford Basin in Connecticut, Newark Basin in New Jersey, Culpeper Basin in Virginia, and Dan River Basin in North Carolina (see Figure 1). Of the 45 million years spanned by Newark sediments, semionotids have been found through a period of 40 million years.

Although semionotid faunas from most Newark lakes are mainly undescribed, we have a general sense of overall diversity for a few other lakes. We illustrate several of these faunas from lakes that filled the Newark basin at various times (Figure 6), but we can not yet assign taxonomic status to any of the fish illustrated here except those from the Early Jurassic Towaco Formation, lake cycle P4.

Each of the four faunas in Figure 6 (A,B,C,D) comes from a discrete sedimentary cycle, separated from one another by millions of years and many thousands of feet of sediment. For stratigraphy of the Newark Basin see Olsen (1980a). The faunas are arranged in the stratigraphic order (A - D) of decreasing age. Each outline drawing in Figure 6C represents a distinct species (McCune 1982). Drawings in 6A, B and D probably represent species, but are pictured here only to give an approximation of diversity.

Of the Late Triassic Newark semionotids, we have only illustrated the fauna in one lake cycle from the Lockatong Formation. However, our sample comes from a large excavation. Results from that excavation, with our prospecting in another 50 Lockatong lake cycles, and the sample from an earlier excavation in North Carolina (Olsen et al. 1978) show that the diversity of semionotids in the Newark lake system throughout the Late Triassic was relatively low. In contrast, semionotids from

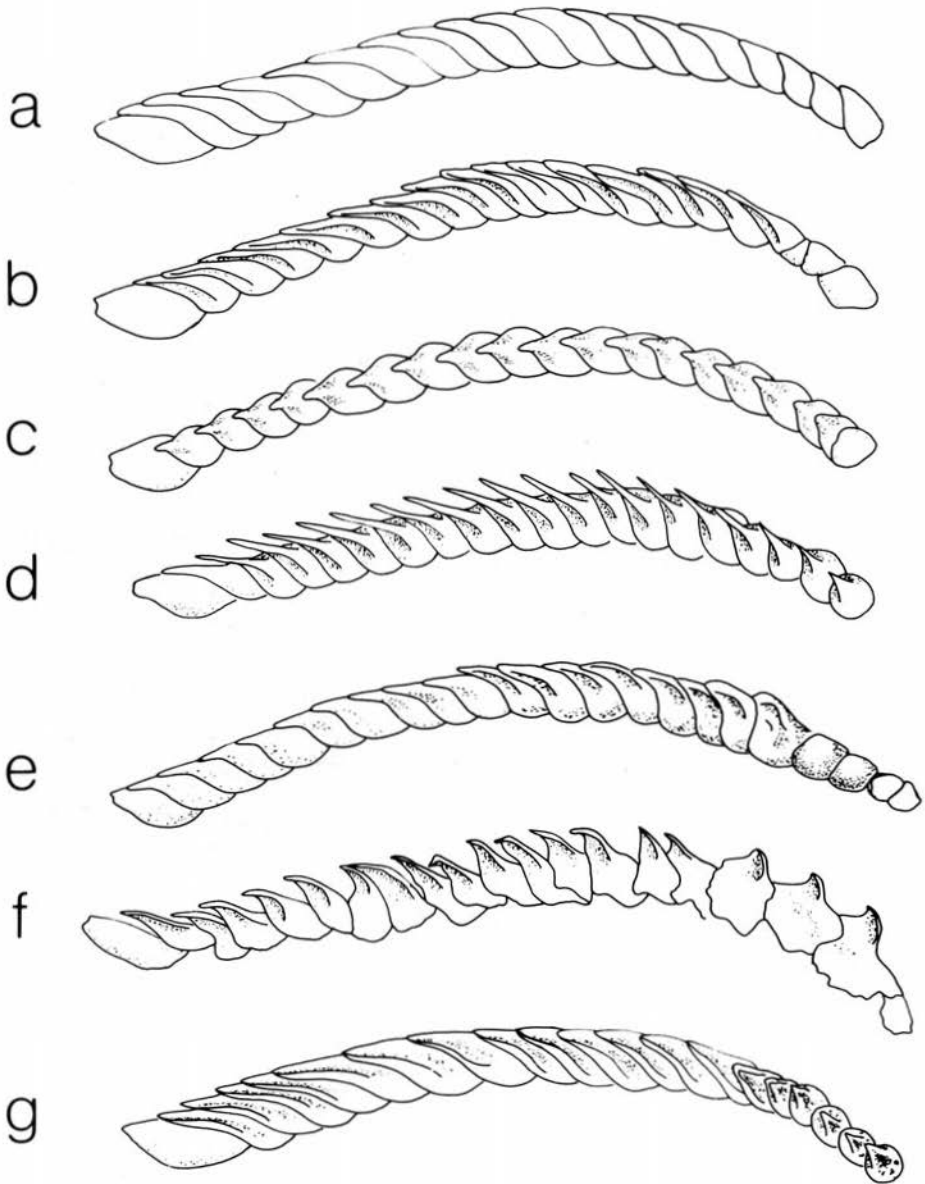


Figure 5. Morphological diversity of the dorsal ridge scales of semionotid fishes from cycle P4, Towaco Formation, Newark Basin. Scales rim the dorsal midline between the nape and the origin of the dorsal fin. The anterior direction is towards the right in each series pictured; spines are directed posteriorly. A: "simple" scales correspond to those of the "simple scale group" (Olsen et al. 1982). B: "modified simple" scales. C: "small" scales, corresponding to those of the "small scale group" (Olsen et al. 1982). D: "thin-spined" scales, corresponding to those of the "*S. Micropterus* group" (Olsen et al. 1982). E: "globular" scales. F: "robust" scales, corresponding to those of the "*S. tenuiceps* group" (Olsen et al. 1982). G: "concave" scales, corresponding to those of the *S. elegans* group" (Olsen et al. 1982).

Early Jurassic lakes from the Felville, Towaco and Boonton formations in the Newark Basin were much more diverse (refer to Figure 6,

B,C,D). The degree to which these faunas were endemic remains to be seen, but the fact that all semionotids from Boonton share the

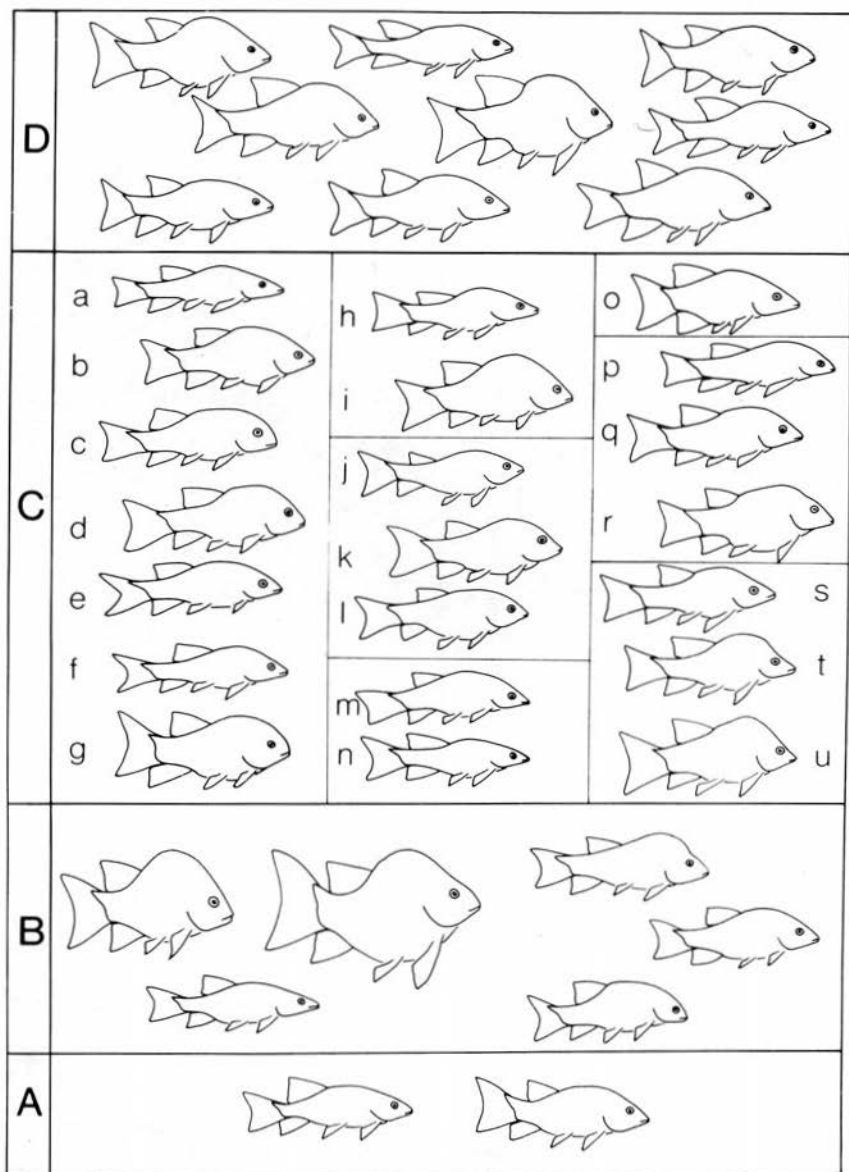


Figure 6. Array of semionotid fishes known from lakes in the Newark Basin, New Jersey. Faunas in stratigraphic order, A,B,C,D, from oldest to youngest. All drawings are based on complete specimens. Names of species are not given because descriptions have not yet been published. Species a - u correspond to those in Figure 7. A. Semionotid fauna from lake cycle W6 of the late Triassic Lockatong Formation. B. Semionotid fauna from Early Jurassic Feltsville Formation. C. Semionotid fauna from cycle P4 Early Jurassic Towaca Formation. Species are grouped by dorsal ridge scale as follows: a - g, simple scales; h, i, modified simple; j, k, l, thin-spined; m, n, concave; o, small; p, q, r, globular; s, t, u, robust.

same dorsal ridge scale morphology suggests a high probability of endemism.

Preliminary diversity data suggest an inverse relationship between the number of semionotid taxa and the number of non-semionotid fish taxa in any given lake cycle. Where the diversity of semionotids is highest, such as Towaco Formation lake cycle P4, there are no non-semionotid fishes. Conversely, there are only one or two semionotids in most Lockatong cycles, but there are minimally three to four other genera of fishes. Our ability to deduce the ecological relationships of these fishes is limited, but we are intrigued by the high diversity of semionotids in the absence of other fishes. Interestingly, the diversity of cichlid and noncichlid fishes is also inversely related in several African lakes (Greenwood 1984). The ephemeral nature of individual Newark lakes and associated drainage patterns may have allowed chance to play an important role in excluding potential non-semionotid predators and competitors in some lakes but not in others. While predation and competition may help maintain diversity in ecological time, the absence of an associated fauna may have been one factor which allowed the evolution of semionotid diversity.

Relationships, Polytomies and Speciation

To understand the evolution of semionotids in the Newark lakes we must elucidate their relationships and distributions in space and time. We initially concentrated our taxonomic studies on the semionotids from Towaco lake cycle P4. Figure 7 shows tentative relationships of 21 species of semionotids from lake cycle P4 and previously described European species. By presenting this cladogram we do not suggest a definitive pattern of relationship for all semionotids. We mean only to organize the information we have so far amassed to facilitate discussion and future work.

The details of relationships within the Semionotidae are still ambiguous and we have not included many undescribed Newark semionotids here. The principal hindrance to working out relationships among semionotids is finding enough synapomorphies to define subgroups. A large portion of the derived characters in the cladogram are autapomorphic (33) rather than synapomorphic (10).

One of the most striking features of the cladogram is the number of unresolved polytomies. Of the 8 nodes defined by one or more synapomorphies, 5 are polytomies — nodes that include 3 to 9 branches. While there is nothing intrinsically wrong with polytomies, they are often thought to arise from "partial ignorance" (Nelson 1980), owing to shortages of specimens, taxa, or characters, particularly in paleontological studies (Patterson, Rosen 1977). However, in Newark semionotids, the kinds of characters and the completeness and high quality of specimens require us to accept the present character distributions until contrary evidence accrues. Further, there are many reasons to believe that polytomies in cladograms of species, especially diverse groups like species swarms, are appropriate to represent true character distributions, and not simply incomplete analyses.

The appeal of fully dichotomous cladograms over those that contain polytomies is their higher information content (Nelson 1980). But higher information content is a formal statement about a dichotomous versus a polytomous branching pattern in the abstract. It is not an evaluation of the degree to which a particular branching pattern reflects the relationships within a group of taxa.

Both Nelson (1980) and Wiley (1981) discuss special circumstances, such as multiple speciation, hybridization, and inclusion of ancestors, when an unresolved polytomy would reflect true character state distributions. Wiley reasoned that if a number of peripheral isolates around the range of a single ancestral species formed new species, they would share only primitive characters with other peripheral isolates and the ancestral species. The cladogram of a group with this character-state distribution would be a polytomy with as many branches as there were taxa. Assuming the same character distribution, if all the descendant species arose from a single common ancestral species that did not change through time, the cladistic pattern would still be a polytomy even if speciation were neither simultaneous nor allopatric. Operationally, the branching sequence of this non-simultaneous case could not be determined from the character distributions. Unless the actual sequence of speciation "events" could be

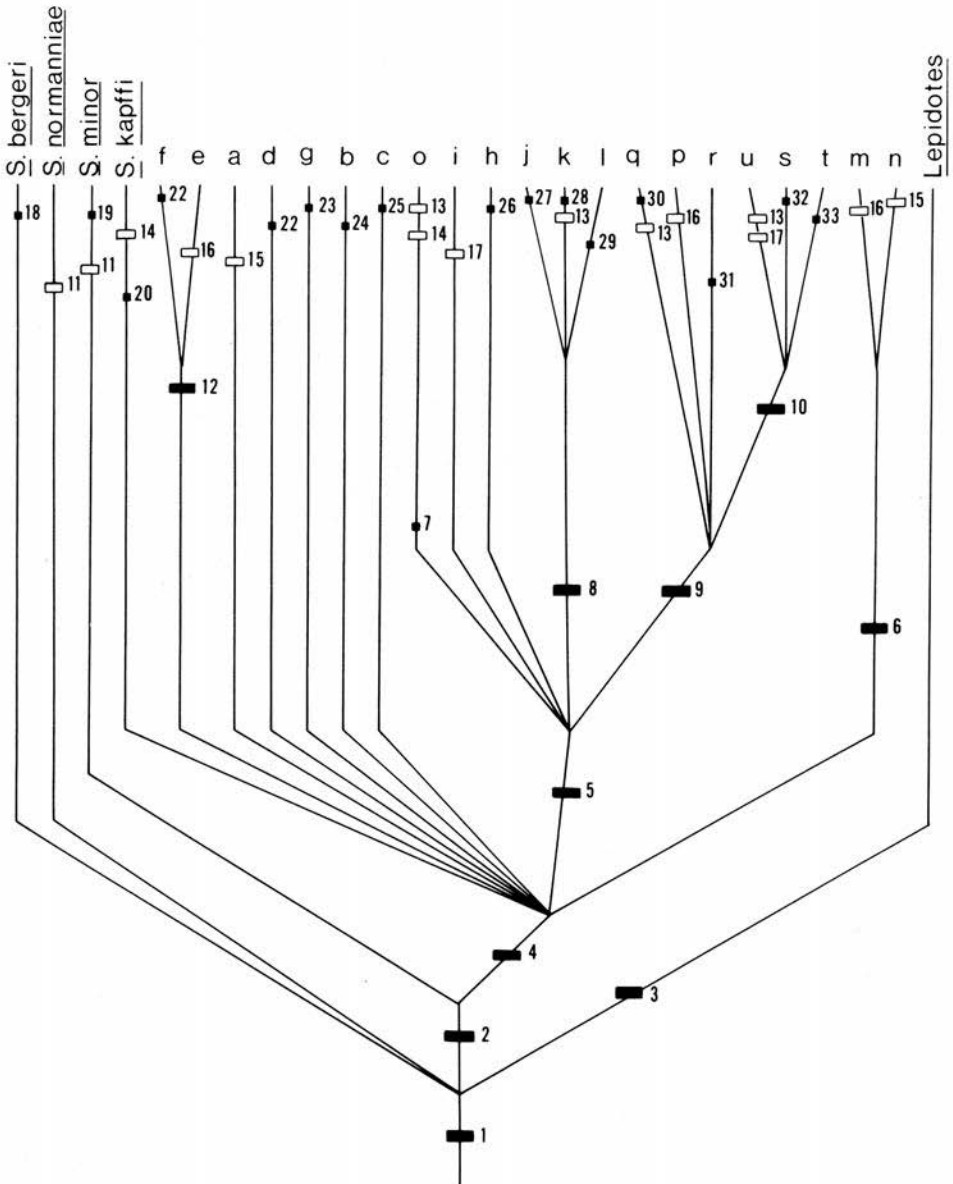


Figure 7. Tentative cladistic relationships for semionotids from P4 and European semionotids. (McCune 1982; McCune ms) Names for species a through u (also in Figure 6C) are not given because descriptions have not yet been published. Large black bars are synapomorphies. White bars represent homoplasies. Primitive character states are not shown. Key to derived character-states is as follows: 1. Dorsal ridge scales present, premaxillae with long rostral process, epiotic with posteriorly directed process, lacrymal serially subdivided. 2. Fringing fulcra reduced in number. 3. Suborbitals number greater than one. 4. Basal fin fulcra reduced in number. 5. Dorsal ridge scales laterally undercut. 6. Dorsal ridge scales concave. 7. Dorsal ridge scales with short spines, dorsal ridge scales small relative to flank scales. 8. Dorsal ridge scale spines very narrow and separated distally from base. 9. Anterior dorsal ridge scales enlarged. 10. Anterior dorsal ridge scales even larger. 11. Flank scales serrated. 12. Caudal fin forked. 13. Horizontal flank scale rows reduced. 14. Vertical flank scale rows reduced. 15. Shape "1". 16. Shape "2". 17. Shape "3". 18-23. Autapomorphic shapes.

scale type (Figure 4a). The cladogram (Figure 7) was based on the latter analysis of dorsal ridge scale morphology. But both schemes of character transformation are only scenarios. Without corroborating characters or understanding of the genetic-developmental control of these morphological transformations, we can not really choose between them. Furthermore, the existence of morphological anomalies suggests that most individuals share the potential to express many or all variants.

Anomalies, Parallelism, and Speciation

In about 2 percent of all Newark semionotids examined, a dorsal ridge scale series of one type will include one or a few "sports" of another type in a single individual (Figure 8). For example, a concave scale may be mixed with simple scales; or simple concave and thin-spined or short-spined scales may occur together; or thin-spined and small scales may appear in a globular series (Figure 8 a - d). Another type of variant involves doubling or tripling of scales in the dorsal ridge series. Several variants involve doublings of only one or two scales (Figure 8 e,f), although in a few instances, a large portion of the series is doubled or tripled (Figure 8 g,h).

Flank scale doubling is concentrated in the anterior epaxial region near the dorsal ridge scales. Interestingly, the anterior flank is the last region to develop scales in *Lepisosteus* (Suttkus 1963), a variety of paleoniscids (D. Bardack, pers. comm.), and probably semionotids. Variability in scale number and shape may be more tolerable in this region because these scales develop late in ontogeny (Goldschmidt 1940:268; deBeer 1930). The occasional complete doubling of scales in the dorsal ridge scale series is particularly interesting since there is a tendency for semionotids and their sister group, the macrosemiids to develop intercalary scale rows (Bartram 1977; McCune 1982; Olsen, McCune ms). The capacity to vary scale shape and number, or tolerance of this variation, appears to be primitive for semionotids and macrosemiids.

What are the implications of this variability for the systematics and evolution of semionotids? Because anomalies occur in

such low frequencies, they do not diminish the conspicuous taxonomic value of dorsal ridge scale characters. But the occurrences of supernumerary spines and dorsal ridge scale "sports" misplaced in series of differing morphologies suggest that all or many semionotid species had the genetic/developmental potential to generate any of the observed dorsal ridge scale patterns, though the potential is rarely expressed. If so, the likelihood of parallelism in closely related species may be very high (Rachootin, Thomson 1981). The same morphology could be less indicative of immediate common ancestry than of shared genetic-developmental potentials (Roth 1984). This would be due to common ancestry on a more general, higher taxonomic, level.

An analogy may be drawn with cichlid trophic polymorphism. It has been suggested that much of the "adaptive radiation" in African cichlids may have been achieved through trophic polymorphism rather than by speciation, because two morphological "species" of cichlids from Cuatro Ciénegas belong to a single biological species (Sage, Selander 1975; Kornfield et al. 1982). While some trophic morphs of African cichlids may have been recognized as species, one can hardly dismiss the African cichlid radiation as taxonomic artifact. It is more interesting that the same complex of characters exhibiting intraspecific variability in the Central American *Cichlasoma* can be used to diagnose species of cichlids from the African lakes. Perhaps this intrinsic variability in trophic structures should be considered pleisiomorphic for cichlids, and viewed as the material for the morphological divergence traditionally associated with speciation. Given appropriate extrinsic conditions, such as large lakes or lack of predators, morphs of ancestral polymorphic species from Africa may have been fixed, through selection or chance, by or along with changes in breeding structure. Instead of asking whether African cichlids are oversplit, we might shift some attention to the potential range of variability in tooth morphology that all cichlids share, and the mechanisms by which particular variants are fixed.

ENVIRONMENTAL CYCLES AND EVOLUTION

Cyclic formation and evaporation of lakes which are permanent on an ecological time

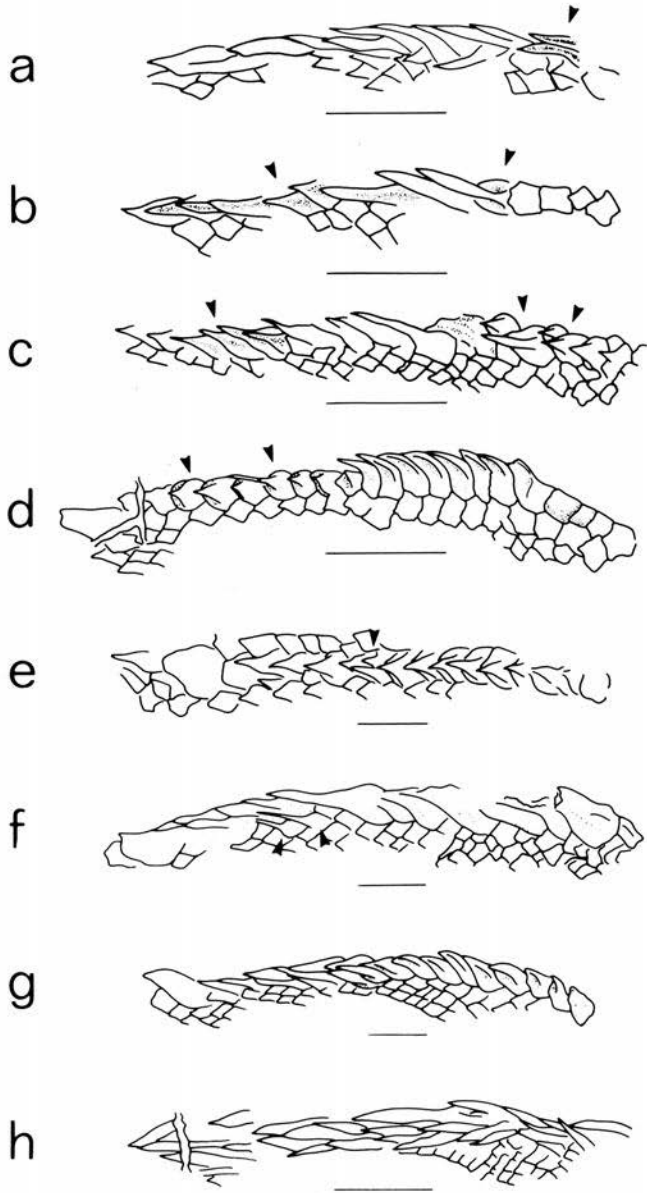


Figure 8. Anomalous variation in dorsal ridge scales from camera lucida drawings of individuals from cycle 4 Towaco Formation, Newark Basin. Specimen numbers refer to Yale Peabody Museum (YPM) specimens. Anterior portion on right dorsal ridge scales point posteriorly. Scale bars = 5 cm. a. Arrow marks two concave scales in a predominantly simple complex series (YPM 8932). b. Anterior arrow marks "thin spined" scales mixed with "simple" scales anteriorly and "concave" scales posteriorly (YPM 8869). c. Central portion comprises "simple" scales while arrows mark "small", "thin-spined" and concave scales anterior to posterior (YPM 8894). d. In this "globular" series, anterior arrow marks thin-spined scale; posterior arrow marks short-spined scale (YPM 8932). e. Arrow marks single scale doubling (YPM 8861). f. Arrows mark scale doublings (YPM 8719). g. Posterior scales are doubled (YPM 8847). h. Entire dorsal ridge scale series tripled or more (YPM 8848).

scale, are not usually discussed in relation to the evolution of fishes. Studies of fishes living in modern lakes cannot reveal the evolutionary effect of such longterm cyclicity because, from an ecological and populational perspective, the rate of climatic change is so slow as to be imperceptible to successive generations of fish. Our retrospective advantage allows us to examine the longterm evolutionary consequences of regular habitat destruction (see also Schindler, 1982), in this case periodic drying, on the species living within a lake episode.

Periodic evaporation of Newark lakes could have extinguished entire communities of fishes. This regular wholesale extinction of communities through geological time deserves consideration separate from natural selection and species selection. While community extinction could be reduced to processes of natural selection, knowledge of cyclic environmental change allows a general prediction of the fate of entire assemblages without consideration of selective factors for individual species. Both community extinction and species selection predict patterns of persistence through geological time, but these predictions are completely different.

In Newark lakes, periodic drying was probably insensitive to most species differences, let alone individual variation. Only fish that could have survived in small isolated saline ponds or found their way up shrunken rivers might have survived a dry phase. If a riverine form was likely to survive better when a lake dried up, then the persistent lineage would have been the one that maintained the riverine lifestyle. Evaporation of a given lake probably would have eradicated most or all of the fishes living in that lake. In regions of high endemism, this sort of environmental change would amount to extinction for many species.

Community extinction and species selection would have occurred on about the same time scale. How do they differ? Stanley (1975:646) suggested that species selection determines the direction of transpecific evolution. Species selection does not invoke a mechanism other than ordinary natural selection. Stanley's point is that evolutionary persistence may be attained by a lineage through a member species that leaves many daughter species, either by a high rate of speciation or by persistent

speciation at a lower rate over a long period of time. This argument is in part probabilistic. If there is a large stochastic component to extinction, then the more descendants a species leaves, the better the chance of survival for that lineage. There may also be an adaptive component to Stanley's proposition. If species adapt by speciating, then a lineage has a better chance of cornering the right direction of adaptation if it speciates frequently. In the case of periodic drying, neither prolific speciation nor adaptation by speciation is relevant. Community extinction would not be stochastic, but decidedly deterministic against lake fishes.

In the case of Newark lake sequences, the hypothesis of the persistence of riverine species could be tested by comparing the faunas of two or more lakes in historical succession. If the species composition was the same in both lakes, then the dry period would appear not to have made any difference to the evolution of the group. If the species in the two lakes are different, and the species in the upper, younger lake are derived from just a few older (riverine?) forms, it would be reasonable to presume that local extinction restarted evolution in the younger lake from persistent riverine forms.

Within individual lake histories, population processes will mold future generations of lake fishes. There probably were both "Red Queen" fish competitively adapting to local conditions (Van Valen 1973), and prolific speciators living in Newark lakes. But as lake habitats disappeared every 21,000 years, whatever evolution occurred within individual lakes may have been largely irrelevant to the longterm pattern of evolution. Stanley's hypothesis of species selection would predict the persistence of species-rich lineages. But in this case, probably only the riverine forms persisted, regardless of their speciation potential. If the effect of periodically drying lakes in the Newark was indeed to select for riverine species, we are forced to see the tremendous diversity of semionotids in various Newark lakes as a kind of noise over evolutionary time.

CLIMATIC CYCLES AND AFRICAN LAKES

What is the relevance of the cyclic expansion and contraction of Newark lakes to other lake systems? How general is periodic climatic

change? Is there any evidence that similar phenomena may have played a role in the history of cichlids in African rift lakes?

Periodic climatic change that produces cyclicity in environmental and sedimentary history appears to be a general phenomenon throughout the Phanerozoic record, and not just an anomaly of the Late Triassic to Early Jurassic Newark record. At tropical latitudes, the laws of celestial mechanics suggest that the precession and eccentricity cycles should produce regular variation of insolation over periods of roughly 21,000 years and 100,000 years. In the Newark Supergroup system, the principal lake level cycle of 21,000 years is modulated by a 100,000 year cycle. Bradley (1929) described a 21,000 year periodicity in lake level in the Eocene Green River Formation of Wyoming, and similar sedimentary lacustrine cycles have been described in the Devonian Old Red Sandstone of Scotland (see Olsen 1983; Donovan 1980).

In the Quaternary, periodic changes in climate—cycles of 21,000, 42,000, and 100,000 years—have been inferred from oxygen isotope ratios in deep sea cores (Berger 1978; Kukla 1977), and ascribed to astronomical causes (Imbrie, Imbrie 1979; Berger 1978; Hays et al. 1976; Imbrie 1982). In the high latitudes, these dramatic, globally synchronous changes in climate were expressed as changes in temperature and ice volume during the Great Ice Ages. In the middle and low latitudes, these climatic fluctuations were expressed as changes in precipitation, influencing the levels of even the largest lakes in East Africa (Livingstone 1975; Hamilton 1982).

Thus far our knowledge of the history of lakes Victoria, Tanganyika, and Malawi extends back through only the last major glacial maximum. For this interval, the sedimentary record indicates that fluctuations in lake level were not equally important in all lakes. Therefore, the degree to which cichlid evolution may have been influenced by lake level changes was probably different in different lakes.

Climatic changes have been most influential in Lake Victoria. Bishop and Trendall (1967) dated the oldest lacustrine sediments associated with Lake Victoria as mid-Pleistocene, about 750,000 years old. But

some evidence suggests that only 14,000 years ago, Lake Victoria was at least 75 m lower than its present maximum depth of about 90 m (Kendall 1969; Livingstone 1975), or perhaps completely dry (Livingstone 1980). If the Lake Victoria basin was dry at that time, the evolution of endemic Lake Victoria cichlids may have occurred in as little as 14,000 years. Such a young age for Lake Victoria is consistent with the electrophoretic data interpreted to mean that speciation in the *Haplochromis* from Lake Victoria has occurred very recently (Sage et al. 1984).

Lake Tanganyika also experienced a major lake level drop at about the same time as Lake Victoria. Hecky and Degens (1973) argue that 14,000 years ago, Lake Tanganyika was at least 600 m lower than it is now, although Livingstone (1975) believes this drop was closer to 300 m. An increase in salinity associated with a decrease in water volume might not affect some cichlids directly, given that many species are euryhaline (Fryer, Iles 1972). However, the decrease in lake area might severely reduce the extent and diversity of habitat, thereby lowering the numbers of individuals and species that could inhabit the lake.

Less is known about Lake Malawi than about any other African Great Lake. Livingstone (pers. comm.) has not yet fully analyzed his cores from Lake Malawi, but he has seen no obvious evidence for massive changes in lake level through the last 20,000 years. Presumably, the climatic changes producing lake level changes in the other lakes had little effect on the cichlids of Malawi.

The record of earlier climatic change in African Great Lakes has not been investigated because of the tremendous logistic problems of taking long, continuous lake cores. Without longer, older cores, it is not possible to observe directly the sedimentological record of periodic fluctuation in lake levels. However, the coincidence of the last great lowering of lakes Victoria and Tanganyika with the most recent glacial advance suggests a 100,000 year periodicity. On the other hand, increased precipitation 9,000 years ago (Hecky, Degens 1973; Hamilton 1982) suggests a precipitation cycle of roughly 20,000 years. Too little is known of the relation between precipitation, solar insolation, and continental

glacier formation to deduce the period of lake level oscillation in any of the African lakes. Yet it seems clear that the African Great Lake levels are under climate control and that this climatic change is periodic.

If climatic changes throughout the Quaternary resulted in very large fluctuations in levels of African lakes, our perceptions of the history and future of the African cichlid radiations may need to be modified. Irrespective of whether Lake Victoria actually dried up completely, we know that both lakes Victoria and Tanganyika experienced severe drying some 14,000 years ago. The historical evidence for this dry episode combined with the evidence for global periodic climatic change throughout the Phanerozoic, emphasizes the ephemeral nature of even the largest lakes. How might these longterm fluctuations influence the persistence of cichlid lineages? Without a longterm perspective we might expect that lineages specialized to lacustrine life would be most likely to persist. And according to the species selection argument (Stanley 1975), we might predict the persistence of *good speciator* lineages. But if African lakes, like Newark lakes, are ephemeral, we might predict that the cichlid lineages most likely to persist would not be the lake-adapted forms nor the prolific speciators, but those with a propensity to migrate or disperse and the ability to survive in small stagnant ponds.

SUMMARY

American semionotid fishes were extremely abundant and diverse in the Late Triassic and Early Jurassic. During that time they dominated the great lakes that filled a series of rift valley basins in eastern North America. The fossil record of this complex of closely related species is particularly conducive to direct historical studies of evolution: 1) Within each of several basins, large, deep, stratified lakes repeatedly formed and evaporated every 21,000 years. Thus, in a given basin there is a geological "stack" of discrete lake histories. Many of these individual lakes, which filled the basin at different times, were dominated by semionotids. 2) The paleontological detail within several individual lake histories is exceptional. Complete articulated fishes are preserved in great abundance. The micro-

layers of sediments, deposited in the anoxic hypolimnion of deep stratified lakes have preserved a yearly chronology of the fish fauna.

The morphological diversity of semionotid fishes from Newark lakes is concentrated in two complex characters—overall body shape, and the morphology of the series of dorsal ridge scales. From a single lake history in the Early Jurassic Towaco Formation of the Newark Basin, 21 species (20 new) have been described. Although most species from Newark have not yet been described, two patterns are apparent. 1) Species diversity is low in the Late Triassic and increases in the Early Jurassic. 2) Semionotid diversity within lake histories is inversely related to the diversity of non-semionotid fish taxa.

Much of the cladogram of relationships of Newark semionotids remains unresolved. Polytomies originate from a shortage of synapomorphies which may, in turn, arise from inadequacy of material or analysis. However, more importantly and more interestingly, a predominance of autapomorphic, not synapomorphic, characters at low taxonomic levels are likely to reflect actual patterns of speciation and real (complete) character distributions, especially in closely related, diverse, and rapidly speciating groups.

Most synapomorphies defining subgroups of semionotids describe features of the dorsal ridge scale series, with about 2 percent showing anomalous deviation from the 7 general types of dorsal ridge scales. The deviations do not diminish the taxonomic value of dorsal ridge scale characters, but they do suggest a pervasive potential for all or most semionotids to produce different dorsal ridge scale morphologies rather easily, increasing the probability of parallelism in these characteristics.

The periodic expansion and contraction of Newark lakes implies a level of selection, extinction of entire communities, that could not be predicted from population processes operating on an ecological time scale. Over the long term, say 22,000 years or more, the evaporation of individual Newark lakes probably "selected for" riverine fishes, and "selected against" lake fishes, irrespective of their propensity to speciate or their

adaptations to local conditions.

The influences of periodic climatic change are not only reflected in the record of Newark lakes, but throughout the Phanerozoic to the present. Similar lake level fluctuations of the modern African rift valley lakes are also under climatic control, although the period of fluctuation is not known. Different lakes appear to have been variously affected by climatic change. Present evidence indicates that Lake Victoria may be as young as 14,000 years, and that Lake Tanganyika experienced as much as a 300-600 meter drop in lake level in the same period. Lake Malawi appears to be relatively stable. The rise and fall of African lakes may have been as important in the evolution of cichlid fishes as the evanescence of Newark lakes was to the evolution of semionotid fishes.

ACKNOWLEDGMENTS

Fellowship support for ARM was provided by the Miller Institute for Basic Research in Science, University of California, Berkeley. Grant support came from the National Science Foundation (DEB-7921746 to KST), National Geographic Society, Theodore Roosevelt Memorial Fund, and Sigma Xi (to ARM). We thank R Boardman for technical assistance, W K Sacco for taking the photographs, Bobb Schaeffer and John Maisey, American Museum of Natural History, and F A Jenkins, MCZ of Harvard University, for loans of specimens, and K Padian, R D Sage, S L Wing, and D W Winkler for reviewing the manuscript.

REFERENCES

- Agassiz L 1833-44 *Recherches sur les Poissons Fossiles*. Neuchatel: Imprimerie de Petitpierre
- Avise J C, J J Smith, F J Ayala 1975 Adaptive differentiation with little genetic change between two native California minnows. *Evolution* 29:411-426
- Bartram A W H 1977 The Macrosemiidae, a Mesozoic family of holostean fish. *Bull Brit Mus (Geol)* 29:137-234
- de Beer Sir G R 1930 *Embryology and Evolution*. Clarendon. Oxford
- Berger A L 1978 Longterm variations of caloric insolation resulting from the earth's orbital elements. *Quart Res* 9:139-167
- Bishop W W, A F Trendall 1967 Erosion surface, tectonics, and volcanic activity in Uganda. *Quart J Geol Soc Lond* 122:385-420
- Bookstein F L 1978 The measurement of biological shape and shape change. *Lecture Notes in Biomathematics* 24 Springer Verlag. New York
- Bradley W 1929 The varves and climate of the Green River Epoch. *U S Geol Surv Prof Papers* 158-E
- Davies G R, S D Ludlam 1973 Origin of laminated and graded sediments, Middle Devonian of Western Canada. *Geol Soc Amer Bull* 84:3527-3546
- Dingus L, P M Sadler 1982 The effects of stratigraphic completeness on estimates of evolutionary rates. *Syst Zool* 31:400-412
- Dobzhansky T 1970 *The Genetics of the Evolutionary Process*. Columbia Univ Press. New York
- Donovan R N 1980 Lacustrine cycles, fish ecology and stratigraphic zonation in the Middle Devonian of Caithness. *Scott J Geol* 16:35-50
- Fryer G, T D Iles 1972 *The Cichlid Fishes of the Great Lakes of Africa*. T F H Publications. Neptune City NJ
- Goldschmidt R 1940 *The Material Basis of Evolution*. Yale Univ Press. New Haven
- Greenwood P H 1979 Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces:Cichlidae) and related taxa, Part I. *Bull Brit Mus Nat Hist (Zool)* 35:265-322
- _____ 1980 Towards a phyletic classification of the 'genus' *Haplochromis* (Pisces:Cichlidae) and related taxa, Part II: The species from Lakes Victoria, Nabugabo, Edward, George, and Kivu. *Bull Brit Mus Nat Hist (Zool)* 39:1-101
- _____ 1981 *The Haplochromine Fishes of the East African Lakes*. Kraus Thomson Organization GmbH. Munich
- _____ 1984 African cichlids and evolutionary theories. 141-154 A A Echelle, I Kornfield eds. *Evolution of Fish Species Flocks*. Univ Maine Press at Orono
- Hamilton A C 1982 *Environmental History of East Africa: A Study of the Quaternary*. Academic Press. New York
- Hays J D, J Imbrie, N J Shackleton 1976 Variations in the earth's orbit: pacemaker of the ice ages. *Science* 194:1121-1132
- Hecky R E, E T Degens 1973 Late Pleistocene-Holocene chemical stratigraphy in the rift valley lakes of Central Africa. *Woods Hole Oceanogr Inst Tech Rpt*. WHOI 73-28
- Hitchcock E 1819 Remarks on the geology and mineralogy of a section in Massachusetts on the Connecticut River, with a part of New Hampshire and Vermont. *Amer J Sci* 1:105-116
- Humphries J M, F L Bookstein, B Chernoff, G R Smith, R L Elder, S G Poss 1981 Multivariate discrimination by shape in relation to size. *Syst Zool* 30:291-308
- Imbrie J 1982 Astronomical theory of the Pleistocene Ice Ages: A brief historical review. *Icarus* 50:408-422
- Imbrie J, K P Imbrie 1979 *Ice Ages: Solving the Mystery*. Enslow. Hillside NJ
- Kendall R L 1969 An ecological history of the Lake Victoria basin. *Ecol Monogr* 39:121-176
- Kornfield I L 1978 Evidence for rapid speciation in African cichlid fishes. *Experientia* 34:335-336
- Kornfield I L, D C Smith, P S Gagnon, J N Taylor 1982 The cichlid fish of Cuarto Cienegas, Mexico: Direct evidence of conspecificity among

- distinct trophic morphs. *Evolution* 36:658-664
- Kukla G L 1977 Pleistocene land-sea correlations. 1. Europe. *Earth Sci Rev* 13:307-374
- Livingstone D A 1965 Sedimentation and the history of water level change in Lake Tanganyika. *Limnol Oceanogr* 10:607-610
- _____ 1975 Late Quaternary climate change in Africa. *Ann Rev Ecol Syst* 6:249-280
- _____ 1980 Environmental change in the Nile headwaters. 339-359 M A J Williams, H Faure eds. *Sahara and the Nile*. Blakema. Rotterdam
- Manspeizer W, H L Cousminer, J H Puffer 1978 Separation of Morocco and eastern North America: A Triassic-Liassic stratigraphic record. *Geol Soc Amer Bull* 89:901-920
- Mayr E 1963 *Animal Species and Evolution*. Harvard Univ Press. Cambridge
- McCune A R 1982 *Early Jurassic Semionotidae (Pisces) from the Newark Supergroup: Systematics and Evolution of a Fossil Species Flock*. PhD Thesis. Yale Univ
- _____ ms A revision of *Semionotus* from the Late Triassic and Jurassic of Europe.
- McDonald N G 1983 History of paleoichthyology in the Newark Supergroup Basins, eastern North America. *Geol Soc Amer Abstr* 15:121
- Nelson G 1980 Multiple branching in cladograms: two interpretations. *Syst Zool* 29:86-91
- Olsen P E 1978 On the use of the term Newark for Triassic and Early Jurassic rocks in eastern North America. *Newsl Stratigr* 7:90-95
- _____ 1980a The latest Triassic and early Jurassic Formations of the Newark Basin (eastern North American Newark Supergroup): Stratigraphy, structure and correlation. *New Jersey Acad Sci Bull* 25:25-51
- _____ 1980b Fossil great lakes of the Newark Supergroup in New Jersey. 352-398 M Manspeizer ed. *Field Studies of New Jersey Geology and Guide to Field Trips*. 52nd Ann Mtg, New York State Geol Assoc. Rutgers Univ. Newark NJ
- _____ 1983 Periodicity of lake-level cycles in the Late Triassic Lockatong Formation of the Newark Basin. (Newark Supergroup, New Jersey and Pennsylvania.) in press D Reidel ed. *Proceedings, NATO ASI Symposium on Milankovitch and Climate*. Dordrecht.
- Olsen P E, C L Remington, B Cornet, K S Thomson 1978 Cyclic changes in Late Triassic Lacustrine Communities. *Science* 201:729-733
- Olsen P E, A R McCune, K S Thomson 1982 Correlation of the early Mesozoic Newark Supergroup by vertebrates, principally fishes. *Amer J Sci* 282:1-44
- Paterson H 1978 More evidence against speciation by reinforcement. *S African J Sci* 74:369-371
- Patterson C 1982 Morphological characters and homology. 21-74 K A Joysey, A E Friday eds. *Problems of Phylogenetic Reconstruction, Systematics Association Spec Vol No 21*. Academic Press. London
- Patterson C, D E Rosen 1977 Review of ichthyodectiform and other Mesozoic teleost fishes and the theory and practice of classifying fossils. *Bull Amer Mus Nat Hist* 158:83-172
- Rachootin S P, K S Thomson 1981 Epigenetics, paleontology and evolution. 181-193 G G E Scudder, J L Reveal eds. *Evolution Today Proc 2nd Internat Congr Syst Evol Biol*. Hunt Inst Bot Documentation, Carnegie-Mellon Univ. Pittsburgh
- Raff R A, T C Kauffman 1982 *Embryos, Genes, and Ancestors*. Macmillan. New York
- Raup D M 1966 Geometric analysis of shell coiling: general problems. *J Paleon* 40:1178-1190
- Rixon A E 1976 *Fossil Animal Remains: Their Preparation and Conservation*. Athlone. London
- Rosen D E 1979 Fishes from the uplands and intermontane basins of Guatemala: revisionary studies and comparative biogeography. *Bull Amer Mus Nat Hist* 162:267-376
- Roth V L 1984 On homology. *Biol J Linn Soc* In press.
- Sage R D, P V Loiselle, P Basasibwake, A C Wilson 1984 Molecular versus morphological change among cichlid fishes (Pisces: Cichlidae) of Lake Victoria. 185-202 A A Echelle, I Kornfield eds. *Evolution of Fish Species Flocks*. Univ Maine Press at Orono
- Sage R D, R K Selander 1975 Trophic radiation through polymorphism in cichlid fishes. *Proc Natl Acad Sci USA* 72:4669-4673
- Schaeffer B 1967 Late Triassic fishes from the western United States. *Bull Amer Mus Nat Hist* 153:287-342
- Schindel D E 1982 Resolution analysis: a new approach to the gaps in the fossil record. *Paleobiol* 8:315-353
- Stanley S 1975 A theory of evolution above the species level. *Proc Nat Acad Sci USA* 72:646-650
- Stebbins G L 1982 Perspectives on macroevolution. *Evolution* 36:1109-1118
- Suttkus R D 1963 Order Lepisosteii. *Fishes of the Western North Atlantic*. Memoir Sears Found for Marine Research. No 1 Pt 3. New Haven
- Thomson K S, A R McCune 1983 Scale structure as evidence of growth patterns in fossil semionotid fishes. *J Vert Paleo* In press.
- Van Couvering J A H 1982 Fossil cichlid fish of Africa. *Spec Pap Paleon* 29. Paleont. Assn. London
- Van Houten F B 1969 Late Triassic Newark Group, north central New Jersey and adjacent Pennsylvania and New York. 314-347 S Subitzki ed. *Geology of Selected Areas in New Jersey and Eastern Pennsylvania*. Rutgers Univ Press. New Brunswick
- Van Valen L 1973 A new evolutionary law. *Evol Theor* 1:1-30
- Wake D 1981 Application of allozyme evidence to problems in evolution of morphology. 257-270 G G E Scudder, J L Reveal eds. *Evolution Today Proc 2nd Internat Congr Syst Evol Biol*. Hunt Inst Bot Documentation, Carnegie-Mellon Univ. Pittsburgh
- Wiley E O 1981 *Phylogenetics: The Theory and Practice of Phylogenetic Systematics*. Academic Press. New York
- Williamson P G 1981 Palaeontological documentation of speciation in Cenozoic molluscs from Turkana Basin. *Nature* 293:437-443