

New Early Jurassic Tetrapod Assemblages Constrain Triassic-Jurassic Tetrapod Extinction Event

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The discovery of the first definitively correlated earliest Jurassic (200 million years before present) tetrapod assemblage (Fundy basin, Newark Supergroup, Nova Scotia) allows reevaluation of the duration of the Triassic-Jurassic tetrapod extinction event. Present are tritheledont and mammal-like reptiles, prosauropod, theropod, and ornithischian dinosaurs, protosuchian and sphenosuchian crocodylomorphs, sphenodontids, and hybodont, semionotid, and palaeonisciform fishes. All of the families are known from Late Triassic and Jurassic strata from elsewhere; however, pollen and spore, radiometric, and geochemical correlation indicate an early Hettangian age for these assemblages. Because all "typical Triassic" forms are absent from these assemblages, most Triassic-Jurassic tetrapod extinctions occurred before this time and without the introduction of new families. As was previously suggested by studies of marine invertebrates, this pattern is consistent with a global extinction event at the Triassic-Jurassic boundary. The Manicouagan impact structure of Quebec provides dates broadly compatible with the Triassic-Jurassic boundary and, following the impact theory of mass extinctions, may be implicated in the cause.

THE TRIASSIC-JURASSIC BOUNDARY marks one of the more significant of the 13 or so (1-5) mass extinctions that punctuate the Phanerozoic. Late Triassic continental faunas were dominated by diverse quadrupedal archosauromorph reptiles, labyrinthodont amphibians, and mammal-like reptiles. By the late Early Jurassic, dinosaurs, crocodylomorphs, mammals, and essentially modern small reptiles and amphibians were dominant and the terrestrial fauna had attained the basic composition it would keep for the next 140 million years (4, 6).

Despite its crucial position, the Triassic-Jurassic tetrapod transition is poorly known, the main problem being the absence of definitive earliest Jurassic deposits (4, 6). These stratigraphic difficulties underlie a range of conflicting hypotheses on the na-

ture of the faunal transition with one extreme suggesting a dramatic, catastrophic turnover (1) and the other suggesting a gradual change spread over tens of millions of years (6). At the time the first hypothesis was formulated, virtually all the strata described in this report as Early Jurassic were considered Triassic in age (1, 6). Their reassignment to the Jurassic extended the range of many supposedly Triassic families

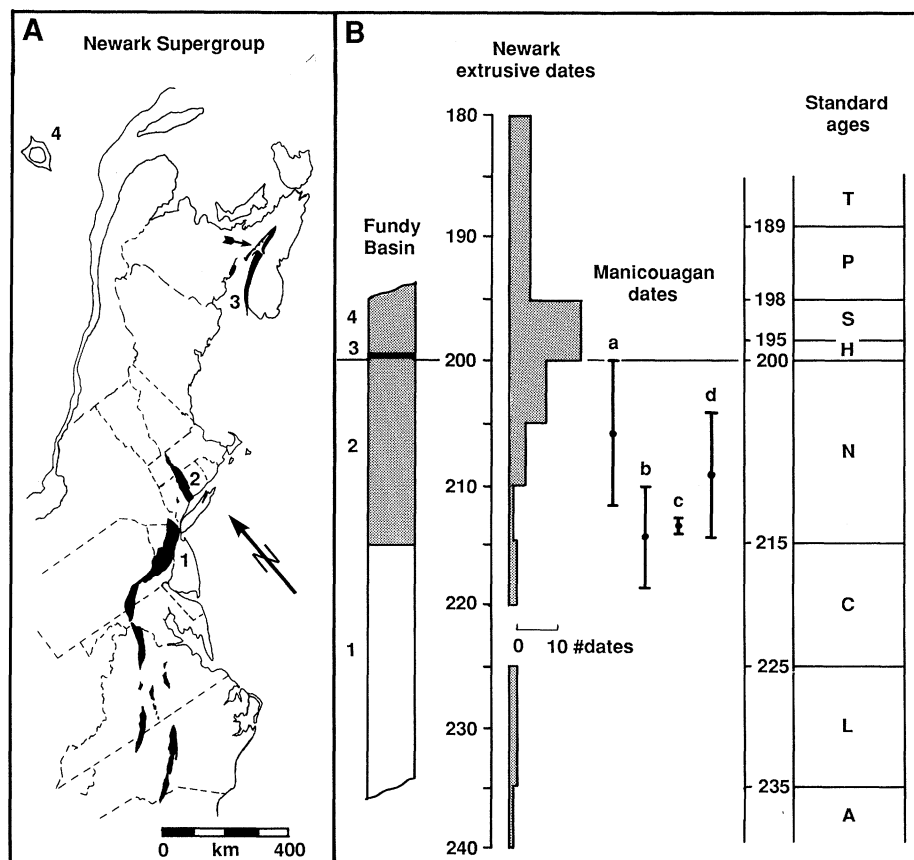
into the Jurassic, thus decreasing the magnitude of the extinction event at the boundary (6). Although more recent discoveries of vertebrates (7, 8) have brought the ranges of many Triassic families to near the Triassic-Jurassic boundary and extended the ranges of many Early Jurassic forms into the Jurassic and Cretaceous (8), the dearth of well-dated earliest Jurassic assemblages has prevented precise dating of the extinctions that occurred at or after the boundary.

We describe four newly discovered diverse vertebrate assemblages within a well-correlated earliest Jurassic sequence from Nova Scotia, Canada, which fill this gap. They are important for four main reasons: (i) the fossil remains are unusually abundant, (ii) a large range of fossil-bearing facies and paleoenvironments is represented, (iii) a high degree of stratigraphic resolution is permitted, and (iv) together with related assemblages, the pattern of extinctions is plausibly representative of global changes. The new data permit a much more refined look at the Triassic-Jurassic transition and

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Fig. 1. (A) The Newark Supergroup (black), showing the position of the Fundy Basin, other Newark Supergroup deposits, and the Manicouagan impact structure: 1, Newark Basin; 2, Hartford Basin; 3, Fundy Basin; and 4, Manicouagan impact structure. **(B)** Correlation of major portions of Fundy Basin section of Newark Supergroup [from (12)], Newark igneous (29) and Manicouagan dates (27), and standard ages. Time scale compiled from Webb and Odin and Kennedy (29). In stratigraphic columns, gray is dominantly cyclic lacustrine sediments, white is dominantly fluvial sediments, and black is extrusive basalt flows. Abbreviations of units are as follows: 1, Wolfville Formation; 2, Blomidon Formation; 3, North Mountain Basalt and sedimentary interbeds; and 4, Scots Bay and McCoy Brook formations. Dates are: a, 206 ± 6 million years (K-Ar); b, 215 ± 4 million years (K-Ar); c, 212.9 ± 0.4 million years (Ar-Ar); d, 209 ± 5 million years (Rb-Sr) (26, 27). Standard ages are: A, Anisian; C, Carnian; H, Hettangian; L, Ladinian; N, Norian; P, Pliensbachian; S, Sinemurian; and T, Toarcian.



may allow tests of the major hypotheses of faunal change.

The tetrapod remains occur within the upper part of the early Mesozoic Fundy Group of the Newark Supergroup, a 1000-m thick sequence consisting of red clastics, minor carbonates, and extrusive tholeiitic basalts. Five conformable formations of Ani-

sian (early Middle Triassic) to Hettangian (earliest Jurassic) age are recognized (Fig. 1 and Table 1). The new assemblages occur in basal beds of the youngest formation of the Fundy Group, the McCoy Brook Formation, at Wasson Bluff near Parrsboro, Nova Scotia. The basal, bone-producing portions of the McCoy Brook Formation fill the

penecontemporaneously faulted and highly irregular upper surface of the extrusive North Mountain Basalt. Four separate facies of the McCoy Brook Formation have produced reptile assemblages at Wasson Bluff: (i) a brown fluvio-lacustrine sandstone, dominated by sphenodontids and protosuchid crocodiles; (ii) thin brown sandstone beds with basalt debris and siltstone chips sandwiched between eolian dune sets, dominated by prosauropods and sphenodontids; (iii) basalt talus cones, dominated by protosuchid and sphenosuchid crocodylomorphs and tritheledont mammal-like reptiles; and (iv) a lacustrine muddy limestone and interbedded basalt talus cone, dominated by semionotid fishes and ornithischian dinosaurs. A faunal list is given in Table 2.

The age of the lower McCoy Brook assemblages is constrained by three lines of data. Pollen and spore assemblages from the upper Blomidon Formation (9, 10), the type Scots Bay Formation (11), and the McCoy Brook Formation (10) are dominated by *Corollina meyeriana*, suggesting a Hettangian or younger age (12). Reptile footprint assemblages from the basal McCoy Brook Formation and Scots Bay Formation are of "Connecticut Valley" aspect (Table 2), which indicates an Early Jurassic age (13). Conventional K-Ar, $^{40}\text{Ar}/^{39}\text{Ar}$, and K-Ar isochron (14) dates from the North Mountain Basalt strongly suggest an Early Jurassic (Hettangian) age.

More precise dating and geographic control are afforded by correlation with the southern Newark basins. The geochemistry of the underlying North Mountain Basalt, pollen and spore data, and lacustrine cycles all point to a close synchronicity of events in the northern and southern Newark basins. Whole rock and trace element geochemistries of the North Mountain Basalt correlate with the oldest of the high Fe_2O_3 -high TiO_2 tholeiites of the more southern Newark basins (15). Strata interbedded between basalts of the more southern basins consistently produce Hettangian palynoflorules and, in the Newark Basin, the Triassic-Jurassic boundary is palynologically fixed at about 30 m below the oldest basalt (Orange Mountain) (12), suggesting that the North Mountain Basalt-Blomidon Formation contact lies within 10 m above the Triassic-Jurassic boundary (9). Finally, in the Newark and Hartford basins, the hierarchy of lacustrine cycles interbedded and below the basalt flows and the igneous cooling and fractionation trends (16) suggest as little as 600,000 years for the entire Newark Supergroup extrusive episode. On these bases, the age of the basal McCoy Brook Formation is between 100,000 and 200,000 years younger than the Triassic-Jurassic boundary (16).

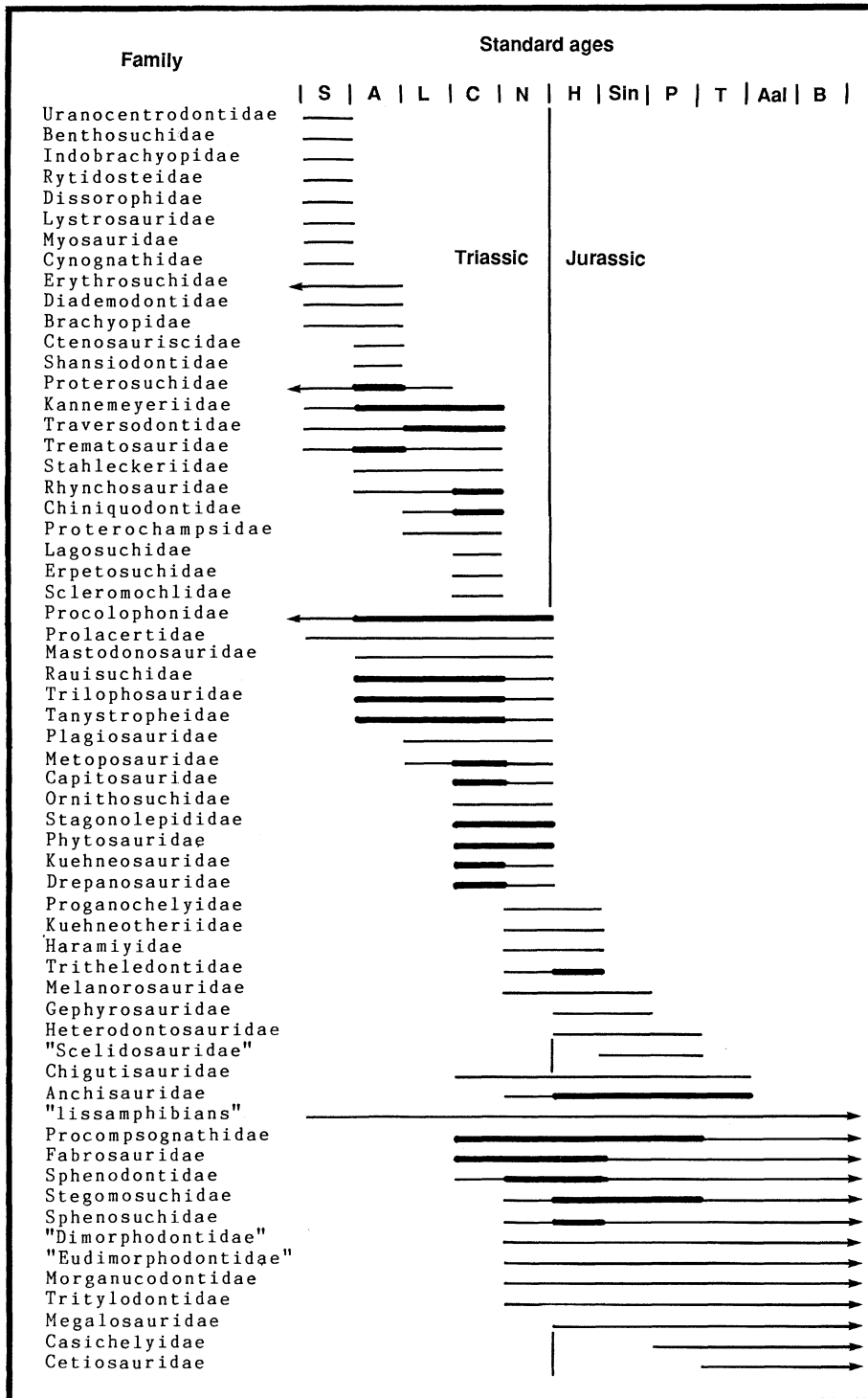


Fig. 2. Range chart for Triassic and Early Jurassic continental reptiles and amphibians [adapted from (7)]. Thin bars indicate compiled global ranges and thick bars represent ranges in Newark Supergroup. Abbreviations for standard ages are as follows: S, Scythian; A, Anisian; L, Ladinian; C, Carnian; N, Norian; H, Hettangian; Sin, Sinemurian; P, Pliensbachian; T, Toarcian; Aal, Aalenian; and B, Bajocian.

A compilation of latest Triassic assemblages from other areas (7) shows that all the families present in the McCoy Brook assemblages were already present during the latest Triassic (Figs. 2 and 3). However, despite the sampling of four different sedimentological facies and the abundance of fossils, the dominant Late Triassic reptiles and amphibians are absent from the McCoy Brook assemblages, or any other syn- or post-extrusive unit in the Newark Supergroup (12, 17). Calibration of the ranges of families in the rest of the Newark Supergroup by lacustrine cycles suggests that the disappearance of dominant Triassic forms was abrupt, occurring in less than 850,000 years (18), not the 15 to 20 million years previously proposed (6).

A similar pattern is shown by a global tabulation of the stage-level faunal transition of the Norian-Hettangian boundary. About 45% of all continental tetrapod families disappear in or at the end of the Norian (7) (Figs. 2 and 3). Counting families present only at the latest Norian (7), at least 32% of the families are extinct by the Hettangian. This implies an abrupt event. In marked contrast to the rather high levels of origina-

tion through the Triassic (7), the Hettangian of the Early Jurassic is distinguished by few if any originations (Fig. 2) (19).

Global tetrapod diversity does not gradually regress before the boundary; on the contrary, familial diversity was at its peak in the Late Triassic (Fig. 2) (20). As continental earliest Jurassic vertebrate faunas are characterized only by the absence of Triassic families, diversity in the Hettangian decreased dramatically. Based on the McCoy Brook and other Newark assemblages, the transition occurred in less than 1 million years.

The Triassic-Jurassic boundary was marked by a major extinction event affecting dominant marine invertebrates (21). All conodonts, nearly half of the bivalve genera and nearly all bivalve species, almost all nautiloid and ammonite families, and most brachiopods disappeared at the Triassic-Jurassic boundary (21). The re-dating of many supposedly Late Triassic continental rocks at first suggested that the terrestrial vertebrate extinctions were not correlative with those of the invertebrates (6, 21). The McCoy Brook assemblages, and our new interpretations of the global pattern of extinctions,

suggest that the tetrapod and invertebrate extinctions were in fact contemporaneous.

The new McCoy Brook discoveries strongly support a sudden and dramatic extinction event at the Triassic-Jurassic boundary. An advantage of this hypothesis of abrupt change is that it is easily falsified by either the discovery of "typical" Triassic or distinctly Jurassic families in the McCoy Brook Formation or correlative strata.

Numerous causal explanations of the Triassic-Jurassic extinctions have been proposed, ranging from ecological explanations that stress the dominant effect of competition (1-3) to geomorphic changes involving major marine transgressions or regressions, anoxic events, and loss of continental relief (21, 22). However, the rapidity and synchronism of the Triassic-Jurassic continental and marine extinctions is difficult to explain by simple gradual mechanisms. Recently, considerable evidence has been presented suggesting that the extinctions marking the Cretaceous-Tertiary boundary resulted from the impact of a large extraterrestrial object (23, 24) and that other major Phanerozoic extinctions might owe their origin to a similar cause (23, 24).

The presence of a large impact structure close in age (Fig. 1) to the Triassic-Jurassic boundary provides an excellent opportunity to test the generality of the impact theory of mass extinction (23, 24). The Manicouagan impact structure (70 km in diameter) in Quebec, Canada, is one of the largest Phanerozoic impact craters and is energetically equivalent (10^{30} ergs) to that proposed for the terminal Cretaceous extinctions (25, 26). However, while tantalizing, it must be noted that due to the large disparity in both defining and dating the Triassic-Jurassic boundary and the large range of dates from the Manicouagan crater (27), the impact could have occurred near the Carnian-Norian boundary (215 to 225 million years before present), where there is also a significant concentration of extinctions (Fig. 2). To refine the time of impact, the impact melt rocks must be re-dated by both $^{40}\text{Ar}/^{39}\text{Ar}$ and Rb-Sr techniques, but no radiometric technique will ever provide the necessary resolution to rigorously test the hypothesis of causation. Therefore, stratigraphic sections in Nova Scotia and elsewhere must be searched for debris from the impact with the hope of making an unambiguous stratigraphic link between the vertebrate extinctions, Triassic-Jurassic boundary, and the impact structure (28).

The Manicouagan impact structure and the Triassic-Jurassic extinctions clearly pose a major challenge to the impact theory of mass extinctions. The impact theory makes the very specific prediction that the extinc-

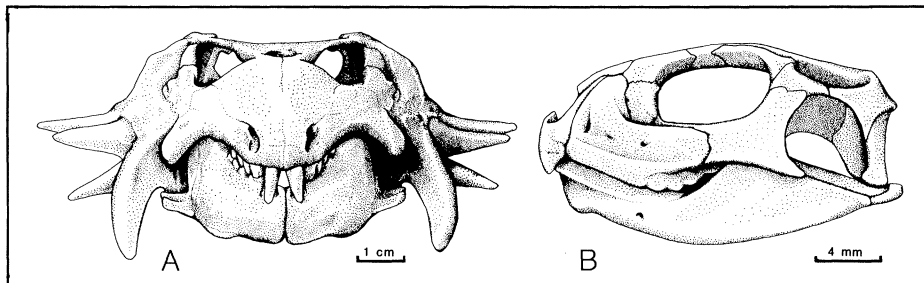


Fig. 3. Reptiles from the Triassic-Jurassic boundary. (A) The procolophonid reptile *Hypsognathus fenneri* from the Late Triassic of Nova Scotia (uppermost Wolfville Formation, Fundy Basin), New Jersey (upper Passaic Formation, Newark Basin), and Connecticut (upper New Haven Arkose, Hartford Basin); procolophonids apparently go extinct at or very near the Triassic-Jurassic boundary. (B) The sphenodontid cf. *Sigmala* sp. from the Early Jurassic fluvio-lacustrine sandstone of the McCoy Brook Formation, Wasson Bluff, Nova Scotia, is a similar, if not congeneric, sphenodontid and is known from Late Triassic upper New Haven Arkose (Hartford Basin); sphenodontids survive to this day.

Table 1. Formations of Fundy Group of the Fundy Basin in Nova Scotia, Canada.

McCoy Brook Formation (+200 m; Hettangian and younger): Red and brown coarse to fine fluvial, deltaic, and lacustrine clastics with locally developed colian sandstones, purple green and white lacustrine limestones, and basalt agglomerates (lateral equivalents of Scots Bay Formation).

Scots Bay Formation (<40 m; Hettangian): White, green, and red lacustrine limestones (partially bioclastic), chert, and minor fluvial brown sandstones.

North Mountain Basalt (maximum of 270 m; Hettangian): Bluish gray to green and red tholeiitic extrusive basalt flows.

Blomidon Formation (maximum of 300 m; ?Carnian-Hettangian): Red, brown, and green cyclic lacustrine and deltaic claystones to sandstones with locally developed brown colian sandstones and purple green conglomerates. Laterally persistent gray, green, and black claystone beds in upper few meters of formation.

Wolfville Formation (maximum of 400 m; Anisian-?Norian): Brown and red fluvial sandstones and conglomerates and subordinate red mudstones with locally developed red and brown deltaic and lacustrine clastics and thick brown colian sandstones.

tions must follow a major impact closely in time. If the debris layer lies above the extinctions or far below them, the general theory would be falsified.

The parallels between the Cretaceous-Tertiary event and that of the Triassic-Jurassic are significant from both a biostratigraphic and a biological view. Biostratigraphically, it may be necessary to define the Triassic-Jurassic boundary by the absence (extinc-

tion) of taxa rather than by the presence of new taxa. Biologically, the catastrophic extinctions represent the most abrupt and large-scale environmental perturbations suffered by global ecosystems. Interestingly, among terrestrial vertebrates, with the exception of the pterosaurs, flightless dinosaurs, and a few mammal-like reptiles, the groups that survived the Triassic are the same groups that survived the Cretaceous.

Table 2. Faunal list of vertebrates found in the McCoy Brook Formation. Abbreviations for localities: BS, Blue Sac; FI, Five Islands Provincial Park; MH, McKay Head; and WB, Wasson Bluff (30). Abbreviations for environments: A, basalt agglomerate with red mudstone matrix; Fl, fluvio-lacustrine sandstone; Ft, footprint facies of fluvio-lacustrine sandstone; La, lacustrine basalt agglomerate; Lc, lacustrine red clastics; and Ll, lacustrine limestone.

Taxon	Locality and environment
<i>Osseous taxa</i>	
Class Chondrichthyes	
Subclass Elasmobranchii	
Order Hybodontiformes	
aff. <i>Hybodus</i> sp.	WB; Ll, La
Class Osteichthyes	
Subclass Actinopterygii	
Order Palaeonisciformes	
Family Redfieldiidae?	
Scales and skull bones	WB; Ll, La
Order Semionotidae	
Family Semionotidae	
<i>Semionotus</i> spp.	WB; Ll, La FI; Lc
Class Reptilia	
Subclass Therapsida	
Order Cynodontia	
Family Tritheledontidae	
<i>Pachygenelus</i> sp.	WB; FI, A
Subclass Lepidosauromorpha	
Order Sphenodontia	
Family Sphenodontidae	
cf. <i>Pelecymala</i> sp.	WB; FI
cf. <i>Sigmala</i> sp.	WB; FI
Subclass Archosauromorpha	
Order Crocodylomorpha	
Family Protosuchidae	
New genera (?)	WB; FI, A, La BS; A
Family Sphenosuchidae	
Genus uncertain	WB; FI, A
Order Saurischia	
Family Anchisauridae	
cf. <i>Ammosaurus</i>	WB; FI
cf. <i>Anchisaurus</i>	WB; A
Family Procompsognathidae	
Genus uncertain	WB; FI, A
Order Ornithischia	
Family Fabrosauridae	
Isolated teeth and postcrania of two new genera	WB; A, La
cf. <i>Scutellostaurus</i>	WB; A
<i>Ichnotaxa</i>	
Ichnofamily Otozoidae	
<i>Otozoum moodii</i> (crocodylomorph or dinosaur)	BS, MH; Ft
Ichnofamily Batrachopodidae	
<i>Batrachopus</i> spp.	WB, BS, MH, FI; Ft
Ichnofamily Grallatoridae	
<i>Grallator</i> (<i>Grallator</i>) spp.	WB, BS, MH, FI; Ft
<i>G. (Anchisauripus)</i> spp.	WB, BS, MH, FI; Ft
<i>G. (Eubrontes)</i> sp.	FI; Ft
Ichnofamily Anomoepodidae	
<i>Anomoepus scambus</i>	BS, MH; Ft

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9. We place the Triassic-Jurassic boundary within the upper 20 m of the Blomidon Formation based on a preponderance of *Corollina meyeriana* [B. Cornet, personal communication; see also (11)], although there is considerable between-locality heterogeneity, an opinion different from that previously expressed (13).
10. J. P. Bujak reports [Mobil Oil Corp., Rep. EPGs-PAL. 3-79 JPB (1977)] palynoflorules strongly dominated by *Corollina meyeriana* in the upper 496-m Blomidon Formation in the Chainamps N-37 well, Bay of Fundy (GSC LOC D-145: 44°56'53"N, 66°35'17"W) and correlates this interval with the portions of the southern Newark Supergroup palynoflorules now thought to be earliest Jurassic (12). The thickness of this interval may be exaggerated by well caving [J. P. Bujak, personal communication; see also A. Traverse, *Geol. Soc. Am. Abst. Prog.* **15** (No. 3), 122 (1983)].
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16. Based on the hierarchy of Milankovitch lacustrine cycles in Jurassic age strata of the Newark and Hartford basins [P. E. Olsen, *Science* **234**, 842 (1986)], the duration of the Newark extrusive episode was less than 600,000 years. This is consistent with the basalt fractionation models of A. Philpotts and I. Reichenbach [*Geol. Soc. Am. Bull.* **96**, 1131 (1985)]. The lacustrine cycles also suggest that the sediments (Feltville Formation) directly over the oldest basalt flow sequence in the Newark Basin are roughly 100,000 years younger than the Triassic-Jurassic boundary. Assuming correlation of the Feltville and basal McCoy Brook formations as suggested by basalt geochemistry (15) and the paleontological data cited above, the new assemblages should be

- between 100,000 and 200,000 years younger than the Triassic-Jurassic boundary.
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 18. The phytosaur ichnotaxon *Apatopus* occurs about 180 m below the Orange Mountain Basalt (N. Resch, personal communication) roughly 160 m below the estimated position of the Triassic-Jurassic boundary. The procolophonid reptile *Hypsognathus* [C. W. Gilmore, *Proc. U.S. Natl. Mus.* **73**, 1 (1928)] has been found roughly 120 m below the same basalt. Sedimentary cycles are not expressed in the areas which produced these remains, but by extrapolating from further southwest where cycles are present (without a change in total thickness of the formation) and under the rationale outlined in (16), these forms should be about 800,000 and 600,000 years older than the Triassic-Jurassic boundary, respectively.
 19. Under close scrutiny the three apparent originations shown in Fig. 2 (Gephyrosauridae, Heterodontosauridae, and Megalosauridae) are questionable: either the stratigraphically oldest specimens assigned to the families are poorly dated or their taxonomic assignment is very doubtful.
 20. All three of the families limited to the Carnian are monotypic and known from single formations and one or two localities; their ranges must be regarded as extremely questionable.
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 28. Another giant impact structure thought to be of early Mesozoic age is the Puchezh-Katuni structure in the Soviet Union which could be Early Triassic to Late Jurassic in age [V. I. Fel'dman, L. V. Sazonova, A. A. Nozova, *Int. Geol. Rev.* **27**, 68 (1985)].
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- G. S. Odin [in *Numerical Dating in Stratigraphy*, G. S. Odin, Ed. (Wiley, New York, 1982), pp. 557–592] by fixing the Triassic-Jurassic boundary at 200 million years and scaling the position of the Hettangian-Sinemurian boundary by the number of ammonite zones. Other boundary dates are unaltered.
30. Geographic coordinates of localities are as follows: Blue Sac, 45°23'50"N to 45°24'15"N, 64°06'30"W to 64°10'00"W; Five Islands, 45°23'20" to 40"N, 64°04'50"W; McKay head, 45°23'40"N, 64°13'00" to 50"W; Wasson Bluff, 45°23'40"N, 64°14'00" to 30"W.
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Organ-Resident, Nonlymphoid Cells Suppress Proliferation of Autoimmune T-Helper Lymphocytes

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Local presentation of autoantigen by organ-resident cells inappropriately expressing Ia determinants has been implicated in organ-specific autoimmunity. Experimental autoimmune uveoretinitis, induced in rats by immunization with retinal soluble antigen, is used as a model of organ-specific autoimmunity. In an *in vitro* system derived from this model, uveitogenic rat T-helper lymphocytes specific to the retinal soluble antigen, or control T-helper lymphocytes reactive to the purified protein derivative of tuberculin, were cocultured with Ia-expressing syngeneic retinal glial cells (Müller cells) in the presence of specific antigen. Antigen presentation was not apparent under ordinary culture conditions, and the Müller cells profoundly suppressed the proliferative response of primed T-helper lymphocytes to antigen presented on conventional antigen-presenting cells, as well as their subsequent interleukin-2 (IL-2)-dependent expansion. Suppression of proliferation was accompanied by inhibition of IL-2 production in response to antigen, as well as by reduction in high-affinity IL-2 receptor expression, and proceeded via a contact-dependent mechanism. These results suggest a role for locally acting suppression mechanisms in immune regulation and maintenance of tissue homeostasis.

IN ORGAN-SPECIFIC AUTOIMMUNE DISEASE the range of interactions between the component cells of a target tissue and the infiltrating autoreactive T cells is largely unknown. Recent observations have suggested active participation of organ-resident cells in tissue-specific autoimmunity. For example, vascular endothelial cells and brain glial cells (astrocytes) are able to express major histocompatibility complex (MHC) class II determinants (Ia) (the restricting elements of self-recognition by the immune system), to present antigen, and to produce interleukin-1 (IL-1)-like factors (1, 2). In fact, presentation of autoantigen by organ-resident cells aberrantly expressing Ia determinants was suggested as one of the major underlying causes in the induction and maintenance of the autoimmune state (3). Control of autoimmunity has been attributed to central suppression mechanisms

(4); very little is known about locally acting mechanisms of suppression.

Experimental autoimmune uveoretinitis (EAU), like experimental allergic encephalomyelitis and adjuvant arthritis (5), serves as a model of organ-specific autoimmune disease and is mediated by T lymphocytes (6, 7). The disease can be induced in rats by immunization with the retinal soluble antigen (SAg) (a 48-kilodalton protein participating in light signal transduction), or by adoptive transfer of SAg-specific T-helper (T_H) lymphocytes (6, 7). EAU is basically a delayed-type hypersensitivity reaction to SAg and manifests itself as an ocular inflammation resulting in irreversible damage to photoreceptor cells, of which the SAg is a major constituent. Retinal glial cells (Müller cells)

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