and hence no skeletal reefs until the Middle Ordovician with the appearance of bryozoa. The only available niche for macroborers from Middle Cambrian to Middle Ordovician, was hard grounds. With the reestablishment of reefs in the Middle Ordovician, and increase in the number and diversity of available hard substrates, macroboring organisms began to radiate and diversify. Therefore, the diversification of macroborings appears to parallel the development and expansion of the reef habitat in the early Paleozoic.

N. P. JAMES
D. R. KOBLUK
Department of Geology,
Memorial University,
St. Johns, Newfoundland
S. G. PEMBERTON
Department of Geology, McMaster
University, Hamilton, Ontario

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1 April 1977

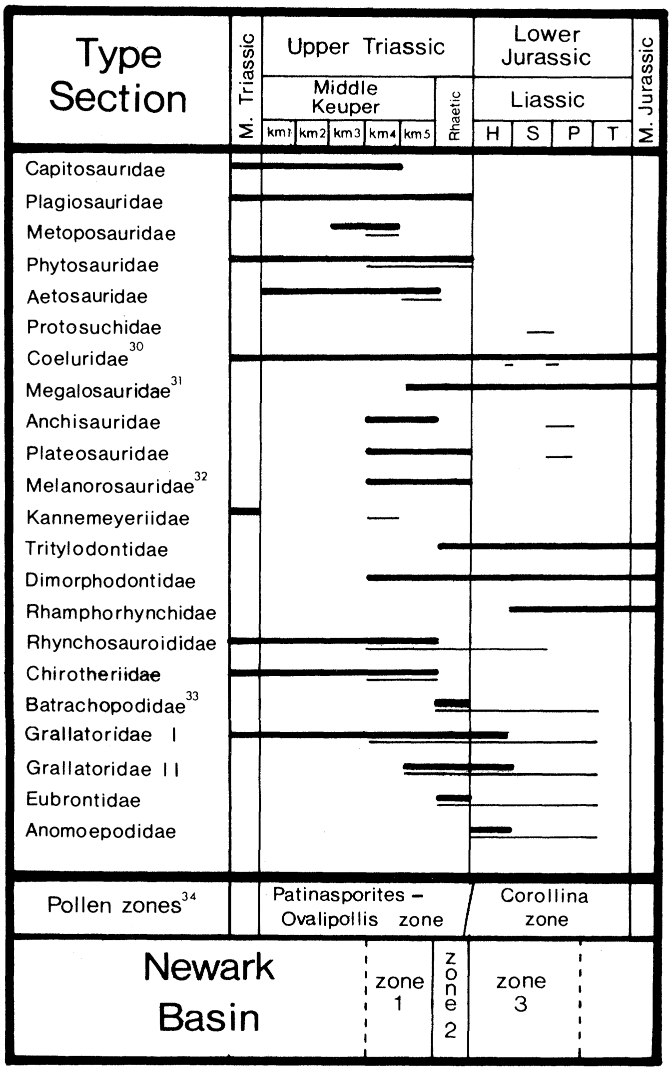
Triassic-Jurassic Tetrapod Extinctions: Are They Real?

Abstract. *Terrestrial vertebrate fossils show that part of the Newark supergroup of the eastern United States, all of the Glen Canyon group of the southwestern United States, and the Upper Stormberg group of southern Africa are Early Jurassic. This new correlation demonstrates that the supposed widespread tetrapod extinction at the Triassic-Jurassic boundary is an artifact of spurious correlation.*

Recent work on the timing of extinctions of higher-level taxa (*1*) is limited by the reliability with which the ranges of those taxa are placed in the geologic time scale. One such mass extinction involving terrestrial vertebrates purportedly occurred at the Triassic-Jurassic boundary (*1*). It has been recently pointed out (*2*) that this "extinction" might be the result of a poor Early Jurassic record. A reappraisal of correlations of early Mesozoic deposits of the world shows that a distinct Early Jurassic terrestrial vertebrate record does exist and that it is transitional between the familiar Late Triassic and Late Jurassic faunas.

The divisions of the early Mesozoic of Europe were originally based on major lithologic changes and hiatuses in the rock succession, so that the boundaries of the major rock units are, by definition, the time-stratigraphic boundaries of the early Mesozoic. The correlation of these time-stratigraphic units from their type areas is limited by whatever time-equivalent data are available (*3*). Vertebrate fossils provide one commonly used means of correlating continental early Mesozoic deposits of the world with the type Triassic and Early Jurassic of Europe. Unfortunately, many faunal data from the type areas are not useful for correlation. The marine and estuarine fish faunas of the German Triassic have more in common with Liassic (Early Jurassic) faunas of northern Europe than either has in common with nonmarine faunas of other early Mesozoic areas (*4*).

Fig. 1. Ranges of correlative vertebrates, and broad palynomorph zones (*34*) of the type areas of the Upper Triassic and Lower Jurassic (Liassic) and the Newark Basin of the Newark supergroup. Heavy horizontal lines represent the ranges of taxa in the European type areas, while light horizontal lines show the ranges for the Newark Basin. The ranges of the Protosuchidae, Coeluridae, Anchisauridae, and Plateosauridae are based on correlation of zone 3 with the Portland formation of the Hartford Basin. Abbreviations of the stages of the Lower (Early) Jurassic: *H*, Hettangian; *S*, Sinemurian; *P*, Pleinsbachian; *T*, Toarcian. Standard divisions of the German Middle Keuper are km 1 to 5. Note that the Lower Keuper and Upper Keuper have been omitted from the figure because they are, more or less, equivalent to parts of the Middle Triassic and Rhaetic, respectively.



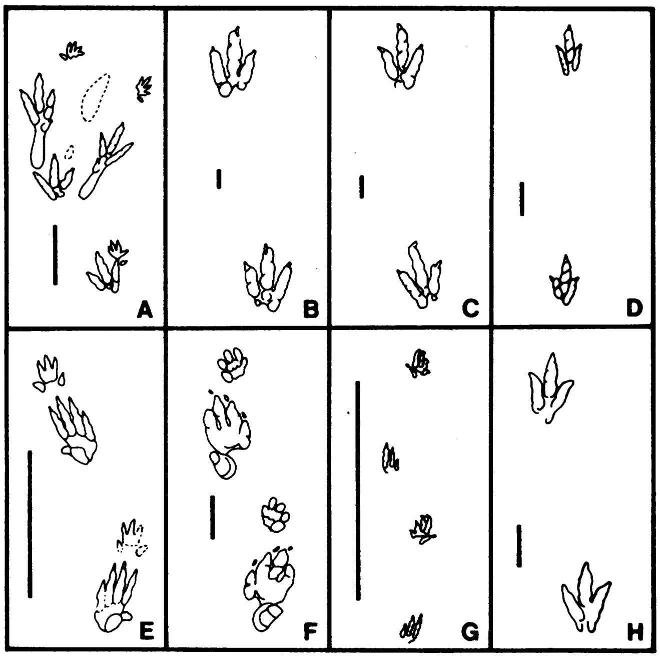


Fig. 2. (A–D) Footprint form–taxa typical of zone 3 of the Newark Basin, the Glen Canyon group, and the Upper Stormberg group: (A) the type of *Anomoepus scambus*; (B) *Eubrontes giganteus*; (C) the type of *Anchisauripus minusculus*; (D) *Anchisauripus sillimani*. (E–H) Footprint form–taxa of zone 1: (E) *Chirotherium lulli*; (F) *Brachychirotherium parvum*; (G) *Rhynchosauroides brunswickii*; (H) *Anchisauripus* sp. (*35*). Scale bars are 10 cm.

Likewise, marine reptiles of the type areas, although common and diverse, are totally absent in most continental deposits. Consequently, amphibians and terrestrial reptiles provide the best means of correlating Jura-Triassic deposits in the absence of other forms of data. For these reasons, however, correlation is strongly biased by the virtual absence of terrestrial forms in the marine Muschelkalk (Middle Triassic) and the European Liassic (*2*), with large numbers of terrestrial vertebrates occurring only in the German Middle Keuper (middle Upper Triassic) and to a lesser extent in the German and English Rhaetic (upper Upper Triassic) (*5*) (see Fig. 1). Significant changes can be observed between the faunas of the lower Middle Keuper, the upper Middle Keuper, and the Rhaetic. The European Liassic presents a significant problem because of the paucity of terrestrial skeletal remains (*6*); therefore, Early Jurassic terrestrial faunas can be examined only in other deposits that can be correlated with the type Liassic by other means. Fortunately, reptilian footprint form–taxa of the European type sections of the Jura-Triassic show consistent trends, with major faunal changes occurring between the Bunter, Keuper, and Rhaetic faunas (see Figs. 1 and 2).

The vertical changes in skeletal and footprint faunas provide a means of correlation between the type areas of the Jura-Triassic and continental deposits of similar age in the world. One major division of the eastern North American Newark supergroup (*7*) is the Newark Basin, which consists of a thickness of 10,000 m of wholly continental clastics and extrusive volcanics. Fossils are common in the sedimentary rocks of the Newark Basin, and, because of the stratigraphic control permitted by lava flows and laterally persistent key-marker beds, faunal and floral zones are clearly demarcated by stratigraphic parameters (Figs. 1 and 2). Three major assemblage zones can be recognized. Zone 1 (the oldest) is clearly correlative with the German middle Middle Keuper, and zone 2 ties in well with the Rhaetic. Zone 3 is found through the 2000 m of sediment and volcanics above zone 2 but seems to have no well-defined European correlate based on vertebrate evidence. Palynomorph studies of the Newark Basin (*8*) show zone 1 to correlate with the German Middle Keuper, zone 2 with the Rhaetic, and zone 3 with the Early Jurassic. Furthermore, potassium-argon dates of the three lava flows in the basal part of zone 3 cluster around 191 to 201 million years B.P. (before present) (*9*), which is in line with a Liassic correlation. The superposition of zone 3 on a Rhaetic correlate, the palynological data, and the potassium-argon dates all suggest an Early Jurassic age for zone 3. It is important to note that the footprint assemblage of zone 3 (see Fig. 2) is a typical "Connecticut Valley" footprint fauna (*10*). A Late Triassic age is usually assigned to a footprint fauna of this type, but there is no valid reason for this because, with the exception of the long-ranging form-family Grallatoridae (*11*) (Figs. 2 and 3), there are no footprint taxa in common between the German Keuper and zone 3.

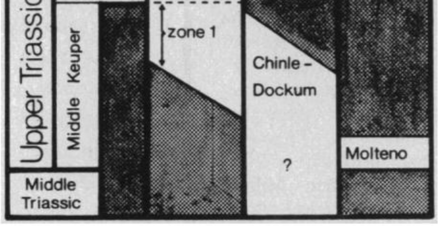


Fig. 3. Correlation of type areas of the early Mesozoic with the Newark Basin of the Newark supergroup, early Mesozoic of the southwestern United States, and the Stormberg group of southern Africa. Abbreviations of Lower Jurassic stages are the same as in Fig. 1. Vertical ruling represents extrusive basalts in the Newark Basin and in the Drakensberg Volcanics of the Stormberg group.

The presence of prosauropod dinosaurs in a unit has often been cited as evidence that it is Triassic in age. Beds correlative with zone 3 in the Hartford Basin of the Newark supergroup have produced the prosauropods *Anchisaurus* (Anchisauridae) and *Ammosaurus* (Plateosauridae) as well as the crocodilian *Stegomosuchus* and a coelurosaur (*12*). Anchisaurids and plateosaurids are known from the German Middle Keuper and fragmentary prosauropods are known from the English Rhaetic (*13*) but, because of the lack of a good terrestrial fauna in the type Liassic, their presence in zone 3 is not in conflict with a Liassic (Early Jurassic) age; rather, it suggests that prosauropods survived into the Early Jurassic.

Transitions in faunas of the early Mesozoic of the western United States are similar to those in the Newark supergroup. The Chinle formation and Dockum group contain vertebrate faunas very similar to zone 1 (see Fig. 3) of the Newark Basin and the correlative Pekin formation (*8*) of the Deep River Basin of the Newark supergroup. Palynomorph studies of the Chinle formation and Dockum group (*14*) suggest correlation with the German Middle Keuper. The Glen Canyon group (*15*) overlies the Chinle formation and contains an entirely different fauna. The advanced mammal-like reptile *Tritylodon* sp. (Tritylodontidae), the crocodilian *Protosuchus* (Protosuchidae), the theropod dinosaurs *Segisaurus* and *Dilophosaurus* [Coeluridae(?)], an undescribed ornithischian dinosaur [Fabrosauridae(?)] (*16*), and the prosauropod dinosaur *Ammosaurus* (Plateosauridae) have been recovered from the Glen Canyon group (*12*). In addition, the presence of a footprint fauna of clear "Connecticut Valley" affinities has recently been confirmed (*17*). The recent discovery of an Early Jurassic–type palynoflora from the basal Glen Canyon group (*18*) adds substantially to the correlation, and heightens the importance of the Glen Canyon fauna.

Recently described footprint faunas from the upper Red Beds and Cave Sandstone of the Stormberg group (*19*) of southern Africa are nearly identical to those of zone 3 of the Newark Basin and its other correlates in the Newark supergroup. Additional evidence for correlation is the presence of *Anchisaurus* in the Upper Stormberg and the zone 3 correlate of the Hartford Basin (*20*). The associated skeletal fauna of the Upper Stormberg is often cited as "typical" Late Triassic in age (*21*), but it must be pointed out that only prosauropods (on a family level) are shared with the German Middle Keuper (*22*). Tritylodonts, eozostrodontid (morganucodontid) mammals, and prosauropods occur in the Upper Stormberg and the Rhaetic (*23*), but tritylodonts and eozostrodontids are known from Liassic fissure fillings of Great Britain (*24*), and tritylodonts are known from the English, Middle Jurassic Stonesfield Slate (*24*). Typical Late Triassic vertebrates such as capitosaurs, plagiosaurs, metoposaurs, aetosaurs, and phytosaurs are completely absent from the Upper Stormberg (*23*) even though these beds have produced a large and varied fauna. Recent authors (*25*) have attributed the gross differences between the faunas of the Keuper and Upper Stormberg to unspecified differences in ecological conditions under the assumption the faunas are of the same age; however, the question of "ecological differences" can be asked only after the ages of the beds are determined by nonvertebrate means. Comparisons with the European type areas suggest a Rhaetic or Liassic correlation for the Upper Stormberg; comparisons with the Newark supergroup suggest a correlation with zone 3 of the Newark Basin; and a correlation with the Glen Canyon group seems justified. From time to time, other authors have noted that at least part of the Stormberg should be Early Jurassic, at least in the eastern areas (*26*), but these suggestions have been largely ignored by paleontologists (*27*). Thus, the most likely age for the Upper Stormberg would seem to be Early Jurassic (*28*). The common assumption that there is a dearth of Early Jurassic terrestrial faunas (*28*) seems to be the result of calling Liassic correlates Late Triassic.

Pangea was beginning to break up in the Early Jurassic, and there may have been few impediments to tetrapod migration (*29*). If the correlation presented here is correct (Fig. 3), then the terrestrial vertebrate fauna was uniform over most of the world, and the known faunal elements included large numbers of prosauropod dinosaurs, small and large theropod dinosaurs, fabrosaurid (and possibly hypsilophodontid), heterodontosaurid, and scelidosaurid ornithischian dinosaurs, a variety of crocodilians including protosuchids and sphenosuchids, pterosaurs (Dimorphodontidae and Rhamphorhynchidae), tritylodonts, and primitive mammals. Many of the groups that are usually cited as becoming extinct at the close of the Triassic actually did so sometime in the Jurassic. When the distribution of terrestrial vertebrates is arranged according to the correlation in Fig. 3, it is clear that the Early Jurassic was essentially transitional between the familiar Keuper and Upper Jurassic in its faunal composition (Fig. 4). The evidence implies that the transition from the Triassic to the Jurassic was not marked by sudden, simultaneous extinctions of large numbers of higher order taxa of vertebrates, but instead was a time of gradual faunal replacement spread over the Late Triassic and at least the Early Jurassic (Fig. 4).

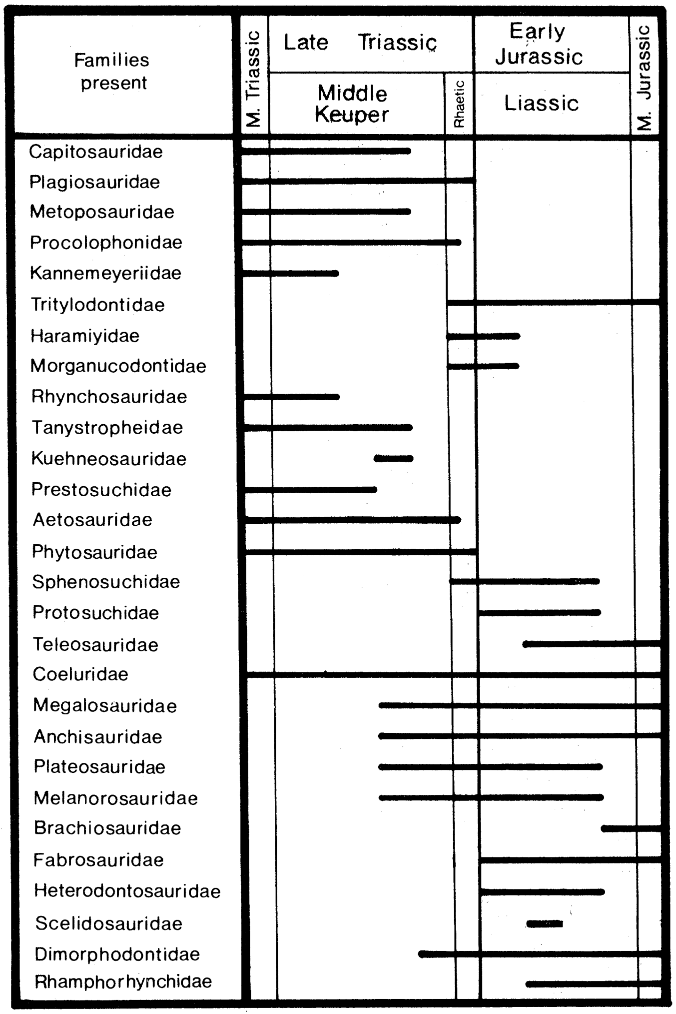


Fig. 4. Revised ranges of amphibians and terrestrial vertebrates in the Late Triassic and Early Jurassic (*36*) based on correlations in Fig. 3.

Paul E. Olsen
Division of Vertebrate Paleontology, Peabody Museum, Yale University, New Haven, Connecticut 06520
Peter M. Galton
Department of Biology, University of Bridgeport, Bridgeport, Connecticut 06602

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3. Article 28, American Commission on Stratigraphic Nomenclature, *Am. Assoc. Pet. Geol. Bull.* **45**, 645 (1961).
4. Five out of eight families of fishes present in the Rhaetic of Germany and England continue into the Lower Liassic. Yet only three out of those same eight families are known from the nonmarine fish faunas of the Newark supergroup of eastern North America and the Beaufort Beds and the Lower Stormberg group of southern Africa.
5. The Rhaetic type section is in Austria. The cor-

relation of S. J. Morbey [*Palaeontogr. Abh. B Palaeophytol.* **152**, 1 (1975)] is used here.

6. Diagnostic material of the ornithischian dinosaurs of the family Scelidosauridae is restricted to the English Lower Liassic [R. Hoffstetter, *Bull. Mus. Hist. Nat. Paris Ser. 2* **29**, 537 (1957)]. Theropod dinosaurs are represented by fragmentary remains of doubtful diagnostic value [M. Waldman, *Palaeontology* **17**, 325 (1974); A. F. Lapparent, *Sciences (Paris)* **51**, 1 (1967)]. The pterosaur families Dimorphodontidae and Rhamphorhynchidae occur throughout the early Mesozoic [A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966)]. R. Zambelli [*Inst. Lombardo Rend. Sci. (B)* **107**, 27 (1973)] reports a dimorphodontid pterosaur from the Norian (Late Triassic) of Cene, Italy. Fragmentary pterosaurs are also reported from the Rhaetic of Germany [M. Schmidt, *Die Lebwelt Unserer Trias* (Hohenloh'sche Buchhandlung Ferdinand Rau, Oehringen, Germany, 1928)].
7. P. E. Olsen, in preparation.
8. B. Cornet, A. Traverse, N. G. McDonald, *Science* **182**, 1245 (1973); B. Cornet and A. Traverse, *Geosci. Man* **11**, 1 (1975).
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11. The form-family Grallatoridae consists of small to large theropod dinosaur footprints. Small forms (Grallatoridae "I" of Figs. 1 and 2) are found throughout the early Mesozoic, while large forms (Grallatoridae "II" of Figs. 1 and 2) are not common until the Rhaetic and Early Jurassic.

→ P. M. Galton, *J. Paleontol.* **45**, 781 (1971); *Postilla* **169**, 1 (1976).

13. H. G. Seeley, *Geol. Mag.* **50**, 1 (1898).
14. R. Dunay and A. Traverse, *Geosci. Man* **3**, 65 (1971); preliminary results of comparisons of Chinle-Dockum samples by B. Cornet (personal communication) (samples provided by S. Ash, Weber State College) with samples from zone 1 of the Newark Basin suggest correlation of both with the German Middle Keuper.
15. According to F. Peterson (personal communication), many geologists now consider the Rock Point member of the Wingate formation to be equivalent to the Church Rock member of the Chinle formation. The Rock Point member contains phytosaurs and should not be considered a part of the Glen Canyon group.
16. D. Lawler (personal communication) reports the discovery of a fabrosaurid(?) ornithischian dinosaur in the Kayenta formation of the Glen Canyon group.
17. S. P. Welles (University of California, Berkeley) has graciously supplied photographs of dinosaur footprints from the Glen Canyon group which show *Anchisauripus sillimani*, *Anchisauripus minusculus*, *Grallator* spp., *Anomoepus crassus*, and *Eubrontes* sp., all of which indicate a "Connecticut Valley" type of footprint assemblage. S. P. Welles [*Geol. Soc. Am. Bull.* **65**, 591 (1954)] has long maintained that the Glen Canyon group is Jurassic.
18. B. Cornet (personal communication) reports that a sample supplied by F. Peterson and C. E. Cristine Turner-Peterson from the Whitmore Point member of the Moenave formation of the Glen Canyon group indicates correlation with the Lower Liassic and zone 3 of the Newark Basin.
19. P. Ellenberger, *Paleovertebrata Mem. Extra.* (1974). Ellenberger has suggested elsewhere [in *Gondwana Stratigraphy, I.U.G.S. Symposium* (Unesco, Paris, 1967)] that the Upper Stormberg footprints indicate a correlation with the Liassic.
20. P. M. Galton and M. A. Cluver, *Ann. S. Afr. Mus.* **69**, 121 (1976).
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22. A. S. Romer [*Brevoria* **395**, 1 (1972)] feels that A. D. Walker's [*Philos. Trans. R. Soc. London Ser. B* **257**, 816 (1970)] placement of the Middle Keuper *Saltoposuchus* in the Sphenosuchidae was not justified.
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25. C. B. Cox, *in The Fossil Record* (Geological Society of London, London, 1967), pp. 77–89; P. L. Robinson, *Palaeontology* **14**, 131 (1971).
26. This is corroborated by F. J. Fitch and J. A. Miller's [*Bull. Volcanol.* **35**, 1 (1971)] radiometric dates of 181 to 165 million years B.P. from the Drakensberg Volcanics overlying and interbedded with the Cave Sandstone of the Stormberg group, a range which is younger than the volcanics in the basal part of zone 3 of the Newark Basin of the Newark supergroup and is certainly Liassic.
27. W. J. Arkell, *Jurassic Geology of the World* (Oliver & Boyd, London, 1956); A. L. Du Toit, *Geology of South Africa* (Oliver & Boyd, Edinburgh, 1954).
28. E. H. Colbert, *The Age of Reptiles* (Norton, New York, 1965); A. S. Romer, *Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1966).
29. F. B. Van Houten, *Bull. Am. Assoc. Pet. Geol.* **61**, 79 (1977).
30. Coeluridae is used in a broad sense to include the Procompsognathidae because separation of these two families is mostly based on the supposed restriction of the Procompsognathidae to the Triassic.
31. The type maxilla of *Teratosaurus* from the Stubensandstein (Middle Keuper) may belong to a megalosaur, and M. Waldman [*Palaeontology* **17**, 325 (1974)] reports that a jaw from the English Rhaetic is indistinguishable from *Megalosaurus*.
32. Some of the larger prosauropod remains from the Middle Keuper are probably melanorosaurid, and *Avalonia* [see (*13*)] from the English Rhaetic certainly is [A. J. Charig, J. Attridge, A. W. Crompton, *Proc. Linn. Soc. London* **176**, 197 (1965)].
33. Data for Rhaetic distribution of footprints are from A. F. deLapparent and C. Montetat [*Mem. Soc. Geol. Fr.* **46**, 1 (1967)] and data for the Liassic record are from P. Ellenberger [*C. R. Acad. Sci.* **260**, 5856 (1965)] and L. Thaler [*C. R. Somm. Sceances Soc. Geol. Fr.* (1962), p. 190].
34. The concurrence of *Patinasporites* and *Ovalipollis* indicate Late Triassic, and a preponderance of *Corollina* (> 90 percent) is typical for the Early Jurassic (B. Cornet, personal communication).
35. Parts A to D of Fig. 2 are from the Pratt Museum of Amherst College, Amherst, Mass., Nos. 16/5, 45/1, 16/1, and 9/14, respectively; Fig. 2E is adapted from D. Baird, *Bull. Mus. Comp. Zool. Harv. Univ.* **111**, 163 (1954); Fig. 2F is adapted from D. Baird, *ibid.* **117**, 449 (1957); Fig. 2G is from Yale Peabody Museum No. 7703; Fig. 2H is from a series of trackways on a slab at the New York State Museum No. V-86.
36. Middle Jurassic faunas are very poorly known, and it is possible that groups which are shown to become extinct (Fig. 4) in the Early Jurassic actually survived into the Middle Jurassic [E. H. Colbert, *The Age of Reptiles* (Norton, New York, 1965)]. The ranges of the Fabrosauridae and the Heterodontosauridae are drawn without the inclusion of several undescribed Newark hypsilophodontid-like forms, or *Pisanosaurus*, or *Tatisaurus*, because of their extremely uncertain taxonomic relationships [P. M. Galton, *Nature (London)* **239**, 464 (1972)].
37. We thank D. Baird, B. Cornet, J. H. Ostrom, F. Peterson, and S. Rachootin for their assistance. This work was supported by grant BM 574-07759 from the National Science Foundation to K. S. Thomson.

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Lunar Surface Chemistry: A New Imaging Technique

Abstract. *Detailed chemical maps of the lunar surface have been constructed by applying a new weighted-filter imaging technique to Apollo 15 and Apollo 16 x-ray fluorescence data. The data quality improvement is amply demonstrated by (i) modes in the frequency distribution, representing highland and mare soil suites, which are not evident before data filtering and (ii) numerous examples of chemical variations which are correlated with small-scale (about 15 kilometer) lunar topographic features.*

The Apollo 15 and Apollo 16 missions to the moon carried an x-ray fluorescence spectrometer, which measured from orbit the aluminum, silicon, and magnesium concentrations in surface soils, using the x-ray emission from the sun as the exciting source (*1, 2*). The primary objective of the experiment was to map the geochemistry of the areas overflown in terms of these major rock-forming elements. Knowledge of the composition and distribution of chemical components is fundamental to a reconstruction of the evolution of the moon, including its origin, accretion, chemical differentiation into rock types, and physical processes which have modified the lunar crust.

The elemental measurements are expressed as intensity ratios (Al/Si, Mg/Si, and Mg/Al) in order to minimize nonchemical effects on the measured signal, such as those caused by differences in sun-moon-spacecraft geometry, shifts in the solar spectrum, and particle size variations on the lunar surface.

The important relationship between orbital x-ray intensity ratios and "ground truth" (returned sample) analyses is based on the fact that the characteristic secondary x-ray intensity is directly related to the element's concentration in surface soils. The conversion factors for intensity to concentration ratios have been determined by correlating orbital data with chemical analyses of returned soils from the Apollo and Soviet Luna missions. This critical link is the basis for extending detailed chemical information from a few specific landing sites to broad areas of the moon traversed by the Apollo 15 and Apollo 16 spacecrafts.

A new technique has recently been developed to convert the digital information from Apollo orbital x-ray data to a color image of chemical variations on the lunar surface. The image shown in Fig. 1 is the first detailed color representation of chemical variations constructed en-

Fig. 1. Map displaying chemical variations across the lunar surface based on data from the Apollo 15 and Apollo 16 orbital x-ray fluorescence experiments. The colors represent different values of Al/Si concentration ratios.