background continuum temperature of Mars. This value is expected to be 200 ± 20 K (*8*). Our absolute measurements of the Mars continuum temperature are not sufficiently accurate to improve upon this value. To first order, the CO absorption signal observed in the Mars spectrum is proportional to the difference between the average atmospheric temperature in the region where the absorption originates and the background continuum temperature. This difference is of the order of ~30 K. The uncertainty of ~±20 K in the background continuum temperature then corresponds to an uncertainty of ~±70 percent in the Mars CO abundance. The martian atmospheric temperature profile might be expected to vary by approximately ± 10 K from the model we used. This amount of variation introduces an additional uncertainty of ~±30 percent in the CO abundance inferred from our data. Therefore, with the information we have available on the background emission and atmospheric temperature of Mars, the uncertainty in our inferred CO abundance is approximately a factor of 2. Since the martian atmosphere is expected to be well mixed (*9*), we have performed calculations using a constant CO mixing ratio profile to determine which CO mixing ratio value gives the calculated spectral line that best fits our measurements as a function of background continuum temperature. The results are given in Table 1, and the calculation for a continuum temperature of 200 K is shown in Fig. 1. There is a suggestion that the measurement gives slightly less absorption at line center than that calculated from a constant CO mixing ratio profile. If this is the case, then the measurement implies a CO mixing ratio profile that decreases slightly at altitudes above ~ 40 km. More precise microwave measurements of the Mars spectrum and continuum emission at 115 Ghz will resolve these uncertainties.

Note added in proof: We have confirmed, by observations in February and April 1977, the variation of the CO signal from Venus with its phase mentioned here. These data indicate more high-altitude CO during nighttime. A similar diurnal variation was also measured for the CO line in the terrestrial mesosphere.

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References and Notes

1. R. K. Kakar, J. W. Waters, W. J. Wilson, *Science* **191**, 379 (1976).
2. J. W. Waters, W. J. Wilson, F. I. Shimabukuro, *ibid.*, p. 1174.
3. L. D. Kaplan, J. Connes, P. Connes, *Astrophys. J.* **157**, L187 (1969).
4. J. Connes, P. Connes, J. P. Maillard, *Atlas of Near Infrared Spectra of Venus, Mars, Jupiter, and Saturn* (Centre National de la Recherche Scientifique, Paris, 1969).
5. L. D. Gray Young, *J. Quant. Spectrosc. Radiat. Transfer* **11**, 385 (1971).
6. R. B. Noll, M. B. McElroy, Y. S. Lou, *NASA Spec. Publ. SP-8010* (1974).
7. P. Varanasi, *J. Quant. Spectrosc. Radiat. Transfer* **15**, 191 (1975).
8. D. O. Muhleman, private communication. This value is based on a theoretical model of microwave emission by the surface of Mars and is expected to be more accurate than measurements that have been made near 3 mm. The uncertainty at millimeter wavelengths has been discussed by J. N. Cuzzi and D. O. Muhleman [*Icarus* **17**, 548 (1972)], C. Sagan and J. Veverka [*ibid.* **14**, 222 (1971)], E. Epstein (*ibid.*, p. 214), and M. A. Janssen and W. J. Welch [*ibid.* **18**, 502 (1973)].
9. M. B. McElroy and J. C. McConnell, *J. Atmos. Sci.* **28**, 879 (1971); S. C. Liu and T. M. Donahue, *Icarus* **28**, 231 (1976).

10. This report presents the results of one phase of research carried out at the Jet Propulsion Laboratory, California Institute of Technology, under NASA contract NAS 7-100. The work at the Aerospace Corporation was jointly supported by an internal research program and by NSF grant MP573-04554. The National Radio Astronomy Observatory is operated by Associated Universities Inc. under contract with the National Science Foundation.

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15 November 1976

Petrolacosaurus, the Oldest Known Diapsid Reptile

Abstract. Petrolacosaurus, *an Upper Pennsylvanian reptile, presents a combination of features that place it within a distinct family of the Eosuchia while also evidencing strong relationships to the ancestral reptiles. It is therefore the earliest and most primitive representative of the largest assemblage of fossil and living reptiles, collectively called diapsids.*

The first fossil remains of one of the oldest reptiles, *Petrolacosaurus kansensis*, were found 45 years ago by a field party from the University of Kansas Natural History Museum. This small reptile from the Upper Pennsylvanian deposits of Garnett, Kansas, has since attracted a great deal of attention. Because of the incompleteness of the specimens and the combination of unusual osteological characters and great age, the taxonomic position and phylogenetic significance of *Petrolacosaurus* have been subjects of considerable dispute (*1*).

The study of recently uncovered specimens, reported here, indicates that *Petrolacosaurus* is the oldest known diapsid reptile. Furthermore, it reveals that this reptile possesses an almost ideal combination of primitive and advanced features to bridge the considerable morphological and evolutionary gap between the stem reptiles and the diapsids (*2*). *Petrolacosaurus* thus appears to be at the base of the largest reptilian radiation, which not only includes three of the four orders of modern reptiles and such extinct groups as eosuchians, thecodonts, rhynchosaurs, pterosaurs, and dinosaurs but also eventually gave rise to birds (Fig. 1). Although diapsids have a long evolutionary history extending into the Late Permian, the early history of this assemblage is not well documented in the fossil record. Consequently, the origins and phyletic relationships of the member groups have been open to question (*3*).

Among stem reptiles the family Romeriidae occupies a central position. Of all the known Paleozoic reptiles, only romeriids are sufficiently generalized to be the ultimate ancestors of any of the subsequent lineages (*4*). The retention in *Petrolacosaurus* of a large number of ro-

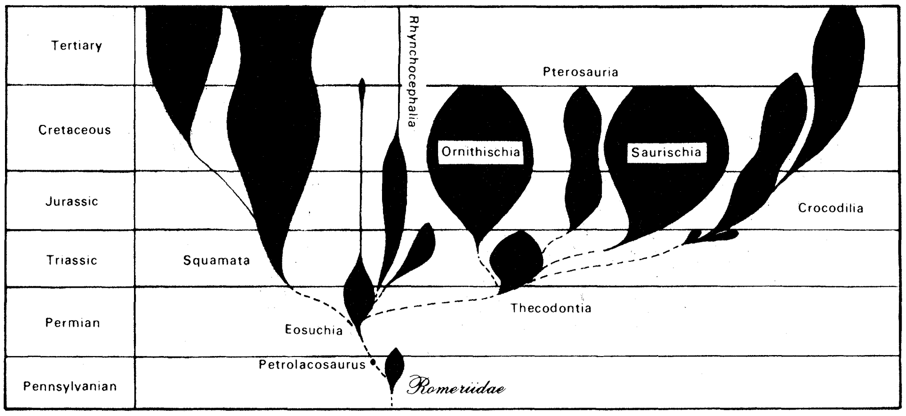

Fig. 1. Phylogeny of diapsid reptiles. The romeriid captorhinomorphs are included at the base of the phylogeny to show the ancestry of *Petrolacosaurus*.

meriid characteristics supports the contention that this reptile is derived from the early romeriid captorhinomorphs. Evolutionary tendencies within the romeriid radiation indicate that the lineage leading to *Petrolacosaurus* separated from the main line of romeriid evolution by the lower part of the Middle Pennsylvanian. Middle Pennsylvanian romeriids such as *Cephalerpeton* and *Paleothyris* are already too specialized in the structure of their atlas-axis complex to have given rise to *Petrolacosaurus*. On the other hand, no known feature of the oldest romeriid, *Hylonomus*, would preclude its being ancestral to *Petrolacosaurus* (*5*).

There are a number of particularly important features that differentiate *Petrolacosaurus* from all members of the family Romeriidae. The most significant departures from the romeriid pattern involve the development of fenestrae, or openings in the skull roof, palate, and occiput (Fig. 2). The upper and lower temporal fenestrae, typical of diapsids, have the same position and orientation in *Petrolacosaurus* as in the earliest diapsids, members of the order Eosuchia. The shape and interrelationship of the circumfenestral bones are modified as a result of diapsidy. In the Upper Permian eosuchian *Youngina* (*3*) and even in the Triassic diapsids *Prolacerta* (*6*), *Kuhneosaurus* (*7*), and *Euparkeria* (*8*), where the skulls are known in great detail, very specific relationships of the postorbital with the surrounding bones are the same as in *Petrolacosaurus*. The lateral portion of each parietal is also modified as a result of fenestration. In romeriids the contact between the parietal and the postorbital and squamosal is extensive. In *Petrolacosaurus*, as in all diapsids, these contacts are greatly reduced and the lateral margin of the parietal is deeply emarginated to form much of the edge of the upper temporal opening. In addition, the parietal in *Petrolacosaurus* has a narrow lateral process in front of this opening, as seen in the above diapsids. The squamosal is modified in *Petrolacosaurus* to form the margins of the upper and lower temporal openings and the intertemporal bar. As in all other diapsids, the contact between the squamosal and postorbital is much reduced compared to that in romeriids. The posterior part of the jugal is modified from a platelike sheet to two relatively narrow bands that extend dorsally and posteriorly. The large suture between the jugal and squamosal of romeriids is replaced in *Petrolacosaurus* by the lower temporal opening.

Suborbital fenestrae, not observed in any romeriid or pelycosaur, are typically found in diapsids. The presence of a pair of suborbital openings on the palate of *Petrolacosaurus* can be associated with certain structural features of the maxillary, palatine, ectopterygoid, and jugal. Similar structural features are found in the diapsids mentioned above. A pair of well-developed posttemporal fenestrae are bounded in *Petrolacosaurus* by the squamosal, the small tabular, the supraoccipital, and the well-developed paroccipital process of the opisthotic. In the eosuchian *Youngina* these fenestrae are somewhat smaller, but of fundamentally similar configuration.

The relative size of the skull, as indicated by the ratio between the skull and the trunk, is considerably smaller in *Petrolacosaurus* and eosuchians than in romeriids. In addition, the postorbital region of the skull is much reduced in *Petrolacosaurus* and eosuchians. The orbits

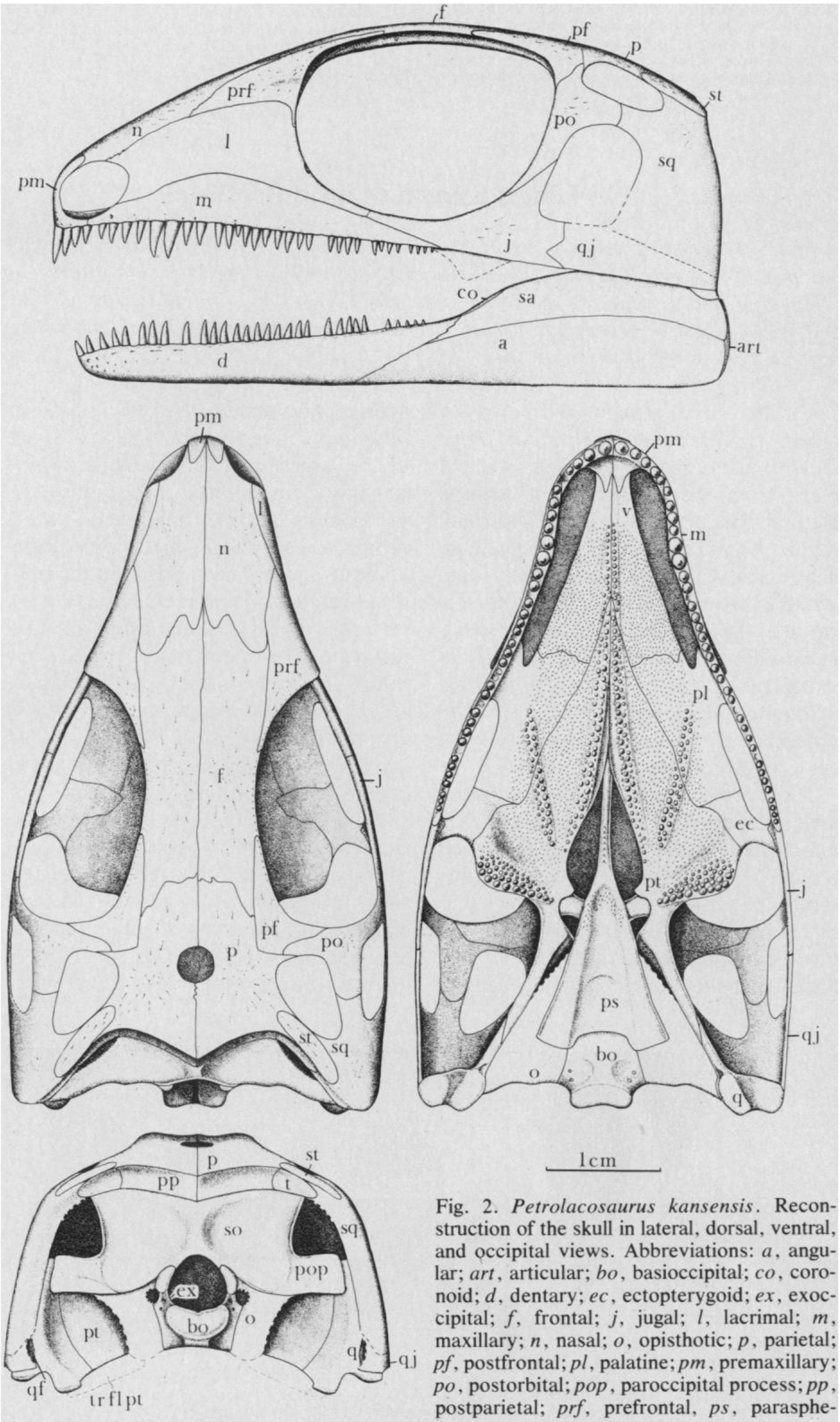

Fig. 2. *Petrolacosaurus kansensis*. Reconstruction of the skull in lateral, dorsal, ventral, and occipital views. Abbreviations: *a*, angular; *art*, articular; *bo*, basioccipital; *co*, coronoid; *d*, dentary; *ec*, ectopterygoid; *ex*, exoccipital; *f*, frontal; *j*, jugal; *l*, lacrimal; *m*, maxillary; *n*, nasal; *o*, opisthotic; *p*, parietal; *pf*, postfrontal; *pl*, palatine; *pm*, premaxillary; *po*, postorbital; *pop*, paroccipital process; *pp*, postparietal; *prf*, prefrontal, *ps*, parasphenoid; *pt*, pterygoid; *q*, quadrate; *qf*, quadrate foramen; *qj*, quadratojugal; *sa*, surangular; *so*, supraoccipital; *sq*, squamosal; *st*, supratemporal; *t*, tabular; *trflpt*, transverse flange of pterygord; *v*, vomer.

are, on the other hand, larger than in romeriids.

In addition to these modifications of the skull, *Petrolacosaurus* is advanced over the romeriid stage in a series of postcranial features. Many of these advanced features are seen in the Late Permian eosuchians *Youngina, Heleosaurus* (*9*), *Galesphyrus*, and *Kenyasaurus* (*10*) and even in Triassic thecodonts and squamates. Seven elongated vertebrae form a long neck; these vertebrae have anteriorly inclined centrosphenes and prominent median ventral keels. Posterior cervical and anterior dorsal vertebrae have well-developed mammilary processes on the sides of the neural spines. The vertebrae from the midcaudal region are also elongate. Some cervical ribs have anterodorsally directed processes near the tubercula. The scapulacoracoid is lightly built. The pelvic girdle, on the other hand, is very massive. The humerus is long and slender, in contrast to the robust femur. Distal limb elements are elongate, slender, and equal in length to the proximal limb elements. The carpus has elongate proximal elements, and the tarsus has an incipient mesotarsal joint, a locked tibioastragalar joint, a single centrale, and a widely divergent fifth metatarsal. The ribs, long bones, and metapodials are hollow.

The large number of highly significant similarities through the skeletons of *Petrolacosaurus* and various eosuchians justify inclusion of this genus within the order Eosuchia. These similarities are not restricted to the advanced features discussed above. Primitive morphological characters seen in the diapsids named above are clearly inherited from a common ancestor, the romeriids. These primitive features, although of little value in establishing phylogenetic relationships, indicate that *Petrolacosaurus* is primitive enough to have given rise to later eosuchians. Certain advanced features of eosuchians, such as cranial modifications toward development of a middle ear system sensitive to airborne sound (*11*), are lacking in *Petrolacosaurus*, necessitating placement of this genus within a separate family, Petrolacosauridae, at the base of the Eosuchia.

Acceptance of *Petrolacosaurus* as an ancestral eosuchian indicates a long hiatus in the fossil record of the eosuchian radiation between the first evidence in the Upper Pennsylvanian and the subsequent differentiation in the Late Permian. The extent of the Early Triassic diapsid radiation confirms that the origin of the eosuchians should be sought much earlier, probably well within the Paleozoic close to the origin of all reptiles, as *Petrolacosaurus* appears to substantiate, but the intervening gap is puzzling. The conditions of preservation and the nature of the fossils at Garnett suggest that *Petrolacosaurus* and other terrestrial tetrapods, invertebrates, and plants were washed into a quiet lagoon from dry ground. The gap in the fossil record can, therefore, be partially explained by the assumption that the early diapsids lived in environmental conditions which were not under normal circumstances conducive to preservation—areas away from standing water.

Recent studies of all the known diapsid species from the Upper Permian and Lower Triassic of south and central Africa (*12*) show that this stage of the diapsid evolution is far more complicated and extensive than was formerly believed. A more complete picture of the early diapsid adaptive radiation is required in order to understand fully how *Petrolacosaurus* is related to later diapsids. It can, however, be stated that the general anatomy of *Petrolacosaurus* and other early eosuchians indicates that they are certainly much closer to the more advanced diapsids and provide a better link with the ancestral romeriids than any other group of Paleozoic reptiles.

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References and Notes

1. H. H. Lane, *Trans. Kans. Acad. Sci.* **47**, 381 (19[illegible] *ibid.* **49**, 289 (1946); F. E. Peabody, *Geol. Soc. Am. Bull.* **60**, 1913 (1949); *Univ. Kans. Paleontol. Contrib. Artic.* **1**, 3 (1952); D. M. S. Watson, *Bull. Mus. Comp. Zool. Harv. Univ.* **111**, 297 (1954); P. P. Vaughn, *ibid.* **113**, 305 (1955); L. P. Tatarinov, *Osn. Paleontol.* **12**, 332 (1964); A. S. Romer, *Osteology of the Reptiles* (Univ. of Chicago Press, Chicago, 1956); J. W. Stovall *et al.*, *Bull. Mus. Comp. Zool. Harv. Univ.* **135**, 1 (1966). Peabody (1952), in the first detailed analysis of *Petrolacosaurus*, tentatively referred this reptile to the Eosuchia. The framentary nature and immaturity of the known specimens led others to reject Peabody's conclusions and place *Petrolacosaurus* in a total of five different suborders within three reptilian subclasses. In 1953 and 1954 Peabody collected more specimens, but he died before he could undertake a reconsideration of the anatomy of *Petrolacosaurus*. His collection forms the basis of the present study with well-preserved adult specimens partially articulated in such critical areas as temporal region and palate (specimens KUMNH 9951, 9952, 33602, and 33603).
2. All living reptiles can be grouped into four orders: Chelonia, Rhynchocephalia, Squamata, and Crocodilia. The latter three can be associated with the largest assemblage of fossil reptiles, collectively called the diapsids. The diapsid condition refers to the presence of two pairs of temporal openings on the skull roof behind the orbit. This condition has been retained in a primitive pattern in the crocodilians and the sole living rhynchocephalian *Sphenodon* but has been modified in the squamates by progressive loss of the dermal bones in the temporal region.
3. D. M. S. Watson, *Philos. Trans. R. Soc. London Ser. B* **240**, 325 (1957); A. S. Romer, *Notes and Comments on Vertebrate Paleontology* (Univ. of Chicago Press, Chicago, 1968), pp. 149–150; C. A. Reig, *Science* **157**, 565 (1967); C. E. Gow, *J. Zool.* **167**, 219 (1972); *Paleontol. Afr.* **18**, 71 (1975).
4. R. L. Carroll and D. Baird, *Bull. Mus. Comp. Zool. Harv. Univ.* **143**, 321 (1972).
5. R. L. Carroll, *J. Linn. Soc. London Zool.* **45**, 61 (1964).
6. P. L. Robinson, *Colloq. Int. CNRS* **163**, 395 (1967).
7. ——, *Proc. Geol. Soc. London* **1601**, 137 (1962).
8. R. F. Ewer, *Philos. Trans. R. Soc. London Ser. B* **248**, 379 (1965).
9. R. L. Carroll, in *Athlon; Essays on Palaeontology in Honour of Loris Shano Russell*, C. S. Churcher, Ed. (Univ. of Toronto Press, Toronto, 1976), p. 58.
10. ——, *Ann. S. Afr. Mus.* **72**, 59 (1976); J. H. Harris and R. L. Carroll, *J. Paleontol.*, in press.
11. The middle ear in romeriids and *Petrolacosaurus* could not function as in most advanced eosuchians and modern reptiles, as a highly sensitive mechanical transformer that amplified small sound pressures impinging on a large, taut tympanum into strong pressures at the small fenestra ovalis. The area behind the skull could not accommodate a large tympanum because the muscle depressor mandibularis hugged the convex posterior edge of the skull. The stapes was very massive and extended to the quadrate bone. A large stapes, immovable by normal sound pressures, would be ideal, however, in transmitting tissue-conducted sounds through the large footplate to the inner ear. It is relatively easy to derive the structural conditions seen in eosuchians and other diapsids from that in romeriids or *Petrolacosaurus* [R. R. Reisz, thesis, McGill University (1975)].
12. R. L. Carroll, *Colloq. Int. CNRS* **218**, 434 (1975.
13. I thank T. H. Eaton, Jr., of the University of Kansas who suggested this study and lent me the specimens of *Petrolacosaurus*.

6 January 1977; revised 10 February 1977

Intermetallic Compounds of the Type MNi_5 as Methanation Catalysts

Abstract. *Catalytic reactions of carbon monoxide with hydrogen have been studied in which intermetallic compounds of the formula* MNi_5 *(where M is thorium, uranium, or zirconium) have been used as the catalysts. The materials perform effectively as methanation catalysts;* $ThNi_5$ *has a specific activity exceeding that of a typical commercial oxide-supported methanation catalyst by a factor of about 5. This material also shows superior resistance to hydrogen sulfide poisoning. Nickel, formed as a decomposition product of the* MNi_5 *intermetallic compound, is probably the active species, but its properties are influenced by the nature of M in the precursor* MNi_5 *system.*

We have studied intermetallic compounds of the formula MNi_5, where M is Th, U, or Zr, with respect to their activity as catalysts in the formation of hydrocarbons (primarily CH_4) from CO and H_2. These materials are a part of a class of compounds represented by the formula MT_5 [where T is Co or Ni, and M is a rare earth (RNi_5), an actinide, or a group IVa element], which are noteworthy as hy-