versus width regression for growth series in each sample; scale as in *C*);

E) Parietal callus thickness for *P. bermudensis zonatus* from western Bermuda (no Shore Hills samples available; in millimeters);

F) Parietal callus thickness for *P. bermudensis zonatus* from eastern Bermuda (stock independent of *E*; in millimeters).

What environmental factors were most important as causes (*7*) of these faunal fluctuations? In comparison with interglacial situations, habitats of glacial Bermuda were cooler, wetter, and lower in calcium carbonate [$CaCO_3$ of red soils may be below 2 percent (*8*), while that of eolian carbonates is, obviously, near 100 percent]. Land snails build their shells of lime extracted from their substrates; in lime-free areas, many species either build very thin shells (*9*) or do not survive at all (*10*). *Gastrocopta* is a known calciphile (*11*), while *Thysanophora* is unusually tolerant of lime-free conditions (*12*). In addition, wide umbilici of glacial *Thysanophora* may reflect thinner shells. I have no explanation for the larger *Carychium* in glacial samples. Thick calluses in interglacial *P. bermudensis zonatus* reflect the availability of lime, as do many other events in this genus not recorded here (*13*). I propose, therefore, that varying access to $CaCO_3$ is the primary environmental cause for the coincident fluctuations of Fig. 1 (*14*).

STEPHEN JAY GOULD
Museum of Comparative Zoology,
Harvard University,
Cambridge, Massachusetts 02138

References and Notes

1. B. Kurtén, *Soc. Sci. Fenn. Comment. Biol.* **21**, 1 (1960); *Acta Zool. Fenn.* **107**, 1 (1965).
2. There is an enormous literature on glacially correlated fluctuation in coiling directions of planktonic foraminifera. See, for example, D. B. Ericson, *Science* **130**, 219 (1959) and A. Longinelli and E. Tongiorgi, *ibid.* **144**, 1004 (1965).
3. S. J. Gould, *Bull. Mus. Comp. Zool.* **138**, 407 (1969).
4. J H. Bretz, *Bull. Geol. Soc. Amer.* **71**, 1729 (1960); L. Land, F. Mackenzie, S. J. Gould, *ibid.* **78**, 993 (1967).
5. The red soils are not solely residual products of carbonate weathering. They contain considerable amounts of wind-blown continental detritus and phosphate leached from guano.
6. Thanks to W. Broecker, we have a firm date of approximately 120,000 years before the present for a shallow-water marine limestone deposited just before the Harrington-Pembroke interglacial eolianites (Fig. 1).
7. Either directly (by phenotypic modification) or indirectly (by setting the direction of natural selection). It is, of course, among a paleontologist's greatest frustrations that he can often establish correlations between organism and environment but can only rarely determine their genetic basis.
8. R. Ruhe, J. Cady, R. Gomez, *Bull. Geol. Soc. Amer.* **72**, 1121 (1961).
9. C. Oldham, *Proc. Malacol. Soc. London* **18**, 143 (1929); *ibid.* **21**, 131 (1934); B. Rensch, *Z. Morphol. Ökol. Tiere* **25**, 857 (1932).
10. V. Lozek, in *Progress in Soil Zoology*, P. W. Murphy, Ed. (Butterworths, London, 1962), p. 334.
11. H. A. Pilsbry, *Manual of Conchology*; vol. 24, *Pupillidae* (*Gastrocoptinae*) (Academy of Natural Sciences, Philadelphia, 1916), p. 7.
12. ———, *Monogr. Acad. Nat. Sci. Philadelphia* **3**, 987 (1940); H. B. Baker, *Occas. Pap. Mus. Zool. Univ. Michigan* **152**, 1 (1924).
13. These are listed in (*3*, p. 491) and include the development of paedomorphic, thin-shelled populations of *P. bermudensis* in red soils and the presence of thick- and thin-shelled subspecies of *P. nelsoni* and *P. superior* in eolianites and red soils, respectively.
14. Coincident fluctuations in land snail assemblages has also been used to distinguish glacial from interglacial deposits over large continental areas of Europe and North America. All this work, to my knowledge, is based on the presences and absences of species, not on quantitative measures of relative abundance or intraspecific variation. For Europe, see (*10*); for North America, see D. W. Taylor, in *The Quaternary of the United States*, H. E. Wright and D. G. Frey, Eds. (Princeton Univ. Press, Princeton, N.J., 1965), pp. 597–611.
15. Supported in part by grant GA 901 from the National Science Foundation. Contribution No. 485 from the Bermuda Biological Station for Research.

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Dentary-Squamosal Joint and the Origin of Mammals

Abstract. *The dentary-squamosal jaw joint evolved more than once in advanced cynodont therapsids or their descendants, probably as a buttress against the reaction force created at the articulation by the adductor jaw musculature. The multiple origin of this joint suggests that additional criteria are required to separate early mammals from advanced therapsids.*

Recently Romer (*1*) described an incipient mammalian jaw articulation in the Middle Triassic cynodont, *Probainognathus*. Romer's report of a dentary-squamosal contact in a cynodont prompts us to stress the importance of cynodont morphology in inferring how, when, and why such a joint developed and to examine the consequences of using this joint to distinguish mammals from therapsid reptiles.

The origin of the dentary-squamosal contact of mammals can be interpreted as part of a major adaptive trend begun in cynodont therapsids, with osteological changes reflecting the evolutionary development of mammalian adductor jaw musculature (*2*). During early cynodont history the dentary expanded and the post-dentary bones diminished in size (Fig. 1). A posteroventral expansion of the dentary, culminating in the formation of an angular region, reflects the differentiation and development of the masseter muscle. A posterodorsal expansion forming a high, broad coronoid process reflects the establishment of a mammal-like insertion of the temporalis muscle. Also, much of the insertion of the pterygoideus musculature was probably transferred from the post-dentary bones to the angular region in cynodonts from the *Cynognathus* Zone (*2, 3*). The capture of this insertion by the dentary may, in part, have been responsible for the reduction in size of the post-dentary bones. These events resulted in the great majority of the adductor jaw musculature being inserted on the dentary in cynodonts from the *Cynognathus* Zone and later.

As the coronoid process developed, the dentary expanded back over the top of the diminishing post-dentary bones. In cynodonts from the *Cynognathus* Zone and later, the base of the coronoid process caps much of the surangular and is continuous with a posteriorly directed process of the dentary which closely approaches the articular region (Fig. 1). This posterior expansion formed a brace which can be interpreted as a means for strengthening the contact between the dentary and the post-dentary elements, which compensated for the great vertical reduction in size of the post-dentary bones (*3*); indeed this brace, by increasing the area of horizontal contact between the bones, probably created the structural conditions which made the reduction of the post-dentary bones possible. This newly formed horizontal contact would have aided in resisting any tendency for the dentary to twist on the post-dentary bones. The existence of such tendencies is suggested by the fact that the major muscular and all the resistance (dietary) forces were applied on the dentary.

In addition, the great mass inferred for the posterodorsally directed temporalis and deep masseteric musculature suggests the existence of a tendency for the lower jaw to be thrust back and up against the skull at the jaw joint. The reaction to this thrust (Fig. 1, *FR*) would have tended to force the post-dentary bones forward and downward on the dentary and thereby would have created support requirements which the horizontal contact would have helped to meet (*4*). This reaction force may have also played a fundamental role in creating the selection pressures leading to the formation of the mammalian jaw joint. The transformation of the posterior process of the dentary into an articular process in contact with the squamosal would have added a buttress to aid the post-dentary bones in resisting such a reaction force and would have minimized the tendency for the post-dentary bones to be forced forward on the dentary.

Once the adductor jaw musculature of cynodonts differentiated to form a mammalian pattern, the development of a contact between the dentary and squamosal would appear to be a probable event. Given the trends for the expansion of the dentary and the reduction of the post-dentary elements accompanying this differentiation of musculature, we would expect any group of descendant cynodonts to have developed a posterior process closely approaching the squamosal as a result of selection for bracing. It is likely that a dentary-squamosal contact could have evolved more than once in advanced cynodonts or their descendants because this contact acted as a buttress against the thrust we believe to have been characteristically imparted by the temporalis and deep masseteric musculature. Fossil evidence indicates that this contact was independently established several times: (i) in the cynodont *Probainognathus* (*1*); (ii) once (but possibly more than once) in the ancestry of the groups generally acknowledged to be mammals (*5*); (iii) in the ictidosaur *Diarthrognathus* (*3*); and (iv) possibly (but not certainly) in the tritylodontids (*6*).

The phylogenetic relations indicated in Fig. 1 express the conclusion that all groups having members with a dentary-squamosal articulation were directly derived from cynodonts. The probability of development of a dentary-squamosal articulation in any group not descended from early cynodonts is extremely low; cynodonts are the only therapsids that show the osteological-muscular changes necessarily antecedent to the development of this joint (*2*). If we exclude *Probainognathus, Diarthrognathus*, and the tritylodontids, which we regard as reptiles despite the presence or possible presence of a dentary-squamosal joint, three distinct groups of early mammals are found in the latest Triassic (*5*). At least two of these mammalian groups possessed a functional articular-quadrate jaw joint lying beside a well-formed dentary-squamosal articulation (*7*). Recent information on molar morphology (*8, 9*), enamel structure (*10*), tooth replacement patterns (*9*), and braincase structure (*9, 11*) suggests that all of the Mesozoic mammals are much more closely related to one another than was previously thought (*11*). In contrast to the theories of the polyphyletic origin of mammals from different ancestral groups of therapsid reptiles, some of this evidence also indicates that mammals were derived from a cynodont ancestor, probably within the family Galesauridae (= Thrinaxodontidae) (*8, 9*).

Romer (*1*) suggests that *Probainognathus* (Chiniquodontidae) lay on or near the line leading to mammals. It differs from a galesaurid such as *Thrinaxodon* in certain features, such as the absence of cingula on the cheek teeth (*12*), which tend to remove it from the direct ancestry of mammals (Fig. 1). However, it is advanced over galesaurids in possessing greatly reduced post-dentary bones and a posterior process of the dentary which is in contact with the squamosal. In this respect, *Probainognathus* illustrates just how far a Middle Triassic cynodont went toward the establishment of a mammalian jaw joint. For this reason an early origin of a dentary-squamosal contact in the cynodont lineage ancestral to mammals would not be unexpected. The degree of diversity of Late Triassic mammals indicates that they shared a common ancestor probably not later than late Middle or early Late Triassic time. We do not know whether this ancestor possessed a mammalian jaw joint, but the available evidence suggests that it did.

Because the dentary-squamosal contact had a multiple origin, its use as the sole criterion for determining what is a mammal has a serious drawback. It does not distinguish between those Late Triassic groups which gave rise to Jurassic and later mammals and those groups which were terminal lineages within the cynodont radiation (Fig. 1). Therefore, additional criteria must be

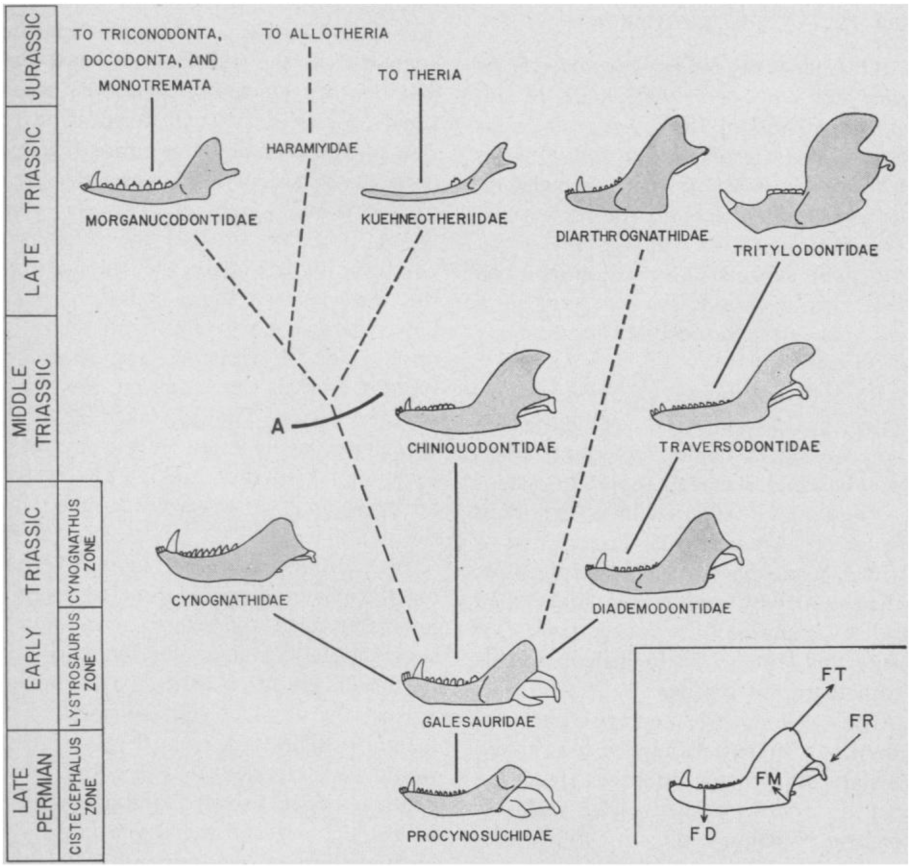

Fig. 1. Phylogenetic relations of cynodonts and their Late Triassic descendants. Line *A* represents the reptilian-mammalian class boundary. The lower jaws show the relative amount of expansion of the dentary (shown by stippling) and reduction of the post-dentary bones in each of the families indicated. (Inset) Diagrammatic representation of the direction and relative magnitude of the forces believed to have been typically applied to the jaw in an advanced cynodont; *FD*, dietary force; *FT*, reconstructed resolved line of action of the force created by the temporalis and deep masseteric musculature; *FM*, same for the superficial masseteric and the pterygoideus musculature; *FR*, reaction force created at the jaw joint. The lengths of the force vectors are scaled to achieve $\Sigma T = 0$, $\Sigma X = 0$, and $\Sigma Y = 0$ assuming that $FM = .33FT$.

used to separate those animals which, on the basis of their phylogenetic relations, we wish to call mammals from those which we wish to retain in the Therapsida. The groups generally considered to be mammals (*5*) appear to be more closely related to one another than to advanced cynodonts or other cynodont-derived groups; thus, it should be possible to find features shared by the former but lacking in the latter which can be used to supplement the definition of a mammal. Hopson and Crompton (*9*) have suggested that the presence of a diphyodont pattern of tooth replacement and possession of cheek teeth of a characteristic pattern be added to the dentary-squamosal contact as criteria for diagnosing what is a mammal. As knowledge of early mammals improves, other, perhaps better, characters can be added to or substituted for these. The problem of mosaic acquisition of these characters will complicate the issue as the record documenting the transition becomes increasingly complete, but we shall also be in an increasingly better position to select the most biologically significant criteria for separating the two classes.

HERBERT R. BARGHUSEN
Departments of Anatomy and Oral Anatomy, University of Illinois Medical Center, Chicago 60680
JAMES A. HOPSON
Department of Anatomy, University of Chicago, Chicago, Illinois 60637

References and Notes

1. A. S. Romer, *Science* **166**, 881 (1969).
2. H. R. Barghusen, *Postilla* **116**, 1 (1968).
3. A. W. Crompton, *Proc. Zool. Soc. London* **140**, 697 (1963).
4. We disagree with Crompton's (*3*) assumption that the horizontal components of the forces created by the adductor jaw musculature completely cancel each other so that the jaw articulation is subjected only to a vertical reaction force.
5. The usually accepted mammalian groups are the orders Triconodonta, Docodonta, Multituberculata, Monotremata, Symmetrodonta, Eupantotheria, Marsupialia, and the placental orders. The Late Triassic Morganucodontidae, Kuehneotheriidae, and Haramiyidae are here included in the Mammalia, but the Ictidosauria and Tritylodontidae are not.
6. S. Fourie, *S. Afr. J. Sci.* **64**, 255 (1968).
7. K. A. Kermack and F. Mussett, *Proc. Roy. Soc. (London) Ser. B* **148**, 204 (1958); D. M. Kermack, K. A. Kermack, F. Mussett, *J. Linn. Soc. London Zool.* **47**, 407 (1968).
8. A. W. Crompton and F. A. Jenkins, Jr., *Biol. Rev.* **43**, 427 (1968).
9. J. A. Hopson and A. W. Crompton, *Evol. Biol.* **3**, 15 (1969).
10. M. L. Moss and K. A. Kermack, *J. Dent. Res.* **46**, 745 (1967); M. L. Moss, *Novitates* **2360**, 1 (1969).
11. K. A. Kermack, *J. Linn. Soc. London Zool.* **47**, 241 (1967).
12. A. S. Romer, personal communication.
13. Supported by institutional research grant, University of Illinois, and by NSF grant GB-7836.

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Radioactivity Induced in Apollo 11 Lunar Surface Material by Solar Flare Protons

Abstract. *Comparison of values of the specific radioactivities reported for lunar surface material from the Apollo 11 mission with analogous data for stone meteorites suggests that energetic particles from the solar flare of 12 April 1969 may have produced most of the cobalt-56 observed.*

Values for the abundances of several radionuclides in eight lunar surface samples returned by the Apollo 11 mission have been reported by the Preliminary Examination Team (PET) (*1*). The preliminary nature of the experimental results was emphasized, and our conclusions must therefore necessarily be considered as tentative also.

One approach to a consideration of these radionuclide results is to compare them with analogous data from stone meteorites. In Table 1 are listed several of the nuclides reported by PET in order of increasing half-life. For each of these, average specific radioactivities in lunar surface material and in typical stone meteorites (*2*), as well as the ratios of these two quantities, are given. Also listed are the types of nuclear reactions by which they may have been formed. Corresponding to each reaction, we present in the last column of Table 1 the ratio of the specific radioactivities, after dividing each by the amount of target element in the sample (*1, 3*). This corrected ratio should be close to unity if the same spectrum and intensity of particles incident on both the lunar surface and the meteorites are responsible for the reaction being considered. It should be borne in mind that, if the relative importance of a given reaction varies greatly between the two classes of materials, the value of this ratio may not be very meaningful.

Perhaps the most striking feature of the PET results is the rather high average ^{56}Co content (≈ 31 dpm kg^{-1}). This ^{56}Co (half-life = 77 days), like most of the other radioactive species reported, is the result of the interaction of energetic particles in space with the lunar surface material; this phenomenon is well known from studies of meteorites and recovered satellites

Table 1. Comparison of specific radioactivities observed in Apollo 11 lunar material and in stone meteorites. d, day; y, year; dpm, disintegrations per minute.

Nuclide	Half-life	Observed specific radioactivities (dpm kg^{-1})		Ratio (lunar/stone)	Possible nuclear reactions	Ratio (lunar/stone)‡
		Average lunar samples*	Typical stone meteorites†			
^{56}Co	77 d	31 ± 4	14 ± 2	2.2 ± 0.4	^{56}Fe (p,n)	4.3 ± 0.8
^{46}Sc	84 d	11 ± 1	12 ± 1	0.9 ± 0.1	$^{46}\mathrm{Ti} + {}^{48}\mathrm{Ti}\left\{\begin{matrix}(p,xpyn)\\(n,xpyn)\end{matrix}\right\}$	0.012 ± 0.002
					$\mathrm{Fe}^{56}\left\{\begin{matrix}(p,6p5n)\\(n,5p6n)\end{matrix}\right\}$	1.8 ± 0.2
^{54}Mn	312 d	29 ± 5	72 ± 7	0.40 ± 0.08	^{54}Cr (p,n)	0.36 ± 0.07
					$^{55}\mathrm{Mn}\left\{\begin{matrix}(p,pn)\\(n,2n)\end{matrix}\right\}$	0.29 ± 0.06
					$^{56}\mathrm{Fe}\left\{\begin{matrix}(p,2pn)\\(n,p2n)\end{matrix}\right\}$	0.79 ± 0.16
^{22}Na	2.6 y	43 ± 4	80 ± 8	0.54 ± 0.08	$^{23}\mathrm{Na}\left\{\begin{matrix}(p,pn)\\(n,2n)\end{matrix}\right\}$	0.96 ± 0.14
					$^{24}\mathrm{Mg}\left\{\begin{matrix}(p,2pn)\\(n,p2n)\end{matrix}\right\}$	1.6 ± 0.2
					$^{28}\mathrm{Si}\left\{\begin{matrix}(p,4p3n)\\(n,3p4n)\end{matrix}\right\}$	0.48 ± 0.07
^{26}Al	7.4×10^5 y	80 ± 7	64 ± 6	1.3 ± 0.2	^{26}Mg (p,n)	3.8 ± 0.5
					$^{27}\mathrm{Al}\left\{\begin{matrix}(p,pn)\\(n,2n)\end{matrix}\right\}$	0.24 ± 0.03
					$^{28}\mathrm{Si}\left\{\begin{matrix}(p,2pn)\\(n,p2n)\end{matrix}\right\}$	1.1 ± 0.2

* Values from (*1*). † Values from (*2*). ‡ Corrected for target abundance.