



---

New Fossil Evidence on the Sister-Group of Mammals and Early Mesozoic Faunal Distributions

Author(s): Neil H. Shubin, A. W. Crompton, Hans-Dieter Sues and Paul E. Olsen

Source: *Science*, New Series, Vol. 251, No. 4997 (Mar. 1, 1991), pp. 1063-1065

Published by: American Association for the Advancement of Science

Stable URL: <http://www.jstor.org/stable/2875224>

Accessed: 03-04-2017 21:50 UTC

---

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://about.jstor.org/terms>



*American Association for the Advancement of Science* is collaborating with JSTOR to digitize, preserve and extend access to *Science*

response to the 1811–1812 New Madrid earthquakes. Such vented sediments are extensive south of the town of New Madrid (Fig. 1), in the epicentral region of the 1811–1812 earthquakes.

11. S. F. Obermeier, *U.S. Geol. Surv. Bull.* 1832 (1988).
12. Wabash Valley seismicity typically originates at a depth of 10 to 20 km, a depth that tends to exceed hypocentral depths in the New Madrid earthquake zone [D. W. Gordon, *U.S. Geol. Surv. Prof. Pap.*

1364 (1988)]. Therefore, in the Wabash Valley, peak shaking near the ground surface may be lower for a local earthquake of a given earthquake magnitude than for an event in the New Madrid zone.

13. Research by the U.S. Geological Survey in the Wabash Valley is supported through the National Earthquakes Hazard Reduction Program in cooperation with the U.S. Nuclear Regulatory Commission.

6 November 1990; accepted 25 January 1991

## New Fossil Evidence on the Sister-Group of Mammals and Early Mesozoic Faunal Distributions

NEIL H. SHUBIN, A. W. CROMPTON, HANS-DIETER SUES,  
PAUL E. OLSEN

Newly discovered remains of highly advanced mammal-like reptiles (Cynodontia: Tritheledontidae) from the Early Jurassic of Nova Scotia, Canada, have revealed that aspects of the characteristic mammalian occlusal pattern are primitive. Mammals and tritheledontids share an homologous pattern of occlusion that is not seen in other cynodonts. The new tritheledontids represent the first definite record of this family from North America. The extreme similarity of North American and African tritheledontids supports the hypothesis that the global distribution of terrestrial tetrapods was homogeneous in the Early Jurassic. This Early Jurassic cosmopolitanism represents the continuation of a trend toward increased global homogeneity among terrestrial tetrapod communities that began in the late Paleozoic.

CURRENT VIEWS OF THE PHYLOGENY and biogeography of early mammals have been hampered by a poor understanding of their sister group. Recently, the tritheledontid synapsids have been hypothesized to be the sister-group of mammals (1). Relatively little material has been described, and consequently the early evolution of characteristic mammalian features remains poorly understood.

The family Tritheledontidae was initially proposed to include the genera *Pachygenelus*, *Diarthrognathus*, and *Tritheledon*, all from the Lower Jurassic upper Stormberg Group of South Africa (1, 2). Subsequently, *Therioherpeton* (Upper Triassic Santa Maria Formation, Brazil) (3), *Chalimimia* (Upper Triassic Los Colorados Formation, Argentina) (4), and a fragmentary jaw referred to *Pachygenelus* (Upper Triassic Dockum Formation, Texas) (5) were referred to the family Tritheledontidae. The single record of *Pachygenelus* from Texas is doubtful and lacks any diagnostic cynodont characters because all the teeth are fused to the jaw and there are no cingula on the postcanine teeth (6). The Nova Scotian tritheledontid, described below, thus constitutes the first def-

inite record of this family from North America.

Tritheledontidae is considered the sister-group of mammals on the basis of the following synapomorphies (1): (i) basicranium foreshortened anteroposteriorly; (ii) prismatic tooth enamel (7); (iii) buccal (external) cingulum on the upper postcanine teeth; (iv) absence of postorbital (and postorbital bar); (v) absence of postfrontal; and (vi) secondary pony palate that extends to the level of the posteriormost postcanine. Another synapomorphy with mammals is the presence of a jaw joint between the dentary and squamosal (8).

The new tritheledontid material was found in the Lower Jurassic sedimentary rocks of the McCoy Brook Formation of the Fundy Group (Newark Supergroup) in Nova Scotia, Canada. The Fundy Group is a >1000-m-thick sequence of predominantly red clastic rocks and extrusive tholeiitic basalts (9). Five formations ranging in age from Middle Triassic to Early Jurassic are recognized, of which the McCoy Brook is the youngest. Tritheledontid remains occur in two distinct facies within the McCoy Brook Formation: a brown, fluvio-lacustrine sandstone and a basalt talus agglomerate. Palynological, footprint, and radiometric data suggest an Hettangian (earliest Jurassic) age for both facies (9). The talus cones contain sandstone-filled fissures with abundant, fragmentary tetrapod remains. The McCoy Brook assemblages are excep-

tional in the number of different stratigraphic controls that support an Early Jurassic age. In contrast, the ages of the tritheledontid-bearing upper Elliot and Clarens formations (upper Stormberg Group) of South Africa are poorly constrained (10).

To date, excellently preserved fragments of two premaxillae, ten maxillae, and six dentaries have been discovered. The coronal configuration of the postcanine teeth and the structure of the dentary and maxilla of these specimens are indistinguishable from those of *Pachygenelus monus* from the upper Stormberg Group of southern Africa (11), and hence the Nova Scotia material is here referred to *Pachygenelus* cf. *P. monus*. The excellent preservation of the dentition allows a detailed analysis of several important aspects of tritheledont dental anatomy, including tooth replacement, enamel structure, and occlusal patterns.

*Pachygenelus* cf. *P. monus* possesses patterns of tooth implantation and replacement similar to those of more generalized cynodonts such as *Thrinaxodon* (12). Tooth replacement is alternating (Fig. 1, A, B, and C). The dental lamina is housed in a small fossa that contains small pits for replacing teeth. The mode of tooth implantation is correlated with the pattern of tooth replacement. Older, well-worn postcanines are fused to the alveoli by a small ring of attachment bone. This feature is highly variable along the tooth row; newly replacing teeth are implanted in the alveoli without any bony attachment.

The molariform teeth of early mammals are distinguished by bifurcated roots that are oriented longitudinally in the jaw (13). The roots of the postcanine teeth of *Pachygenelus* cf. *P. monus* are intermediate in this condition in that they incipiently divided longitudinally (Fig. 1D).

Several aspects of the dentition of *Pachygenelus* are similar to primitive mammals (1) such as *Morganucodon* and *Megazostrodon* and are therefore derived with respect to other nonmammalian cynodonts. In both *Pachygenelus* cf. *P. monus* and the *Morganucodontidae* (*Megazostrodon* and *Morganucodon*) the enamel consists of closely packed crystallites with a small difference in orientation between prismatic and interprismatic enamel. No clear prismatic sheath is present. A herringbone arrangement of crystallites is present within each prismatic domain (14). This pattern is not seen in any other nonmammalian cynodont.

Mammals have long been thought to be distinguished by consistent patterns of occlusal wear that suggest stereotyped patterns of jaw movement (13). *Pachygenelus* cf. *P. monus* provides the first evidence that several aspects of this pattern are primitive. A char-

N. H. Shubin, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104.

A. W. Crompton, Museum of Comparative Zoology, Harvard University, Cambridge, MA 02138.

H.-D. Sues, Department of Paleobiology, NHB MRC 121, National Museum of Natural History, Washington, DC 20560.

P. E. Olsen, Lamont-Doherty Geological Observatory of Columbia University, Palisades, N.Y. 10964.

acteristic feature of undisputed Mesozoic mammals is unilateral occlusion. The lower jaw on the active side moves dorsomedially relative to the upper teeth during occlusion. This movement produces wear facets on the lingual face of the uppers and the buccal face of the lowers. In mammals this pattern of jaw movement produces complex and consistent multiple wear facets on the molars. In these taxa the teeth are progressively added from front to back and are not replaced. In contrast to other nonmammalian cynodonts, *Pachygenelus* cf. *P. monus* also possesses unilateral occlusion but lacks precise, matching wear facets. The matching facets on the teeth of *Pachygenelus* extend over the entire lingual surface of the upper postcanines and the buccal surface of the lower postcanines (Fig. 1A). Occlusal wear facets are also present on the incisors and canines of *Pachygenelus* cf. *P. monus* (Fig. 1F). In *Pachygenelus* cf. *P. monus* the postcanine teeth are replaced alternately and this process appears to have continued throughout life. As new postcanines erupted, they contacted opposing teeth on the opposite jaw. This resulted in the less well-defined facets on the postcanines of *Pachygenelus* cf. *P. monus*. The other putative mammalian sister-group, the Trityledontidae, have postcanine wear facets that lack buccal-lingual postcanine wear and do not suggest patterns of unilateral occlusion. Consequently, the trityledontid and mammal-tritheledontid occlusal patterns cannot be homologized as a single character as has been suggested (15).

In *Pachygenelus* cf. *P. monus*, there is a close coupling of enamel distribution on the teeth to patterns of occlusal wear: enamel that borders on the occluding surfaces is thin whereas enamel on nonoccluding surfaces is thick (as seen on the apical portion of the principal postcanine cusp). Once the thin enamel is worn away the apical edge of thick enamel is exposed. This feature provides a resistant cutting edge on the apical surface of the tooth.

*Pachygenelus* and *Diarthrognathus* are also characterized by a contact between the dentary and the squamosal that is lateral to the articular-quadrate joint. This new jaw articulation develops on the postero-lateral aspect of the articular process of the dentary and is probably homologous to the well-developed condyle on the dentary of mammals.

Tritheledontidae can be distinguished from other nonmammalian cynodonts by the following dental features: (i) presence of only two upper and two lower incisors (1); (ii) transversely expanded upper postcanines (1, 8); (iii) longitudinally ovate postcanines with large anterior cusp followed by one or two posterior accessory cusps and a lingual

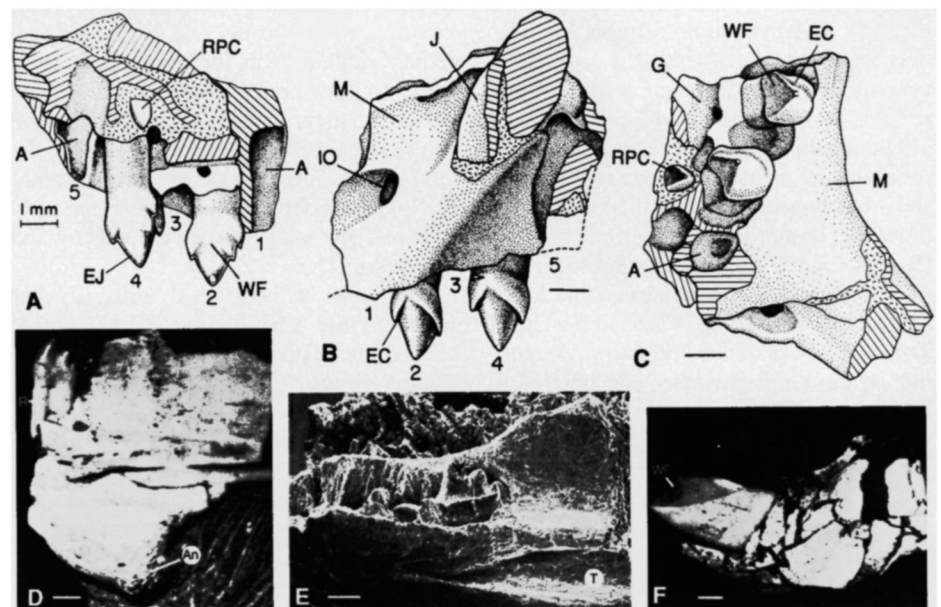
cingulum; (iv) upper postcanines with a buccal cingulum; (v) postcanine teeth with incipiently divided, massive roots. From these features, the family Tritheledontidae is hypothesized to include the genera *Diarthrognathus*, *Pachygenelus*, and *Tritheledon*. The dentition of *Tritheledon* is poorly known but closely resembles that of *Diarthrognathus* in the buccolingual expansion of the upper postcanine teeth (1, 2, 11). *Therioherpeton* does not possess any of the features above and cannot be considered to be a tritheledontid. The phylogenetic status of *Chalimimia* is uncertain because of the poor preservation of the only known specimen.

The newly discovered tritheledonts mainly support the cynodont phylogeny originally proposed by Hopson and Barghusen (1). Dental characteristics such as the development of a buccal cingulum on the upper teeth, matching occlusal wear on the buccal surface of the lower postcanines and the lingual surface of the upper postcanines, and contact between the dentary and squamosal bones apparently evolved only once among cynodonts.

The occurrence of *Pachygenelus* cf. *P. monus* in Nova Scotia underscores a pattern of wide, in many cases virtually cosmopolitan, distribution of Early Jurassic taxa of terrestrial tetrapods. Other tetrapod taxa from the McCoy Brook Formation, particularly the sphenodontian lepidosaurs and the proto-

suchid crocodyliform archosaurs, reveal further close similarities among continental tetrapod assemblages of Early Jurassic age. The sphenodontian *Clevoosaurus* is known from Upper Triassic fissure-fillings in England (16), and closely related forms are known from the Forest Sandstone of Zimbabwe and the lower Lufeng Formation of Yunnan, China, both of which are Early Jurassic in age (17). The protosuchid *Protosuchus* is known elsewhere from the Lower Jurassic Glen Canyon Group of the southwestern United States and the upper Stormberg Group of southern Africa (18). The dinosaurian material from the McCoy Brook Formation recovered to date is fragmentary but it includes an anchisaurid prosauropod and teeth of an ornithischian indistinguishable from *Lesothosaurus* from southern Africa. Both dinosaurian families appear to have a worldwide distribution during the Early Jurassic.

The homogeneity of tetrapod distributions during the Early Jurassic represents the continuation of a trend toward increased cosmopolitanism that began in the late Paleozoic (19). Similar cosmopolitan distributions are also seen in Early Jurassic terrestrial floral assemblages that are dominated by cheirolepidaceous conifers (10). This trend in terrestrial biotic cosmopolitanism is broadly contemporaneous with the initial stages of the breakup of Pangaea. These



**Fig. 1.** (A) Lingual view of left maxilla of *Pachygenelus* cf. *P. monus* (NSM 988GF11.1) showing wear patterns (WF), replacing teeth (RPC), empty aveoli (A), and dentine-enamel junction (EJ). (B) Buccal view of NSM 988GF11.1 showing external cingulum (EC), infraorbital foramen (IO), and jugal (J). (C) Occlusal view of NSM 988GF11.1 showing gubernaculum for the dental lamina (G). (D) Lingual view of right dentary of *Pachygenelus* cf. *P. monus* (MCZ 9139) showing large angle (An) and incipiently bifurcated postcanine roots (R). (E) Right dentary of *Pachygenelus* cf. *P. monus* (NSM 988GF10.1) showing trough for post-dentary bones (T). (F) Dentary of *Pachygenelus* cf. *P. monus* (NSM 988GF12.1) showing enlarged canine with occlusal wear (WF). Numbers 1 through 5 pertain to the number of individual postcanine teeth. Institutional abbreviations: NSM, Nova Scotia Museum; MCZ, Museum of Comparative Zoology, Harvard University. Scale bar, 1 mm.

patterns suggest that the persistence of Pan-gaea throughout the Triassic provided few barriers for the migration of terrestrial vertebrates. The initial stages of rifting in the Late Triassic resulted in no corresponding provinciality of terrestrial vertebrate distribution by the Early Jurassic.

REFERENCES AND NOTES

1. J. A. Hopson and H. Barghusen, in *The Ecology and Biology of Mammal-like Reptiles*, N. Hotton, P. D. MacLean, J. J. Roth, E. C. Roth, Eds. (Smithsonian Institution Press, Washington, DC, 1986), pp. 83–106; T. S. Kemp, *Mammal-like Reptiles and the Origin of Mammals* (Academic Press, New York, 1982).  
 2. J. A. Hopson and J. W. Kitching, *Palaentol. Afr.* **14**, 71 (1972).  
 3. J. F. Bonaparte and M. C. Barberena, *J. Paleontol.* **49**, 931 (1975).  
 4. J. F. Bonaparte, *Actas 2 Congr. Argent. Paleontol.*

*Biostratigr. 1 Congr. Latinoam. Paleontol. (Buenos Aires)* **2**, 123 (1980).  
 5. S. Chatterjee, *Science* **220**, 1151 (1983).  
 6. J. A. Hopson and A. W. Crompton, in preparation.  
 7. F. E. Grine, C. E. Gow, J. W. Kitching, *Proc. Electron Microsc. Soc. S. Afr.* **9**, 99 (1979).  
 8. A. W. Crompton, *Proc. Zool. Soc. London Ser. B* **130**, 183 (1958).  
 9. P. E. Olsen, N. H. Shubin, M. H. Anders, *Science* **237**, 1025 (1987).  
 10. P. E. Olsen and P. M. Galton, *Palaentol. Afr.* **25**, 87 (1984).  
 11. C. E. Gow, *Proc. R. Soc. London Ser. B* **208**, 461 (1980).  
 12. A. W. Crompton, *Ann. S. Afr. Mus.* **46**, 479 (1963); *Proc. Zool. Soc. London Ser. B* **140**, 697 (1963); \_\_\_\_\_ and F. Ellenberger, *Ann. S. Afr. Mus.* **44**, 1 (1957).  
 13. A. W. Crompton and F. A. Jenkins, Jr., *Annu. Rev. Earth Planet. Sci.* **1**, 131 (1973); in *Mesozoic Mammals: The First Two-Thirds of Mammalian History*, J. Lillegraven, Z. Kielan-Jaworowska, W. Clemens, Eds. (Univ. of California Press, Berkeley, 1979), pp. 59–73.

14. D. Stern and A. W. Crompton, *J. Dent. Res.* **67**, 231 (1988); D. Stern, thesis, Harvard University (1989).  
 15. T. Rowe, *J. Vertebr. Paleontol.* **8**, 241 (1988).  
 16. N. C. Fraser, *Philos. Trans. Roy. Soc. London Ser. B* **321**, 125 (1988).  
 17. H.-D. Sues et al., in preparation.  
 18. J. M. Clark, thesis, University of Chicago, Chicago, IL (1986).  
 19. N. H. Shubin and H.-D. Sues, in preparation.  
 21. W. W. Amaral, W. A. Clemens, N. Greenwald, J. A. Hopson, K. Padian, M. Russell, and M. Seidl provided helpful discussion and comments on the manuscript. F. A. Jenkins, Jr., and W. W. Amaral provided facilities and extraordinary expertise for laboratory and field investigation. Field permits and logistical support were provided by the Nova Scotia Museum, Halifax, Nova Scotia. Supported by grants from the National Geographic Society, the Museum of Comparative Zoology of Harvard University, and the Department of Biology of the University of Pennsylvania.

10 September 1990; accepted 29 November 1990

## Salicornia bigelovii Torr.: An Oilseed Halophyte for Seawater Irrigation

EDWARD P. GLENN, JAMES W. O'LEARY,\* M. CAROLYN WATSON, T. LEWIS THOMPSON, ROBERT O. KUEHL

The terrestrial halophyte, *Salicornia bigelovii* Torr., was evaluated as an oilseed crop for direct seawater irrigation during 6 years of field trials in an extreme coastal desert environment. Yields of seed and biomass equaled or exceeded freshwater oilseed crops such as soybean and sunflower. The seed contained 26 to 33 percent oil, 31 percent protein, and was low in fiber and ash (5 to 7 percent). The oil and meal were extracted by normal milling equipment, and the oil was high in linoleic acid (73 to 75 percent) and could replace soybean oil in chicken diets. The meal had antigrowth factors, attributed to saponins, but could replace soybean meal in chicken diets amended with the saponin antagonist, cholesterol. *Salicornia bigelovii* appears to be a potentially valuable new oilseed crop for subtropical coastal deserts.

THERE ARE TWO APPROACHES TO DEVELOPING crops tolerant of seawater-concentration salinity. One is to increase the tolerance of present crops (1), but the difference between the upper limit of salt tolerance currently exhibited by crop plants and that required to tolerate seawater salinity is great (2). An alternative is to select from the large pool of halophytes, plants which already have the requisite salt tolerance, those that might make desirable crops (3).

*Salicornia bigelovii* Torr. is a leafless, annual salt-marsh plant with green, jointed, succulent stems that ultimately form terminal fruiting spikes in which seeds are borne (4). In subtropical regions it may grow to be a large, upright plant, 50 cm tall, with most

of the seed spikes on the upper one-third of the plant. The seeds are approximately 1 mg and germinate directly on seawater. *Salicornia bigelovii* emerged as a potential seawater oilseed crop from a screening of wild halophytes (5–7) and was selected for seawater field trials including determination of seed yield and seed analyses.

The trials were conducted at Puerto Peñasco, Sonora, Mexico, in an extreme coastal

desert environment at the northern Gulf of California. Seeds were collected near Puerto Peñasco in Estero Morua. Trials in 1982 were conducted in the same 1-ha field and with the same methods previously described for other halophytes (6). Trials from 1984 to 1988 were conducted in a 0.5-ha field nearby. Both fields had sandy soils typical of light agricultural soils in the region and were divided into individually irrigated, 200 m<sup>2</sup> flood plots. At both sites irrigation water with a salinity range of 38 to 42 per mil was supplied daily from seawater wells. In field 1, seawater that passed through a shrimp aquaculture facility, which added nitrogen and other nutrients to the water, was used, and no supplemental fertilizer was needed. Field 2 was irrigated with unenriched seawater, and plots received fertilizer additions equivalent to 200 kg of N per hectare or more, as urea, diammonium phosphate, or ammonium nitrate. Rainfall was less than 90 mm annually and the soil in the root zone was at seawater salinity or higher at all times (6).

The standard seeding rate of 25 kg ha<sup>-1</sup> produced a mean plant density at harvest of 323 plants/m<sup>2</sup> (SD, 249; n = 49; observa-

**Table 1.** Summary of annual *Salicornia bigelovii* seed and biomass yields at field 2, Puerto Peñasco, Sonora, Mexico (n, number of plots). Crops were sown during a 2- to 3-week period during the months indicated and were harvested the following September or October in the year indicated. In 1986 12 plots were planted in February and 12 in April.

Month sown	Year	Biomass (kg m <sup>-2</sup> )	SE	n	Seed (g m <sup>-2</sup> )	SE	n
December	1984	2.46	0.18	9	233	13	9
	1985	1.39	0.04	15	208	11	15
April	1986	1.27	0.05	12	177	5	12
	1986	1.51	0.08	12	193	10	12
	1987	1.98	0.04	15	246	7	15
	1988	1.44	0.09	20	139	11	20

E. P. Glenn, J. W. O'Leary, M. C. Watson, T. L. Thompson, Environmental Research Laboratory, 2601 East Airport Drive, Tucson, AZ 85706.  
 R. O. Kuehl, Statistical Support Unit, College of Agriculture, University of Arizona, Tucson, AZ 85721.

\*Present address: Bioresources Research Facility, 250 East Valencia Road, Tucson, AZ 85706.