<sup>18</sup>O and solar activity. If the positive relationship between <sup>18</sup>O concentration and temperature is determined by temperature trends that are induced by variation in solar activity, then the negative relationship between <sup>18</sup>O concentration and <sup>14</sup>C variation noted by Dansgaard et al. (1) may be the indirect result of solar variation, since there is a significant negative correlation over the past 2 millennia between solar activity and <sup>14</sup>C variation (2), for which a possible physical explanation is available (6).

The significant correlation between <sup>18</sup>O in the Camp Century core and the

solar activity index is indirect evidence of the validity of the index and of the solar-climate (4) and solar-14C relationships that are based on the index.

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# **Coincidence of Climatic and Faunal Fluctuations**

## in Pleistocene Bermuda

Abstract. As the climate of Pleistocene Bermuda oscillated during the last two glacial cycles, coincident variation occurred for a variety of independent events in the form and diversity of land snails. This variation was influenced primarily by the availability of calcium carbonate for shell construction.

The relationship between organism and environment is the common ground of two disciplines. Evolutionists probe environments for the selective forces that lead to adaptation, while paleoclimatologists, lacking direct measures, hope to read climate from its organic results. These goals can only rarely be attained in the immense complexity of vast time spans in large areas. The Pleistocene glaciations, however, provide a natural experiment for testing hypotheses of precise climatic influence

upon organic form and diversity-the time span is short, the climatic cycle proceeded several times in approximately the same manner, and all the advantages of a time-slice near our own are available (precision in radiometric dating and good preservation of animals that have survived in known habitats). If each glacial cycle is a replication, then the experiment has succeeded when climatic and faunal fluctuations coincide for several cycles. Successes have been recorded for such diverse



Fig. 1. Coincidence of faunal and climatic fluctuations for six independent events in the Bermudian Pleistocene. See text for explanation.

phenomena as size in mammals (1) and coiling directions in foraminifera (2). Previously, I noted (3) several cases of coincidence for shell thickness in the large, endemic land snail Poecilozonites in Bermuda. I now add several instances for both form and diversity of Bermuda's microgastropods (< 3 mm in length) and present this synthesis of an unusual situation in which environmental factors exerted a very exact control upon a large group of diverse events in very different size ranges.

The eolian carbonate dunes of Pleistocene Bermuda are peripheral, rapidly cemented deposits that did not migrate far inland (4). During interglacial times, they accumulated on the area of modern Bermuda. During glacial times, they were deposited on the edge of an emergent platform that is now well under water; at the same time, dunes of previous interglacials were weathered in the central areas of greater glacial Bermuda (modern Bermuda), and red soils formed (5). The sequence of red soil-eolian carbonate may be read as glacial-interglacial; it occurs at least three times in the preserved Pleistocene deposits of Bermuda. Land snails are common in both lithologies.

I collected bulk samples from 48 localities representing the last two cycles (6) and sorted out all the microgastropods. I found 12 species in samples ranging from 45 to 513 individuals (only 18 samples with < 100 snails) and calculated percentage abundances for all species in all localities. I also studied the shell form of two common species that seemed, on the basis of diversity, to prefer interglacial and glacial habitats, respectively.

Figure 1 presents a few of the many events, of various types, that exhibit coincidence with environmental changes through time—A and B for the diversity of microgastropods, C and D for the form of microgastropods, and Eand F for shell thickness in Poecilozonites. These events are:

A) Percentage abundance of Gastrocopta rupicola (points, in all cases, are grand means of sample means for each time period);

B) Percentage abundance of Thysànophora hypolepta;

C) Height of adult Carychium bermudense (20 specimens per sample; scale in micrometer units at 29 = 1mm);

D) Umbilical width of Thysanophora hypolepta (expected value at width, 2 mm, calculated from umbilical width

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<sub>3</sub> 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).

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- 5. The red soils are not solely residual products of carbonate weathering. They contain considerable amounts of wind-blown continenta detritus and phosphate leached from guano. continental
- 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 collamites (Fig. 1). 7. Either directly (by phenotypic modification) or
- indirectly (by setting the direction of natural selection). It is, of course, among a paleon-tologist's greatest frustrations that he can often establish correlations between organism and environment but can only rarely determine
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  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 and red soils, respectively. anites and red soils, respectively
- 14. Coincident fluctuations in land snail assemblages has also been used to distinguish schinges in a las also been acted to the singless 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 relaspecies, not on quantitative measures of rela-tive 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.
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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 postdentary 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 postdentary 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 squamo-