

(8, 9); resulting volcanic edifices need not always erupt along narrow linear trends comparable in width to that of the seamounts themselves.

Using the mean ages of  $22.6 \times 10^6$  years for Kodiak Seamount and  $19.9 \times 10^6$  years for Giacomini Guyot and their separation of 177.8 km, we calculate a Pacific-plate motion of 6.6 cm/year during early Miocene time. This calculation assumes a hypothesis of seamount generation by plate motion over a fixed hot spot in the mantle (8); it also assumes that the time of construction of each volcanic edifice was short, and, therefore, that dates measured on dredged samples are reasonable estimates for the times of initiation of volcanic activity at each seamount. These assumptions are well documented for the more extensively studied Hawaiian-Emperor chain (9), although the second assumption can be strictly applied only to the tholeiitic, shield-building stage of volcanic activity.

Our data, combined with plate tectonic concepts, suggest that the Pratt-Welker seamount chain consists of a series of volcanoes, all younger than  $23 \times 10^6$  years, cutting obliquely across structural trends shown by magnetic anomaly patterns in an older north-eastern Pacific sea floor (Fig. 2). The oldest dated volcanic edifice is in the Aleutian Trench, apparently about to be subducted. Future dating of successive seamounts southeastward along the chain from Giacomini Guyot should show a corresponding decrease in age and provide significant data on Pacific-plate motion during the last  $23 \times 10^6$  years.

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## Earthquakes of Strike-Slip Type in Central California: Evidence on the Question of Dilatancy

**Abstract.** *The travel times of compressional waves from quarry explosions of well-known origin times, measured at the University of California network of seismographic stations for the period 1961 to the present, have been examined for evidence of premonitory changes prior to earthquakes of moderate magnitudes in the region. Velocities to seven station sites are generally constant to within  $\pm 1$  percent, with occasional deviations of  $\pm 2$  percent. Variations seem to bear no correlation to earthquake occurrence and are probably due to a combination of reading errors and changes in the source location within the quarry.*

Evidence is accumulating in support of premonitory variations in seismic wave velocities in the source regions of earthquakes. Studies in the Soviet Union (1) and in New York (2) indicate that this premonitory change is seen in the ratio of the compressional and shear velocities,  $V_P/V_S$ , which usually has a value of about 1.75. Recent data of Whitcomb *et al.*

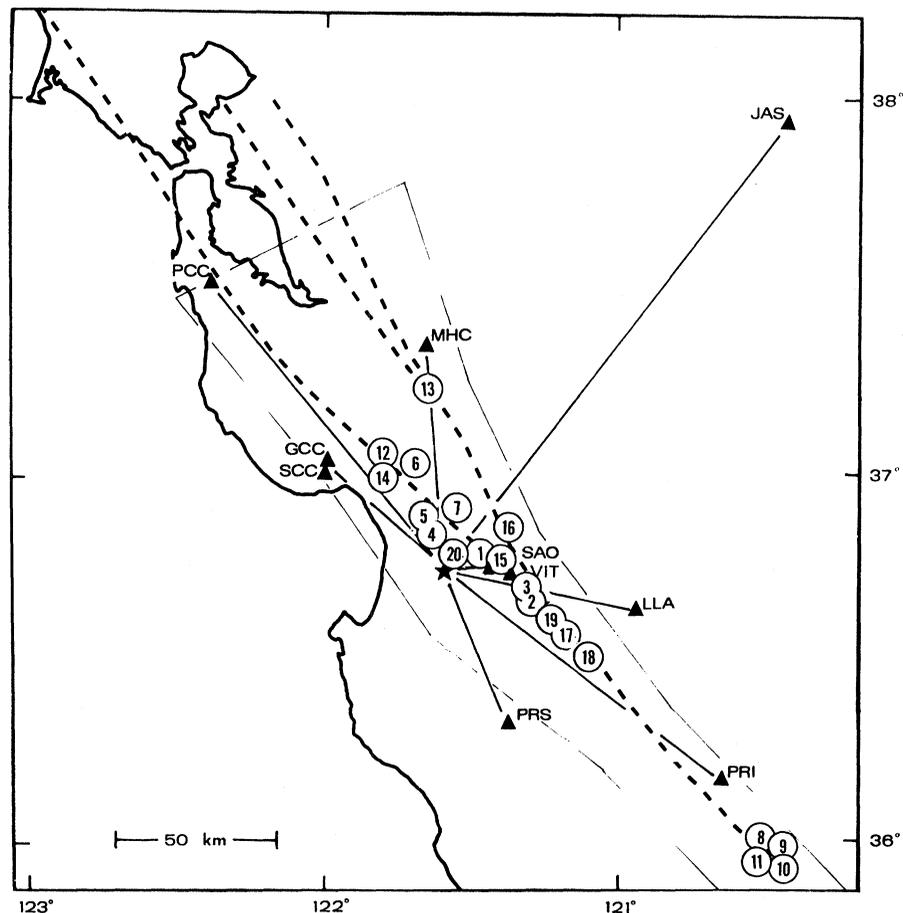


Fig. 1. Map of central California showing the quarry location (star) and seismographic stations (triangles) used in this study. Circled numbers give the locations of all earthquakes since 1960 with  $M \geq 4.5$  within the outlined region.

(3) on the San Fernando earthquake along with the studies of Nur (4) and Scholz *et al.* (5) suggest that the phenomenon of dilatancy (6) occurs in the stress cycle preceding the failure point represented by the earthquake occurrence. Laboratory studies of rocks show that dilatancy, an increase in volume due to microfracturing under stress, reaches a maximum well before failure. Compressional wave velocities can be reduced in the dila-

tancy process whereas shear wave velocities are less affected. This process provides an explanation for the  $V_P/V_S$  reduction and implies that the premonitory change should be apparent in  $V_P$ . Such changes have been reported for the 1971 San Fernando earthquake (3).

Data on file at the University of California seismographic stations provide the basis for a severe test of this hypothesis as applicable to earthquakes

in the magnitude ( $M$ ) range 4.5 to 5.5 and of the strike-slip source type common along the San Andreas fault system in central California. In 1960-1961 a network of seismographic stations was established in that region with signals telemetered to Berkeley and recorded together on 16-mm film with common timing. Immediately studies of crustal structure were undertaken in which several of the large quarries in the area were used as

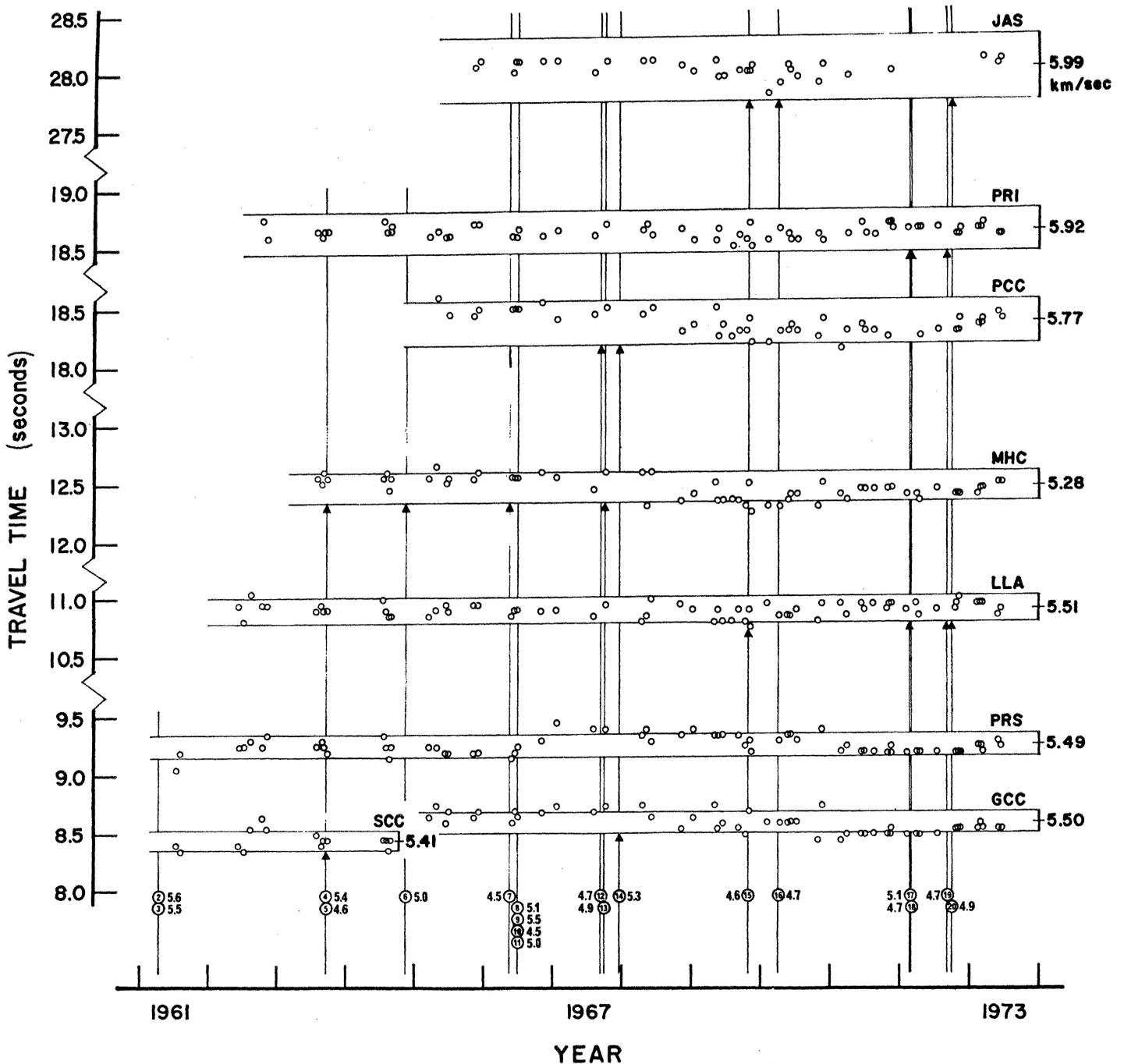


Fig. 2. Travel times of P-waves for 1961-1973 from 68 explosions to seven seismographic stations. Horizontal lines bracket  $\pm 1$  percent variation from the mean. Numbers on the right are the mean velocities for the paths. Vertical lines are the times of earthquakes, shown as circled numbers keyed to Fig. 1, with magnitudes given adjacent to the index numbers.

sources. Precise origin times were measured by telemetering the firing time signals to Berkeley where they were recorded along with the seismic data channels, allowing travel times to be measured with a precision of 0.05 second without the concern of absolute timing accuracy since all signals were recorded on the same film. During the period 1961 to 1964, 16 explosions were so timed at one quarry, the Kaiser Natividad installation near Salinas, California. This source is used in the study reported here.

Waves from the explosions are well recorded at several stations in the network which have been in operation continuously since their installation in the early 1960's. The nearest station to the quarry is some 13 km distant, with a P-wave travel time of 2.5 seconds. The origin times of blasts not timed at the quarry can be inferred within an estimated precision of 0.1 second on the basis of the P-wave arrival time at this station.

Records have been analyzed for 68 explosions from 12 July 1961 to 14 June 1973. Arrival times were measured for the crustal  $P_g$  phase at eight stations shown in Fig. 1. Times at station SAO or VIT were used to infer origin times, thus providing travel times to the other seven stations throughout the 12-year period. The circled numbers in Fig. 1 give the locations of all  $M \geq 4.5$  earthquakes since 1960 in the region outlined on the map. Distances (in kilometers) from the quarry to the stations are as follows: SCC, 46; GCC, 47; PRS, 51; LLA, 60; MHC, 66; PCC, 109; PRI, 107; and JAS, 168.

We estimate the uncertainties introduced in reading the P-wave arrival times to be  $\leq 0.1$  second since the wave forms at the stations have remained virtually identical throughout the 12-year period, thus allowing a timing consistency not usually found in measuring earthquake signals. Further uncertainty is introduced in using the SAO or VIT arrival time to estimate origin times if either the explosion site is moved relative to the 1961–1964 locations or the velocity is changing as a result of dilatancy between the station and the quarry. The former source of error can be evaluated by considering the areal extent of the quarry. The extreme variation in source position is less than 0.5 km from the quarry center and could produce an error in origin time of up to

0.1 second and a change in travel time of up to 0.1 second to a particular station where distance is changed by the full 1 km. Errors due to dilatancy, causing, say, a 10 percent decrease in velocity along the wave path to station SAO, could effectively introduce an additional 0.25-second error into the estimated origin times. Considering the worst possible extremes, when all potential errors are additive, a range of arrival times at a particular station might vary by as much as  $\pm 0.4$  second from a mean value. For mean travel times of 8.6 to 28.0 seconds to the seven stations used in this study the extreme variations due to the above errors would correspond to between  $\pm 5$  percent at short distances and  $\pm 1.5$  percent at the more distant stations. In fact, observed extreme values show less than half this possible deviation from the mean travel time.

Data are presented in Fig. 2. Travel times (and equivalent mean velocities) are given for the 12-year period at the seven stations indicated in Fig. 1. The times of earthquakes are shown as vertical lines keyed by number to Fig. 1, and the magnitudes are given (standard Wood-Anderson  $M_L$  values). Horizontal lines indicate  $\pm 1$  percent variations from the mean travel time.

Existing data (1–3) on premonitory velocity changes associated with earthquakes indicate that, for shocks in the range  $M = 4.5$  to 5.5, the precursor time during which the velocity decrease may exceed 10 percent is some 2 to 5 months. The velocity is expected to increase slowly thereafter, reaching a normal value just prior to the earthquake. It would seem that the relatively dense sampling provided by the quarry explosions should certainly give clear indication of such behavior in velocity.

The data of Fig. 2 show maximum variations in velocity of  $\pm 2$  percent from the mean values, with most measurements within  $\pm 1$  percent. Furthermore, many anomalous points show systematic differences most easily explained in terms of the previously described errors associated with changes in source location and errors in origin time. There are no clear indications of premonitory velocity changes prior to earthquakes.

Several interpretations of these results are possible:

1) The dilatancy effect exists but

was missed because of inadequate sampling in time. This argument seems weak—somewhere a change greater than 2 percent should have been encountered, particularly if we consider the much larger numbers of  $M < 4.5$  earthquakes occurring within the area.

2) The dilatancy effect exists but was missed because of inadequate sampling in space. This is a stronger argument but requires that affected source areas for earthquakes of  $M = 4.5$  to 5.5 are smaller than 10 to 20 km in diameter so that the proportional effect of a 10 percent or greater velocity decrease in the source area would be below the 2 percent variations seen. Evidence based on reasonable crustal velocity distributions indicates that ray paths except to the most distant station reach depths no greater than about 15 km. Earthquake foci in the region range in depths to about 15 km.

3) The region is uniformly dilated as a result of ongoing seismicity throughout central California or a future major ( $M > 7$ ) earthquake. This explanation is plausible except that the value of  $V_P/V_S$ , based on other observations, seems normal (about 1.75) in the area.

4) Dilatancy is not a significant effect in the source region of a major strike-slip fault such as the San Andreas fault in central California. Possible reasons for this may be that fault creep and ongoing major seismicity have produced a near stable environment of slippage without attendant large fluctuations in stress levels during the earthquake cycle or that stress levels around the source region remain below those sufficient to cause dilatancy.

Of these possibilities, hypotheses 2 and 4 seem the most likely. Continued monitoring of quarry explosions and the installation of velocity-monitoring arrays in more local regions will be required to differentiate among the alternative interpretations of the data presented here. It is fairly clear, however, that compressional velocities along paths several tens of kilometers in length are not affected significantly by San Andreas type earthquakes of  $M$  up to 5.5.

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## Functional Organelles in Prokaryotes: Polyhedral Inclusions (Carboxysomes) of *Thiobacillus neapolitanus*

**Abstract.** *The polyhedral inclusions of Thiobacillus neapolitanus have been isolated; they contain ribulose diphosphate carboxylase.*

Prokaryotic cells have not been reported to have metabolically functional organelles. Many blue-green algae and chemoautotrophic bacteria contain polyhedral inclusions that have identical appearances in thin section (1, 2). We have isolated these inclusions from *Thiobacillus neapolitanus* (Fig. 1) and have discovered that they contain the enzyme ribulose diphosphate carboxylase (E.C. 4.1.1.39). We propose that these organelles, responsible for carbon dioxide fixation, be called carboxysomes.

The bacteria were grown in a 200-liter fermentor with constant aeration and pH control (pH 7.0) in the medium described by Vishniac and Santer (3). After the cells reached the maximum stationary phase of growth they were collected by centrifugation, packed in plastic petri dishes, frozen, and stored (-10°C) until used.

The purification procedures were monitored by electron microscopy and enzymatic assay. Fractions were collected, fixed with glutaraldehyde (1 percent final concentration), dialyzed, negatively stained (potassium phosphotungstate, pH 7.0) on carbon-coated, Formvar covered grids, and observed in a Siemens Elmiskop 1A equipped with a short focal length objective. Ribulose diphosphate carboxylase was assayed by modification of the method of McFadden and Denend (4). The final reaction mixture at pH 8.0 contained 0.01M tris(hydroxymethyl)aminomethane-HCl, 0.01M MgCl<sub>2</sub>, 0.001M dithiothreitol, 0.001M ribulose diphosphate (tetrasodium salt, Sigma, St. Louis), and 0.02M NaH<sup>14</sup>CO<sub>3</sub> (0.167 μc/μmole; New England Nuclear). The reaction was initiated by adding ribulose diphosphate after a 10-minute incubation period at 25°C.

Table 1. Results of the purification of carboxysomes and ribulose diphosphate carboxylase of *Thiobacillus neapolitanus*. The numbers in parentheses indicate the amount of material carried forward to the next step in the purification. The specific activity of a fraction is the number of enzyme units divided by the protein in that fraction.

Fraction	Enzyme units	Protein (mg)	Specific activity
Cells	13.6 (12.9)	1620 (1539)	0.008
Pressate	180.5 (142.5)	1520 (1200)	0.12
<i>Differential centrifugation</i>			
Supernatant	28.6	561	0.05
Fluffy layer	58.7 (55.2)	283 (266)	0.21
Hard pellet	53.0	258	0.21
<i>Sucrose step gradient</i>			
Sample layer and 45 percent sucrose layer	16.0	235	0.07
60 percent sucrose layer	28.9 (27.2)	20.7 (19.5)	1.4
65 percent sucrose layer	4.5	6.7	0.67
<i>(NH<sub>4</sub>)<sub>2</sub>SO<sub>4</sub> precipitate</i>			
	11.6 (9.5)	9.4 (7.7)	1.2
<i>Linear sucrose gradient</i>			
Band 1 (25 percent sucrose)	4.4	2.0	2.2
Band 2 (55 percent sucrose)	1.4	3.4	0.41

At desired intervals (0.5 to 2.0 minutes), the reaction was terminated by transferring aliquots into scintillation vials that contained an equal volume of glacial acetic acid. We used the scintillation fluid of Patterson and Greene (5) and a Packard Tricarb liquid scintillation spectrometer (model 3320) to measure radioactivity and a [<sup>14</sup>C]toluene standard (New England Nuclear) to determine counting efficiency. One unit of ribulose diphosphate carboxylase catalyzes the fixation of 1 μmole of CO<sub>2</sub> per minute at 25°C under the conditions specified. All enzyme activities have been corrected for the minimal background fixation that takes place in the absence of ribulose diphosphate. Specific activities are expressed as the number of enzyme units per milligram of protein. Protein was estimated by the method of Lowry *et al.* (6) with bovine serum albumin as the standard.

The purification methodology, including the results of protein and enzyme assays, is presented in Table 1. Frozen packed cells (8 to 10 g) were resuspended in distilled water to a final volume of 20 ml. This suspension, containing 1620 mg of protein, had low enzyme activity; ribulose diphosphate does not effectively penetrate the cells. Deoxyribonuclease I (Sigma) was added (final concentration, 10 μg/ml), and the suspension was passed through a French pressure cell at 20,000 pounds per square inch external pressure. Nearly all the protein was recovered in the material that passed through the press (pressate), and the enzyme activity increased 15-fold (specific activity, 0.12).

After passing the material through the pressure cell, we performed all manipulations (resuspending, gradients) in the following buffer: tris(hydroxymethyl)aminomethane-HCl, 0.005M; ethylenediaminetetraacetic acid, 0.001M; MgCl<sub>2</sub>, 0.001M; and NaHCO<sub>3</sub>, 0.02M; pH 8.0.

The pressate was centrifuged in a Sorvall RC2-B refrigerated centrifuge (SS-34 rotor) for 1 hour at 48,000g. There were three readily separable fractions: the supernatant, the fluffy layer (easily resuspended by light shaking), and the hard pellet (resuspended only by using a stirring rod and hard shaking). About 80 percent of the total enzymatic activity was sedimented (fluffy layer and hard pellet). The results of MacElroy *et al.* (7) who reported that the ribulose diphosphate carboxylase of either *Thiobacillus thio-*