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The Process of Formation of Ocean Crust

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Between 50 and 60 percent of the earth's surface is covered by ocean with a depth greater than 2 kilometers. Underlying most of this ocean is a zone of the solid earth called the crust, which in turn overlies the mantle. Ocean crust is formed at the mid-ocean ridge system.

Summary. Ocean crust is the outermost layer of earth under the oceans. It is separated from the underlying mantle by a seismic transition zone called the Moho. A widely held view is that the Moho represents a petrologic change from basaltic-type rocks to a mantle composed mostly of olivine and pyroxene. According to this view, crust is formed by a steady segregation of basaltic melt, derived from partial melting of the mantle, into a crustal magma chamber wherein cooling and crystallization bring about steady-state accretion to the continuously spreading plates. There is sufficient disagreement between the predictions of this hypothesis and marine geophysical data to cause one to doubt the validity of this formation process. At least two other processes are more compatible with the geophysical data. In one, the crust is formed from the episodic injection of basaltic dikes from a mantle reservoir and the Moho is a primary petrologic boundary. In the other, the crust is treated as a mechanical boundary layer in which thermal contraction results in cracking; by comparison, in the mantle thermal contraction is accommodated by flow. The upper part of the crust is formed from episodic extrusion and intrusion of basaltic melt. The lower crust is formed by rapid hydrothermal alteration of mantle that may be continuously or episodically injected by viscous flow at temperatures below the melting temperature.

This identification of the place of formation of ocean crust is based on geological and geophysical data collected over the last 15 years [for a review, see (*1*)]. Now that the source of ocean crust has been identified, the next level of inquiry concerns the process by which it is formed. The discovery of sulfide deposits (*1*) on the mid-ocean ridges, which may be of economic interest, has served to stimulate this inquiry. In this article I will first review the evidence for the existance of an ocean crust, then present geophysical and geological constraints on the formation process, and finally consider which models of the process are consistent with the data.

Ocean Crust, a Background

Investigators with different backgrounds often perceive ocean crust in different ways, and therefore it is useful to define the term. In a strict sense, knowledge of the existence of an ocean crust is based solely on seismological data. These data indicate a zone characterized by a rapid change of compressional wave velocity (from about 7 to 8 km/sec) at depths of 8 to 11 km below the sea surface. This zone represents the base of the oceanic crust (the Moho, named after its discoverer Mohorovičić). From a geological viewpoint, the existence of a crust is inferred from studies of igneous rocks obtained from the sea floor. These are almost always basalts. Geochemical studies suggest that these basalts derive from partial melting of a rock of a different composition (the mantle). Hence the inference of a basaltic crust. However, a one-to-one correspondence between the geological and seismological crusts has yet to be proved, as we will see. The seismological definition of the crust will be used here.

Geological Data on the Crust

Direct evidence of the structure and composition of the crust below the sea floor comes only from deep-sea drilling. Although such drilling has been very successful, it has only scratched the surface of the crust. In the Atlantic Ocean several holes have penetrated about 500 meters, and in the Pacific Ocean one hole near Costa Rica has recently penetrated 1 km (*2*). Most of the other attempts have achieved only a few hundred or tens of meters. Nonetheless, the available data indicate significant differences between the Atlantic and Pacific crusts. In the Atlantic serpentinized peridotites and ultramafic rocks (rocks thought to represent the mantle which have been hydrothermally altered) have been found interspersed among lava flows and pillow basalts in the top few hundred meters (*3*). In the Pacific the top few hundred meters are usually composed of alternating lava flows and pillow basalts in varying proportions. In the Costa Rica hole vertical dikes were penetrated in the lower section of the hole (*2*).

The drilling results support what has been learned about the process of crust formation by other methods (*4*). That is, the upper few hundred meters of crust are formed by the extrusion of lava flows and pillow basalts which are often ponded in small valleys. Below this depth in the Pacific are vertically injected dikes, which must have also served as the feeders for the extrusives. The greater diversity of rock types in the Atlantic indicates that the process is causing a mixture of basaltic melt and upper mantle source rocks to be emplaced near the sea floor. This finding suggests that in the Atlantic the amount of basaltic melt is less than that at most Pacific spreading centers.

Ophiolites (thought to be sections of ocean crust exposed on land) are another source of information on submarine igne-

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ous processes, whether or not they are actually indicative of present-day ocean crust processes. A schematic synthesis of ophiolites (*5, 6*) is shown in Fig. 1. Ophiolites are typified by the sequence pillow basalts, dikes, gabbros, cumulate gabbros, and ultramafics. In most cases the ultramafics show hydrothermal alteration, but only in the Xigazê example can the alteration be shown to have occurred in situ. It is generally held that in the other cases the alteration occurred after emplacement on land. The wide thickness variation of the basaltic sections indicates significant variations in the quantity of basaltic melt available for the formation of these sections. Since the degree of melting is very sensitive to temperature, one could infer from these data that these sections were formed in areas with different mantle temperatures.

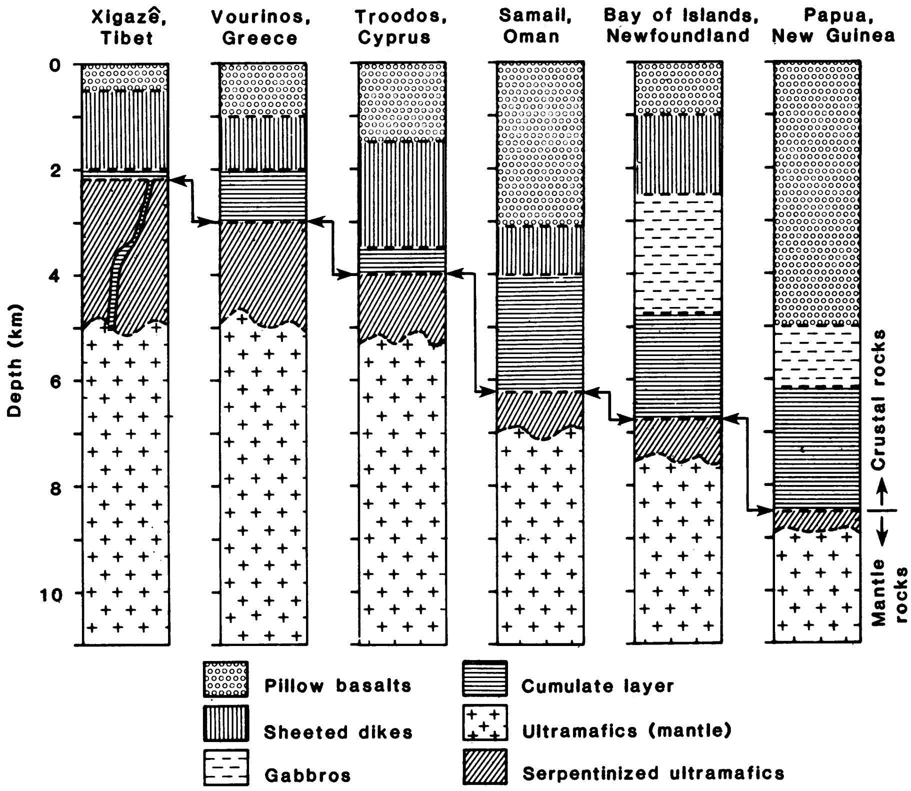

Fig. 1. Schematic sections of ophiolites (*5, 6*). The basaltic section varies in thickness from 2 km (Xigazê) to about 8.5 km (Papua).

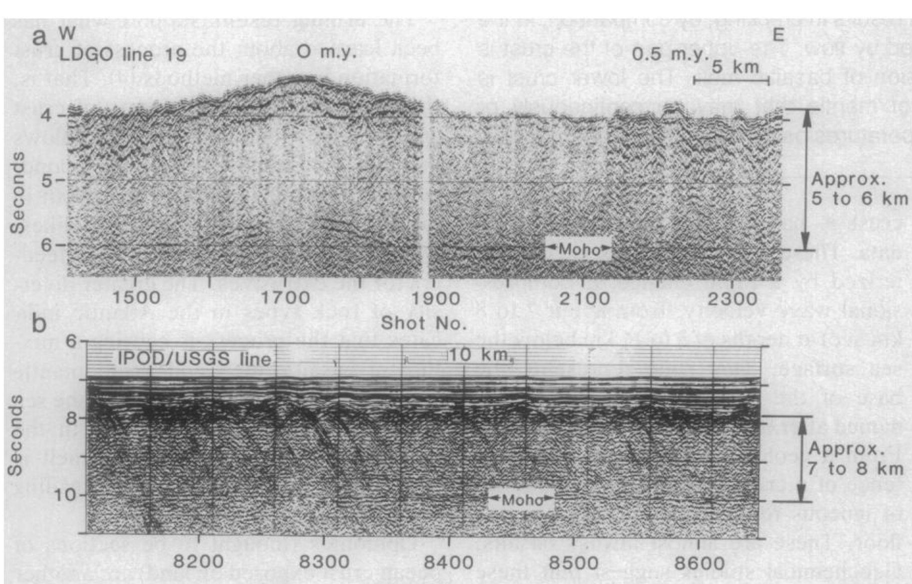

Fig. 2. Multichannel seismic reflection profiles from (a) the East Pacific Rise at 9°30′N (*8*) and (b) Atlantic crust 135 million years (*m.y.*) old. The seismic Moho occurs at a two-way travel time of about 2.1 seconds in both profiles. There is no evidence of an increase in travel time under the East Pacific Rise axis due to low-velocity magma.

A widely used justification for equating ophiolites to ocean crust is the approximate agreement between velocities measured on small (1-centimeter) ophiolite samples and seismic refraction velocities (representing averages over about a kilometer) (*7*). A difficulty in making these comparisons is lack of knowledge of cracks and pore water pressure, which can have large effects on velocity. These effects are well known in the upper crust where porosities can reach 25 percent, but they are ignored in the lower crust where it is assumed that cracks do not occur. This assumption requires verification under mid-ocean ridge stress conditions before it can be properly applied. High-pressure experiments with large-volume samples containing cracks have been initiated by N. I. Christensen at the University of Washington.

Because of the effects of serpentinization on velocity, the seismic Moho in the Xigazê ophiolite would be not at the base of the basaltic section but at the base of the serpentinized zone, which is at a depth of about 5 km (*6*).

Constraints from Seismology

Seismic refraction data (*7*) have shown that the rate of transition from crust to mantle is variable, occurring in some cases over a depth range of several kilometers and in others over a few hundred meters. Often the transition is sufficiently sharp to allow the reflection of vertically incident seismic waves with a frequency of less than 6 to 8 hertz, or a wavelength of about 1 km. Figure 2 shows such data from the East Pacific Rise and from Atlantic crust 135 million years old. These data show the crust-mantle transition zone. Several features of these data are important to this discussion. The two-way travel time of seismic waves through the crust (excluding sediments) is about 2.1 seconds in both examples, and there appears to be no discernible anomaly under the East Pacific Rise axis. To convert travel time to thickness we require knowledge of the rock velocities. These can be obtained from refraction data. Results (*8, 9*) indicate that these sections do not have the same thickness, primarily because the upper crustal velocities are higher in the Atlantic section than in the Pacific section. It has been shown that there is often an increase in the upper crustal velocity with age (*10*). If this were all that was occurring, we would expect the two-way travel time to the Moho to decrease with age. It does not, and this indicates that the crust may thicken with age (*11*).

The data in Fig. 2 also show that the Moho is formed in a very short time, that the process of ocean crust formation has not changed substantially over hundreds of millions of years, and that the formation process is independent of the ocean we are studying (at least seismologically).

Seismic data also show that the formation process results in a crustal thickness that is independent of plate divergence rate and ridge axis morphology (that is, the presence of an axial high or axial valley). Two examples from the Pacific and two from the Atlantic are shown in Fig. 3.

To understand the process of ocean crust formation, it is important to know if steady-state magma chambers exist in the crust under the rise axes. Evidence for these chambers must come from remote-sensing data. Seismology is the most useful technique because velocities are sensitive to the rigidity modulus, which is sensitive to temperature and the degree of melting. Initial experiments on the East Pacific Rise designed to detect partial-melt (low-velocity) zones (*12*) were refraction experiments along the axis of the ridge. These data were interpreted in terms of horizontal homogeneous layers, and no allowance was made for three-dimensional wave propagation effects. This is a serious simplification, because the velocity variations perpendicular to the ridge can be as large as the depth variations. Although there is evidence for a decrease of velocity with depth in these data, they provide little constraint on the width or depth of this zone. In spite of this, rather elaborate models which invoked a magma chamber about 10 km wide were developed on the basis of these data (*13*). These data were taken at 9°30′N on the East Pacific Rise over the same ground traversed by the reflection data in Fig. 2. The reflection data do not support such a large low-velocity zone. More recent experiments (*14, 15*) on the Juan de Fuca Ridge and at 12°N on the East Pacific Rise were designed specifically to constrain the structure in the lower crust under the axis. These experiments were conducted perpendicular to the ridge and showed that any low-velocity zone in the lower crust is either absent or less than about 2 km wide. This result is more consistent with the reflection data.

Mid-Atlantic Ridge refraction data exhibit no evidence for low-velocity zones in the lower or upper crust that would be indicative of partial melt (*16. 17*). In fact, shear waves propagate across the ridge and earthquakes occur in the mantle below the axis of spreading (*16, 18*). The earthquake data show that on parts of

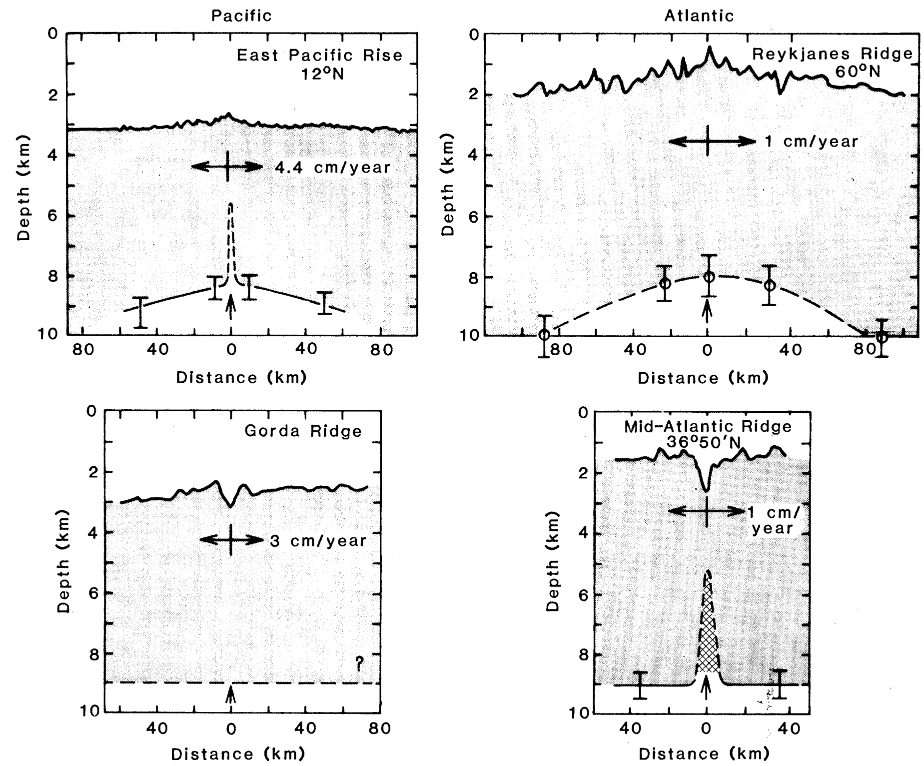

Fig. 3. Four sections across Pacific and Atlantic spreading centers showing the depths to the Moho as determined from seismic refraction experiments. The 12°N section (*15*) has either no axial low-velocity zone or one less than about 2 km wide. The Reykjanes Ridge section (*17*) showed no evidence for a distinct axial low-velocity zone. The 36°50′N section (*16*) has a thin crust at the axis, an absence of a Moho under the axis, but no low velocities under the axis that would indicate a magma chamber. For the Gorda Ridge section, well-determined crustal thickness data are lacking. Earthquake data (*35*) show seismicity extending below depths of 9 km, as was found on the Mid-Atlantic Ridge (*18*); these results suggest an absence of a crustal magma chamber.

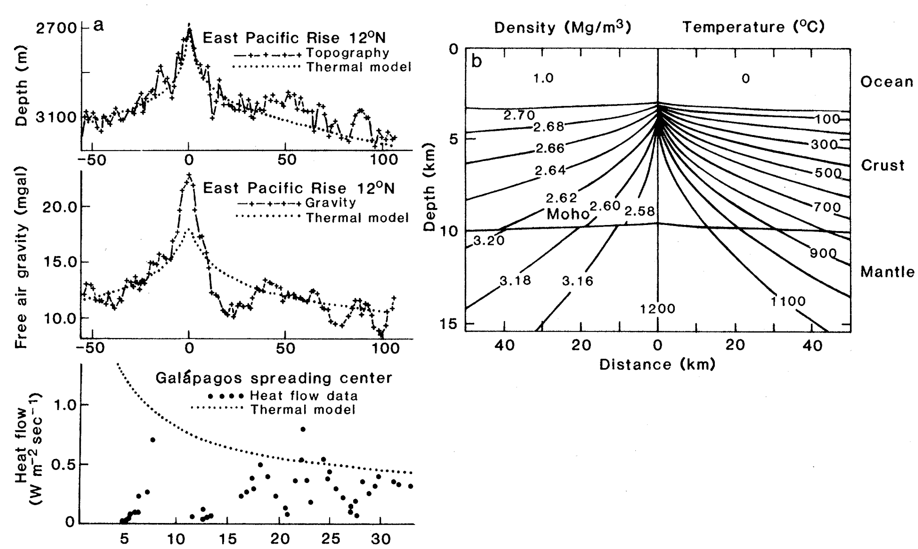

Fig. 4. (a) Bathymetry and gravity data from 12°N and heat flow data from the Galápagos spreading center compared to predictions from the thermal model with a conductively cooled crust. The gravity data are higher and the heat flow data lower than the model predictions. (b) Densities and temperatures from the thermal model with a conductively cooled crust. The topography, gravity, and heat flow data from this model are shown in (a).

the Mid-Atlantic Ridge even the upper mantle is at a sufficiently low temperature to allow stress to be relieved by brittle fracture.

The evidence for a very narrow intrusion zone under the axis is also more consistent with the results of detailed geological mapping based on the use of deep-towed cameras and manned submersibles (*4*). These data show that on every ridge studied to date the width of the zone of intrusion near the sea floor is less than a few kilometers. This has been verified in the Pacific by magnetic anomaly transition widths (*1*). Another conclusion from the mapping data is that the extrusion process is episodic in both space and time (*4*). The data are clear that on the Mid-Atlantic Ridge and at least on some parts of the East Pacific Rise there are presently no magma chambers underlying the axis of spreading. We shall see that this is not inconsistent with density and thermal data.

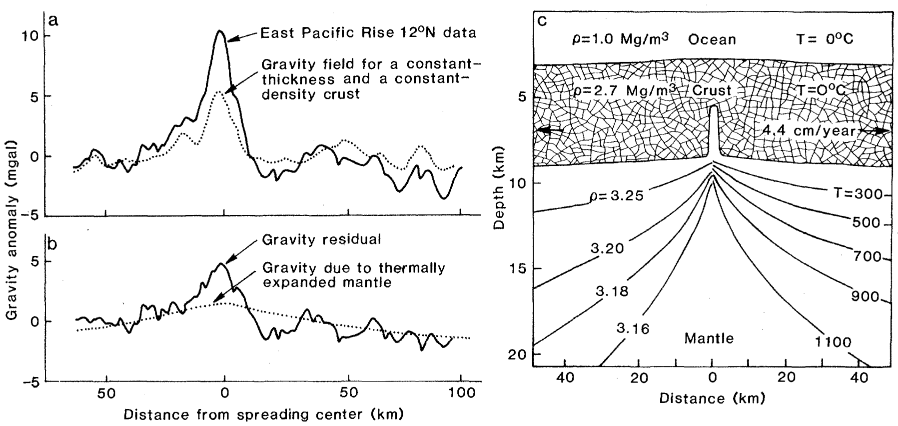

Fig. 5. (a and b) The 12°N gravity data compared to the calculated gravity for a constant-thickness and constant-density (ρ = 2.7 Mg/m^3) two-dimensional crust. The difference between the observed and calculated gravity (residual) has a narrow gravity high (b) that cannot be accounted for in terms of the thermally expanded mantle. This result indicates a zone of high density in the crust under the axis. (c) A schematic cross section of the axis at 12°N that is consistent with the gravity, seismic, and topographic data. The crust is assumed to be rapidly cooled by water circulating through cracks that are induced by thermal contraction. The gravity high has been interpreted as a 1-km-wide diapiric intrusion of mantle into the crust (*23*).

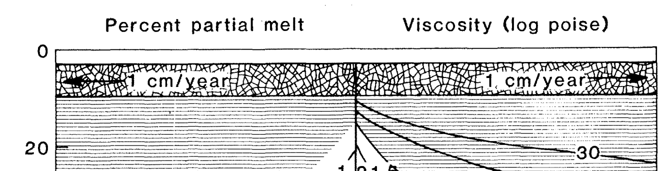

Fig. 6. Estimates of the percentage of partial melt and viscosity (see text) based on the thermal model for spreading rates of 1 and 4.4 cm/year and a temperature of the upwelling mantle of 1100° and 1200°C. The crust is assumed to be rapidly cooled by hydrothermal circulation (cracked pattern). Horizontal stipling indicates mantle viscosities greater than 10^{22} poise. Most of the mantle flow will occur at viscosities less than this value. Variations in spreading rate and mantle temperature can lead to substantial differences in partial melt and viscosity. These will cause variations in the basaltic magma available in the crust and will influence the ridge crest morphology (*29*).

Constraints from Gravity

One of the major advances in understanding plate tectonic processes was the formulation of a simple thermal model that explains the increase in depth of the oceans away from the mid-ocean ridges (*19*). In this model loss of heat through the sea floor by conductive cooling results in thermal contraction of the crust and mantle and a deepening of the oceans with age. In computing the thermal contraction, the volumetric expansion coefficient was assumed. This assumption implies that contraction is accommodated by flow in the rock. If the linear expansion coefficient were assumed, cracks would result, which is the case at low temperatures and pressures but unlikely at high temperatures and pressures. Thermal contraction results in a density change, and therefore this model should predict topography, gravity, and heat flow data as a function of crustal age. The model does explain the major depth-age patterns in the oceans, the general features of the gravity field, and heat flow variations well away from the ridge axis (*20*). When we try to use this model to explain the details of the mid-ocean ridge processes, however, we run into trouble. We often find in the Atlantic a deep axial valley at the ridge axis and a gravity anomaly less than that predicted by the model. We find in the Pacific that the topography near the axis is reasonably well modeled, but the observed gravity is greater and the conductive heat flow is less than the predicted values (*21, 22*).

Examples of topography and gravity from the East Pacific Rise at 12°N and heat flow data from the Galápagos Ridge are shown in Fig. 4a together with the predictions of the thermal model. The density and temperature distributions for the 12°N spreading rate are shown in Fig. 4b. The discrepancies between the model and the data are probably the result of the application of the volumetric expansion coefficient to the crust. If the linear coefficient is used, that is, if we allow cracks, and if we allow convective cooling of the crust by seawater circulation through these cracks, heat is removed from the crust far more rapidly and the density structure can be significantly altered.

Seismic reflection and refraction data from the East Pacific Rise near 12°N indicate a crust of near constant thickness adjacent to and under the rise axis. Therefore, as a first approximation we can consider the crust as a constant-thickness and constant-density layer of variable depth overlying a thermally expanded mantle. Differences between the observed and theoretical gravity fields should indicate where this approximation is weak. Figure 5a shows the 12°N data and the gravity effect of a constant-thickness and constant-density crust of variable depth. Figure 5b also shows that the gravity residuals still contain a positive anomaly over the ridge axis, and this anomaly is too narrow to be accounted for in terms of the thermally (volumetrically) expanded mantle (*23*). The data therefore indicate that higher densities are required under the rise axis. This anomaly can be explained in terms of a narrow (1 to 2 km wide) dikelike body in the lower crust that is more dense than the surrounding crust (*23*) (Fig. 5c).

This result cannot be interpreted simply as the filling of cracks, generated by thermal contraction, with water, because the water adds mass to the crust which exacerbates the gravity problem. One possibility is that strain is imparted to the crust near the ridge axis by plate driving forces, and this strain results in a volume increase (density decrease) that is accommodated by hydrothermal alteration. Stated another way, this result can be interpreted in terms of hydrothermal alteration of mantle material with an associated volume increase and no mass flow out of the lower crust. The gravity data do not allow low-density material in the lower crust under the ridge axis.

Constraints from Heat Flow

The observed conductive heat flow near the rise axis is considerably less than that predicted by the thermal model (Fig. 4a). This discrepancy is accounted for in terms of convective heat transport through seawater circulation. There is now abundant and spectacular evidence for convective cooling by seawater, for example, the hot-water vents found on the East Pacific Rise (*1*). The rate of heat removal by a single vent with an exit temperature of 300°C is about 6×10^7 calories per second, and at 21°N there is about one vent every kilometer over the limited area where they occur (*1*). The plate divergence rate here is about 6 centimeters per year, which implies that 6 m of new crust must be generated every 100 years (on average). If we assume a latent heat of freezing of 300 calories per cubic centimeter, a specific heat of 0.9 calorie per cubic centimeter per degree Celsius, and a temperature of 1200°C, this implies a rate of heat injection into the crust (5 km thick) over a 1-km length of axis of 6×10^{16} calories per 100 years. The rate of heat removal by a single vent is 18×10^{16} calories per 100 years. Therefore, the rate of heat removal is about three times that of heat emplacement. Stated another way, if we had a 6-m-wide injection of magma every 100 years, the convective cooling would cool 5 km of crust to 0°C in about 30 years. Although this explains the low values of conductive heat flow near the axis, these data do not strongly constrain the depth of hydrothermal circulation.

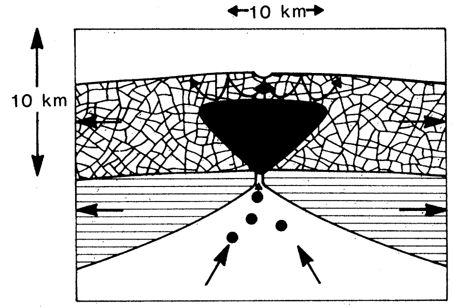

Fig. 7. Diagram of the model of ocean crust formation that invokes a large steady-state crustal magma chamber (*1*). In this model the Moho is a petrologic boundary. Such a large magma chamber is not supported by the seismic data. This model is not consistent with the gravity data, and it does not adequately explain the narrow extrusion zone at the ridge axes.

Possibly the strongest constraint on the depth of circulation comes from the seismic results. The absence of low seismic velocities in the lower crust within a few kilometers of the rise axis indicates that the temperature here is well below that predicted by the conductive cooling model (*23*). This would be indicative of cooling throughout the crust. This idea is supported by observations from the Oman ophiolite (*24*) and the Xigazê ophiolite (*6*). These observations are also consistent with cracking theory (*25*).

One further comment about the thermal history of the crust should be made. The heat flow data approach the theoretical curve away from the ridge (Fig. 4a). This result suggests that, away from the ridge, the cracks become sealed, probably with precipitation from seawater solutions, and the crust will tend to a conductive cooling regime (*26*). This implies that the crust must undergo a reheating before cooling again at much greater ages, which could result in metamorphic overprinting of textures and mineralogy acquired near the ridge axis that would complicate interpretation of these rocks, were they to be exposed eventually on land.

To place the process of ocean crust formation in the larger context of mantle flow, it is instructive to consider models of the upper mantle that are based on the thermal model and include data on partial melting and viscosity. I have incorporated partial melting data (*27*) and viscosity estimates that include temperature and pressure effects (*28*) into the thermal model, using calculations that I have described (*21*). In these calculations I have assumed that the crust is cooled very rapidly by seawater circula-

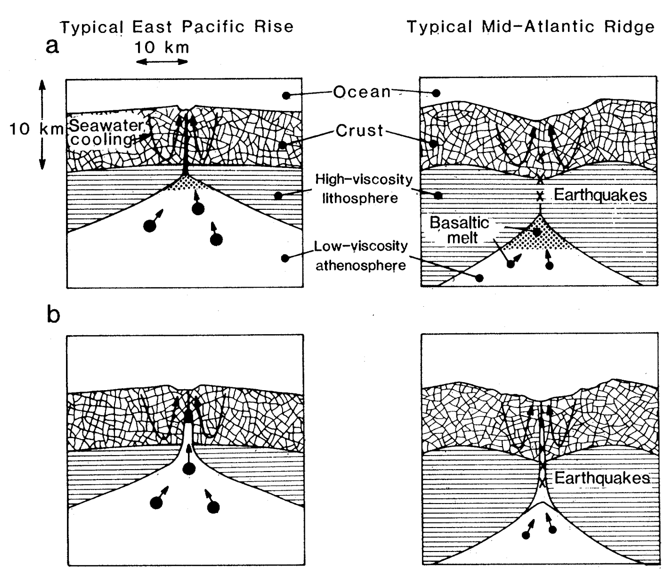

Fig. 8. (a) Diagram of the model of ocean crust formation in which the crust is formed by episodic injection of basaltic dikes from a mantle reservoir and the Moho is a petrologic boundary. This model requires that the amount of basaltic melt is independent of spreading rate and all the melt is available to form crust. (b) Diagram of the model of ocean crust formation that invokes diapiric intrusion of mantle containing basaltic partial melt. The depth to the Moho in this model is controlled by the depth to which hydrothermal circulation and metamorphism extend (if the thickness of the basaltic section is less than about 5 km). This model accounts for the fairly uniform depth to the Moho (independent of spreading rate and mantle temperature), the absence of steady-state crustal magma chambers, the gravity data on the East Pacific Rise, and the seismic data.

tion and therefore does not participate in the conductive cooling process. Moreover, two spreading rates (1 and 4.4 cm/year) and two assumptions for the mantle temperature (1100° and 1200°C) were considered. The results are shown in Fig. 6. At slow spreading rates and low temperatures (Mid-Atlantic Ridge?), the existence of partial melt even near the top of the mantle is unlikely because the rate of conductive cooling is large as compared to the spreading rate. The predicted viscosity is sufficiently high to allow brittle fracture. This idea is supported by the observation of earthquakes under the axis in the mantle (*18*). These high viscosities could also be responsible for the existence of the axial valley (*29*). For higher mantle temperatures (hence lower viscosities and more partial melt) the axial valley may disappear (Reykjanes Ridge). At very high temperatures (hot spots), sufficient partial melt may be generated to form basaltic crust of very great thickness [Iceland (*30*) and possibly some ophiolites]. These models suggest that in the Atlantic it is extremely unlikely (impossible) that steady-state crustal magma chambers exist (*31*). Therefore, the process of ocean crust formation must be episodic.

In the Pacific the faster spreading rates will allow melt to occur closer to the top of the mantle, but we would not expect to find large steady-state magma chambers in the crust. Short-lived small magma chambers are more likely. In the case of low mantle temperatures and high viscosities, axial valleys may also occur on faster spreading ridges (Gorda Ridge?).

Models of the Process

Any viable model of the process of ocean crust formation must account for the following: (i) for the formation of crust whose thickness is largely independent of spreading rate and ridge crest morphology; (ii) for the apparent occurrence of mantle material interlayered with lava flows and pillow basalts in the Atlantic and their absence in the Pacific; (iii) for the episodic nature of the process; and (iv) for the absence of low densities in the lower crust under the ridge axis in the Pacific. Three models are considered.

Model 1. This model (Fig. 7) represents a widely held view (*1*) that the process of ocean crust formation is steady state. It is based on studies of the Samail ophiolite. In this model basaltic melt migrates upward from the mantle and accumulates in a large crustal magma chamber. A large part of the crust is formed by steady accretion resulting from the freezing of crystals to the sides and roof of the chamber and by accumulation of crystals settling to the floor. The upper crust is formed by episodic intrusion and extrusion of basalts, although it is not clear why the extrusion would be limited to the axial zone. In this model the Moho is a petrologic boundary.

This model is not viable for many reasons. It does not explain how Atlantic crust is formed (where there are no steady-state magma chambers). It is not consistent with seismic data on the East Pacific Rise. It is not consistent with gravity data, since the model would require a low-density zone in the lower crust. There is also the difficulty of accounting for how such a large magma chamber would survive in the presence of active hydrothermal cooling.

Model 2. In this model most of the crust is composed of dikes injected episodically and the Moho represents a petrologic boundary between basaltic-type rocks and ultramafics (Fig. 8a). This model requires that the amount of melt available from the mantle is constant on all ridges (in order to produce constant-thickness crust). This requirement implies that the mantle temperature must vary by just the right amount to compensate for the spreading rate–dependent cooling and that all the melt migrate to the surface. Although this constitutes a highly unlikely scenario, it cannot be ruled out at this time.

Model 3. The principal feature of this model (Fig. 8b) is the injection of a mixture of mantle rock and basaltic melt into the crust. The basaltic melt, being lighter, migrates through the viscous mantle and accumulates near the top of the injection diapir where it reaches the surface episodically through dikes and forms lava flows and pillow basalts at the sea floor. The quantity of melt available depends on the initial temperature of the mantle and the spreading rate–dependent cooling.

Hydrothermal circulation rapidly cools the rock mass by the propagation of cracks associated with thermal contraction down to depths where the cracks no longer can remain open, about 5 to 7 km. This depth depends on rock mechanical properties and not on spreading rate or mantle temperature. Thus it is likely to be constant over widely varying ridge crest conditions. Hydrothermal alteration of the ultramafics to a lower density and velocity is facilitated by continual strain imparted by the diverging plates. This strain may explain how the increase in volume (decrease in density) occurs without an embarrassingly large mass transfer. A limiting factor on the amount of alteration would be the mechanical strength, that is, the point at which the rock is sufficiently weakened by the alteration that cracks cannot remain open. In this model the Moho therefore represents the depth to which cracking, water penetration, and hydrothermal alteration extend.

Problems with this model concern geochemical fluxes. It has been argued (*32*) on the basis of global chemical fluxes that alteration to the extent involved in this model is unlikely and that hydrothermal circulation extends to a depth of only 1 to 2 km. However, counterarguments (*33*) based on sulfur oxidation suggest alteration to depths of about 5 km, or the full thickness of the crust.

Conclusions

Geophysical data in the Pacific and Atlantic indicate that the process of formation of ocean crust is not consistent with large steady-state magma chambers containing low-density melt. A process consistent with seismic, gravity, and thermal data consists of episodic or steady flow of a partially molten mantle diapir into the crust and rapid hydrothermal cooling and alteration. To account for a Moho whose depth is largely independent of the thermal regime (spreading rate and mantle temperature) and hence the quantity of partial melt, the most reasonable proposition appears to be that the Moho represents the depth to which water penetrates. If this is the process by which the Moho is formed, greater understanding of the mechanisms of water penetration through stressed hot rock and the associated chemical reactions is needed to explain the details of this process. Drilling into the lower crust could resolve some of these problems but the demise of the Ocean Margin Drilling Program (*34*), which had this problem as one of its investigative goals, appears to preclude this possibility.

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Molecular Biological Mechanisms of Speciation

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Recent discoveries in molecular biology have prompted speculation regarding their significance for evolution, with new synthetic hypotheses receiving great attention (*1–16*). Unfortunately, the intuitive appeal or conceptual breadth of a theory is not an infallible guide to its validity. Here we examine the empirical status of some of these new hypotheses in evolutionary molecular biology, those relating the origin of species to the evolutionary behaviors of repetitive DNA's.

Summary. Growing recognition that much of the evolutionary history of eukaryotic genomes reflects the operation of turnover processes involving repetitive DNA sequences has led to the recent formulation of models describing speciation as a consequence of such turnover. These models are of three general kinds: those attributing hybrid infertility to the process of transposition, those attributing hybrid infertility to mispairing between chromosomes of divergent repetitive DNA composition, and those assuming that change in repetitive DNA's can reset coordinated gene regulation. These models are discussed with respect to the kinds of evidence needed for their corroboration and to their significance for questions related to macroevolutionary punctuated equilibria and genetic revolutions.

Because of the diversity of new molecular biological proposals for speciation mechanisms, we find it convenient to group them under three headings, and to assess each of them in terms of four lines of evidence. At least these four are needed to test the new molecular biological proposals properly. First, there must be a known biological effect that can lead to reproductive incompatibility. Second, the molecular mechanisms presumed responsible for that effect must be known to operate in species in which the effect is observed. Third, there must be evidence that molecular mechanism and biological effect are coupled. Fourth, there must be parallels between biological effect and speciation, such as instances within related species in which the effect can reasonably be interpreted as primarily responsible for, and not secondarily a consequence of, reproductive isolation.

By speciation, we mean the establishment of biological characteristics (i) that preclude fertilization of members of one population by those of another (prezygotic reproductive isolation) or (ii) that give rise to pathologies among hybrids, or hybrid descendants, which in turn preclude gene flow between these populations (postzygotic reproductive isolation) (*17*).

Molecular Mechanism I: Genomic Disease

The view that many, although not all, transposable elements provide no functional benefit to the organism is now commonplace (*11–14*). Whether or not such elements decrease organismal fitness is as yet uncertain. It is clear on theoretical grounds that transposable elements can decrease fitness and yet be maintained within Mendelian populations (*18*).

Transposable elements are potentially important for the phyletic (within-species) evolution of both Mendelian and asexual populations (*10, 14, 19*). An analogy with disease suggests that they might also be important in the formation of new species, a process that can be uncoupled from phyletic evolution. If an isolated population has either lost or failed to acquire transposable elements that have spread throughout remaining populations of the species, then it may lack some property establishing immunity to these elements. Matings between individuals of that isolate and individuals of other populations could lead to abnormalities resulting from proliferation of the novel, disruptive, transposable element (*20*). Such abnormalities could lead to sterility of F_1 or F_2 hybrid progeny, thereby establishing postzygotic reproductive isolation. To avoid gamete wastage, natural selection might then act to establish behavioral or mechanical (or both) prezygotic barriers to mating. This is in effect a "genomic disease" model for speciation.

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