Reports

Model Simulation of the Cretaceous Ocean Circulation

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Three-dimensional numerical ocean circulation model experiments that were designed to evaluate the circulation characteristics for the mid-Cretaceous (~ 100 million years ago) show that the primary direction of flow through the Tethys Ocean was eastward; in contrast, a westward flowing circumglobal Tethys current has been a consistent feature of earlier reconstructions of Cretaceous ocean circulation. The model studies demonstrate that (i) ocean circulation is sufficiently sensitive to the role of continental positions, sea level, and climate to limit the application of modern analogs to past circulations, and (ii) reconstructions based on limited biogeographic data may not provide unique surface circulation patterns.

THE TETHYS OCEAN IS ONE OF THE most distinctive features of the paleogeography for much of the Mesozoic and Cenozoic. Tethys separated the North American and Eurasian continents from the southern continents of Africa, South America, and India and provided a circumglobal oceanic connection at low paleolatitudes. The paleocirculation in Tethys is of considerable interest because of this geography. Particularly for the Cretaceous, much of the well-studied marine sedimentological and paleontological record for this warm time period is associated with the Tethys Seaway and adjacent epicontinental seas.

A westward flowing surface current that circled the globe at the tropics and flowed through the Tethys Ocean (Fig. 1) has been hypothesized on the basis of early laboratory circulation experiments (1) and reconstructions based on Cretaceous biogeography (2, 3). Luyendyk *et al.* (1) simulated the surface circulation for the Late Cretaceous using a curved rotating disk with an applied wind stress and reconstructed Cretaceous continental geometries. Results from these laboratory experiments suggested that a westward circumglobal current system dominated the flow through the Tethys Ocean.

Biogeographic evidence (1, 2) for such a current includes: (i) the homogeneity and distinctiveness of Tethyan faunas, which is indicative of a well-connected and well-defined biogeographic regime; (ii) the occurrence of fauna with Tethyan affinities, and therefore an implied Caribbean source, on mid-Pacific guyots; (iii) evidence of a warm climate in Europe that may be related

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to the poleward deflection of Tethyan waters associated with the bulge of Africa; and (iv) evidence that the migration of larger foraminifera (4) was mostly east to west. Based on this evidence, the concept of a westward flowing circumglobal Tethys current has become an accepted feature of Cretaceous paleoceanography.

The development of ocean models that simulate three-dimensional temperature, salinity, and flow fields from specification of geometry, atmospheric boundary conditions for wind stress, heat and moisture balance, and physical laws has proceeded rapidly during the last two decades (5, 6). However, application of these models to paleoceanography has been limited (7, 8). In this report, we describe results from global, numerical ocean model experiments for Cretaceous geography. These experiments suggest that the hypothesis of a westward flowing circumglobal Tethys current may be incorrect.

The ocean model (9) is based on the primitive equations for a hydrostatic, Boussinesq (the differences in density are small and the mean density is utilized in the governing equations except in the computation of the buoyancy term) ocean with a rigid lid. The numerical scheme is that of Bryan (10). The horizontal resolution is 5° by 5°, and the vertical levels and bathymetry are based on grid thicknesses of 50, 450, 1500, and 2000 m. Because the model has a relatively coarse grid resolution, diffusion processes are used to account for mesoscale eddy effects. Vertical mixing is parameterized as a function of static stability. The large-scale features of the global ocean are accurately simulated with this type of model, although the resolution and vertical mixing parameterizations must be considered as limiting factors in any interpretation. This model allows the prediction of the threedimensional fields of velocity, temperature, and salinity in an ocean of any specified geometry given the atmospheric conditions at the ocean surface. The wind stress, surface heating, evaporation, and precipitation at the ocean surface can be specified from observations or from the results of atmospheric general circulation models (GCMs).

The mid-Cretaceous continental reconstructions and distribution of epicontinental seas, as given by Barron et al. (11) for 100 million years ago, were digitized and then transformed into the 5° by 5° ocean model resolution (Fig. 2). The continental positions for the mid-Cretaceous are reasonably well known. However, because of the difficulty of reconstructing accurately Cretaceous ocean bathymetry (12), a simple bowllike ocean bathymetry was utilized for all oceanic regions other than epicontinental seas. The bathymetry simply was decreased by one vertical level with each grid-point distance from the continental margin until the maximum model depth was reached. A



Fig. 1. A reconstruction of mid-Cretaceous surface ocean currents, based on biogeography and hypothesized controls on ocean circulation after Gordon (2). The continents are labeled NA, North America; AS, Asia; SA, South America; AF, Africa; IN, India; AU, Australia; M, Madagascar; and AN, Antarctica. Tethys is the region between NA-EU-AS and SA-AF-IN.

sensitivity experiment, in which oceanic plateaus in the Pacific and shallow depths at the ends of the Tethys Seaway were included, was performed to evaluate the importance of the bathymetry assumptions on the simulated pattern of ocean circulation.

The atmospheric conditions specified at the ocean surface were derived from a mean annual atmospheric GCM (13) for mid-Cretaceous geography (11). As one test of the sensitivity of the model to specified atmospheric forcing, we also used parameters derived from a GCM experiment for mid-Cretaceous geography and four times the present-day atmospheric carbon dioxide concentration (14) (a warmer Cretaceous case). In both of these cases, the atmospheric forcing is consistent with the Cretaceous continental geometries and only the degree of global warmth is different.

In both of the sensitivity experiments, the pattern of circumglobal flow through Tethys is similar to that in the principal simulation, indicating that these results are not sensitive to reasonable variations in the forcing parameters or in the bathymetry. Consequently, the model results can be taken as a reasonably robust simulation of the surface current patterns for the reconstructed mid-Cretaceous geography.

The current vectors and streamlines (Fig. 2) simulated for the surface layer (upper 50 m) of the ocean circulation model with mid-Cretaceous geography are significantly different from those of earlier reconstructions of Tethyan flow patterns (1-3). Although westward flow occurs throughout the tropical Pacific, a predominant westward flow through Tethys does not occur. Rather, circulation in the Tethys is dominated by clockwise flow, which produces a general easterly flow along the northern margin of the ocean basin. The clockwise, gyre-type circulations that develop between North America and South America and between Eurasia and Africa yield components of westward flow and components of eastward flow.

In retrospect, the previously proposed hypothesis that there was a westward circumglobal circulation pattern seems unreasonable on the basis of the GCM wind stresses and the geometry of Tethys. In the earlier reconstructions, the westward flow in the tropical Pacific and the poleward deflection by the land barrier of Africa are analogs of the modern tropical surface currents and the poleward moving Gulf Stream or Kurioshio currents. However, in the Luyendyk et al. (1) reconstruction, the Tethys current turned again westward near 30°N and then southward around Africa. In the reconstruction in Fig. 1, the Tethys current also appears to go around the bulge of Africa. In both of these cases, the flow appears to follow the geometry of Tethys rather than to be controlled by the nature of the wind stress or by an angular momentum balance. In the numerical ocean model, the poleward moving surface flow turns eastward (because of the position of the westerly winds), developing gyre-like circulations in Tethys much like those in the modern mid-latitude oceans.

Why are the results from the numerical model so different from those of the pioneering laboratory experiments by Luyendyk et al. (1)? Much of the difference might be ascribed to the physical problems of representing ocean circulation by a rotating dish and by the specific problems associated with representing the equator in these laboratory experiments. Differences in boundary conditions between the laboratory experiments and our model may also be important. The Cretaceous continental reconstruction in the laboratory experiment placed Asia too far equatorward, compared to its position in more recent reconstructions, and hence Tethys was simulated as a small (less broad) ocean. Furthermore, the laboratory reconstruction had modern continental outlines and did not include epicontinental seas. The lack of realistic continental outlines also resulted in a narrower and more sinuous Tethys than indicated by more recent reconstructions.

Equally important, Luyendyk *et al.* (1) assumed that during the warm Cretaceous, the westerlies would be displaced from 30° to 60° N to 40° to 60° N latitude. This

assumption of a warm climate was based on a modern "summer" analog. In an additional laboratory experiment based on present-day mean winds (no poleward displacement) and Cretaceous geography, a gyre developed adjacent to the eastern margin of North America, although the westward circumglobal flow remained the dominant component of the circulation. In contrast, our atmospheric GCM experiments for warmer climates and Cretaceous geography show no evidence of a poleward displacement of the westerlies (15). The large differences in applied wind stresses and the differences in the shape and size of Tethys may well have contributed to the differences in results between laboratory and numerical models. This last point also indicates that the flow in Tethys may have been sensitive to changing size and configuration as a function of continental positions and changing sea level. This point was not recognized, however, in earlier reconstructions, as the circumglobal flow through Tethys appears to be a ubiquitous feature of paleoceanographic reconstructions even though continental geometry and sea level evolved during the Cretaceous and Early Cenozoic (2, 3).

The primary test of the model simulations should be comparisons with observations. Interestingly, despite the large differences between the numerical ocean model simulations and earlier reconstructions based on biogeographic data, the model results are apparently not at odds with the data. The homogeneity and distinctiveness of the Tethyan faunas can still be reasonably ex-

Fig. 2. Simulated mid-Cretaceous surface ocean circulation illustrated by (A) current vectors (in centimeters per second) with maximum vector length shown and (B) streamlines. Streamlines are lines that follow the flow of the fluid. The continents given with the model resolution of 5° by 5° are labeled as in Fig. 1.



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plained. The apparent warmth of Europe is accounted for by the poleward flow along the eastern margin of North America and through the poleward deflection of westward flow by the bulge of Africa. The mid-Pacific guyots are in a zone of westward flow and the Tethyan affinities could easily have a western Caribbean source. Finally, the model simulation provides opportunities for both east-to-west and west-to-east faunal migrations in Tethys. This result suggests that the biogeography, either because of an incomplete record or because the relations between biogeography and ocean circulation patterns are not fully understood, may not provide uniquely determined surface circulation patterns. Physically consistent and comprehensive reconstructions of ocean circulations, which can only be derived from fully resolved ocean circulation models, may be required to assess past ocean circulations.

The results of the numerical ocean model experiments for Cretaceous paleogeography indicate that the concept of a westward flowing circumglobal equatorial current for the Cretaceous and for much of the Mesozoic and Cenozoic must be re-assessed. At a minimum, earlier reconstructions are probably too simplistic and the circulation may have changed substantially as a function of ocean geometry (continental positions and sea level). The concept of poleward displacement of atmospheric winds during warm time periods, which has not been substantiated with GCM studies, apparently influenced earlier paleoceanographic reconstructions. Furthermore, ocean surface current reconstructions based on limited biogeographic data may not tightly constrain surface circulation patterns.

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Hearing in Honey Bees: Detection of **Air-Particle Oscillations**

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Although the airborne sounds produced by dancing honey bees seem essential in the bees' dance communication, attempts to show directly that bees can detect airborne sounds have been unsuccessful. It is shown here that bees can in fact detect airborne sounds and that they do so by detecting air-particle movements. Most vertebrates, by contrast, detect pressure oscillations. Because all traveling sound waves have both components, either can be used in sound detection. The bees' acoustic sense appears to be sensitive enough to allow bees to detect the air-particle movements that occur within several millimeters of a sound-emitting dancer.

LTHOUGH MUCH IS KNOWN ABOUT the orientation of honey bee (Apis *mellifera*) dancers and the role of the dance language in a colony's overall biology, we still do not know through which sensory modalities the dance communication occurs (1). Sounds, however, are evidently essential: dancers produce sounds by vibrating their wings (2), and the dances of bees with clipped wings and of the mutant diminutive wings are ineffective (3), as are silent dances by bees with normal wings (4). Further, a mechanical model of a dancing bee can successfully communicate with its "nestmates" only when its artificial wings generate normal sounds (5). The vibrations of a dancer's wings generate strong air-particle oscillations within a few millimeters of the dancer's abdomen, but only relatively weak pressure oscillations (2, 6) and no comb vibrations (7), suggesting that the sounds may be detected by dance followers as airparticle movements (8). Uninformed by these insights, previous attempts to elicit responses by bees to airborne sounds have been unsuccessful (9). Here we report our efforts to condition bees to respond to artificial airborne vibrations similar to those produced by dancers.

Individual bees visiting a feeder were trained to associate the presentation of a 5-slong sound (conditioned stimulus, CS) with

a mild electric shock. On each training trial, the shock was delivered 4 s after the sound's onset and caused the bee immediately to withdraw from the feeder (10). The sounds were generated at the open end of a narrow glass tube by driving the air column in the tube with a loudspeaker (11). The open end of such a tube is a site of strong air-particle oscillations and relatively weaker pressure oscillations (6). Two different frequencies of sound were used as CS at different times: 14 Hz, the frequency of a dancer's abdominal waggling, and 265 Hz, the frequency of the dance sounds (12). On each training trial, the bee was scored as responding to the sound if she withdrew from the feeder in the 4-s CS-only interval, before the shock.

Twenty-four bees were individually trained to withdraw from the feeder in response to one of the sound frequencies (CS+) until each bee responded positively on at least five out of ten sequential trials (13). Sixteen of these trained bees, eight with 265 Hz as CS+ and eight with 14 Hz as CS+, were then used in a 20-trial frequency-discrimination procedure. In this procedure, each bee was given her CS+ and the alternative frequency (CS-) for ten trials each in pseudorandom order. The results, shown in Fig. 1, indicate that the bees can detect and learn to respond to both frequencies (acquisition, left) and that they can discriminate each frequency from the other (discrimination, right).

Because bees are highly sensitive to substrate vibrations, such vibrations in these experiments were measured and held below the bees' known physiological thresholds (14). Furthermore, eight additional bees trained to associate the 265-Hz sound with shock

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