earth's atmosphere (*18*). Clear connections are seen in the upper atmosphere (above 90 km), but below that it has been difficult to establish relationships based on the use of earlier measurements. The results presented here clearly demonstrate such a solar-terrestrial connection in the stratosphere.

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Species Formation Through Punctuated Gradualism in Planktonic Foraminifera

Abstract. *Detailed analysis of evolutionary changes in a 10-million-year long Late Neogene lineage of planktonic foraminifera has revealed a pattern that is not consistent with either the gradualistic or the punctuational model of evolution. The lineage was in stasis over a considerable part of its total duration but underwent relatively rapid, but not geologically instantaneous, gradual morphologic change that did not lead to lineage splitting. The term* punctuated gradualism *is suggested for this evolutionary modality.*

The question of whether new species arise through the slow and gradual phyletic transformation of entire populations leading to an unbroken, gradational chain of species (orthogenesis or phyletic gradualism) or whether they evolve rapidly (on a geologic time scale) in genetically isolated subpopulations (allopatric speciation or punctuated equilibrium) (*1*) has been discussed for more than a decade. It remains unclear which, if any, of these models predominates in the paleontological record. Many factors contribute to this uncertainty, but the most important is the scarcity of detailed quantitative studies of phyletic changes through long intervals of time in most fossil groups. Rather than forcing poorly documented patterns of evolutionary change to fit theoretical models, the evolutionary models should be formulated from studies of existing fossil lineages.

Evolutionary studies of fossil lineages, properly conducted, are laborious, but the time spent in generating the necessary data base should pay off by increasing our understanding of the nature of evolutionary patterns as well as of possible differences in patterns among organism groups. Morphologic changes need to be quantified from analyses of large numbers of specimens in long continuous sequences spanning several million years. Stratigraphic completeness and time resolution for a particular sampling density need to be evaluated (*2*). Patterns need to be tested statistically, for example, for precision of data, unidirectionality, stasis, and stepwise change. The geographic validity of an observed pattern must be confirmed to rule out the possibility that it has a nongenetic origin (migration).

We have analyzed the warmwater planktonic foraminiferal lineage *Globorotalia tumida* through the last 10 million years of its evolutionary history (Late Miocene–Recent) in DSDP Site 214 from the southern Indian Ocean (11°S, 89°E; water depth 1665 m). We were interested in determining long-term patterns of evolutionary change and, particularly, the evolutionary transition from *G. plesiotumida* to *G. tumida* across the Miocene-Pliocene boundary. We examined 105 samples taken at 10- to 30-cm intervals across the Miocene-Pliocene boundary and at about 2-m intervals in other parts. Sampling resolution was very good, between 5×10^3 and 15×10^3 years across the boundary and 2×10^5 years otherwise. Biochronologic analyses indicate a complete sequence across the Miocene-Pliocene boundary, whereas about 3 million years of sediments appear to be missing in the Late Miocene (in the interval between 10.4 and 6.4 million years ago).

About 50 specimens were picked at random from each sample. The specimens were oriented in an edge view. This view permits measuring of the elongation and inflation of the test; both are known to be responsible for evolutionary change in this lineage (*3*). The outline contour of the shape in this orientation was analyzed with the use of eigenshape analysis (*4*). This method represents the greatest proportion of variation observed among a collection of shapes by the least number of different shapes. The shape variable in eigenshape analysis is independent of size, which eases comparisons of different sized specimens.

The Late Miocene part of the sequence (*G. plesiotumida*) displays some variation in mean morphotype (Fig. 1), but most of this variation is clearly within the range of the precision of the data. Overall, these fluctuations were nondirectional and did not lead to any net phyletic change (*5*). Populations were thus more or less in stasis for about 5 million years. In the latest Miocene (about 5.6 million years ago) the shape began to change (at about the sample denoted 2 in Fig. 1); it changed gradually across the Miocene-Pliocene boundary, completing the transition from *G. plesiotumida* to *G. tumida* in the earliest Pliocene (about 5.0 million years ago; sample denoted 3). The rate of evolution was not constant during the transition (*6*); rather, the transition was marked by irregular fluctuations in morphotype in one general direction that caused the net change (*7*). This pattern appears to be a common mode of evolutionary change in those few lineages that are well documented through quantitative analysis (*6*).

Raup and Crick (*8*) have suggested the importance in evolutionary studies to

test an evolutionary pattern against the hypothesis that the pattern results from a random walk. Use of two of the test procedures described by them suggests that the transformation from *G. plesiotumida* to *G. tumida* may be a random walk (*9*). However, Charlesworth (*6*) has pointed out that these tests have a low power of detectability of deviations from a random walk. He argued that an inhomogeneity in evolutionary rate variance between the transitional and post-transitional period in the *G. tumida* lineage is inconsistent with the random walk hypothesis.

Once the new morphotype (*G. tumida*) was established, no further major modifications of the shape took place through the remainder of the Pliocene-Pleistocene (*10*). The pattern is one of gentle fluctuations about a stationary morphotype. Populations were thus again in relative stasis during about 5 million years.

The transition from *G. plesiotumida* to *G. tumida* was accomplished through changes in the test of the proportions of ventral to dorsal heights and an increase in test size. The shapes (Fig. 1) are typical morphologies reconstructed from the eigenshape analysis; size is plotted to scale. In the Late Miocene, the ventral side (left-hand side in our orientation) was higher than the dorsal side, whereas in the Pliocene-Pleistocene forms, the dorsal side was the most inflated. Ventral and dorsal heights of transitional forms showed greater similarity.

It is not likely that the shape changes across the Miocene-Pliocene boundary are not evolutionary, but a result of migration of a coexisting but ecologically different morphotype across the site:

1) *Globorotalia tumida* has not been observed in Late Miocene sediments. Likewise, no Plio-Pleistocene sediments are dominated by the typical *G. plesiotumida* morphotype.

2) The transition from *G. plesiotumida* to *G. tumida* can be observed in most Miocene-Pliocene boundary sections from Indo-Pacific equatorial regions and to a lesser extent in the Atlantic Ocean. In complete sections the transition occurs at the same level in a succession of well-documented and well-dated biostratigraphic events associated with the boundary, precluding any major time-transgressiveness of the transition.

3) We did not find any bimodality in the shape variable across the Miocene-Pliocene boundary, which is conclusive evidence that changes in proportions of two distinct morphotypes did not contribute to the observed change, but that the change was due to evolutionary transformation of entire populations.

Our result shows that the *G. tumida* lineage, although remaining in stasis over a considerable part of its total duration, underwent relatively rapid morphologic change that did not involve lineage branching. This pattern does not conform to the gradualistic model because that would assume gradual changes through most of the history of the lineage. It is not consistent with the punctuational model either because (i) there was no lineage branching in the *G. tumida* lineage and (ii) the transition was not sufficiently rapid. Gould (*11*) has suggested that the transitional period should be shorter than 1 percent of the duration of the descendant species to qualify for punctuationism. The transition of *G. plesiotumida* to *G. tumida* comprised about 12 percent of the total duration of *G. tumida*. At present, *G. tumida* is alive and well in the modern ocean, and this percentage will continue to decrease as long as the species survives. However, it will have to survive for another 55 million years for the percentage to drop to 1 percent, which seems unlikely in the normally rapidly evolving *Globorotalia* (*12*).

In conclusion, we see no evidence of either punctuational or gradualistic evolution in the *G. tumida* lineage. We propose the term "punctuated gradualism" for an evolutionary pattern of the type observed here in which populations are in stasis for long periods of time and in which these periods are interrupted by relatively rapid, gradual phyletic trans-

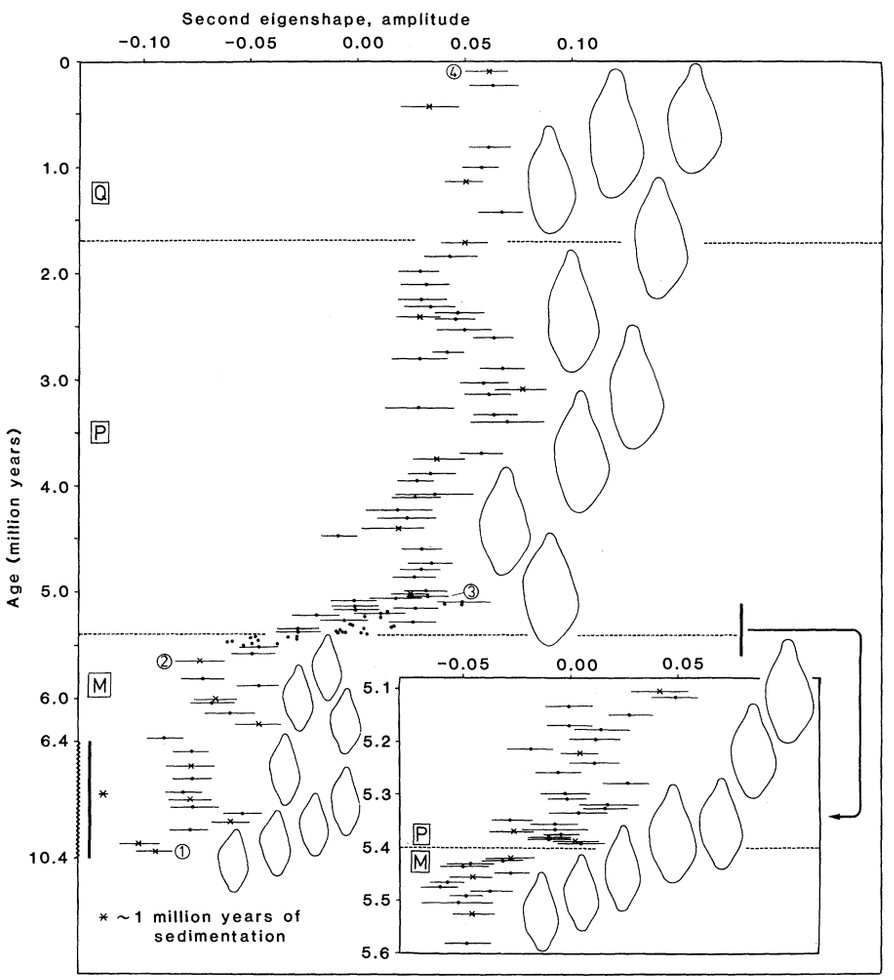

Fig. 1. Evolutionary changes in the *Globorotalia tumida* lineage through the Late Neogene (DSDP Site 214 from the southern Indian Ocean). Values plotted are the mean phenotypic scores on the second eigenshape axis (bars are 80 percent confidence intervals). (M, Miocene; P, Pliocene; Q, Quaternary.) About 3 million years of sediments are probably missing from the Late Miocene record (in the interval between 6.4 and 10.4 million years ago). The inset is a close-up of the changes across the boundary. Sampling resolution is here about 5×10^3 to 15×10^3 years; resolution is 2×10^5 years in the rest of the sequence. Specimens shown in the figure represent typical morphologies in some samples (marked by crosses). Specimens were oriented in edge view (final chamber is oriented upward and umbilical side is to the left). The size of the specimens is plotted to scale.

formations (species formations) without lineage splitting. This model differs from the punctuational model in that new species are not assumed to evolve through lineage splitting and in that the transformations are not assumed to be geologically instantaneous.

The acceleration of evolution that led to the transition of *G. plesiotumida* to *G. tumida* may have been driven by an increase in selection pressure across the Miocene-Pliocene boundary. Density changes in the upper water column associated with the Mediterranean salinity crisis (*13*) could have caused the morphologic changes. Density changes may induce morphologic adaptations in planktonic foraminifera in order to maintain buoyancy in the water column (*14*).

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An Endogenous Peptide Stimulates Secretory Activity in the Elasmobranch Rectal Gland

Abstract. *Extraction and partial purification of peptide material from the intestine of the elasmobranch* Scyliorhinus canicula *yielded a fraction that shows potent stimulatory activity in the rectal gland. The extracted material appears to contain an endogenous peptide (or peptides) that represents the natural hormone responsible for the control of rectal gland secretion in vivo.*

The elasmobranch rectal gland is an extrarenal salt-secreting organ that is important in maintaining the overall ionic balance of the animal (*1*). The secretion rate in the isolated gland is greatly increased by the cyclic nucleotide analog dibutryl adenosine 3′,5′-monophosphate (cyclic AMP) and the phosphodiesterase inhibitor theophylline (*2*). This stimulation of secretion is associated with marked increases in ouabain binding and ouabain-sensitive oxygen consumption (*3, 4*), which presumably reflect increased sodium pump activity. The cyclic AMP stimulation of sodium pump activity, however, is an indirect effect of a cyclic AMP–induced increase in sodium entry via a furosemide-sensitive chloride-coupled cotransport system (*4, 5*). The participation of cyclic AMP in regulating secretion implies a hormonal control. Stoff *et al.* (*6*) therefore investigated a range of exogenous peptide hormones and neurohormonal factors for stimulatory activity in the isolated perfused gland of *Squalus acanthias*. Of the substances tested, only the polypeptide vasoactive intestinal peptide (VIP) stimulated secretion. However, it has been reported that VIP has no effect on rectal gland secretion in another elasmobranch *Scyliorhinus canicula* (*7*), thereby raising doubts that VIP is the natural hormone responsible for controlling rectal gland secretion in elasmobranchs in vivo. We now report the results of an alternative approach, that of isolating the native endogenous secretagogue from elasmobranch tissues.

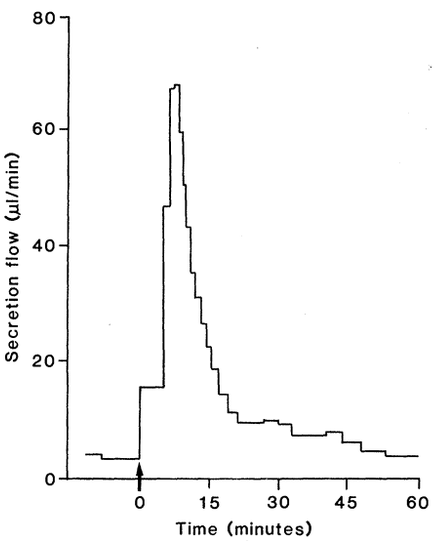

Fig. 1. The effect of fraction 13 on secretion rate in the perfused gland of *Squalus* showing a typical result. The gland was isolated and perfused at a constant pressure (20 mmHg). Secreted fluid was collected by a cannula in the secretory duct, and the flow rate was determined by a microprocessor-controlled flowmeter connected to a drop detector. Output from the flowmeter was proportional to flow rate and was recorded on a chart recorder. Perfusion flow rate was 2.8 ml g^{-1} min^{-1}, and a bolus injection of 100 µl of saline containing 100 µg of fraction 13 was introduced into the afferent perfusion line at time zero.

Extracts of intestines (ileum plus rectum) obtained from freshly killed *Scyliorhinus* were prepared by standard procedures for peptide isolation (*8*). Boiling of the intestines in water for 10 minutes was followed by acidification with acetic acid (final concentration 3 percent) and extraction overnight at 5°C. After filtration, peptides were absorbed to alginic acid and then eluted with dilute hydrochloric acid (0.2 mol/liter). Sequential purification of peptide material was carried out by means of Sephadex gel filtration, ion-exchange chromatography (carboxymethyl cellulose; ammonium bicarbonate stepwise gradient, 0.01 to 0.2 mol/liter) and reversed-phase high-performance liquid chromatography (HPLC). A 0.05 percent trifluoroacetic acid–acetonitrile gradient (20 to 50 percent) was used for HPLC, which was performed with two Waters M6000A pumps and a µBondapak C_{18} column with a model 441 detector operating at 214 nm. Eluted material was freeze-dried after evaporation of acetonitrile under dry nitrogen. This yielded a series of partially purified peptide fractions, which were screened at each stage in the separation procedure for biological activity in the rectal gland by determining their effect on oxygen consumption in slices of the gland of *Scyliorhinus*. Only one of the HPLC fractions (fraction 13) had a potent stimulatory action in the slices from *Scyliorhinus*. This fraction was tested further for activity in *Squalus* and in the ray *Raja clavata*. The peptide content of the tested fractions was determined by biuret analysis of peptide