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Geographic Origin of Benthic Foraminiferal Species

MARTIN A. BUZAS AND STEPHEN J. CULVER

Museum collections were used to document the worldwide Pliocene and Pleistocene fossil record of 59 species that now occur on the Atlantic continental margin of North America. Tabulation of these data indicates that benthic foraminifera evolve at all latitudes and in all parts of the world ocean rather than from some center or centers of origin. Dispersal in geologic time is very rapid.

THE CENTERS OF ORIGIN OF SPECIES have been discussed in the literature of biogeography and evolution for over a century. The classic scenario maintains that species evolve in the tropics and then disperse toward the higher latitudes (*1*). Recently, the Arctic and Antarctic were invoked as possible centers of origin (*2*). Much of this research centered on the origination of higher taxonomic units. In this report we examine the concept of centers of origin at the species level for benthic foraminifera.

The benthic foraminifera are abundant and ubiquitous and have an excellent fossil record. Thus they are ideal for biogeographic and evolutionary studies. Moreover, they have been the subject of intense study for over a century. The collection at the U.S. National Museum of Natural History contains about a half million identified slides of foraminifera. This collection and 11 others (*3*) are the basis for the data presented here.

The geographic distribution of over 800 species has been documented on the Atlantic continental margin of North America (*4*). These species also often occur elsewhere, and many benthic foraminiferal species are distributed worldwide (*5*). About one third of the modern species have a fossil record. Using collections, we documented the species durations for benthic foraminifera that occur on the Atlantic continental margin of North America (*6*). Our observations indicate that those species with a fossil record extending to the Miocene or older occur in sediments over a wide geographic area. Consequently, at our level of stratigraphic resolution, the geographic origination of a species cannot be determined. Attempting to minimize this difficulty, we examined the worldwide fossil record of species currently occurring on the Atlantic continental margin of North America and originating in the Pleistocene and Pliocene.

Table 1 shows the present distribution on the Atlantic continental margin and the fossil localities of species originating in the Pleistocene. Most of the sediments are late Pleistocene (younger than 12,000 years), and, even so, three species have their first fossil occurrence in both Alaska and Maine. Actually, the simultaneous recording of species from widely separated geographic areas is more common than the table shows because some of the species recorded in Alaska, Vancouver, and Maine have also been reported from Scandinavia and Baffin Island (*7*). (We have not included them in the table because we have not seen the specimens.) We do not, however, doubt that many of the species occur in North America as well as on the European continent, testifying to the rapid dispersal ability of benthic foraminifera. Of the 23 species that today are restricted to the north of Cape Hatteras, 22 were first recorded in the higher latitudes (Table 1). The three species restricted to the south of Cape Hatteras were first recorded in the lower latitudes. The three species that today occur from Florida to Newfoundland

Table 1. Modern distribution of benthic foraminifera on the Atlantic continental margin of North America and Pleistocene fossil localities. Abbreviations: CH, Cape Hatteras; NF, Newfoundland; FL, Florida; *n*, number of species.

Modern distribution	First fossil occurrence	*n*
CH–NF	Alaska	9
CH–NF	Netherlands	1
CH–NF	Alaska, Maine	3
CH–NF	Germany	2
CH–NF	Vancouver	2
CH–NF	Montreal	1
CH–NF	Maine	1
CH–NF	Massachusetts	2
CH–NF	Long Island	1
CH–NF	Southern California	1
FL–NF	Alaska	1
FL–NF	Vancouver	1
FL–NF	Maine	1
FL–CH	Southern California	1
FL–CH	Aruba	1
FL–CH	Northern Australia	1

Table 2. Modern distribution of benthic foraminifera on the Atlantic continental margin of North America and Pliocene fossil localities. For abbreviations used, see Table 1.

Modern distribution	First fossil occurrence	*n*
CH–NF	Netherlands	1
CH–NF	Northern California, Georges Bank	1
CH–NF	Italy	1
CH–NF	Southern California	2
CH–NF	Okinawa	1
CH–NF	Jamaica	1
FL–NF	Alaska	1
FL–NF	Georges Bank	1
FL–NF	Italy	1
FL–NF	Southern California	2
FL–NF	Jamaica	1
FL–NF	Dominican Republic	1
FL–CH	Italy	2
FL–CH	Southern California	1
FL–CH	North Carolina	1
FL–CH	Japan	1
FL–CH	Isle of Rhodes	1
FL–CH	Okinawa	1
FL–CH	Jamaica	5
FL–CH	Jamaica, Dominican Republic	1
FL–CH	Dominican Republic	2
FL–CH	Nicobar Island	1

M. A. Buzas, Department of Paleobiology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560.
S. J. Culver, Department of Geological Sciences, Old Dominion University, Norfolk, VA 23508.

have their first fossil occurrence in the higher latitudes.

Table 2 shows the present distribution on the Atlantic continental margin and the fossil localities of species originating in the Pliocene. Sixteen of the 30 species are restricted to south of Cape Hatteras. Their first fossil records are from mid- and lower latitudes. Today seven of the species occur only north of Cape Hatteras, and their first occurrences were in mid- and higher latitudes. Seven species today occur from Florida to Newfoundland. Five of these have their first occurrence in mid- to lower latitudes. In both the Pliocene and the Pleistocene, the first recordings are from all over the world.

These data do not support the concept of a center of origin in either the higher or the lower latitudes. Our data indicate that benthic foraminifera are continuously evolving, albeit at different rates (*6*), at all latitudes all over the world. Dispersal of species is extremely rapid and worldwide within certain latitudinal limits. Their rapid dispersal makes any vicariance events insignificant (*8*).

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Technical Comments

Measurement of Brain Deoxyglucose Metabolism by NMR

Deuel *et al.* (*1*) have shown by phosphorus-31 nuclear magnetic resonance (^{31}P NMR) spectroscopy that deoxyglucose-6-phosphate (DG6P) accumulates in rat brain for at least 40 minutes after administration of an intravenous dose of deoxyglucose at 500 mg/kg and then at some time between 40 and 60 minutes begins to decline, with an apparent half-life of 120 minutes. Similar results were obtained by gas chromatography–mass spectroscopy analysis of derivatized DG6P extracted from brains of similarly treated rats. This is a rate of loss of DG6P that is greater than is commonly believed (*2*). The time course obtained by Deuel *et al.* (*1*) is, however, remarkably similar to the time course of calculated cerebral glucose utilization (LCGU) reported by Sokoloff (*3*) in 1982. The LCGU values of Sokoloff and the data of Deuel *et al.* (*1*) have been replotted in Fig. 1 after normalization to maximum values.

The agreement between the NMR curve and the data of Sokoloff is remarkably close between 40 and 120 minutes after administration of DG6P. The curves of Deuel *et al.* represent concentrations of phosphorylated deoxyglucose compounds in brain, whereas LCGU is largely determined by the ratio of the deoxyglucose metabolites to the integrated precursor-specific activity in the brain. The LCGU values are constant as long as deoxyglucose metabolites remain trapped; the fall in LCGU value after 45 minutes reflects almost entirely loss of products of deoxyglucose phosphorylation. The results of Deuel *et al.* (*1*) confirm this observation of Sokoloff and provide further evidence that glucose 6-phosphatase (G6Pase) has little if any effect in the first 45 minutes after administration of ^{14}C-labeled 2-deoxyglucose, the experimental period prescribed by the deoxyglucose method (*4*).

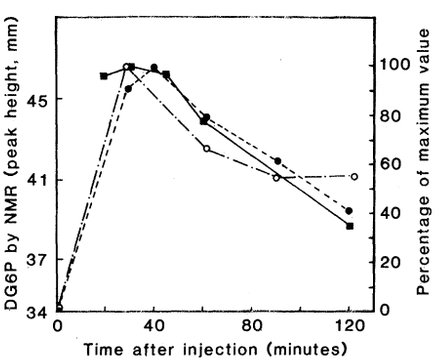

Fig. 1. Time courses of DG6P concentration (*1*) and LCGU (*2*) in rat brain after intravenous administration of deoxyglucose. Left ordinate, DG6P (NMR peak height). Right ordinate, percentage of maximum value of LCGU (■) and DG6P [gas chromatography–mass spectrometry (GC-MS)] (○) (*2*). Abscissa, portion of time course in (*1*) corresponding to same time period examined in (*2*). NMR data in (*1*), (●).

After this time the effects of G6Pase activity become apparent and develop progressively more influence on the results (*3*).

The data of Sokoloff (*3*) demonstrating that the influence of phosphatase activity is initially absent can be understood in light of the slow transport of G6P into the compartment containing the enzyme. Fishman and Karnovsky (*5*) have shown that the lag in appearance of G6Pase activity in the normal brain is due to the absence of a carrier for G6P, which delays substrate entry into the microsomal compartment where G6Pase is located.

The results of Sokoloff (*3*) demonstrate that there is no significant phosphatase activity up to 45 minutes after administration of tracer doses of deoxyglucose. The results of Deuel *et al.* (*1*) obtained with pharmacological doses of deoxyglucose are consistent with the conclusions of Sokoloff (*3*), and the demonstration of significant late G6Pase activity does not affect the validity of the deoxyglucose method for experiments concluded within 45 minutes after the administration of the tracer (*6*).

THOMAS NELSON
GIOVANNI LUCIGNANI
LOUIS SOKOLOFF
Laboratory of Cerebral Metabolism, National Institute of Mental Health, Bethesda, MD 20205

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