

Continuity and Crisis in the Reef Community¹

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This Symposium has for its theme reef biology in the Indo-Pacific; it is particularly concerned with the present state of faunistic information in this area, and the extent to which biogeographic patterns are reflected in the structure and morphology of local reef communities. The tropical Indo-Pacific, from the east coast of Africa, Madagascar, and the Red Sea to the easternmost Tuamotus, is one of extraordinary uniformity in shallow benthic marine biota. This applies not only to the more conspicuous components of the coral reefs, but also to many intricate associations of plants and animals found in this environment. This fact alone, based though it is on a patchy and limited sampling of reefs, nevertheless represents a remarkable paradox, for it exists in spite of recurrent crises in the reef seas which reached their peak during the period of Pleistocene glaciations and which are probably not over yet.

Many workers have, of course, drawn attention to a disharmony between modern reef growth and relatively recent reef formation. Vaughan's work on Cuba and the Lesser Antilles was perhaps the first to demonstrate the paucity of present reef accumulation; Wainwright in the Red Sea drew a most useful distinction between 'coral communities' and 'reefs' and showed that the former were not necessarily genetically or spatially related to the latter; and more recently workers in areas as distant as Melanesia and the western Indian Ocean have reached similar conclusions.

These disharmonies represent the culmination of a long and continuing period of reef development, with reefs still adjusting to the most recent environmental changes. To understand these adjustments we need to study the fine structure of change: the nature and extent of the environmental crises, the effects on individual taxa of plants and animals, the continuity of reef communities, and the variability over time and space of present distributions. Fine questions of course require fine data: hence the increasing interest in extending and completing primary biogeographic distribution data.

The western Pacific area is particularly appropriate in which to discuss these issues. Many centers of recent reef studies, such as Hawaii, the Tuamotus, Tuléar and Aldabra, lie on the fringes of this central area; even the southern Marshalls, better known than any other major reef province, have an attenuated biota by

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comparison with insular and peninsular south and east Asia. The gradients of faunal and floral attenuation away from this central zone are frequently steep and even abrupt. To move inwards from the Cook Islands to Tonga is to move from eastern Polynesia almost to Melanesia, from bare barren reef-flats to communities of sea-grasses and mangroves, abundant ophiuroids and asteroids, and probably twice as many genera of reef-building corals. Only within the central area, from Malaya to Fiji, and to some extent extending to southern Micronesia and Tonga, can the full diversity of the Indo-Pacific reef biota be observed.

It was in the Pacific too that Charles Darwin on the *Beagle* in 1835–36 first formulated his theory of the origin of atolls, a theory which he at once saw in terms of ocean-wide areas of subsidence balancing continent-wide areas of elevation (Darwin, 1838). The simplicity and power of Darwin's theory led to its immediate acceptance, although scientific exploration of the reef seas was only then beginning. The first serious criticism of Darwin's theory, thirty years later, also came from the west Pacific, with Semper's observation in Palau of the close juxtaposition of atoll, barrier, and fringing reefs in a single group and of the prevalence of raised rather than of subsided reefs (Semper, 1880). After the *Challenger* expedition in 1872–76 had demonstrated the importance of pelagic sedimentation in the oceans, Guppy found similar thin raised reefs in the Solomon Islands, overlying what appeared to be pelagic sediments, apparently demonstrating the possibility of reef formation in areas of uplift (Guppy, 1886).

As a result, the 'coral reef problem' came to be seen entirely in terms of the evolutionary development of atolls and other reefs in a structural and geomorphological sense. Questions of the nature of reef communities and the distribution of constituent organisms were, if treated at all, purely ancillary. This is no longer true. Following the deep borings in the southern Marshall Islands, and later at Midway and Mururoa, the evolution of open-ocean atolls in the manner envisaged by Darwin is no longer in doubt. Ever since the Great Barrier Reef Expedition of 1928–29, led by Maurice Yonge, moreover, there has been an increasing emphasis on coral reefs as biological communities, complex assemblages of specialized plants and animals, and this approach was given great impetus by the work of Drs. Eguchi, Takahashi, Abe, Matsui and Motoda, all present during this Symposium, and their colleagues at the Palao Tropical Biological Station from 1935 to 1944. The time has clearly come to re-examine the questions which pre-occupied Darwin, Semper and Guppy, to ask how the history of the reefs has affected present reef communities and the biogeography of the reef biota, and to see whether a wider synthesis is possible than the purely geological or the purely biological.

Coral Reefs and Ocean Evolution

Nowhere is this need for reappraisal more clearly demonstrated than in the plate tectonics revolution. Whereas classical reef theory stressed the importance of vertical movements, it has now been clearly shown that horizontal changes in

location are taking place at rates two to three orders of magnitude faster than subsidence rates derived from deep drilling on atolls. These horizontal rates are so substantial that we can no longer consider the development of reefs in post-Cretaceous time within a static spatial framework; and this alone has substantial biogeographic implications.

Three kinds of evidence bear on the problem of horizontal movement. First, deep drilling in the ocean floor during the JOIDES programme, combined with analysis of magnetic lineations, has yielded rates of movements for oceanic plates. Thus the mid-Pacific plate has moved at a mean rate of 8 cm/yr over the last 21 million years (Winterer, 1973; Hammond *et al.*, 1974). Second, potassium-argon dating of lavas from oceanic islands, which in the Pacific are frequently arranged in spatial series, has allowed a time parameter to be fitted to the migration of subsiding oceanic volcanoes: see, for example, McDougall (1964) on Hawaii, Krummenacher and Noetzlin (1966) on the Australs, Brousse *et al.* (1972) on the Gambiers, and Duncan and McDougall (1974) on the Marquesas. Rates of migration so derived average 15 cm/yr for Hawaii, 9 cm/yr in the Austral Islands, 10 cm/yr in the Marquesas. These rates compare with mean rates of 0.002–0.003 cm/yr for Darwinian subsidence. Thirdly, we have data derived from the study of individual islands. Dating and paleomagnetic study of basalts underlying Midway Atoll indicate a migration through 13° of latitude over 18 million years, or a movement of 1400 km (Grommé and Vine, 1972). This is an atoll actively moving *out* of the reef seas. Conversely, Pitcairn, at 24°S., is a presently reefless island moving along a NW-SE trajectory *into* the reef seas at a rate of 11 cm/yr (Duncan *et al.*, 1974).

These rates are substantial, and the convergence of evidence impressive. They mean that we can no longer interpret, for example, the thickness of post-Cretaceous reef deposits as indicating a gross temperature control reflecting proximity to the present equator, as was done only a few years ago. They also suggest, in terms of the plate-tectonic mechanism, that substantial spatial discontinuities exist, notably at subduction zones, which must be reflected in reef histories and biogeographic patterns. Thus the spectacular biotic discontinuity between Tonga and the Cook Islands, already noted, coincides with the location of the Tonga Trench, with high islands, recent volcanoes, and elevated reef limestones dating back to the Eocene to the west, and later Tertiary subsiding volcanoes and atolls to the east.

Our knowledge of the fauna of much of the Pacific is based on a very coarse grid: the uniformity of distribution and the regularity of decrease in diversity away from the southeast Asian area may reflect the coarseness of the sampling grid rather than the detail of the pattern. With increasing knowledge we may well find that our distributions fall into a series of discrete steps determined by the overall pattern of ocean histories. If we follow Carr and Coleman's (1974) recent analysis of Atlantic Green Turtle migrations, then plate tectonics can provide a clue even to the distribution of highly motile creatures over distances as great as those separating Ascension Island and Brazil; and their suggestion could well be applied to turtles in the Pacific (migrating between Tahiti and Melanesia) and the Indian Ocean

(between Madagascar and Seychelles) with profit.

What is demonstrated is that, in the geological perspective over which the present reefs have grown, the geographic frame of reference is not a static one. This has only recently been realized, and its implications for marine biogeography are only beginning to be worked out (Valentine, 1971, 1973).

Pleistocene Events

In the Tertiary, time is inevitably telescoped and the emphasis is hence on relatively gross geographic changes. In the Pleistocene, time is relatively expanded, space more nearly constant, and the emphasis shifts to environmental change. R. A. Daly, in a long series of publications from 1910 to 1948, first emphasised what he termed the 'glacial control' of reef form and structure. He at first argued that with lowered sea-levels, lowered temperatures and increased water turbidity during the glacials there was widespread extinction of living reefs, with the formation of abrasional platforms at low sea levels which were subsequently colonized by reefs as the sea rose in inter- and post-glacial times.

We now have much more information on what happened to reefs during the Pleistocene than Daly did. We know from oxygen isotope paleotemperature measurements that near-equatorial sea-surface temperatures during the last glaciation fell by about 3–4°C in the Pacific, 4–5°C in the Indian Ocean, 5–6°C in the Atlantic Ocean, and 7–8°C in the more northerly, land-locked Caribbean (Emiliani, 1971; Oba, 1969). Except in the Caribbean, this cooling would not have been sufficient to have seriously affected reefs, except at the mid-latitude limits of the reef seas and possibly in some areas where upwelling was intensified as a consequence of increased meridional circulation patterns. The study of modern emergent reefs also gives little support to the idea of greatly increased turbidity during periods of lowered sea-level. We know also from the histories of individual reefs that coral growth could continue during full glacial conditions, though in many cases (well documented for example, at Aldabra Atoll) it was interrupted simply because of the sea-level change. By studying tectonically active areas where reefs have been continuously elevated above present sea-level (such as Barbados, rising at 0.3 m/1000 yr, or the Huon Peninsula, New Guinea, rising at 3 m/1000 yr), it is possible to recognize sequences of Pleistocene reefs. In New Guinea, Chappell (1974) found no less than 20 reef complexes, six of which lie in the range 5000–107,000 yr B.P., *i.e.*, during the last full glacial period. Interruptions in growth resulted from sea level change rather than other environmental effects.

This continuity of reef growth avoids one dilemma posed by Daly's original hypothesis—the uniformity of the Indo-Pacific reef biota, which, on his argument, would have had to have been re-established from an East Indies refuge (itself then largely dry land) in the last 10,000 years of Flandrian time. While the complexity of the reefs suggests that this was inherently unlikely, there must nevertheless have been, if not extinction, at least recurrent local crises in the reef communities as

sea-level fell and the reefs contracted from the broad flat summits of atolls to the steep-sided flanks of limestone mountains. If the area-diversity relations of MacArthur and Wilson (1967) hold for the marine environment, then we could hypothesize that such a reduction in area would result in massive local extinctions: instead of the sheltered shallow lagoon, the reef flat and the reef edge, the main locus of Pleistocene reef growth would have been the present drop-off and the upper seaward slope. The hypothesis would involve the interesting corollary that changes in diversity in the marine reef environment would be out of phase with those in the terrestrial. Many characteristic reef-flat species must have undergone extreme environmental stress, with results at present unknown. In terms of light, bracket and foliaceous corals must have been at advantage over massive growth forms, and the latter must have been physically ill-adapted to steep substrate situations. In few places can we yet determine the effects of these stresses on the present biota. In some places we see faunal discontinuities between modern and Pleistocene reefs (e.g., presence of *Fungia* in the Pleistocene and absence in the modern reefs of Formosa; presence of *Acropora* in the fossil reefs and absence in the modern reefs of Hawaii), but in general such differences still reflect differences in knowledge rather than in distributions.

It is also apparent that Daly greatly overemphasized the efficiency of marine erosion during the glacial periods. Radiometric dating has established a fall of sea-level during the last glaciation to about -150 m at about 20,000 B.P., with a previous high stand *ca.* 100,000 B.P. Multiple oscillations of this amplitude occurred throughout the 2.5 million years of Pleistocene time. Recent quantitative studies of erosion rates by Trudgill at Aldabra Atoll have yielded rates of marine erosion of the order of 1 mm/yr: it would thus take one million years to bevel a reef 1 km wide. Rates of subaerial denudation are an order of magnitude slower: it would take 150,000 yr to remove an emerged limestone mountain 150 m high at the rate of 0.1 mm/yr. These are gross approximations, and the rates themselves probably vary by an order of magnitude in response to differences in wave energy, rainfall, mineralogy and cementation. But they indicate that glacial low stands of the sea were simply not long enough and Daly's processes not efficient enough for major changes in form of elevated reefs to occur. Coral communities which retreated downslope as the sea-level fell advanced back up as it rose again over a terrain substantially the same as that they had left, though modified in detail by karst erosion. This is borne out by the widespread remnants of last interglacial reefs on and under modern reef flats, as well as by geophysical surveys of modern reef structures and studies of contemporary karst geomorphology. The case for the inheritance of modern reef topography from karst-modified reef structures of earlier age has recently been made in greater detail by Stoddart (1973), Purdy (1974a, 1974b), and Bloom (1974).

There is a further line of evidence which it is becoming possible to explore: oceanic weather, wave and circulation patterns during full glacial times (Lamb and Woodroffe, 1972; Wilson and Hendy, 1971). Attempts have been made, either

using historical analogs or numerical simulations, to model glacial conditions, but these have the disadvantage that they are based on continental weather stations and that they generally omit consideration of oceanic circulation patterns (Alyea, 1972; Williams *et al.*, 1973). It is likely that with increased meridional gradients there were significant changes in patterns of oceanic currents and upwelling. A modern analog might be found in the Central Pacific dry zone, characterized by upwelling of cool, nutrient-rich water of high productivity, and in consequence the site of the old 'on the Line' whale fishery, of many seabird islands, and of contemporary guano deposition. This zone usually extends from the Peruvian coast to the southern Gilberts. Occasionally it extends into the Carolines, but quite frequently the upwelling is suppressed, the sea warms, aridity gives way to heavy rain, and seabirds die. Quite apart from the repercussions of this situation on global climate (Bjerknes, 1969), could not this situation locally provide an indicator of glacial/interglacial conditions? The great phosphate islands of Ocean and Nauru lie immediately downwind of this arid zone; Niue, otherwise geologically similar, lies in a different atmospheric and oceanic regime, and lacks phosphate deposits. In the Indian Ocean it is difficult to imagine the phosphorites of Christmas Island being formed under present humid conditions. Present-day linkages between climate, ocean conditions, seabird populations and guano deposition may thus yield clues about similar though more extensive changes during glacial times.

Reefs in the Holocene

The most severe environmental change experienced by the modern reefs has also been the most recent: the Flandrian transgression triggered by the melting of the glacial ice. Bemused as we are by uniformitarian doctrine, it is difficult to realize the scale and rate of this catastrophe. The Laurentide ice sheet, some 4000 km wide, collapsed in 4000 years and had largely disappeared by 6000 B.P. At times the ice front was retreating by 5 m/week (Andrews, 1973). Sealevel rise as a result averaged 1 m/100 yr over several thousand years to 6000 B.P. The transgression did not end there, however. Partly because of decantation resulting from isostatic recovery of the unloaded crust (*e.g.*, in the Hudson's Bay area), partly because of the phenomenon of hydroisostasy or differential adjustment of the crust to the new load of water, the transgression has continued, though at a declining rate, to the present day (Bloom, 1971; Jensen, 1972; Walcott, 1972).

Two points might be made about the Flandrian event. First, it was so brief. Sea-level has stood close to its present level for only 2000–3000 yr, or 0.1 per cent of Pleistocene time. Modern reefs have had little time to adjust to this new condition. Second, the transgression meant a change in shoreline not only in a vertical but also in a horizontal sense. In some areas, such as the East Indies, the sea transgressed across flat-lying lands at rates of up to 10–15 m/day. Hence reefs growing at Pleistocene shorelines might be separated spatially by many kilometers from reefs round present coasts: in many areas of the East Indies and the Solomon

Islands reef patterns only make sense when interpreted in terms of Pleistocene rather than present shoreline locations.

Other consequences also follow. Some shallow shelf areas have only been marine for a few thousand years. The Persian Gulf, for example, lacks *Halimeda*, *Penicillus*, all larger molluscs, and many corals (Hughes Clark and Keij, 1973). Other areas, especially of the continental borderlands, at present islands, were formerly contiguous land-masses: thus the former continuity of land between Bougainville and islands almost all the way to Guadalcanal has been shown to have had considerable influence on the present terrestrial butterfly and bird faunas, and cannot have been without significance for the littoral biotas too. Salvat (1969) has also drawn attention to differences between closed and open atolls in the eastern Pacific, the former flooded by the sea only when it overtopped the peripheral reefs, the latter inundated when the sea reached the lips of the reef-gaps, and he has shown how differences in faunal diversity and biomass in atoll lagoons stem from this difference in history.

Reefs during the transgression must have had optimal conditions for vertical growth. Chave *et al.* (1972) estimate a potential vertical growth of 7 m/1000 yr (rather more than half the transgression rate), reducing to a net increment of 2 m/1000 yr (or one-fifth the transgression rate). Once the transgression slowed, reef-growth could catch up with it and ultimately form reef-flats. Successional changes, similar to those seen in elevated reefs (Mesolella *et al.*, 1970; Chappell, 1974), must have occurred as reef morphology also altered. The ubiquity of recently dead microatolls on reef-flats undoubtedly represents the transition between unconstrained vertical reef-growth and the constraint of a near-stationary sea-level (Scoffin and Stoddart, *in litt.*). There is still controversy over what happened in the comparatively brief interval of time between the retardation of the transgression and reef-growth reaching sea-level. Many aggradational features of reef-flats (reef blocks, shingle ramparts, cemented shingle ridges, apparently slightly elevated reefs) have been radiometrically dated to just this period (2500–6000 B.P.). They have been explained either by slightly higher sea-levels than at present, or by a period of storminess greater than the present: probably they represent the time-lag between the stabilization of sea-level and the protection of coasts by actively growing corals.

Conclusion

These, then, are the successive crises undergone by the reef communities. This is the context of the evolution of the Indo-Pacific reef biota over at least 70 million years. One could go further and add a further category of crisis, to do with pollution, human interference, and perhaps the *Acanthaster* problem, on yet a shorter time scale, and one could certainly add much on the effects of brief high-intensity events such as hurricanes, earthquakes and volcanic eruptions. Perhaps the earlier crises will supply a perspective for such present perturbations, and will

suggest that reefs are inherently more resilient phenomena than they are sometimes considered to be. The picture I have sketched is one in very general terms, but it prompts many detailed questions and presupposes much more detailed data. The purpose of this Symposium is to assess the status of our information over the Indo-Pacific reef seas, to define the questions which need to be asked, and to determine where and how we need to improve our knowledge of the reefs in order to answer the questions we now realize to be important in the light of these new advances of the last few years.

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References Cited

- Alyea, F. N. 1972. Numerical simulation of an ice age paleoclimate. Colorado State Univ. Atmospheric Sci. Pap. 193: 1-120.
- Andrews, J. T. 1973. The Wisconsin Laurentide ice sheet: Dispersal centers, problems of rates of retreat, and climatic implications. Arctic Alpine Res. 5: 185-199.
- Bjerknes, J. 1969. Atmospheric teleconnections from the equatorial Pacific. Mon. Weath. Rev. 97: 163-172.
- Bloom, A. L. 1971. Glacial-eustatic and isostatic controls of sea level since the last glaciation. p. 355-379. In K. K. Turekian (ed.), The late Cenozoic glacial ages. Yale Univ. Press, New Haven. xii+606 p.
- . 1974. Geomorphology of reef complexes. Spec. Publ. Soc. Econ. Paleontol. Mineral. 18: 1-8.
- Brousse, R., J.-C. Philippet, G. Guille, and H. Bellon. 1972. Géochronometrie des Iles Gambier (Océan Pacifique). C. r. hebdom. Séanc. Acad. Sci., Paris, 274: 1995-1998.
- Carr, A., and P. J. Coleman. 1974. Seafloor spreading theory and the odyssey of the Green Turtle. Nature, Lond. 249: 128-130.
- Chappell, J. 1974. Geology of coral terraces, Huon Peninsula, New Guinea: A study of Quaternary tectonic movements and sea-level changes. Bull. Geol. Soc. Am. 85: 553-570.
- Chave, K. E., S. V. Smith, and K. J. Roy. 1972. Carbonate production by coral reefs. Marine Geol. 12: 123-140.
- Darwin, C. R. 1838. On certain areas of elevation and subsidence in the Pacific and Indian Oceans, as deduced from the study of coral formations. Proc. Geol. Soc. Lond. 2: 552-554.
- Duncan, R. A., and I. McDougall. 1974. Migration of volcanism with time in the Marquesas Islands, French Polynesia. Earth Plan. Sci. Lett. 21: 414-420.
- Duncan, R. A., I. McDougall, R. M. Carter, and D. S. Coombs. 1974. Pitcairn Island—another Pacific hot spot? Nature, Lond. 251: 679-682.
- Emiliani, C. 1971. The amplitude of Pleistocene climatic cycles at low latitudes and the isotopic composition of glacial ice. p. 183-197. In K. K. Turekian (ed.), The late Cenozoic glacial ages. Yale Univ. Press, New Haven. xii+606 p.
- Grommé, S., and F. J. Vine. 1972. Paleomagnetism of Midway Atoll lavas and northward movement of the Pacific plate. Earth. Plan. Sci. Lett. 17: 159-168.
- Guppy, H. B. 1886. Notes on the characters and mode of formation of the coral reefs of the Solomon Islands. Proc. R. Soc. Edinb. 13: 857-904.

- Hammond, S. R., F. Theyer, and G. H. Sutton. 1974. Paleomagnetic evidence of northward movement of the Pacific Plate in deep-sea cores from the central Pacific basin. *Earth Plan. Sci. Lett.* 22: 22-28.
- Hughes Clark, M. W., and A. J. Keij. 1973. Organisms as producers of carbonate sediment and indicators of environment in the southern Persian Gulf. p. 33-56. *In* B. H. Purser (ed.), *The Persian Gulf*. Springer-Verlag, Berlin. viii+471 p.
- Jensen, H. 1972. Holocene sea-level and geoid deformation. *Bull. Geol. Soc. Denmark*, 21: 374-381.
- Krummenacher, D., and J. Noetzelin. 1966. Ages isotopiques K/A de roches prélevées dans les possessions françaises du Pacifique. *Bull. Soc. Géol. Fr.* 8: 173-175.
- Lamb, H. H., and A. Woodroffe. 1972. Atmospheric circulation during the last ice age. *Quat. Res.* 1: 29-58.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton Univ. Press, Princeton. 203 p.
- McDougall, I. 1964. Potassium-argon ages from lavas of the Hawaiian Islands. *Bull. Geol. Soc. Am.* 75: 107-128.
- Mesoellea, K. J., H. A. Sealy, and R. K. Matthews. 1970. Facies geometries within Pleistocene reefs of Barbados, West Indies. *Bull. Am. Ass. Petrol. Geol.* 54: 1899-1917.
- Oba, T. 1969. Biostratigraphy and isotopic paleotemperatures of some deep-sea cores from the Indian Ocean. *Scient. Rep. Tohoku Univ.* (2) 41: 129-195.
- Purdy, E. G. 1974a. Reef configurations: cause and effect. *Spec. Publ. Soc. Econ. Paleontol. Mineral.* 18: 9-76.
- . 1974b. Karst-determined facies patterns in British Honduras: holocene carbonate sedimentation model. *Bull. Ass. Am. Petrol. Geol.* 58: 825-855.
- Salvat, B. 1969. Dominance biologique de quelques mollusques dans les atolls fermés (Tuamotu, Polynésie); phénomène récent—conséquences actuelles. *Malacologia* 9: 187-189.
- Scoffin, T. P., and D. R. Stoddart. *In* *Litt. Nature and origin of microatolls*.
- Semper, C. 1880. *Die natürliche Existenzbedingungen der Thiere*. Leipzig.
- Stoddart, D. R. 1973. Coral reefs: The last two million years. *Geography* 58: 313-323.
- Valentine, J. W. 1971. Plate tectonics and shallow marine diversity and endemism, an actualistic model. *Syst. Zool.* 20: 253-264.
- . 1973. *Evolutionary paleoecology of the marine biosphere*. Prentice Hall, Englewood Cliffs. xv+511 p.
- Walcott, R. I. 1972. Past sea levels, eustasy and deformation of the earth. *Quat. Res.* 2: 1-14.
- Williams, J., R. G. Barry, and W. M. Washington. 1973. Simulation of the climate at the last glacial maximum using the NCAR global circulation model. *Inst. Arctic Alpine Res., Univ. Colorado Occas. Pap.* 5: 1-23.
- Winterer, E. L. 1973. Sedimentary facies and plate tectonics of equatorial Pacific. *Bull. Am. Ass. Petrol. Geol.* 57: 265-282.
- Wislon, A. T., and C. H. Hendy. 1971. Past wind strengths from isotope studies. *Nature, Lond.* 234: 344-345.