ments are made using the "pump-probe" technique, in which a strong "pump" pulse excites a collection of molecules into an initial energetic state, followed by a weaker time-delayed "probe" pulse that samples changes in the molecular behavior such as optical absorption. By recording many samples at different pump-probe time delays, one can construct a time-domain picture of the molecular response to excitation, which provides insights into its chemistry. The resolution of this technique depends directly on the pump and probe pulse durations, and therefore the extremely short pulses demonstrated by Drescher *et al.* offer substantially improved accuracy in these measurements. Furthermore, it might be possible to extend such studies to the analysis of atomic dynamics, which occur on much faster time scales than molecular vibrations. In their paper, Drescher *et al.* suggest that ultrashort x-ray pulses might be used to study the rapid motions of inner-shell electrons, which are tightly bound to the nucleus, or could provide information about fast ionization processes.

The route to attosecond science has been paved over the last decade by huge advances in the generation and manipulation of ultrashort laser pulses (*2–8*). Durations of optical pulses are now approaching a fundamental plateau at two optical cycles (see the figure), or about 5 fs for electromagnetic waves in the visible and near infrared. To achieve substantially shorter pulses therefore requires working at shorter wavelengths. Fortunately, it is possible to generate laserlike beams of x-ray pulses by focusing high-intensity ultrashort laser pulses onto a suitable target, such as the neon gas cell used by Drescher *et al.* The mechanism by which short optical pulses can generate even shorter x-ray pulses relies on the principle of harmonic generation. Any mechanical system that experiences a restoring force dependent on its displacement from some equilibrium position can oscillate at a well-defined resonant frequency. An isolated atom is one example of such a system, in which the outer electrons experience a restoring force due to the nuclear Coulomb field. These electrons are easily perturbed from their equilibrium position by a strong optical field, and the combination of restoring and applied forces results in complex motion involving frequencies much higher than that of the incident wave. As they respond to these forces, the electrons dissipate energy as high-frequency electromagnetic radiation, and wavelengths in the x-ray region are generated at harmonics of the original optical frequency.

In their experiment, Drescher *et al.* isolated the highest frequency harmonics and, using a novel method, measured the duration of these x-ray pulses. The method uses a portion of the original laser pulse that created the x-ray pulse like a fast shutter to gate the intensity of different parts of the x-ray pulse profile. The authors demonstrate pulse durations of around 2.5 fs—certainly the fastest events ever recorded and slightly shorter than the optical period of the generating optical wave. Truly attosecond-domain pulses still remain just out of reach, but the generation and measurement tools demonstrated here bring them another step closer.

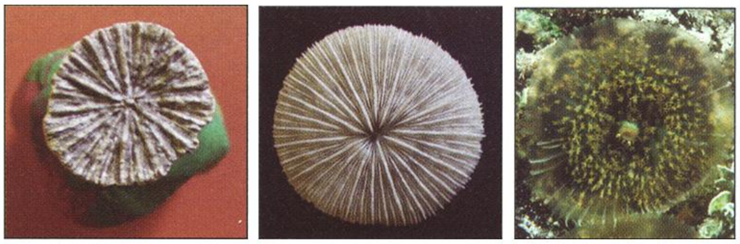
References

1. M. Drescher *et al.*, *Science* **291**, 1923 (2001); published online 15 February 2001 (10.1126/science.1058561).
2. C. P. Huang *et al.*, *Opt. Lett.* **17**, 1289 (1992).
3. P. F. Curley *et al.*, *Opt. Lett.* **18**, 54 (1993).
4. I. P. Christov *et al.*, *Opt. Lett.* **19**, 1465 (1994).
5. A. Stingl *et al.*, *Opt. Lett.* **20**, 602 (1995).
6. L. Xu, C. Spielmann, F. Krausz, R. Szipocs, *Opt. Lett.* **21**, 1259 (1996).
7. I. D. Jung *et al.*, *Opt. Lett.* **22**, 1009 (1997).
8. D. H. Sutter *et al.*, *Opt. Lett.* **24**, 631 (1999).

PERSPECTIVES: PALEONTOLOGY AND EVOLUTION

The Origins of Modern Corals

George D. Stanley Jr. and Daphne G. Fautin



Searching for the ancestors. (Left) A fossil scleractinian coral of Triassic age. **(Middle)** The calcified skeleton of a modern scleractinian. **(Right)** A living corallimorpharian polyp, a soft-bodied species. Were the ancestors and some descendants of living corals soft-bodied?

CREDIT: RIGHT IMAGE/JOEL ELLIOTT

Corals belonging to the order Scleractinia are the animals primarily responsible for creating the framework of reefs. These marine invertebrates (see the first figure) are important today and in the geologic past because of their prodigious ability to calcify. Massive deposits of calcium carbonate, some holding important hydrocarbon reserves, trace their origin to ancient coral reefs. Modern reefs exert important controls on global climate and the marine environment, especially in the recycling of carbon. Despite a rich fossil record, however, the origin of Scleractinia has remained shrouded in controversy. Recent work suggests that apparent disagreements and ambiguities may be reconciled.

Most calcifying multicellular animals, or metazoans, made their debut about 540 million years ago (Ma) during the Cambrian period, soon after the start of the Paleozoic era, which saw the explosion of life's diversity in the sea. Molecular evidence indicates that most Paleozoic metazoans originated much earlier, in the Precambrian (*1*). Scleractinians are relative latecomers, appearing in the fossil record during the Triassic period about 237 Ma (see the second figure) (*2–4*)—14 million years after Earth's most devastating mass extinction at the close of the Permian period. Not reef-builders at first (*5*), Middle Triassic scleractinians belong to nine or ten families in at least three suborders. This early diversity implies a history unrecognized or unrecorded in the fossil record.

The absence of coral fossils in the first 14 million years of the Triassic coincides with a time when carbonate deposition was suppressed globally (*5*), long after most marine life had been extinguished at the end of the Permian (*6*). This gap is one stumbling block to the old theory that scleractinians were derived from Paleozoic corals. It has been postulated that some survived but that post-extinction abundances were so low, and the resulting fossils so rare, as to elude detection. Another theory is that they survived the 14-million-year gap in as-yet-undiscovered refugia. Both ideas seem tenuous in light of the intense global scrutiny of Lower Triassic rocks.

Moreover, the Paleozoic corals most often proposed as scleractinian ancestors, members of order Rugosa (see the second figure), differ morphologically from scler-

---

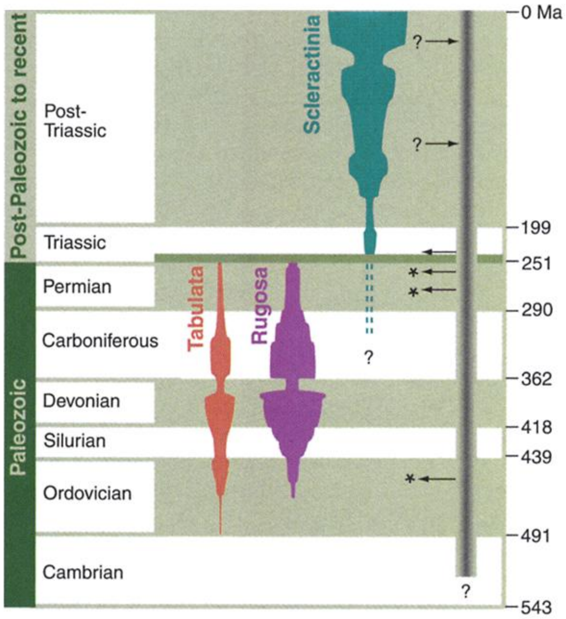
G. D. Stanley is at the Department of Geology, University of Montana, Missoula, MT 59812, USA. E-mail: fossil@selway.umt.edu D. G. Fautin is at the Department of Ecology and Evolutionary Biology, Natural History Museum and Biodiversity Research Center, University of Kansas, Lawrence, KS 66045, USA. E-mail: fautin@ukans.edu

actinians (*7*): Rugosans have a different symmetry, their radial skeletal elements commonly grow sequentially rather than cyclically, and the crystal form of their calcium carbonate skeleton is calcite, whereas it is aragonite in scleractinians. Some rare, reputedly aragonitic Paleozoic corals, termed "scleractiniamorphs" because they resemble scleractinians (*8*–*11*), may be evolutionary dead ends or progenitors of modern Scleractinia (*8*, *10*). At least one scleractiniamorph was proposed as a Paleozoic member of Scleractinia (*10*), but this view has been challenged (*11*, *12*). Molecular data indicate that two lineages of scleractinians diverged about 300 Ma, in the Late Carboniferous (*13*), and by implication survived the Permian extinction. With such ambiguous data, how are we to construct a credible picture of scleractinian phylogeny?

The sudden appearance of scleractinians in the Middle Triassic may mark the time when soft-bodied ancestors (*14*) acquired the ability to form skeletons. Recent data support the idea that physicochemical conditions of seawater influence skeleton formation in scleractinians. In many corals that harbor symbiotic algae called zooxanthellae, calcification declines with decreasing calcium carbonate saturation of seawater (*15*). If scleractinian ability to calcify decreases when conditions become unfavorable, it may increase under favorable conditions.

The Early Triassic was characterized by anoxic deep ocean turnover, elevated CO_2, and shifts in global ocean chemistry that reduced carbonate deposition (*16*). The environment of the Middle Triassic, which was favorable to aragonite calcification (*17*), could have allowed soft-bodied ancestors of scleractinians of several lineages to secrete skeletons. Molecular data suggest that scleractinian skeletons may have evolved as many as four times (*18*). This indicates that the skeleton may be ephemeral, that is, a lineage may lose and subsequently reacquire hard parts as conditions favorable to calcification wane and wax (*19*). The 14-million-year gap would then be more of a step than a stumbling block.

Did the numerous coral lineages that appeared in the mid-Triassic descend from a single ancestor or was there more than one ancestor? If skeletalization is ephemeral, the fossil record is unlikely to resolve this question. The latest phylogenetic diagram (*20*), based on fossils, is not a tree or even a bush—it is a lawn that lacks the ancestor-descendant links among lineages shown in previous trees. Most DNA data support a single ancestor, but sequences of some genes, other molecular data, and morphological analyses do not (*21*). Moreover, at least some molecular data are incompatible with the current higher level classification of Scleractinia based on microstructural or traditional skeletal morphology (*18*).



Corals and their kin through time. The vertical length of the spindle diagrams indicates the temporal extent of the three major orders of calcified corals, and the thickness indicates their relative diversity and abundance. The colored line at the base of the Triassic indicates the coral gap. The vertical bar to the right represents soft-bodied forms, for which the fossil record is very poor or nonexistent. The figure is therefore not meant to imply a continuous lineage for any group nor that all of the soft-bodied forms are one another's closest relatives. Asterisks indicate occurrences of calcified scleractiniamorphs. Right arrows suggest times of loss and left arrows times of gain of calcified skeletons, which may have occurred several times during geologic time. [Modified from (*9*)]

All analyses include some or all animals of order Corallimorpharia (which lack a skeleton) within the Scleractinia or as a sister group. The morphological similarity of some corallimorpharian and scleractinian polyps casts doubt on whether a skeleton is an essential attribute of Scleractinia (*22*) and is consistent with the idea of a skeleton being ephemeral. It may be more phylogenetically accurate to merge the Scleractinia with the soft-bodied orders Actiniaria and Corallimorpharia (*19*, *23*). Indeed, there is cause to wonder whether some apparently extinct lineages of Scleractinia persist as anemones.

Many apparent ambiguities and conflicts in previous analyses can be reconciled if lineages of corals have lost and redeveloped skeletons repeatedly through their history in response to environmental conditions. To test this idea, future research should explore biochemical mechanisms of calcification, establish phylogenetic relationships between scleractinians and morphologically similar soft-bodied animals, analyze if and how skeletal structure of scleractinian groups corresponds with molecular data, and seek evidence of geochemical changes in geologic history that correlate with changes in the robustness of coral skeletons and appearances or disappearances of various coral groups

References and Notes

1. G. A. Wray, J. S. Levinton, L. H. Shapiro, *Science* **274**, 568 (1996).
2. Z. Deng, L. Kong, *Acta Paleontol. Sinica* **23**, 489 (1984).
3. W. Qi, *Palaeontgr. Am.* **54**, 187 (1984).
4. E. Morycowa, *Acta Palaeontol. Pol.* **33**, 91 (1988).
5. G. D. Stanley Jr., *Palaios* **3**, 170 (1988).
6. D. H. Erwin, *The Great Paleozoic Crisis: Life and Death in the Permian* (Columbia Univ. Press, New York, 1993).
7. W. A. Oliver Jr., *Paleobiology* **6**, 146 (1980).
8. C. T. Scrutton, *Geol. Today* **15**, 184 (1999).
9. Y. Ezaki, *Palaeontology* **43**, 199 (2000).
10. Y. Ezaki, *Paleobiology* **24**, 227 (1998).
11. C. T. Scrutton, *Proc. Yorks. Geol. Soc.* **51**, 177 (1997).
12. J. Fedorowski, *Acta Palaeontol. Pol.* **42**, 446 (1997).
13. S. L. Romano, S. R. Palumbi, *Science* **271**, 640 (1996).
14. Hypothetical scleractinian ancestors are referred to as "anemones" in the paleontologic literature. This terminology is unfortunate because the word anemone commonly refers to actiniarians and occasionally to corallimorpharians, orders of soft-bodied animals that have no known ancestors. Trace fossils of "anemones" from Lower Triassic rocks cannot be assigned to any order.
15. J.-P. Gattuso, D. Allemand, M. Frankignoulle, *Am. Zool.* **39**, 160 (1999).
16. A. H. Knoll, R. K. Bambach, D. E. Canfield, J. P. Grotzinger, *Science* **273**, 452 (1996).
17. P. A. Sandberg, *Nature* **305**, 19 (1983).
18. S. L. Romano, S. D. Cairns, *Bull. Mar. Sci.* **67**, 1043 (2000).
19. D. G. Fautin, J. M. Lowenstein, *Proc. Seventh Int. Coral Reef Symp.* **2**, 665 (1994).
20. J. E. N. Veron, *Corals of the World* (Australian Institute of Marine Science, Townsville, Australia, 2000), vol. 1.
21. D. G. Fautin, S. L. Romano, W. A. Oliver Jr., see http://phylogeny.arizona.edu/eukaryotes/animals/cnidaria/anthozoa/zoantharia.html.
22. In Cnidarian class Hydrozoa, the ability to form a calcareous skeleton is no longer considered a major taxonomic feature. Hydrozoa previously consisted of three orders containing mostly animals with chitinous skeletons or no skeletons, and two orders that secreted calcium carbonate skeletons. Now, the animals that secrete calcium carbonate are placed in one of the other three orders (*24*).
23. W. A. Oliver, Jr., in *Paleobiology and Biology of Corals*, G. D. Stanley Jr., Ed. (Paleontological Society, Pittsburgh, PA, 1996), vol. 1, pp. 107–135.
24. K. W. Petersen, in *Biology and Systematics of Colonial Organisms*, G. Larwood, B. R. Rosen, Eds. (Academic Press, London, 1979), pp. 105–139.
25. NSF grants are acknowledged: EAR 9624501 to G.D.S. and DEB 9521819 and 9978106 to D.G.F.