



Intermittent Plate Tectonics?

Paul G. Silver, *et al.*
Science **319**, 85 (2008);
DOI: 10.1126/science.1148397

The following resources related to this article are available online at www.sciencemag.org (this information is current as of January 20, 2008):

Updated information and services, including high-resolution figures, can be found in the online version of this article at:

<http://www.sciencemag.org/cgi/content/full/319/5859/85>

Supporting Online Material can be found at:

<http://www.sciencemag.org/cgi/content/full/319/5859/85/DC1>

This article **cites 35 articles**, 6 of which can be accessed for free:

<http://www.sciencemag.org/cgi/content/full/319/5859/85#otherarticles>

This article appears in the following **subject collections**:

Geochemistry, Geophysics

http://www.sciencemag.org/cgi/collection/geochem_phys

Information about obtaining **reprints** of this article or about obtaining **permission to reproduce this article** in whole or in part can be found at:

<http://www.sciencemag.org/about/permissions.dtl>

Intermittent Plate Tectonics?

Paul G. Silver^{1*} and Mark D. Behn²

Although it is commonly assumed that subduction has operated continuously on Earth without interruption, subduction zones are routinely terminated by ocean closure and supercontinent assembly. Under certain circumstances, this could lead to a dramatic loss of subduction, globally. Closure of a Pacific-type basin, for example, would eliminate most subduction, unless this loss were compensated for by comparable subduction initiation elsewhere. Given the evidence for Pacific-type closure in Earth's past, the absence of a direct mechanism for termination/initiation compensation, and recent data supporting a minimum in subduction flux in the Mesoproterozoic, we hypothesize that dramatic reductions or temporary cessations of subduction have occurred in Earth's history. Such deviations in the continuity of plate tectonics have important consequences for Earth's thermal and continental evolution.

Plate tectonic theory originated to explain how oceanic lithosphere is created at spreading centers and consumed at subduction zones. The continental component of this theory was added by Wilson (1), who proposed that there is an cycle of continental breakup and collision that accompanies the opening and closing of ocean basins. One of the most intriguing aspects of this theory is the formation of supercontinents after ocean closure. In particular, supercontinent assembly has the potential to dramatically reduce subduction flux by the termination of subduction via continent-continent collision. For example, consider the Atlantic Ocean basin, which has been growing in area at the expense of the Pacific since its opening at 200 million years ago (Ma). If this trend continues, relative plate-motion models (2) predict that in ~350 million years (My), the Pacific will effectively close, leading to widespread continent-continent collisions and the termination of subduction in the Pacific basin. This would eliminate most of Earth's subduction zones, resulting in an order of magnitude reduction in global subduction flux.

Despite the plausibility of such an event, it is commonly assumed that reductions in global subduction flux of this magnitude do not occur (3). The goal of this study is to critically evaluate this assumption and to consider the alternative hypothesis that there have been dramatic reductions in subduction flux over Earth's history. There are two main factors that must be considered when evaluating the continuity of subduction flux: the mode of ocean closure and the characteristics of subduction initiation. If the Atlantic closed (A-type closure), instead of the Pacific (P-type closure), then Pacific subduction would survive intact (Fig. 1). A-type closure occurs when an interior ocean closes after the breakup of a previous supercontinent. In contrast, P-type closure represents the closing of an external ocean (4). The key distinction between these two modes, in terms of subduction flux, is

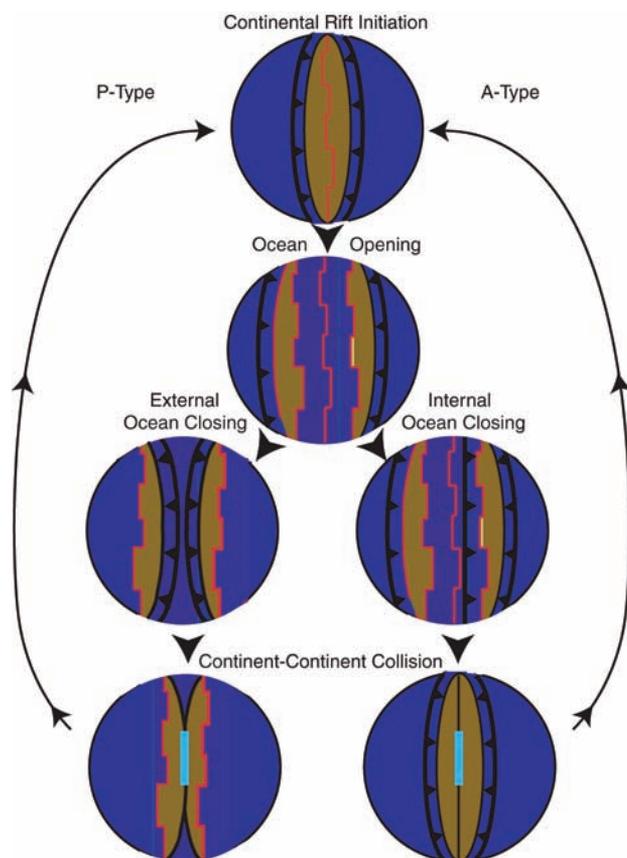
that P-type closure has the potential to dramatically reduce or even eliminate subduction flux, whereas A-type closure does not (Fig. 1). Closure mode can be determined by dating the former oceanic crust (preserved as ophiolites in sutures) after supercontinent assembly. For A-type closure, the (former) ocean crust from the internal ocean is always younger than the age of breakup of the previous supercontinent (Fig. 1). For P-type closure, this crust can be older (because subduction predates the breakup of the previous supercon-

tinent), as exemplified today by the circum-Pacific ophiolite belts, some of which possess early Paleozoic ages (such as the Trinity ophiolite of northern California) and predate the breakup of Pangaea (4).

P-type and A-type closure represent two end-member cases, and in practice the mode of closure is likely to be a mixture of the two. It nevertheless appears that supercontinent assembly is typically predominantly produced by one or the other (4). The supercontinent Pangaea, which was formed by the closing of the Iapetus Ocean, appears to have formed primarily by A-type closure (4). In contrast, presently available evidence suggests that both the supercontinents Pannotia (5, 4) and Rodinia formed primarily by P-type closure (6, 4). Finally, the earlier hypothesized supercontinent Nuna may have formed by A-type closure, although this is highly uncertain (4) (Table 1).

For Rodinia, the evidence for P-type closure is based on (i) the greater age of oceanic-affinity rocks (such as ophiolites), as compared to the age of breakup of Nuna (4); (ii) the fact that the Superior province faced an open ocean for ~0.8 billion years (4); and (iii) that the Grenville orogen, which ultimately created Rodinia, ap-

Fig. 1. Schematic of two modes of ocean closure: P-type and A-type (4). **(Top)** Supercontinent (brown), surrounded by subduction zones (black), begins rifting, initiating continental breakup and the creation of an internal ocean (red lines). **(Middle top)** Breakup continues, increasing the size of the internal ocean at the expense of the external ocean. **(Middle bottom)** In A-type closure, subduction begins at a passive margin of the internal ocean and the internal ocean begins to close. In P-type closure, the internal ocean continues to grow and becomes the largest ocean basin (the other side of Earth is shown). **(Bottom)** Supercontinent assembly. In A-type closure, the internal ocean closes, shutting down subduction zones in the internal ocean, while subduction (and sea-floor spreading) in the external ocean continues. In P-type closure, the external ocean closes, shutting down all subduction. A-type and P-type closure can be distinguished by the age of former oceanic crustal material (such as ophiolites) that is trapped in the suture zone upon supercontinent assembly (light blue rectangle) (4). In A-type closure, it is younger than the age of breakup of the previous supercontinent (because subduction initiation postdates the previous breakup), whereas in the case of P-type closure, oceanic crustal material can predate the breakup of the previous supercontinent (because subduction initiation predates breakup).



¹Department of Terrestrial Magnetism, Carnegie Institution of Washington, 5241 Broad Branch Road, NW, Washington, DC 20015, USA. ²Department of Geology and Geophysics, Woods Hole Oceanographic Institution, Mail Stop 22, Woods Hole, MA 02543, USA.

*To whom correspondence should be addressed.

pears to have been a collision between two active margins (6). These observations suggest that this collision stopped an extensive (~20,000 km) length of active margin stretching from southwestern North America to Baltica (~10,000 km) (7) on the western side and an equally long active margin to the east. Thus, the geologic record suggests a predominantly P-type closure mode and points to a drastic reduction in subduction flux.

The second factor in assessing the continuity of subduction flux is subduction initiation, probably the least well-understood aspect of plate tectonic theory (8, 9). The Wilson cycle predicts that the Atlantic will close again to form a second Pangaea through widespread initiation of subduction in the Atlantic basin (1, 10). Yet, with the exceptions of the narrow Caribbean and Scotia arcs, there is no evidence for subduction initiation (either intra-oceanic or at passive margins) within this ocean basin, despite 100- to 200-million-year-old passive margin sequences. From a thermal point of view, for ages greater than ~80 My, the flattening of the sea-floor-age relation (11) suggests little further change in passive margin thermal structure (and by extension little change in passive margin stability). Thus, the passage of time does not appear to increase the probability of subduction initiation in the Atlantic basin,

suggesting that P-type closure remains a likely closure mode for the future.

If most of the world's subduction zones were indeed lost through P-type ocean closure, roughly constant subduction flux could still be maintained if subduction initiation approximately balanced subduction termination. This requires that there be a causal relationship between the two processes corresponding to an approximate "conservation law" for subduction flux; namely, that order-of-magnitude fluctuations in subduction flux do not occur. Is there such a law? The most likely mechanism would be through a transfer of stress induced by a collision, leading to "forced" subduction initiation elsewhere (8). Yet the response to recent collisions suggests otherwise. The formation of the Alpine-Himalayan chain represents the collision of India and Africa with Eurasia at about 35 to 50 Ma in the closure of the Tethys Ocean. If large-scale collisional stress transfer occurred, we would expect subduction to have initiated elsewhere within the Indian and African plates. However, no new subduction zones have initiated south of either India or Africa to compensate for the loss of subduction by this ocean closure. The Indian plate does exhibit extensive internal deformation related to the collision (12); yet more than 50 My

have elapsed without the initiation of subduction. In fact, the only subduction initiation that has occurred in the past 80 My (with the notable exception of the 600-km-long Scotia Arc) has been intra-oceanic and entirely within the Pacific basin (8). As such, it would prevent neither the ultimate closure of the Pacific basin nor the loss of Pacific-basin subduction zones. These examples illustrate that (i) an internal ocean can exist for at least 200 My (and probably much longer) without subduction initiation, and (ii) subduction does not immediately begin in response to a continent-continent collision, lagging by at least tens and perhaps hundreds of millions of years. Given the evidence that supercontinent assembly has occurred by P-type closure in the past and appears to be occurring in the present, and the absence of evidence for a subduction flux "conservation law," we conclude that supercontinent assembly has the potential to substantially reduce subduction flux or even temporarily eliminate it.

Although a direct record of subduction flux earlier than 200 Ma is not available, we can look for proxies from which to estimate this flux. Here we define subduction flux, F_s , as the globally integrated product of trench length and convergence velocity. One promising approach is to make use of subduction-related magmatism. The primary magmatic product of subduction is arc volcanism, and it is reasonable to assume that the global arc magmatic production rate, M , is proportional to F_s . This assumption is supported by numerical modeling results (13), by comparisons with local geology (14), and by the positive correlation between magmatic production rates and convergence velocity for several subduction zones in the Pacific (fig. S2). If arc magmatism is reflected in mantle depletion, we can then use the time history of mantle depletion as a proxy for subduction flux.

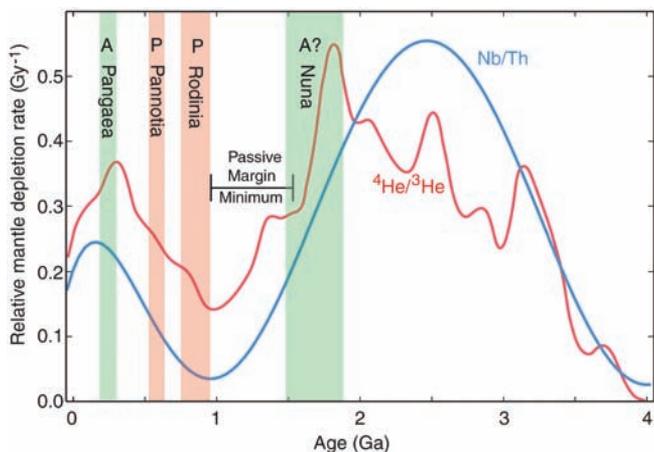
As an illustration, we choose two geochemical indicators of mantle depletion history proposed in the literature. The first is based primarily on Nb/Th ratios (15), whereas the second is based on the statistical distribution of $^4\text{He}/^3\text{He}$ ratios in ocean island basalts (16, 17). These two independent measures exhibit the same overall basic features, namely a maximum in the Neoproterozoic, a minimum around 1.0 billion years ago (Ga), and a second maximum in the Phanerozoic (Fig. 2). Interpreted as subduction flux, this variation is distinctly different from the expected gradual reduction in subduction flux over the age of Earth inferred from the secular decline in mantle temperature (18). These geochemical proxies therefore suggest a minimum in subduction flux corresponding in time to the formation of Rodinia by P-type closure.

Other proxies for plate tectonic activity can also be used. Assuming that continental crust is predominantly derived from arc volcanism, a continental growth-rate curve could be used as a subduction flux proxy. Although there are concerns about biased sampling of the crust, the role

Table 1. History (formation age, breakup age, and duration) and ocean closure mode for the last four supercontinents.

Supercontinent	Formation (Ma)	Breakup (Ma)	Duration (My)	Mode	Ref.
Pangaea	350	250	100	Atlantic	(4)
Pannotia/Gondwanaland	650	550	100	Pacific	(4, 5)
Rodinia	900	760	140	Pacific	(4, 6, 39)
Nuna	1800	1500	300	Atlantic?	(4)

Fig. 2. Estimated mantle depletion-rate curves as inferred from two independent sources. Blue curve: relative mantle depletion rate obtained from a derivative of polynomial fit to measurements of Nb/Th ratios and other geochemical and geophysical estimates (15). Red curve: $^4\text{He}/^3\text{He}$ ratios (16) of ocean island basalts, with an inferred time scale based on a He evolution model that matches peaks in the distribution of crustal zircons. The two



curves are broadly similar, characterized by a peak at ~2.5 Ga, a minimum around 1.0 Ga, and a second maximum in the Phanerozoic. The units of the blue curve are relative mantle depletion rate (Gy^{-1}), whereas the $^4\text{He}/^3\text{He}$ curve has no well-defined units but should also reflect relative mantle depletion. Assuming that the depletion-rate curves are proxies for subduction flux, then they should reflect the rate of plate tectonic activity and predict relatively low tectonic activity in the Mesoproterozoic and early Neoproterozoic. The minimum in passive margin formation (denoted by the black time bracket), thought to be another proxy for plate tectonic activity (26), also occurs roughly at this time (black bracket). Also shown are the lifetimes of the known supercontinents, denoting whether they were formed primarily by A-type (A, green) or P-type (P, orange) closure. Grenville collision occurred at the formation time of Rodinia (~1 Ga).

of recycling, and the difficulty of distinguishing between juvenile and reworked crust, it has become increasingly clear that continental growth is episodic rather than continuous (15, 16, 19–24). The conventional explanation is that this episodicity reflects dramatic events in the mantle, such as superplumes and mantle overturn events, implicitly arguing that crustal addition is unrelated to subduction. However, we propose that an equally plausible alternative is that the episodicity of crust formation reflects the episodicity of subduction flux (25). Another possible proxy for subduction flux is the occurrence of passive margins throughout Earth's history (26). It has been found that passive margins do not occur with a higher frequency (that is, with shorter passive margin lifetimes) at earlier times in Earth's history, as would be expected from the secular decline in mantle temperature. Instead, there is a near absence of passive margins in the Mesoproterozoic between 1.75 and 1.0 Ga as compared to periods before and after. The one exception corresponds to the longest-lived passive margin, with a lifetime of 600 My, suggesting a decrease in plate tectonic activity during this period. This timing is broadly consistent with the mantle depletion curves shown in Fig. 2 and provides additional support for a reduction in subduction flux during this time.

A dramatic reduction in subduction flux would have important implications for the thermal history of Earth. For example, an order of magnitude decrease would, from a thermal point of view, constitute a switch to stagnant-lid or sluggish-lid convection, with little or no subduction or sea-floor spreading (27). There is increasing evidence that Earth has lost heat much more slowly than is predicted from a backward extrapolation of present-day plate tectonic rates. Indeed, such an extrapolation assuming a present-day Urey ratio, γ_0 , of 0.3 leads to unacceptably high mantle temperatures for ages >1 Ga

(28, 29) [so-called thermal catastrophe (Fig. 3)]. A value of $\gamma_0 = 0.7$ avoids this problem, although this appears to be an unacceptably high value, given present estimates of the concentration of heat-producing elements (28). Although there have been other hypothesized solutions to this problem, such as more sluggish plate tectonics in the past due to thicker chemical boundary layers formed at higher mantle temperature (29), a minimum in slab flux would dramatically lower the rate of heat loss and provide a simple means of resolving this paradox (Fig. 3). As an illustration, we have performed a thermal history calculation by parameterizing the heat flux Q as a function of internal temperature (29), multiplied by an index of plate tectonic “efficiency” (a value between 0 and 1), based on the gross characteristics of the mantle depletion-rate curves in Fig. 2 (17). The curve is scaled so that the two peaks (at the present and at 2.5 Ga) correspond to 100% efficiency, with the greater peak height at 2.5 Ga reflecting higher mantle temperatures at that time. In addition, the minimum in crustal growth rate at 1.0 Ga is constrained to be at 10% efficiency [corresponding to a 90% reduction in subduction flux or ~5000 km of subduction length remaining (fig. S1)]. Using $\gamma_0 = 0.3$, we find that the variable slab-flux model yields a thermal history that does not result in thermal catastrophe back to 4 Ga (Fig. 3).

These global calculations also imply that on shorter time scales, an order of magnitude reduction in slab flux should correspond to a period of increased mantle temperature whose magnitude depends on the assumed radioactive heat production. For $\gamma_0 = 0.3$ (0.7), the heating rate would be about 5°C (12°C)/100 My in the recent past and 18°C (42°C)/100 My in the early Archean, when heat production was thought to be several times greater (29). Thus, periods of attenuated plate tectonic activity may also be reflected in in-

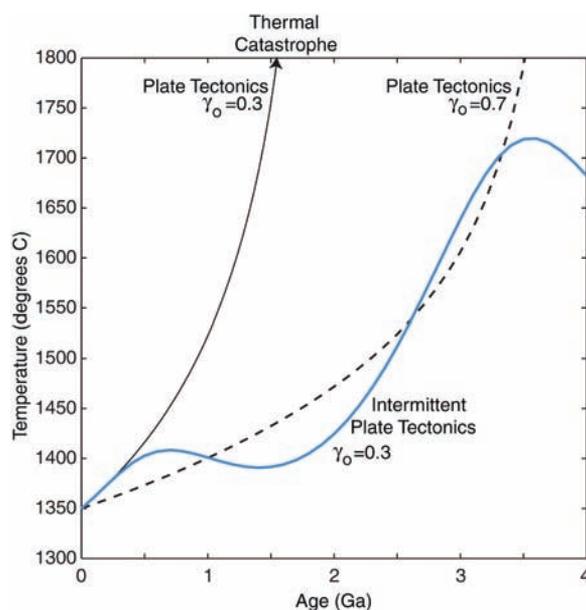
creased non-subduction-related magmatic activity. For example, the major emplacement period of “anorogenic” granites at 1.6 to 1.3 Ga corresponds in time to the suggested period of reduced plate tectonic activity in the Mesoproterozoic. These granites are difficult to explain by plate tectonic (orogenic) mechanisms (30, 31), and proposals for their emplacement have appealed to supercontinent formation and subsequent insulation of the underlying mantle (32, 33). Decreased subduction flux constitutes another viable mechanism, and the worldwide occurrence of these granites suggests a global increase in upper mantle temperature.

It has been implicitly assumed that the oceanic and continental components of plate tectonics, namely sea-floor spreading/subduction and the Wilson cycle, interact only weakly. As we have shown, however, supercontinent assembly, through its impact on subduction zones, has the potential to produce a very strong interaction, possibly to the point of temporarily stopping plate tectonics altogether. If this is correct, then the Wilson cycle takes on new meaning, representing a cycle in the operation of plate tectonics itself.

References and Notes

1. J. T. Wilson, *Nature* **211**, 676 (1966).
2. C. DeMets, R. G. Gordon, D. F. Argus, S. Stein, *Geophys. J. Int.* **101**, 425 (1990).
3. We are assuming that plate tectonics began to operate early in Earth's history. This sidesteps the important problem of plate tectonic initiation. Some have argued that plate tectonics began as late as the Neoproterozoic (34–37).
4. J. B. Murphy, R. D. Nance, *Int. Geol. Rev.* **47**, 591 (2005).
5. P. F. Hoffman, *Science* **252**, 1409 (1991).
6. I. W. D. Dalziel, S. Mosher, L. M. Gahagan, *J. Geol.* **108**, 499 (2000).
7. K. E. Karlstrom *et al.*, *Precambrian Res.* **111**, 5 (2001).
8. M. Gurnis, C. Hall, L. Lavier, *Geochem. Geophys. Geosys.* **5**, Q07001 (2004).
9. R. J. Stern, *Earth Planet. Sci. Lett.* **226**, 275 (2004).
10. J. F. Casey, J. F. Dewey, *Geol. Soc. Spec. Publ.* **13**, 269 (1984).
11. C. Stein, S. Stein, *Nature* **359**, 123 (1992).
12. M. Gerbault, *Earth Planet. Sci. Lett.* **178**, 165 (2000).
13. A. M. Cagnioncle, E. M. Parmentier, L. T. Elkins-Tanton, *J. Geophys. Res.* **112**, B09402 (2007).
14. P. Clift, P. Vannucchi, *Rev. Geophys.* **42**, RG2001 (2004).
15. K. D. Collerson, B. S. Kamber, *Science* **283**, 1519 (1999).
16. S. W. Parman, *Nature* **446**, 900 (2007).
17. Materials and methods are available as supporting material on Science Online.
18. G. F. Davies, *Dynamic Earth: Plates Plumes and Mantle Convection* (Cambridge Univ. Press, Cambridge, 1999).
19. J. D. Kramers, I. N. Tolstikhin, *Chem. Geol.* **139**, 75 (1997).
20. K. C. Condie, *Earth Planet. Sci. Lett.* **163**, 97 (1998).
21. K. C. Condie, *Tectonophysics* **322**, 153 (2000).
22. S. Rino *et al.*, *Physics Earth Planet. Int.* **146**, 369 (2004).
23. A. I. S. Kemp, C. J. Hawkesworth, B. A. Paterson, P. D. Kinny, *Nature* **439**, 580 (2006).
24. C. J. Hawkesworth, A. I. S. Kemp, *Nature* **443**, 811 (2006).
25. C. O'Neill, A. Lenardic, L. N. Moresi, T. H. Torsvik, C.-T. A. Lee, *Earth Planet. Sci. Lett.* **262**, 552 (2007).
26. D. C. Bradley, *Eos* **88**, U44A-03 (2007).
27. N. H. Sleep, *J. Geophys. Res.* **105**, 17563 (2000).
28. J. Korenaga, *Geophys. Res. Lett.* **30**, 1437 (2003).
29. J. Korenaga, *Archean Geodynamics and the Thermal Evolution of Earth*, K. Benn, J. C. Mareschal, K. Condie,

Fig. 3. Estimated thermal history of Earth under variable subduction flux (blue curve). We assume that heat flux Q is the product of a function of internal temperature [used by (29)] and a measure of plate tectonic efficiency (between 0 and 1) based on the basic features of the mantle depletion-rate curves (Fig. 2). An initial Urey number, γ_0 , of 0.3 is assumed. Also shown are full plate tectonic efficiency with $\gamma_0 = 0.3$ (solid black curve), which leads to a thermal catastrophe (unreasonably high mantle temperatures) before about 1.0 Ga, and $\gamma_0 = 0.70$ (dashed curve), which avoids the catastrophe before 3.0 Ga but is thought to be an unrealistically high value (29). A variable slab-flux model predicts reasonable mantle temperatures back to 4.0 Ga (no thermal catastrophe) for plate tectonics working on average at about 50% efficiency and with realistic γ_0 .



- Eds., vol. 164 of *Geophysical Monograph Series: Archean Geodynamics and Environments* (American Geophysical Union, Washington, DC, 2006), pp. 7–32.
30. J. L. Anderson, J. Morrison, *Lithos* **80**, 45 (2005).
31. There is also evidence for anorogenic magmatism associated with Pannotia, the other supercontinent formed by P-type closure (38).
32. P. F. Hoffman, *Geology* **17**, 135 (1989).
33. J. L. Anderson, E. E. Bender, *Lithos* **23**, 19 (1989).
34. A. E. J. Engel, S. P. Ison, C. G. Engel, D. M. Stickney, E. J. Cray Jr., *Geol. Soc. Am. Bull.* **85**, 843 (1974).

35. W. B. Hamilton, *Precambrian Res.* **91**, 143 (1998).
36. R. J. Stern, *Geology* **33**, 557 (2005).
37. R. J. Stern, *Chin. Sci. Bull.* **52**, 578 (2007).
38. M. Doblaz, J. Lopez-Ruiz, J.-M. Cebria, N. Youbi, E. Degroote, *Geology* **30**, 839 (2002).
39. Z. X. Li et al., *Precambrian Res.* **160**, 179 (2008).
40. We thank S. Shirey, P. Hoffman, D. Rumble, G. Davies, D. Anderson, A. Shaw, W. Bleeker, D. Bradley, B. Kamber, K. Cooper, D. Weeraratne, M. Fogel, S. Parman, R. Stern, A. Levander, and three anonymous reviewers. This work is supported by the Department of Terrestrial Magnetism,

Carnegie Institution of Washington, and the Woods Hole Oceanographic Institution.

Supporting Online Material

www.sciencemag.org/cgi/content/full/319/5859/85/DC1
SOM Text
Figs. S1 and S2
References

26 July 2007; accepted 27 November 2007
10.1126/science.1148397

A Mosaic of Chemical Coevolution in a Large Blue Butterfly

David R. Nash,^{1*} Thomas D. Als,^{2†} Roland Maile,^{3‡} Graeme R. Jones,³ Jacobus J. Boomsma¹

Mechanisms of recognition are essential to the evolution of mutualistic and parasitic interactions between species. One such example is the larval mimicry that *Maculinea* butterfly caterpillars use to parasitize *Myrmica* ant colonies. We found that the greater the match between the surface chemistry of *Maculinea alcon* and two of its host *Myrmica* species, the more easily ant colonies were exploited. The geographic patterns of surface chemistry indicate an ongoing coevolutionary arms race between the butterflies and *Myrmica rubra*, which has significant genetic differentiation between populations, but not between the butterflies and a second, sympatric host, *Myrmica ruginodis*, which has panmictic populations. Alternative hosts may therefore provide an evolutionary refuge for a parasite during periods of counteradaptation by their preferred hosts.

Social and brood parasites often use mimicry to exploit their hosts (1, 2). These parasites typically affect a small proportion of host populations, so that selection for costly defensive discrimination between kin and parasites by the host (2, 3) may be weak (4). This allows social parasites of ants, bees, and wasps to parasitize multiple host species (5–7). However, when parasites are common enough, selection on hosts to avoid being parasitized fuels coevolutionary arms races, in which parasites evolve better mimicry and hosts improve their recognition of parasites (8, 9).

The dynamics of parasite density and distribution can be explained by geographic mosaic

models of coevolution (10), which allow different degrees of interaction and adaptation between local populations. In these models, mutual coadaptation is restricted to sites of intense and lasting interactions (hotspots), whereas parasites and hosts may evolve independently in other populations (coldspots). Theoretical studies have explored geographic mosaic models (11, 12), but there have been few empirical tests of ecological systems in which the mechanisms of coevolution and the patterns of interaction were known (10).

The Alcon blue butterfly, *Maculinea alcon*, is socially parasitic on two species of *Myrmica* ants in Denmark (13). The butterfly's caterpillars initially develop on marsh gentian plants, *Gentiana*

pneumonanthe (Fig. 1A), before being “adopted” by a foraging *Myrmica* worker (Fig. 1B). Once inside the host ant nest, caterpillars are fed by the ants in preference to their own larvae (14), reducing host fitness, particularly in small colonies (15) (Fig. 1C and fig. S2). The overlap in distribution of the widespread host ants and the rare host plant is small, both locally and regionally, and there is geographic variation in the abundance and use of the two host ant species (13). Populations of the Alcon blue are therefore patchy, and only a small fraction of host ant populations are parasitized and potentially subject to selection for resistance. The parasite is absent from most host populations, which are therefore coevolutionary coldspots (10, 11). In much of Europe, a third ant species, *Myrmica scabrinodis*, is also a host of the Alcon blue (16), but infection of this species has never been observed in Denmark, despite its abundance on Danish *M. alcon* sites (13).

¹Institute of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark. ²Department of Genetics and Ecology, University of Aarhus, DK-8000 Århus C, Denmark. ³School of Chemistry, Keele University, Keele, Staffordshire ST5 5BG, UK.

*To whom correspondence should be addressed. E-mail: DRNash@bi.ku.dk

†Present address: Population Genetics Laboratory, Danish Institute for Fisheries Research, Vejlsøvej 39, DK-8600 Silkeborg, Denmark.

‡Present address: Trivadis GmbH, D-70565 Stuttgart, Germany.

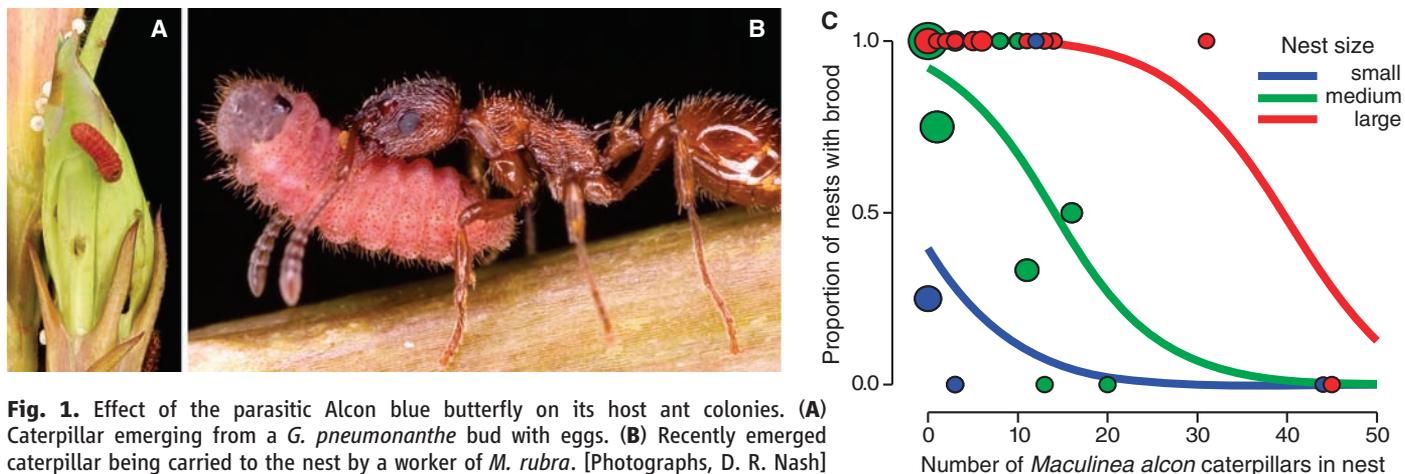


Fig. 1. Effect of the parasitic Alcon blue butterfly on its host ant colonies. (A) Caterpillar emerging from a *G. pneumonanthe* bud with eggs. (B) Recently emerged caterpillar being carried to the nest by a worker of *M. rubra*. [Photographs, D. R. Nash] (C) Relationship between the number of caterpillars present in small, medium, and large *M. rubra* nests (SOM text) in late spring and the probability of ant brood being present. The area of each symbol is proportional to the number of nests observed with that number of caterpillars. Lines are fitted logistic regressions.