

# Making continental crust

Roberta L. Rudnick

**The continental crust has an andesitic bulk composition, which cannot have been produced by the basaltic magmatism that dominates sites of present-day crustal growth—at both convergent margins and within plates. These observations suggest that there may have been a different mode of continental crust generation in Archaean times, and may point to delamination of the lower crust as an important recycling process.**

ONE of the Earth's unique features when compared with other rocky planets in our Solar System is the presence of a chemically 'evolved' crust—the continental crust<sup>1</sup>. The continental crust covers ~40% of the Earth's surface area, and is defined laterally on the basis of the slope break on continental shelves<sup>2</sup> and vertically by a jump in seismic wave speeds to values greater than 7.6–8.0 km s<sup>-1</sup> (the Mohorovičić discontinuity). In contrast to the Earth's oceanic crust, which is predominantly thin, basaltic and young (<200 Myr), the continental crust is thick (20–60 km), with an average thickness of 39 km (ref. 3) and contains virtually every rock type known to geologists, including the oldest rocks found on Earth (presently the Acasta gneisses of Canada at 3.96 Gyr (ref. 4)). The composition of the continental crust is established by independent methods to be intermediate between basalt and rhyolite (in other words, andesitic), and it contains a significant fraction of incompatible trace elements—those that do not fit readily into crystal lattice sites and are therefore concentrated in melts. Thus the continental crust, although volumetrically insignificant (~0.57% of the mass of the mantle) is an important reservoir for the most incompatible elements.

Although the continents constitute one of the more accessible regions of the Earth, compared with the mantle, core and even the oceanic crust, there is considerable debate regarding how and when they formed and the processes responsible for their unique composition. Did the present mass of continents form very early in Earth's history (>4.0 Gyr ago), with past and present growth counterbalanced by recycling of crust into the mantle? If so, what were the main processes that formed the early crust and how do they compare with those operating today? And by what means are large masses of continental crust recycled into the convecting mantle? Alternatively, has the crust grown progressively, with important contributions having occurred after 2.5 Gyr, by processes roughly similar to those occurring now (island arc accretion, oceanic plateau accretion and basaltic underplating)?

Perhaps the greatest dilemma facing those interested in understanding how the continents formed is their composition. The continental crust is believed to be derived by partial melting of the mantle, and forms a complementary geochemical reservoir to the Earth's depleted mantle<sup>5</sup>. Yet most melting experiments carried out on mantle peridotite produce magmas that are considerably less evolved (for example, basalts and picrites) than the bulk continental crust (see, for example, refs 6 and 7).

To explain this paradox several models have been proposed. One suggests that the higher heat flow believed to be present earlier in Earth's history led to significant production of mantle-derived intermediate to silicic melts. These may have formed by melting of subducted oceanic crust<sup>8,9</sup>, by reaction between these melts and overlying peridotite<sup>10,11</sup>, or by shallow melting of wet, metasomatized peridotite<sup>12–14</sup>. The second<sup>15–18</sup> proposes that the crust grows by addition of basaltic magmas derived from the mantle (or by tectonic accretion of basaltic crust formed in island arcs or oceanic plateaus), which undergo intracrustal differentiation to form evolved melts and their complementary residues.

The former ascend buoyantly while the latter transform to a dense mineralogy (eclogite) in the deep crust and are lost to the convecting mantle during 'delamination' events that occur during continental collisions<sup>18</sup>. A third explanation is that chemical weathering of surface rocks leads to depletion in MgO, which exchanges with CaO during mid-ocean-ridge hydrothermal alteration and is ultimately returned to the mantle through subduction, thereby driving the crust towards more evolved compositions<sup>15</sup>. Finally, a fourth possible explanation is that ultramafic complements to the crust exist within the upper mantle as either eclogites or olivine-rich cumulates<sup>19,20</sup>, having high densities and acoustic velocities that are indistinguishable from those of residual peridotite<sup>21</sup>. This last suggestion is not borne out by studies of upper-mantle rocks brought to the surface as xenoliths in continental regions<sup>22,23</sup>, suggesting that if such voluminous cumulates did exist beneath the Moho, they have been largely lost from the lithosphere, perhaps by delamination.

Thus the first three explanations remain as possibilities and call for more detailed examination. These explanations are not mutually exclusive and it is possible that all have operated to some extent during the course of Earth history.

## When did the continents grow?

The timing of continental growth has been the topic of myriad papers over the past three decades and a definitive answer to this question has yet to be determined. Although space does not permit a thorough discourse on this issue, the following points are relevant here.

(1) The present age distribution of the crust, as determined from model age studies using the Sm–Nd isotope system (for example, refs 24–27) provides a minimum estimate of the crustal growth rate. These curves suggest that 35–60% of the present crustal mass formed in the Archaean, a considerably larger amount than the present areal extent of Archaean crust (14%, ref. 28). (2) The present age distribution of the crust does not constrain the maximum growth rate, owing to the occurrence of crustal recycling by means of sediment subduction, tectonic erosion at convergent margins and, perhaps, lower-crustal delamination<sup>29,30</sup>. Recent estimates of the flux of crustal material returned to the mantle at subduction zones are 1.3–1.8 km<sup>3</sup> yr<sup>-1</sup> (ref. 31), of which only a small portion returns to the crust in convergent margin magmas<sup>31,32</sup>. This volume is roughly comparable to current crustal production rates (for example, 1.65 km<sup>3</sup> yr<sup>-1</sup>, ref. 33) and it is uncertain how these rates may have changed in the past. Thus, anywhere between 40 to 100% of the present mass of the continents may have existed since the end of the Archaean.

Irrespective of when the continents attained their present mass, isotopic data demonstrate that continental formation has been occurring throughout Earth history. That is, continents are forming, but the net mass of the continents may or may not be changing. We can therefore use the cumulative mass curves determined from neodymium model ages to define approximately when the present mass of continents grew. It is the pro-

cesses responsible for this crust formation that are of interest here.

**Continental crust composition**

Fundamental to understanding crustal growth is knowledge of the bulk crust composition. Thus it is appropriate in a review of crustal growth processes to begin by discussing the crust composition and evaluating how well it is known.

Estimates of bulk crust composition are derived from observations of the rock types present in the upper continental crust and models of lower-crust composition. The latter are derived from (1) proportions of rocks observed in outcrops of granulites (granulite terrains) that have equilibrated at lower-crustal pressures<sup>34, 36</sup>, (2) relating observed deep-crustal seismic velocities with rock types observed in both granulite xenoliths and terrains<sup>3, 37, 38</sup>, or (3) mixing mafic and silicic rock types in appropriate proportions to satisfy observed heat flow<sup>39</sup>. Thus current geochemical estimates of the continental crust rely on diverse geochemical data bases (some specific to certain regions<sup>34, 36</sup>, others more global in nature<sup>37, 39</sup>); some make geophysical constraints cornerstones of the model<sup>37-39</sup>, others do not<sup>34, 35</sup>.

Table 1 lists a current estimate of the bulk continental crust composition<sup>37</sup>. The major-element composition is fairly well defined, with various estimates falling within 30% of one another for most major elements (Fig. 1a). In contrast, there is variation of more than a factor of 2 in the estimates of K concentration, as well as those of other highly incompatible elements (for example, Cs, Rb, Th, U). The same is true for some compatible elements (for example, Ni, Fe, Fig. 1a). Such variations give rise to large uncertainties when calculating the amount of mantle that differentiated to form the crust (see, for example, refs 40, 41).

These uncertainties aside, there are some striking similarities in the crust compositional estimates reviewed above: they are all 'intermediate' in composition, with 57-64% SiO<sub>2</sub> and Mg# (defined as 100 × molar Mg/(Mg + Σ Fe)) between 50 and 56; they are all enriched in light rare-earth elements (REE), and have similar incompatible element ratios, with Nb and Ti depleted and Pb strongly enriched relative to the REE (Fig. 1b). Considering the diverse methods and observations used to create the crust compositional models, these similarities can be considered robust features of the continents with which any model of crustal growth must be in harmony. Below I explore how these features might be produced.

**Crustal growth processes**

Continental growth is generally ascribed to two distinct plate tectonic settings: intraplate and convergent margins. Crustal growth at convergent margins, where lithospheric plates converge and basaltic oceanic crust is subducted into the mantle, may be accomplished by tectonic accretion of intra-oceanic island arcs or magmatic additions at continental arcs. Growth of continents in intraplate settings occurs in response to plume-related magmatism. This can happen within continents, such as in flood basalt provinces, or in ocean basins, resulting in anomalously thick oceanic crust (oceanic plateaus) that is difficult to subduct and is consequently accreted to continents during subduction-driven collisional events. Crustal growth in each of these settings is discussed in turn.

**The andesite model and its variants.** The andesitic composition of the continental crust, coupled with the spectacular andesite volcanism that occurs at convergent margin settings, led Taylor<sup>42, 43</sup> to propose that the continents form by accretion of island arcs of andesitic composition. This 'andesite model' of crustal growth appealed to uniformitarian sensibilities, in that processes we see occurring today could account for the formation of the continents. Subsequent investigations of continental crust and island arcs, however, have demonstrated the difficulties with this simple model. The andesite model of crust formation cannot account for the bulk-crust Cr and Ni contents (average

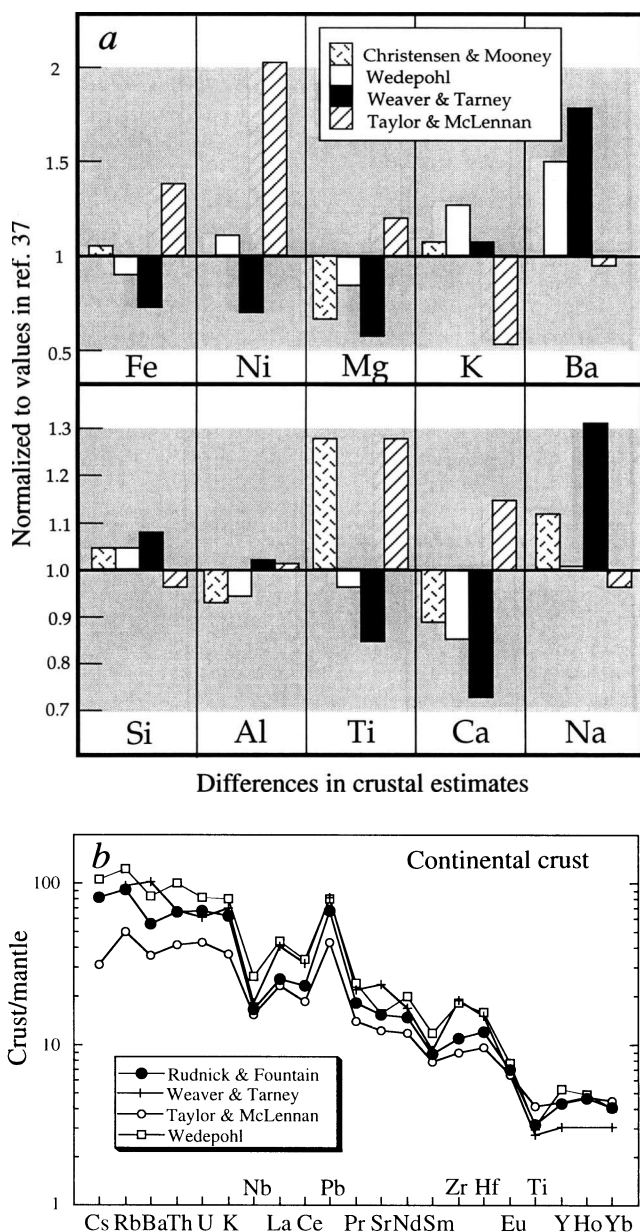


FIG. 1 a, Differences in elemental abundances between the various crust composition models. Values from Christensen and Mooney<sup>3</sup>, Weaver and Tarney<sup>34</sup>, Taylor and McLennan<sup>39</sup> and Wedepohl<sup>38</sup> are normalized to those of Rudnick and Fountain<sup>37</sup>. For the elements shown in the upper panel, variations between models are within a factor of two (shaded region), whereas for elements shown in the lower panel, variations are within 30% of the Rudnick and Fountain model (shaded region). b, Trace-element compositions of the continental crust. Data are normalized to primitive mantle<sup>73</sup> and plotted in order of their relative incompatibilities during mantle melting, as deduced from studies of oceanic basalts<sup>73</sup>. All models show high La/Nb, low Ce/Pb and similar Sr/Nd compared to undifferentiated mantle. These are considered robust features of continent composition.

andesites have abundances that are too low) nor its Th/U ratio<sup>39</sup>. Furthermore, a large portion of the continents probably formed during Archaean times (see above) and andesites are uncommon in Archaean volcanic sequences. This led Taylor and McLennan<sup>39</sup> to suggest that only post-Archaean crustal growth is accomplished by island arc accretion.

Perhaps most problematic for the andesite model, however, is that intra-oceanic island arcs are estimated to have basaltic, rather than andesitic bulk compositions<sup>15, 44, 46</sup>. This is consistent

with the observation that generally only basaltic or more magnesian magmas (for example, picrites or komatiites) are produced in high-pressure experimental melting studies of mantle peridotite. High-Mg# andesites and boninites that have equilibrated with mantle peridotite are thought to form under rather special  $P$ - $T$ - $X_{H_2O}$  ( $X_{H_2O}$  is molar proportion of water) conditions in modern arcs (that is, shallow, hot and wet)<sup>47,48</sup>, consistent with their relative rarity in arc settings. Thus accretion of modern island arcs produces basaltic crustal additions and cannot account for the intermediate composition of post-Archaean crust.

Andesites are more common in continental arc settings (such as the Andes, Cascades and central America) compared to intra-oceanic island arcs, presumably due to the effects of pre-existing continental crust on primary mantle-derived basaltic magmas (for example, ref. 16). But primary arc magmas in continental settings are estimated to have basaltic compositions, similar to those in intra-oceanic settings<sup>15</sup>.

To overcome the above difficulties, several variations on the andesite model for crustal growth have been proposed. One of these suggests that during the Archaean, mantle temperatures may have been significantly higher than at present, leading to generation of mantle-derived intermediate to silicic melts. This may have occurred by melting of metasomatically enriched peridotite to produce intermediate melts<sup>7-9</sup> (the 'sanukatoids' of Shirey and Hanson<sup>12</sup>), which then differentiated to form silicic plutons, the so-called 'TTGs' (for tonalite-trondhjemite-granodiorite) that dominate in Archaean cratons. Alternatively, TTGs may have formed by direct melting of subducted oceanic crust, leaving behind a complementary eclogitic residue that is returned to the convecting mantle<sup>8,9</sup>. An important and distinctive feature

of TTGs is their trace-element compositions: they are enriched in incompatible trace elements and have strongly fractionated heavy REE patterns, suggesting that garnet played a role in their genesis (see ref. 49 and references therein).

Experimental studies have shown that production of andesite (or monzodiorites or quartz monzodiorites, as their intrusive equivalents are called) by melting of peridotite is possible under certain  $T$ - $X_{H_2O}$  conditions at uppermost mantle pressures. These include, at 1.0 GPa, temperatures in excess of 1,150 °C and magmatic water contents of 4-7 wt% (refs 20, 47, 48). A recent study produced andesite by 2% melting of anhydrous spinel lherzolite<sup>50</sup>, but a follow-up investigation has called these results into question (D. H. Green and T. Falloon, personal communication). Irrespective of the final resolution of this controversy, the very high viscosities of these melts<sup>50</sup> make them an unlikely means by which to generate the continents. Thus, volumetrically significant andesite production in the uppermost mantle appears to be limited to rather special hot and wet conditions that may have been more common in the Archaean than today<sup>14</sup>. Moreover, peridotite melting, whether hydrous or anhydrous, is not able to generate silicic melts with high Mg# nor the distinctive incompatible trace-element signatures of TTG. These features of TTGs, coupled with their primitive Nd-isotope compositions, require significant metasomatic enrichment of the peridotite source shortly before TTG genesis.

In contrast, production of tonalite and trondhjemite by partial melting of mafic rocks is well documented experimentally<sup>51-55</sup> and yields the requisite REE and Nb concentrations of TTGs, provided garnet and rutile are residual phases. In detail, the TiO<sub>2</sub> and Al<sub>2</sub>O<sub>3</sub> contents of these experimentally produced melts are generally higher than those observed in Archaean TTGs at simi-

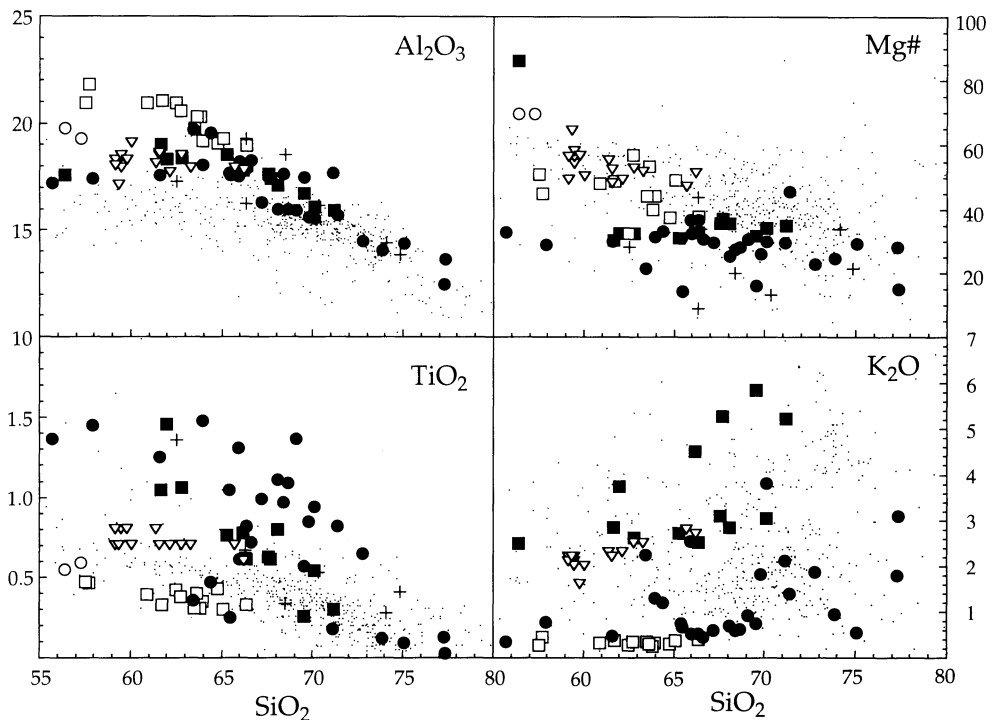
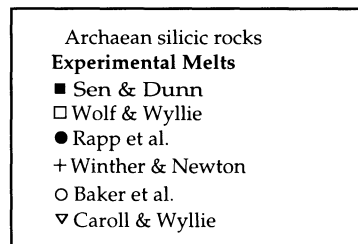


FIG. 2 Major-element variation diagrams comparing Archaean silicic rocks with melt compositions generated in experiments on amphibolite melting (Sen and Dunn<sup>54</sup>, Wolf and Wyllie<sup>55</sup>, Rapp *et al.*<sup>52</sup>, and Winther and Newton<sup>53</sup>), peridotite melting (Baker *et al.*<sup>50</sup>) and mixed peridotite-tonalite melting (Caroll and Wyllie<sup>61</sup>).



lar SiO<sub>2</sub> values (Fig. 2), whereas their Mg # are lower (especially at high SiO<sub>2</sub> values). These discrepancies are probably due to the choice of experimental starting composition. Archaean basalts have, on average, higher MgO contents and Mg # and lower Al<sub>2</sub>O<sub>3</sub> and TiO<sub>2</sub> contents than the basaltic compositions used in the amphibolite melting experiments (Fig. 3). Similarly, the relatively high Ni contents of some Archaean TTGs (see, for example, ref. 14) may reflect the Ni-rich character of Archaean basalts<sup>56</sup> coupled with a relatively low bulk partition coefficient for Ni during eclogite melting, where garnet, omphacite and rutile are likely to be residual phases. Unaltered Archaean basalts are expected to have low K<sub>2</sub>O contents (≤0.1%), but if the chemical effects of sea-floor alteration in the Archaean were similar to those observed today (see, for example, ref. 57), then K<sub>2</sub>O contents may be enhanced by an order of magnitude in altered Archaean oceanic basalts, thereby providing the K<sub>2</sub>O necessary to form TTGs. Thus, despite some discrepancies between existing experimental melts and TTGs, choice of a starting composition that more closely matches altered Archaean basalts should yield silicic melts that are indistinguishable from Archaean TTGs.

What is not clear from the geochemistry of Archaean TTGs is at what depth they were generated; melting may have occurred within the lower continental crust, within subducted mafic crust or within metasomatized peridotitic mantle. If the first, the problem remains that voluminous mafic residues (garnet granulite or eclogite) are not present in either the lower crust or uppermost mantle of Archaean cratons<sup>58</sup>. The slab-melting model provides a convenient means of disposing of these residues, but it remains unclear what will happen to the silicic melts as they migrate through the overlying peridotitic wedge. Finally, the third model,

melting of metasomatized peridotite, can produce only high-Mg # andesites, yet these compositions are far outweighed by the more siliceous rocks of the Archaean crust (Fig. 2), some of which have equally high Mg #. These latter rocks cannot be produced from a metasomatized peridotite source.

As the trace-element characteristics of TTGs are the same as those predicted for a melt derived from subducted oceanic crust, it would seem that the two models of TTG genesis (slab versus peridotite melts) might profitably be combined into a model where TTGs are generated either by melting shallow mantle that has been hydrated and hybridized to pyroxenite by introduction of a silicic, slab-derived melt or by interaction of such a melt with overlying mantle wedge (see refs 10, 11 and references therein). It is possible that the volatile content of the hydrated crust served to buffer the degree of slab melting and that these melts interacted to variable extents on their way up through the mantle, thereby producing the distinctive and sub-parallel<sup>14</sup> trace-element patterns observed in TTGs (see Fig. 7 in ref. 10). Such models may also explain the presence of enstatite-rich peridotite found in some cratonic mantle xenolith suites<sup>59</sup> (for example, Kaapvaal craton<sup>60</sup>). Indeed, experimental investigations of peridotite-tonalite mixtures have produced silicic melts with high Mg #, similar to TTGs (Fig. 2) and reaction residues of orthopyroxene + garnet ± clinopyroxene<sup>61</sup>.

Another variation on the andesite model has recently been proposed<sup>11</sup> in which andesites form in the mantle through interaction between rising basalts or silicic melts (the latter derived from subducted slabs) and peridotitic wall rock. In this model, young as well as ancient crust forms through direct addition of high-Mg # andesites. As the Mg # of the continental crust is significantly lower than that predicted for andesites which have

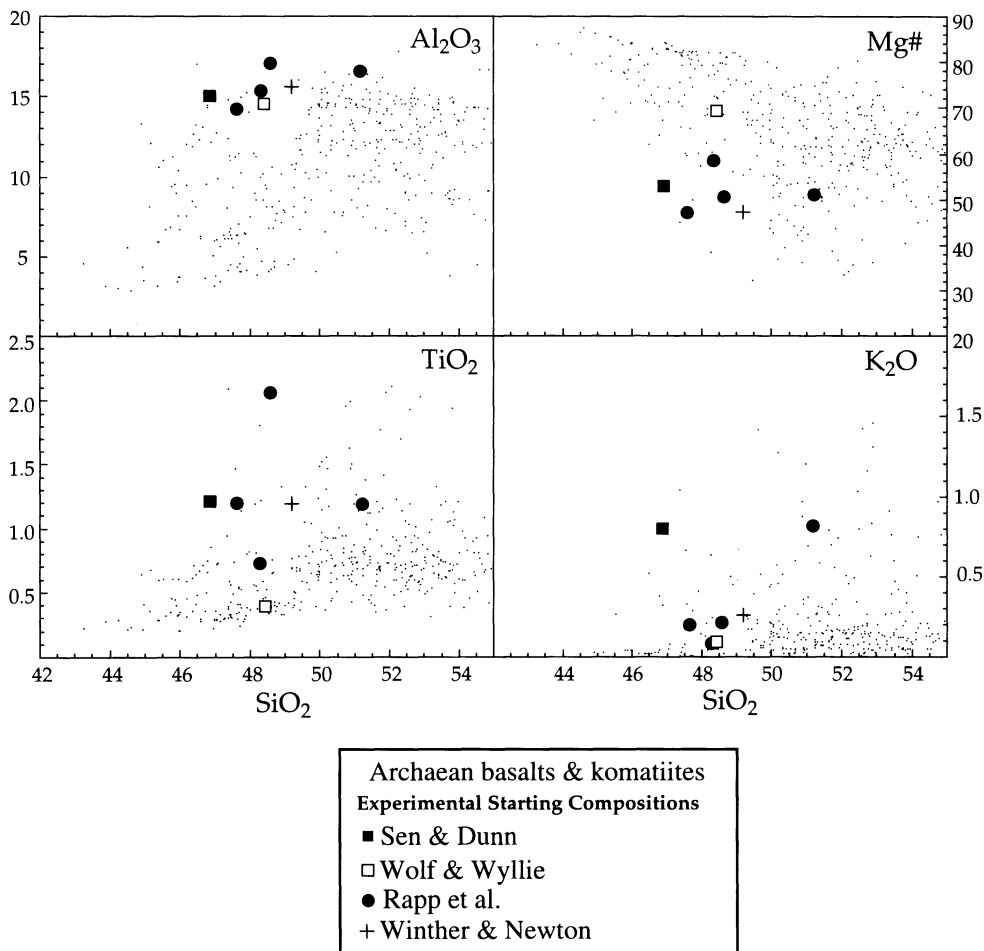


FIG. 3 Major-element variation diagrams comparing Archaean basalt and basaltic komatiite compositions with starting compositions used in amphibolite melting experiments (see Fig. 2). Data normalized to 100% anhydrous. In general, the Archaean lavas have lower Al<sub>2</sub>O<sub>3</sub> and TiO<sub>2</sub> and higher Mg # than the compositions chosen for experimental investigation. K<sub>2</sub>O contents for all but two of the basaltic starting compositions overlap values seen in Archaean basalts. It is possible that even higher K<sub>2</sub>O contents were present in hydrothermally altered Archaean sea-floor basalts (see text).

equilibrated with peridotite (that is,  $Mg\# = 50\text{--}54$  for bulk crust, compared to  $>70$  for melts in equilibrium with peridotite), this model would require loss of high- $Mg\#$  cumulates from the crust or lithospheric mantle, as discussed above. Moreover, this model faces some of the same difficulties as the original andesite model for the generation of continental crust: namely, that intra-oceanic island arcs appear to have basaltic bulk compositions<sup>15,44,46,62</sup> and andesites are uncommon constituents of Archaean-aged crust<sup>63</sup>.

**Intraplate crustal growth.** During the Cenozoic, crustal growth at plate margins is estimated to outstrip growth at intraplate settings by a factor of 3 (1.1 versus  $0.3\text{ km}^3\text{ yr}^{-1}$ , ref. 33), but it is not clear that this has always been the case. Large tracts of crust in west Africa<sup>64</sup> are interpreted to have grown by accretion of oceanic plateaus, considered to have formed by plume-related magmatism. In addition, oceanic plateaus make up about one-third of the accreted Wrangellia terrain in northwestern North America<sup>65,66</sup> and plume-associated magmatism has been estimated to contribute between 15% and  $>50\%$  of some Archaean greenstone belts<sup>67,68</sup>. Intraplate magmatism may also contribute significant mass to continental crust via basaltic underplating in flood basalt provinces<sup>69,70</sup>. Plume-generated intraplate crustal growth may be episodic, volumetrically significant and ultimately related to mantle convection patterns<sup>71</sup>.

Can any limits be placed on the amount of crust generated in intraplate settings? As illustrated in Fig. 1 and discussed above, the continental crust has trace-element characteristics broadly similar to magmatic rocks generated in convergent margin settings. In detail, however, significant differences exist. Convergent margin magmas are characterized by variable, but generally high, Sr/Nd ratios compared to that of the primitive mantle (that is, 15; ref. 72). The Sr/Nd ratio of the continental crust overlaps these values, but lies at the lower end of the range (Fig. 4). That is, the continental crust has a lower Sr/Nd than is typical of convergent margin magmas. Likewise, the characteristic depletion in Nb relative to La in convergent margin magmas is also seen in the continental crust, but to a lesser degree (Fig. 4).

Convergent margin magmas with low Sr/Nd ratios also have negative Eu anomalies, owing to plagioclase fractionation. Thus, lower Sr/Nd in the continental crust compared with average arc volcanics may indicate that plagioclase-bearing cumulates, converted to plagioclase-free eclogitic mineralogies at the base of the thickened crust, have been lost from the continents by delamination of the lower crust (see below). The negative Eu anomaly seen in the bulk crust models of Gao *et al.*<sup>36</sup>, Wedepohl<sup>38</sup> and, to a lesser extent, Rudnick and Fountain<sup>37</sup> support this contention (Table 1). But, this process cannot explain the discrepancy between the La/Nb of the crust and convergent margin magmas because La/Nb, unlike Sr/Nd, does not vary significantly with depth in the continental crust<sup>37</sup> (that is, La/Nb is not significantly fractionated by intracrustal processes).

An alternative explanation of the trace-element characteristics of the crust is that they reflect growth through a mixture of convergent margin and intraplate magmatism. Intraplate magmas through time have Sr/Nd similar to the chondritic ratio (that is, 16) and La/Nb generally  $<1.0$  (refs 73, 74). Mixing relations between an intraplate basalt and possible convergent margin magmas are illustrated in Fig. 5. Between 10 and 35% of an intraplate component is required to explain the continental crust's La/Nb ratio.

It has been suggested on the basis of the light-REE enrichment of continental crust that its trace-element budget is dominated by the influence of small melt fractions from the mantle<sup>75</sup>. The dominantly arc-like trace-element characteristics of the continents highlighted above suggest that continent growth occurs mainly at convergent margins. In modern arcs, the role of fluids versus slab melts in generating the distinctive arc trace-element

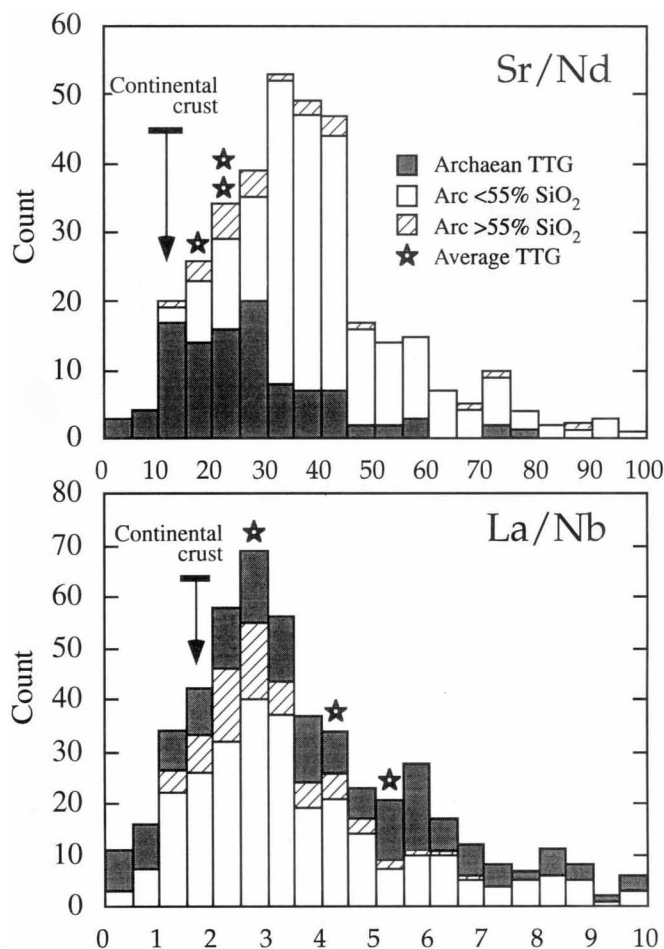


FIG. 4 Histograms of Sr/Nd and La/Nb ratios of arc magmas and Archaean TTGs (tonalites–trondhjemites–granodiorites) compared with bulk continental crust. To remove the effects of intracrustal differentiation on the Sr/Nd ratio, only rocks with  $0.90 < Eu/Eu^* < 1.10$  were included in the Sr/Nd plot ( $Eu/Eu^* = Eu_N / (Sm_N \times Gd_N)^{0.5}$ , where the subscripted N indicates the values are normalized to chondritic meteorites). Stars represent values of average TTG from refs 38, 49, 99.

signature is still debated, but most investigators acknowledge the importance of fluid transfer from slab to overlying mantle wedge (ref. 76 and references therein). The relative importance of these processes in the Archaean is more poorly constrained, but the models for TTG genesis discussed above suggest that slab melts of 10–20% may have been important. Thus, small-volume melts are not required to explain the crust's trace-element composition; fluid-transfer processes and slab melting may have played a more important role in generating the crust's composition.

In contrast to La/Nb, the Sr/Nd ratio of the continental crust is too low to be simply explained as a mixture of intraplate and convergent margin magmas (Fig. 5b). There are several possible explanations for this: (1) plagioclase-rich cumulates are under-represented in the lower-crustal xenolith populations that were used to model the composition of the lower crust, (2) Sr has been preferentially lost from the continents owing to carbonate precipitation in altered oceanic crust<sup>77</sup>, or (3) plagioclase-bearing cumulates have been lost from the base of the crust through delamination. Although the first explanation cannot be ruled out (because there are only  $\sim 70$  determinations of Eu anomalies in mafic xenoliths currently available<sup>37</sup>), the other explanations are more appealing. Preferential Sr recycling is supported by the high Sr/Nd ratios observed in altered oceanic crust composites<sup>57</sup>, and delamination of a mafic to ultramafic layer from the base

TABLE 1 Bulk compositional estimate of the continental crust

|                                |      |        |        |
|--------------------------------|------|--------|--------|
| SiO <sub>2</sub>               | 59.1 | Ba     | 390    |
| TiO <sub>2</sub>               | 0.7  | La     | 18     |
| Al <sub>2</sub> O <sub>3</sub> | 15.8 | Ce     | 42     |
| FeO*                           | 6.6  | Pr     | 5.0    |
| MnO                            | 0.11 | Nd     | 20     |
| MgO                            | 4.4  | Sm     | 3.9    |
| CaO                            | 6.4  | Eu     | 1.2    |
| Na <sub>2</sub> O              | 3.2  | Gd     | 3.6    |
| K <sub>2</sub> O               | 1.9  | Tb     | 0.56   |
| P <sub>2</sub> O <sub>5</sub>  | 0.2  | Dy     | 3.5    |
|                                |      | Ho     | 0.76   |
| Mg#                            | 54.4 | Er     | 2.2    |
| Li                             | 11   | Yb     | 2.0    |
| Sc                             | 22   | Lu     | 0.33   |
| V                              | 131  | Hf     | 3.7    |
| Cr                             | 119  | Ta     | 1.1    |
| Co                             | 25   | Pb     | 12.6   |
| Ni                             | 51   | Th     | 5.6    |
| Cu                             | 24   | U      | 1.4    |
| Zn                             | 73   | K/U    | 10,100 |
| Ga                             | 16   | Sr/Nd  | 16     |
| Rb                             | 58   | La/Nb  | 1.5    |
| Sr                             | 325  | Ce/Pb  | 3.3    |
| Y                              | 20   | Nb/U   | 8.6    |
| Zr                             | 123  | Th/U   | 3.9    |
| Nb                             | 12   | Eu/Eu* | 0.96   |
| Cs                             | 2.6  |        |        |

These estimates are taken from ref. 37. Symbols used: Mg# = 100 × molar Mg/(Mg + Σ Fe); FeO\*, total Fe as FeO; Eu\*, Eu value interpolated from REE pattern (see Fig. 4 legend).

of the crust could explain the major-element compositional paradox of the continental crust.

**Continental delamination.** Delamination of continental lithospheric mantle, owing to a density inversion between lithospheric and underlying asthenospheric mantle, was originally proposed to explain uplift of the Colorado plateau<sup>78</sup> and high-temperature metamorphism in the Himalayas<sup>79,80</sup>. Subsequently, delamination of the lower continental crust has been proposed to account for the intermediate composition of the continental crust<sup>17,18,81</sup>. A critical feature of lower-crustal delamination models is a density inversion between mafic or ultramafic lower crust and the underlying depleted peridotitic mantle. In these models, high-density lower crust may form as (1) ultramafic crystal cumulates from fractionating basaltic magmas at the base of the crust; these are rich in iron and hence denser ( $\rho = 3.4\text{--}3.6\text{ g cm}^{-3}$ ) than refractory mantle composed of forsteritic olivine ( $\rho = 3.3\text{ g cm}^{-3}$ , ref. 12) or (2) mafic lithologies (cumulates, restites or ponded melts) that convert to eclogite ( $\rho > 3.3\text{ g cm}^{-3}$ ) at the base of an anomalously thick crust<sup>17,18</sup>.

Although the lower crust has yet to be included in numerical models of delamination, it appears that lithospheric thickening (such as occurs at sites of continental-scale collisions) is required to achieve delamination<sup>18,80</sup>. Thickening serves two purposes: (1) it promotes transformation of mafic lower crust into dense eclogite, and (2) it depresses cold, and presumably denser, lithospheric mantle into hotter and more buoyant asthenosphere, thereby providing the driving force for delamination. (Note, however, that compositional contrasts between fertile, asthenospheric peridotite and refractory peridotite, which may be characteristic of lithospheric mantle beneath arcs (for example, ref. 82) and Archaean cratons<sup>60,83</sup>, tend to counteract the density contrast caused by temperature differences). Previous or concurrent delamination of the underlying lithospheric mantle seems a prerequisite for ultimate loss of lower-crustal materials from the lithosphere<sup>18</sup>.

Although delamination of mafic to ultramafic rocks from the lower portions of the continents provides a means of explaining the non-basaltic composition of the crust, it is a difficult process

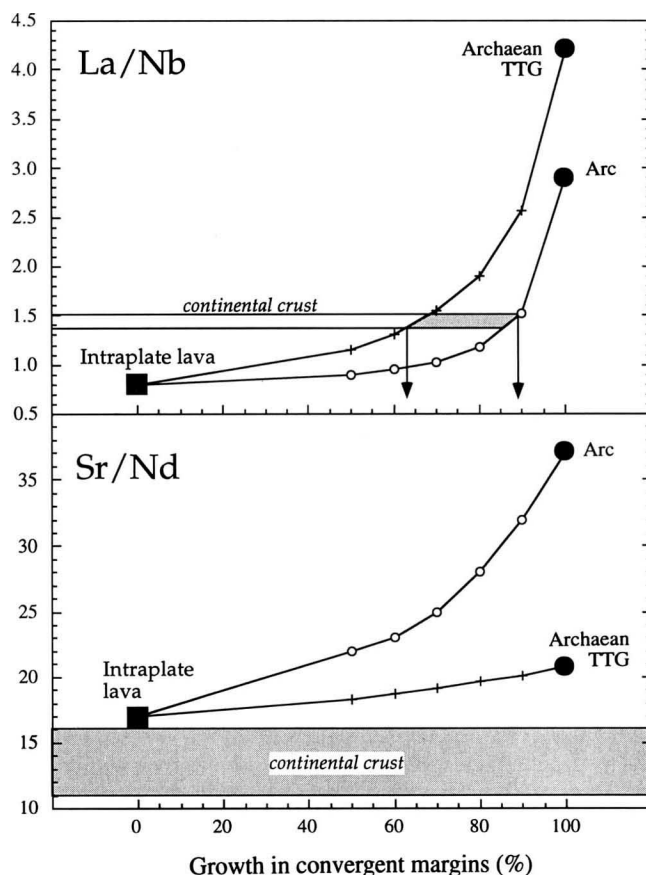


FIG. 5 Mixing relationships between convergent margin magmas (arc and Archaean TTG) and intraplate magma (average ocean island basalt from ref. 73); crosses and circles on curves represent 10% increments. Arc and Archaean TTG are median values from several hundred analyses compiled from the literature and plotted in Fig. 4. Continental crust bars represent range of ratios from estimates of refs 36–39. The model of Weaver and Tarney<sup>34</sup> is not considered here, as their choice of middle and lower crust is composed dominantly of Archaean TTG. Horizontal bars and shaded regions on both diagrams represent range of values for continental crust. Where these intersect the continental crust composition for La/Nb, the percentage of intraplate component can be read from the x-axis (marked by arrows). For Sr/Nd, the crust's ratio is lower than that of its potential 'building blocks', suggesting that the crust's Sr/Nd has been affected by other processes, such as preferential Sr loss during weathering or delamination of high-Sr/Nd material from the base of the crust. See text for full discussion.

to document. Some maintain that the geochemical characteristics of delaminated continental lithosphere are seen in plume-derived magmas from the ocean basins<sup>17,84</sup>, but these speculations are not evidence that the phenomenon occurs. Kay and Kay<sup>85</sup> and Kay *et al.*<sup>86</sup> suggest that sites of delamination in modern convergent margin settings may be recognized by rapid uplift and stress change (from compressional to extensional), low velocities and high attenuation of seismic waves (both features of hot mantle), and a temporal change in the composition of regional magmatism. The latter is regarded by Kay and Kay as providing the most geologically enduring evidence for delamination. They document changes in magmatism from the southern Puna plateau in Argentina that they attribute to delamination of the lower crust and upper mantle. Intrusions of granitic magmas, having geochemical evidence of being derived from a garnet-bearing source region (the thickened mafic lower crust in their model), are succeeded by basaltic magmas with intraplate chemistries (produced in response to incursion of hot asthenospheric mantle in the gap where the lithosphere used to be). It is possible, however, to produce these geochemical signatures in a variety

of ways. For example, a 'garnet signature' in granitic rocks may indicate partial melting of a mafic source at either the base of an anomalously thick lower crust, or within the basaltic layer of a subducted slab (as discussed above). Moreover, basalts having ocean-island type chemical characteristics, although uncommon, have been reported from a number of arcs (see discussion in ref. 87), which do not exhibit other evidence for lithospheric delamination. Given these uncertainties, recognizing delamination in older regions remains a difficult proposition.

It is desirable to determine whether delamination has occurred widely beneath the continents. The lower Sr/Nd ratio of the continental crust relative to its potential 'building blocks' (island arcs and oceanic plateaus) may argue for loss of rocks with high Sr/Nd from the base of the crust, as described above. Another way in which the importance of delamination might be tested is by evaluation of Os model ages for peridotite xenoliths derived from the continental lithospheric mantle. Unlike the other commonly utilized isotopic systems (Rb–Sr, Sm–Nd, U–Pb and Lu–Hf), the Re–Os isotopic system has the potential to date melt extraction, hence 'growth' and stabilization of lithospheric mantle<sup>88</sup>. If delamination occurs significantly after crustal growth, as may occur at sites of continental collision events, then lithospheric mantle in these regions should be younger than the overlying crust. To date, Os model ages are available for peridotites from only a few areas. In these areas the oldest Os model ages correspond well with the oldest ages observed in the overlying crust<sup>88–92</sup>. Thus, from the currently limited database, the Os model ages suggest either that (1) delamination has not occurred in these regions, or (2) if delamination occurred, it happened so close in time to original crustal growth that it is not detectable from the Os isotopic systematics (that is, within about 100 Myr). The latter may be true of continental regions that grow by accretion of island arcs or oceanic plateaus, where delamination occurs in response to their tectonic accretion to pre-existing crust shortly after their formation.

**Preferential Mg recycling.** The final process that may serve to shift the composition of the continental crust from basalt to andesite is preferential recycling of Mg to the mantle. Chemical weathering of igneous rocks results in loss of MgO, Na<sub>2</sub>O and CaO to solution; SiO<sub>2</sub>, Fe<sub>2</sub>O<sub>3</sub>, Al<sub>2</sub>O<sub>3</sub>, TiO<sub>2</sub> and K<sub>2</sub>O generally remain in the residues either as oxides or within or absorbed onto clay minerals<sup>93</sup>. Of the dissolved species, CaO is precipitated as carbonate and Na<sub>2</sub>O remains in solution or precipitates in evaporites. (Evaporites form the only known sedimentary sink for Na<sub>2</sub>O, but their volumes are so small (~5% of the sedimentary mass<sup>93</sup>) that they are not believed to influence the Na<sub>2</sub>O budget significantly<sup>94</sup>.) MgO may also precipitate in carbonates but a significant portion is fixed in oceanic crust through hydrothermal exchange with Ca at mid-ocean ridge spreading centres (ref. 95 and references therein). Thus, upon subduction of altered oceanic crust, Mg is preferentially recycled back to the mantle.

The recycling of Mg is occurring today and may have been even greater in the past if more extensive hydrothermal systems were present, perhaps due to greater ocean spreading-centre lengths. This process would serve to deplete the crust in MgO while other soluble elements are retained in, or returned to, the crust as sediments. However, Na<sub>2</sub>O is problematical because evaporites are uncommon and a good portion of the Na<sub>2</sub>O remains dissolved in the oceans. Attempts to recombine sedimentary rocks to form an 'average' igneous rock highlight the problems with Na<sub>2</sub>O (ref. 96).

Some limits on the effectiveness of chemical weathering in determining crust composition might be gained from the compositions of average sediments. As described above, fine-grained, clastic sedimentary rocks are notably depleted in Na<sub>2</sub>O and CaO. Sedimentary rocks of any sort comprise only a small fraction of the crust (~8% by mass<sup>39</sup>), so to shift the composition of continental crust by chemical weathering one must argue that many of the crystalline rocks in the crust contain a significant portion of formerly sedimentary material. Reprocessing of sedi-

ments within the crust produces crystalline rocks that are deficient in Na and probably Ca (depending on how much carbonate was present) relative to primary igneous rocks. S-type (sedimentary-type) granites<sup>97</sup> are an example of such a rock type. However, these granites are estimated to form less than 2% of all granitoids<sup>98</sup>. Indeed, the metaluminous composition of the bulk crust (Table 1) argues against the presence of a volumetrically significant weathered component within the crust.

In summary, preferential Mg recycling from the continents to the mantle due to chemical weathering has undoubtedly occurred for as long as subduction processes have been active on Earth. This process will drive the continents towards a more evolved bulk composition, but is unlikely to be the primary process by which the continental crust attained its present composition.

## Future directions

It is likely that each of the processes reviewed here has contributed to the production of the present continental crust. Future studies of the continents should develop tests of the relative importance of these processes in crustal growth and evolution. In the case of Archaean crustal growth and TTG genesis, experimental melting studies are needed for mafic compositions that better approximate Archaean basalts (lower TiO<sub>2</sub> and Al<sub>2</sub>O<sub>3</sub>, higher Mg# relative to modern basalts). Further experimental investigations into the interaction between hydrous silicic melts and refractory to fertile peridotite compositions would help in understanding the complex processes occurring in both ancient and modern subduction settings. Supporting evidence for crustal delamination can be sought in Os isotope studies; regions in which the lithospheric mantle is demonstrably younger than overlying crust might be *prima facie* evidence of delamination, although a coincidence in age of crust and mantle lithosphere is non-definitive. Numerical models of lower-crustal delamination that incorporate likely lithospheric temperature distributions at convergent margin settings and petrological constraints on phase transitions would aid in understanding the relative importance of the various driving forces behind delamination. Additional integrated geophysical, petrological and geochemical studies of potential present-day sites of lower-crustal delamination (such as the Tibetan plateau and the central Andes) would go far towards establishing the viability of this process. Finally, refinement of existing empirical estimates of continental crust composition are needed in order to place more quantitative constraints on models of crustal growth. □

R. L. Rudnick is at the Department of Earth and Planetary Sciences, Harvard University, 20 Oxford Street, Cambridge, Massachusetts 02138, USA.

- Taylor, S. R. *Tectonophysics* **161**, 147–156 (1989).
- Cogley, J. G. *Rev. Geophys. Space Phys.* **22**, 101–122 (1984).
- Christensen, N. I. & Mooney, W. D. *J. geophys. Res.* **100**, 9761–9788 (1995).
- Bowring, S. A., Williams, I. S. & Compston, W. *Geology* **17**, 971–974 (1989).
- Hofmann, A. W. *Earth planet. Sci. Lett.* **90**, 297–314 (1988).
- Jaques, A. L. & Green, D. H. *Contr. Miner. Petrol.* **73**, 287–310 (1980).
- Hirose, K. & Kushiro, I. *Earth planet. Sci. Lett.* **114**, 477–489 (1993).
- Martin, H. *Geology* **14**, 753–756 (1986).
- Drummond, M. S. & Defant, M. J. *J. geophys. Res.* **95**, 21503–21521 (1990).
- Kelemen, P. B., Shimizu, N. & Dunn, T. *Earth planet. Sci. Lett.* **120**, 111–134 (1993).
- Kelemen, P. B. *Contr. Miner. Petrol.* **120**, 1–19 (1995).
- Shirey, S. B. & Hanson, G. N. *Nature* **310**, 222–225 (1984).
- Stern, R. A. & Hanson, G. N. *J. Petrol.* **32**, 201–238 (1991).
- Evans, O. C. & Hanson, G. N. in *Tectonic Evolution of Greenstone Belts* (eds Ashwal, L. & de Wit, M.) (Oxford Univ. Press, in the press).
- Anderson, A. T. *J. geophys. Res.* **87**, 7047–7060 (1982).
- Gromet, L. P. & Silver, L. T. *J. Petrol.* **28**, 75–125 (1987).
- Arndt, N. T. & Goldstein, S. L. *Tectonophysics* **161**, 201–212 (1989).
- Kay, R. W. & Kay, S. M. *Geol. Rundschau* **80**, 259–278 (1991).
- Kay, S. M. & Kay, R. W. *Geology* **13**, 461–464 (1985).
- Kushiro, I. *J. geophys. Res.* **95**, 15929–15939 (1990).
- Griffin, W. L. & O'Reilly, S. Y. *Geology* **15**, 241–244 (1987).
- Wilshire, H. W. et al. *Mafic and Ultramafic Xenoliths from Volcanic Rocks of the Western United States* (US Geological Survey, Washington DC, 1988).
- Nixon, P. H. *Mantle Xenoliths* (Wiley, New York, 1987).
- Patchett, P. J. & Arndt, N. T. *Earth planet. Sci. Lett.* **78**, 329–338 (1986).
- McCulloch, M. T. in *Proterozoic Lithosphere Evolution* (ed. Kröner, A.) 115–130 (Am. Geophys. Union, Washington DC, 1987).
- Jacobsen, S. B. *Geochim. cosmochim. Acta* **52**, 1341–1350 (1988).
- DePaolo, D. J., Linn, A. M. & Schubert, G. *J. geophys. Res.* **96**, 2071–2088 (1991).
- Goodwin, A. M. *Precambrian Geology* (Academic, London, 1991).

29. Armstrong, R. L. *Phil. Trans. R. Soc. Lond. A* **301**, 443–472 (1981).
30. Armstrong, R. L. *Aust. J. Earth Sci.* **38**, 613–630 (1991).
31. von Huene, R. & Scholl, D. W. *Rev. Geophys.* **29**, 279–316 (1991).
32. Plank, T. & Langmuir, C. H. *Nature* **362**, 739–743 (1993).
33. Reymer, A. & Schubert, G. *Tectonics* **3**, 63–77 (1984).
34. Weaver, B. L. & Tarney, J. *Nature* **310**, 575–577 (1984).
35. Shaw, D. M., Cramer, J. J., Higgins, M. D. & Truscott, M. G. in *The Nature of the Lower Continental Crust* (eds Dawson, J. B., Carswell, D. A., Hall, J. & Wedepohl, K. H.) 257–282 (Geol. Soc. London, London, 1986).
36. Gao, S. et al. *Geochim. cosmochim. Acta* **56**, 3933–3950 (1992).
37. Rudnick, R. L. & Fountain, D. M. *Rev. Geophys.* **33**, 267–309 (1995).
38. Wedepohl, H. *Geochim. cosmochim. Acta* **59**, 1217–1232 (1995).
39. Taylor, S. R. & McLennan, S. M. *The Continental Crust: its Composition and Evolution* (Blackwell, Oxford, 1985).
40. Allègre, C. J., Hart, S. R. & Minster, J.-F. *Earth planet. Sci. Lett.* **66**, 191–213 (1983).
41. Hofmann, A. W., Jochum, K. P., Seufert, M. & White, W. M. *Earth planet. Sci. Lett.* **79**, 33–45 (1986).
42. Taylor, S. R. *Tectonophysics* **4**, 17–34 (1966).
43. Taylor, S. R. in *Island Arcs Deep Sea Trenches and Back-arc Basins* (eds Talwani, M. & Pitman, W. C.) 325–336 (Am. Geophys. Union, Washington DC, 1977).
44. Arculus, R. J. *Tectonophysics* **75**, 113–133 (1981).
45. Ellam, R. M. & Hawkesworth, C. J. *Geology* **16**, 314–317 (1988).
46. Pearcey, L. G., DeBari, S. M. & Sleep, N. H. *Earth planet. Sci. Lett.* **96**, 427–442 (1990).
47. Tatsumi, Y. *Earth planet. Sci. Lett.* **60**, 305–317 (1982).
48. Baker, M. B., Grove, T. L. & Price, R. *Contr. Miner. Petrol.* **118**, 111–129 (1994).
49. Martin, H. in *Archaean Crustal Evolution* (ed. Condie, K. C.) 205–259 (Elsevier, Amsterdam, 1994).
50. Baker, M. B., Hirschmann, M. M., Ghiorso, M. S. & Stolper, E. M. *Nature* **375**, 308–311 (1995).
51. Stern, C. R. & Wyllie, P. J. *Am. Miner.* **63**, 641–663 (1978).
52. Rapp, R. P., Watson, E. B. & Miller, C. F. *Precamb. Res.* **51**, 1–25 (1991).
53. Winther, K. T. & Newton, R. C. *Bull. Geol. Soc. Denmark* **39**, 213–228 (1991).
54. Sen, C. & Dunn, T. *Contr. Miner. Petrol.* **117**, 394–409 (1994).
55. Wolf, M. B. & Wyllie, P. J. *Contr. Miner. Petrol.* **115**, 369–383 (1994).
56. Arndt, N. T. *Tectonophysics* **187**, 411–419 (1991).
57. Staudigel, H., Davies, G. R., Hart, S. R., Marchant, K. M. & Smith, B. M. *Earth planet. Sci. Lett.* **130**, 169–185 (1995).
58. Ireland, T. R., Rudnick, R. L. & Spetsius, Z. *Earth planet. Sci. Lett.* **128**, 199–213 (1994).
59. Rudnick, R. L., McDonough, W. F. & Orpin, A. in *Kimberlites, Related Rocks and Mantle Xenoliths* Vol. 1 (eds Meyer, H. O. A. & Leonardos, O.) 336–353 (Proc. 5th Int. Kimb. Conf., C.P.R.M., Brasilia, 1994).
60. Boyd, F. R. *Earth planet. Sci. Lett.* **96**, 15–26 (1989).
61. Carroll, M. R. & Wyllie, P. J. *J. Petrol.* **30**, 1351–1382 (1989).
62. Arculus, R. J. *Lithos* **33**, 189–208 (1994).
63. Condie, K. C. *Precamb. Res.* **32**, 261–278 (1986).
64. Abouchami, W., Boher, M., Michard, A. & Albarede, F. *J. geophys. Res.* **95**, 17605–17629 (1990).
65. Ben-Avraham, Z., Nur, A., Jones, D. & Cox, A. *Science* **213**, 47–54 (1981).
66. Richards, M. A., Jones, D. L., Duncan, R. A. & DePaolo, D. J. *Science* **254**, 263–267 (1991).
67. Hill, R. L., Campbell, I. H., Davies, G. F. & Griffiths, R. W. *Science* **256**, 186–193 (1992).
68. Vervoot, J. & White, W. M. *Eos* (abstr.) **73**, 617 (1992).
69. Cox, K. G. *J. Petrol.* **21**, 629–650 (1980).
70. Coffin, M. F. & Eldholm, O. *Rev. Geophys.* **32**, 1–36 (1994).
71. Stein, M. & Hofmann, A. W. *Nature* **372**, 63–68 (1994).
72. McDonough, W. F. *Earth planet. Sci. Lett.* **101**, 1–18 (1990).
73. Sun, S.-s. & McDonough, W. F. in *Migmatism in the Ocean Basins* (eds Saunders, A. D. & Norry, M. J.) 313–345 (Spec. Pub. 42, Geol. Soc. Lond., 1989).
74. McDonough, W. F. & Ireland, T. R. *Nature* **365**, 432–434 (1994).
75. O'Nions, R. K. & McKenzie, D. P. *Earth planet. Sci. Lett.* **90**, 449–456 (1988).
76. Stolper, E. & Newman, S. *Earth planet. Sci. Lett.* **121**, 293–325 (1994).
77. Goldstein, S. L. *Nature* **336**, 733–738 (1989).
78. Bird, P. *J. geophys. Res.* **84**, 7561–7571 (1979).
79. Bird, P. *J. geophys. Res.* **83**, 4975–4987 (1978).
80. Houseman, G. A., McKenzie, D. P. & Molnar, P. *J. geophys. Res.* **86**, 6115–6132 (1981).
81. Nelson, K. D. *Geophys. J. Int.* **105**, 25–35 (1991).
82. Jaques, A. L. & Chappell, B. W. *Contr. Miner. Petrol.* **75**, 55–70 (1980).
83. Jordan, P. H. in *The Mantle Sample: Inclusions in Kimberlites and other Volcanics* (eds Boyd, F. R. & Meyer, H. O. A.) 1–14 (Am. Geophys. Union, Washington DC, 1979).
84. McKenzie, D. & O'Nions, R. K. *Nature* **301**, 229–231 (1983).
85. Kay, R. W. & Kay, S. M. *Tectonophysics* **219**, 177–189 (1993).
86. Kay, S. M., Coira, B. & Viramonte, J. *J. geophys. Res.* **99**, 24323–24339 (1994).
87. Briggs, R. M. & McDonough, W. F. *J. Petrol.* **31**, 813–851 (1990).
88. Walker, R. J., Carlson, R. W., Shirey, S. B. & Boyd, F. R. *Geochim. cosmochim. Acta* **53**, 1583–1595 (1989).
89. Pearson, D. G. et al. *Mineralog. Mag.* **58A**, 703–704 (1994).
90. Carlson, R. W. & Irving, A. J. *Earth planet. Sci. Lett.* **126**, 457–472 (1994).
91. Pearson, D. G. et al. *Geochim. cosmochim. Acta* **59**, 959–977 (1995).
92. Pearson, D. G., Carlson, R. W., Shirey, S. B., Boyd, F. R. & Nixon, P. H. *Earth planet. Sci. Lett.* **134**, 341–357 (1995).
93. Garrels, R. M. & McKenzie, F. T. *Evolution of Sedimentary Rocks* (Norton, New York, 1971).
94. Goldschmidt, V. M. *Geochemistry* (Oxford Univ. Press, 1958).
95. Holland, H. D. *The Chemical Evolution of the Atmosphere and Oceans* (Princeton Univ. Press, Princeton, NJ, 1984).
96. Garrels, R. M. & McKenzie, F. T. *Evolution of Sedimentary Rocks* 242–243 (Norton, New York, 1971).
97. Chappell, B. W. & White, A. J. R. *Pacific Geol.* **8**, 173 (1974).
98. Miller, C. F. *Geology* **14**, 804–805 (1986).
99. Condie, K. C. *Chem. Geol.* **104**, 1–37 (1993).

ACKNOWLEDGEMENTS. We thank P. Hoffman and B. McDonough for providing helpful criticisms of the first draft. The final review has benefited from reviews by S. McLennan, P. Kelemen, R. Kay, J. Patchett, D. Abbott and C. Hawkesworth, and discussions with S. Eggins, W. McDonough and S. Jacobsen.

## ARTICLES

# Nucleation of microtubule assembly by a $\gamma$ -tubulin-containing ring complex

Yixian Zheng<sup>\*</sup>, Mei Lie Wong<sup>\*</sup>, Bruce Alberts<sup>\*†</sup> & Tim Mitchison<sup>†</sup>

<sup>\*</sup> Department of Biochemistry and Biophysics, <sup>†</sup> Department of Pharmacology, University of California at San Francisco, San Francisco, California 94143-0448, USA

**The highly conserved protein  $\gamma$ -tubulin is required for microtubule nucleation *in vivo*. When viewed in the electron microscope, a highly purified  $\gamma$ -tubulin complex from *Xenopus* consisting of at least seven different proteins is seen to have an open ring structure. This complex acts as an active microtubule-nucleating unit which can cap the minus ends of microtubules *in vitro*.**

ALL eukaryotes use the microtubule cytoskeleton for mitosis and cytoplasmic organization. Microtubules are long, hollow cylindrical structures (25 nm in diameter) formed from  $\alpha$ - and  $\beta$ -tubulin heterodimers<sup>1,3</sup>. Each microtubule is a polar structure with a plus and a minus end. The formation of a microtubule involves the addition of GTP-bound tubulin molecules to the growing end of the microtubule. *In vitro* studies show that a microtubule grows at a rate that is proportional to the concentration of free tubulin, and that at high tubulin concentrations the plus end grows approximately three times faster than the minus end<sup>4</sup>. *In vivo*, microtubule-organizing centres (MTOCs) nucleate microtubules and orient them so that each growing plus

end is distal to the MTOC. An MTOC catalyses nucleation at tubulin concentrations that are too low to promote spontaneous microtubule nucleation. In metazoa, the primary MTOC is the centrosome, consisting of a pair of centrioles surrounded by a cloud of electron-dense pericentriolar material (PCM), which is also known as the centrosome matrix. It is the PCM that is responsible for microtubule nucleation<sup>5</sup>. Microtubules nucleated from the PCM *in vivo* or *in vitro* have 13 protofilaments, whereas spontaneously assembled microtubules *in vitro* mostly have 14 protofilaments, with 13 and 15 protofilaments sometimes being found; it is therefore believed that MTOCs specify the exact structure of the microtubules that they nucleate<sup>6</sup>.

A very minor species of tubulin,  $\gamma$ -tubulin, has been identified as a new member of the tubulin superfamily<sup>7</sup>. Subsequently,  $\gamma$ -tubulin was found to be a highly conserved component of the

<sup>†</sup> Present address: National Academy of Sciences, 2101 Constitution Avenue NW, Washington, DC 20418, USA.