1. Batiza, R. & Vanko, D. *J. geophys. Res.* **26**, 564–602 (1984).
2. Allan, J. F., Batiza, R. & Lonsdale, P. *Seamounts, Islands, and Atolls, Geophys. Monogr.* No. 43 (eds Keating, B. H. *et al.*) 255–282 (Am. geophys. Un., Washington, DC, 1987).
3. Allan, J. F., Batiza, R., Perfit, M. R., Fornari, D. J. & Sack, R. O. *J. Petrol.* (submitted).
4. Fornari, D. J., Perfit, M. R., Allan, J. F. & Batiza, R. *Nature* **331**, 511–513 (1988).
5. Zindler, A., Studigel, H. & Batiza, R. *Earth planet. Sci. Lett.* **70**, 175–195 (1984).
6. Fornari, D. J. *et al. Earth planet Sci. Lett.* **89**, 63–83 (1988).
7. Graham, D. W. *et al. Contr. Miner. Petr.* **99**, 446–463 (1988).
8. Batiza, R., Melson, W. G. & O'Hearn, T. *Nature* **335**, 428–431 (1988).
9. Batiza, R. *et al. J. Geol.* **97**, 209–220 (1989).
10. Hanan, B. B., Kingsley, R. H. & Schilling, J.-G. *Nature* **322**, 137–144 (1986).
11. McKenzie, D. P. *Earth planet. Sci. Lett.* **74**, 81–91 (1985).
12. Sleep, N. H. *J. geophys. Res.* **89**, 10029–10041 (1984).
13. Castillo, P. *Nature* **336**, 667–670 (1988).
14. Shirey, S., Bender, J. F. & Langmuir, C. H. *Nature* **325**, 217–223 (1987).
15. Schilling, J.-G., Hanan, B. B. & McCully, B. *Eos* **69**, 1426 (1988).
16. White, W. M., Hofmann, A. W. & Puchelt, H. *J. geophys. Res.* **92**, 4881–4893 (1987).
17. Ito, E., White, W. M. & Gopel, C. *Chem. Geol.* **62**, 157–176 (1987).
18. Schilling, J.-G. *Earth planet. Sci. Lett.* **25**, 103–115 (1975).
19. Schilling, J.-G. *Nature* **314**, 62–67 (1985).
20. Klein, E. M., Langmuir, C., Zindler, A., Staudigel, H. & Hamelin, B. *Nature* **333**, 623–629 (1988).
21. Mahoney, J. J. *et al. J. geophys. Res.* **94**, 4033–4052 (1989).
22. Castillo, P. *Eos* **69**, 490 (1988).
23. Silver, P. G., Carlson, R. W. & Olson, P. A. *A. Rev. Earth planet. Sci.* **16**, 477–541 (1988).
24. Dziewonski, A. M. *J. geophys. Res.* **89**, 5929–5952 (1984).
25. Hager, B. H. *J. geophys. Res.* **89**, 6003–6015 (1984).
26. Cazenave, A., Souriau, A. & Dominh, K. *Nature* **340**, 54–57 (1989).
27. Cohen, R. S. & O'Nions, R. K. *J. Petrol.* **23**, 299–239 (1982).
28. Allègre, C. J., Hamelin, B. & Dupre, B. *Earth planet Sci. Lett.* **71**, 71–84 (1984).
29. Macdougal, J. D. & Lugmair, G. W. *Earth planet Sci. Lett.* **77**, 273–284 (1986).
30. Catanzaro, E. J., Murphy, T. J., Shields, W. R. & Garner, E. L. *J. Res. natn. Bur. Stand.* **72A** (1968).

Young high-temperature granulites from the base of the crust in central Mexico

J. L. Hayob*, E. J. Essene*, J. Ruiz†, F. Ortega-Gutiérrez‡ & J. J. Aranda-Gómez§

* Department of Geological Sciences, University of Michigan, Ann Arbor, Michigan 48109, USA
† Department of Geosciences, University of Arizona, Tucson, Arizona 85721, USA
‡ Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Mexico City, Mexico
§ Instituto de Geologia, Universidad Nacional Autonoma de Mexico, Guanajuato, Mexico

CHARACTERIZATION of the lower continental crust is essential to understanding processes of crustal formation and evolution. Many workers have concluded that the lower crust is composed of granulite-facies rocks (see, for example, refs 1, 2), but many exposed granulite-facies terranes seem to have mid-crustal rather than lower-crustal origins[3–5]. Here we present new data from direct samples of the lower continental crust, in the form of metapelitic rock fragments brought to the surface by Quaternary volcanism in central Mexico. These xenoliths contain exsolved ternary feldspars that record extremely high minimum metamorphic temperatures of 950–1,100 °C, the highest yet known to be preserved in deep-seated metamorphic rocks. The metamorphism seems to be the result of underplating by basaltic magma and to be regional in extent. Our barometry on these samples demonstrates that granulite-facies metamorphic rocks are present in the lower crust, and provides important constraints on tectonic models and interpretations of geophysical data. Chemical and textural evidence suggest that the xenoliths were not able to cool to below 850–900 °C before being entrained in their host magmas, indicating that the granulite-facies metamorphism occurred no more than ~30 Myr ago.

So far most studies of xenoliths have focused on characterization of samples from the Earth's upper mantle[6], and only limited mineralogical and geochemical data have been obtained on xenoliths believed to be from the lower crust. In addition, most studies of deep crustal xenoliths have concentrated on mafic and intermediate orthogneisses[6]. Although modally less abundant than mafic orthogneisses, xenoliths with sedimentary protoliths may be more useful in providing definitive pressure information, because their mineralogy is often more appropriate for applying existing geobarometers[7–10].

Xenoliths of garnet-sillimanite paragneiss, occurring in Quaternary basanitic tuffs[11] from the central Mexican plateau in the state of San Luis Potosí, contain the assemblage garnet-sillimanite-mesoperthite-quartz-rutile-graphite, ±plagioclase-ilmenite-zircon-monazite. The paragneisses are the major lithology at El Toro and represent ~10% of the xenolith population at La Joya Honda and Los Palau; mafic and felsic orthogneisses are the dominant lithologies at these two localities. Here we present the pressure (P)-temperature (T) conditions of last equilibration for the paragneisses, and discuss the crustal level from which these samples were derived and the information they reveal about the crust beneath central Mexico.

The paragneiss xenoliths were selected for detailed study based on mineralogical and textural similarities and the presence of univariant mineral assemblages with respect to barometric reactions. Five samples are from the El Toro (ET) cinder cone, three are from La Joya Honda (LJH) maar, and two are from Los Palau (LP) maar. Field relations are given elsewhere[11–13]. The xenoliths range from 4 to 10 cm in diameter and appear fresh. In general, all samples have similar mineral chemistries. None of the selected samples exhibit distinct layering or mineral zoning. Evidence of partial fusion is given by the ubiquitous occurrence of devitrified melt rims around garnets (see, for example, refs 14, 15). Quench textures in the melt rims consist of intergrowths of euhedral orthopyroxene, hercynite-spinel$_{ss}$, and interstitial glass and/or calcic plagioclase. Stähle[14] has suggested that the breakdown of almandine garnet to orthopyroxene + hercynite + glass occurs rapidly at ~1,100 °C and 0.1–0.3 GPa.

The compositions of the feldspars may provide constraints on the thermal histories of the xenoliths. Plagioclase lamellae occurring within an alkali feldspar host and large plagioclase crystals not hosted by an alkali feldspar have very similar anorthite contents, within a given sample. The plagioclase lamellae are typically slightly more potassic, indicating that the larger plagioclase crystals formed during cooling from an initially homogeneous alkali feldspar[16]. Exsolution lamellae in feldspars are typically 10–30 μm in width. Exsolved feldspar compositions are given in Fig. 1a and Tables 1 and 2. The calculated

TABLE 1 Representative host, lamellae and reintegrated feldspar analyses from a single mesoperthite crystal in sample ET24

	Kfs host	Pl lam.	Reintegrated		
SiO_2	64.15	58.98	60.64	60.85	61.22
Al_2O_3	19.51	25.53	22.98	23.33	23.47
Fe_2O_3	0.01	0.19	ND*	ND*	ND*
CaO	0.77	7.41	4.30	4.42	4.81
Na_2O	3.12	6.42	5.21	5.24	5.30
K_2O	11.60	1.56	5.82	5.45	5.23
Total	99.16	100.09	98.95	99.29	100.03

Formulae normalized to 5 cations

Si	2.94	2.63	2.76	2.76	2.76
Al	1.06	1.35	1.23	1.25	1.25
Fe^{3+}	0.00	0.01	ND*	ND*	ND*
Ca	0.04	0.36	0.21	0.21	0.23
Na	0.28	0.56	0.46	0.46	0.46
K	0.68	0.09	0.34	0.32	0.30
O	7.99	7.98	7.97	7.99	8.00

* Fe_2O_3 was not determined (ND) for the reintegrated analyses.
Kfs, alkali-feldspar; Pl lam, plagioclase lamella.

TABLE 2 Component mole percentages for each sample from averaged mineral analyses

| Sample number | Garnet | | | Rutile | Ilmenite | Fs host | | Fs lam. | | Integ. | | Temperature (°C) | |
	Al	Py	Gr	TiO_2	$FeTiO_3$	An	Or	An	Or	An	Or	Int.	Exs.
ET11	55	39	5	98	95	4	73	39	10	20	40	1,100	880
ET16	52	43	4	98	—	3	69	34	10	10	54	1,000	890
										23*	30*	1,050	890
ET24	49	46	4	98	98	4	69	35	9	22	32	1,050	880
ET38	55	40	4	97	—	3	73	36	10	23	33	1,075	880
ET42	55	40	4	97	—	4	65	30	12	18	34	1,025	890
LJH14	49	45	4	97	—	3	66	32	14	15	44	1,050	910
LJH15	54	42	3	98	—	6	52	27	17	19	28	1,000	965
LJH32	53	43	3	98	89	6	51	26	15	19	26	975	940
LP7	54	42	3	98	84	5	59	33	14	23	30	1,050	950
LP8	50	45	3	97	81	4	56	23	24	9	49	950	950

Sample locality abbreviations are given in the text.
Mineral abbreviations: Al, almandine; Py, pyrope; Gr, grossular; An, anorthite; Or, orthoclase; Fs, feldspar; Lam., lamellae. Spessartine and albite can be calculated by difference from 100. Int., average minimum reintegrated temperature, and Exs., average temperature of exsolution using the model of Lindsley and Nekvasil[17].
* Bimodal distribution of reintegrated analyses observed for this sample.

tie lines for 900 °C from the ternary feldspar model of Lindsley and Nekvasil[17] are shown at $P = 1.0$ GPa; the pressure dependence of the feldspar equilibria is from ref. 18. The mesoperthites contain lamellar plagioclase ($An_{20-40}Ab_{49-62}Or_{8-28}$) and alkali feldspar ($An_{3-7}Ab_{20-45}Or_{47-76}$) (Tables 1 and 2). Graphical use of the ternary two-feldspar thermometer in ref. 17 yields temperatures of ~800–950 °C for lamellae and host feldspars (Fig. 1a and Table 2). These temperatures are much higher than any recorded by exsolved feldspars of exposed granulites[16,19]. Reintegration of the mesoperthites by image analysis and broad-beam energy-dispersive analysis yields former ternary feldspar compositions of $An_{6-24}Ab_{35-57}Or_{22-55}$ (Tables 1 and 2). The compositions are among the most ternary reported from rocks of undoubted metamorphic origin[16,20–23]. The isotherms of the ref. 17 model require minimum temperatures of 950–1,125 °C (Table 2 and Fig. 1b) for the reintegrated feldspars to be stable.

Tie lines connecting exsolved alkali feldspar and plagioclase compositions for El Toro samples agree well with calculated tie lines[17] (Fig. 1a). La Joya Honda and Los Palau samples give mixed results for exsolved compositions, as tie lines cross, indicating that these compositions may not represent equili-

brium assemblages. Nevertheless, the reintegrated values give similar minimum temperatures of 950–1,125 °C for the three localities. Regardless of the details of exsolution processes, these mesoperthites yield minimum reintegrated temperatures that are considerably higher than those typically obtained for exposed granulites[16,19].

Figure 2 is a back-scattered electron image of a mesoperthite from sample ET24; quartz and rutile are also present. The regular and continuous exsolution texture is typical of the mesoperthites, and is interpreted as evidence for slow cooling after regional metamorphism. If the mesoperthites were produced during or after transport to the surface it is highly unlikely that the intergrowths would be so coarse and regular. The homogeneity of lamellae and host compositions within each xenolith suggests that equilibrium between the feldspars was commonly attained, and no chemical gradients across lamellae have been identified with the electron microprobe. The occurrence of mesoperthite inclusions in unzoned garnets from three samples (LP7, LP8, LJH32) seems to exclude an origin by epitaxial growth, as proposed[23] for mesoperthites from Kilbourne Hole (New Mexico), and indicates that the garnets
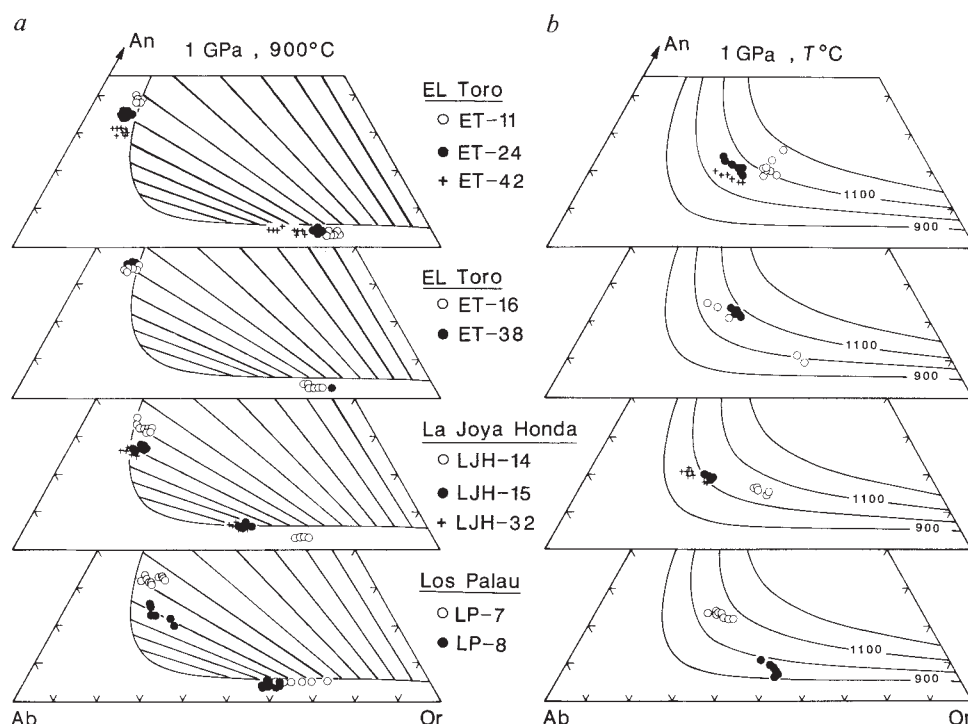

FIG. 1 a, Exsolved feldspar compositions, for each xenolith, plotted on stacked anorthite (An)–albite (Ab)–orthoclase (Or) diagrams. Symbols correspond to sample numbers as shown. Isotherm and tie lines for 900 °C are shown at 1.0 GPa (ref. 17). b, Reintegrated feldspar compositions plotted as in a. Isotherms are shown at 1.0 GPa for 900, 1,000, 1,100 and 1,200 °C (ref. 17).

equilibrated with homogeneous ternary feldspars. Diffusion through the garnet would be required to permit re-equilibration of exsolved plagioclase compositions with matrix sillimanite.

The paragneiss garnets are homogeneous, with almandine ranging from 49 to 55 mol %, pyrope from 39 to 47 mol % and grossular from 3 to 5 mol % (Table 2). Garnets contain abundant inclusions of quartz, sillimanite and rutile. If the garnet in each sample equilibrated with the reintegrated ternary feldspar, sillimanite ($X_{Al_2SiO_5} = 0.99$), rutile ($X_{TiO_2} = 0.97$-0.98), ilmenite ($X_{FeTiO_3} = 0.81$-0.98) and quartz, barometry may be applied using the feldspar activity/composition relations of ref. 17. For garnet we have used the mixing model of Anovitz and Essene[24]. An ideal-solution model was used for rutile, sillimanite and ilmenite, and the activity of quartz was assumed to be unity. The garnet-sillimanite-quartz-plagioclase barometer[8] yields pressures of 0.9-1.4 GPa at $T = 950$-$1,200$ °C; the garnet-rutile-ilmenite-plagioclase-quartz barometer[9] also gives pressures of ~0.9-1.3 GPa. If lower pressure limits from the five samples that lack ilmenite are excluded, pressures of 0.9-1.3 GPa are obtained with the garnet-rutile-sillimanite-ilmenite-quartz barometer[10]. Pressures deduced from the three barometers correspond to depths of ~33-48 km (depending on temperature and the average specific gravity of the crustal rock column, chosen here to be 2.7). These depths are consistent with the estimated crustal thickness (35-45 km) in the study area[25-27], and show that the xenoliths sample the region of the crust/mantle boundary in central Mexico.

The mesoperthites provide evidence for regional metamorphism at $T > 950$-$1,125$ °C, higher than any temperatures recorded previously in regionally metamorphosed rocks of undoubted sedimentary parentage. The metamorphism spanned an area of at least 100 km^2 in central Mexico and may be related to the occurrence of similar metapelitic xenoliths 1,600 km to the north at Kilbourne Hole in New Mexico in the United States. We conclude that the lowermost crust of central Mexico was heated to ~1,100 °C by underplated basaltic magmas[5,28]. The base of the crust was subsequently cooled to ~900 °C, as recorded by the exsolved feldspars. We believe the xenoliths never equilibrated below 900 °C and were excavated from nearly the depth they record by ascending basanitic magmas. Such extreme

quench temperatures (800-950 °C) for the feldspars suggest recent granulite facies metamorphism of the base of the crust in central Mexico; a mid-Tertiary underplating event would be consistent with moderate cooling rates of 5-10 °C Myr^{-1} for a regional terrane. These inferences are consistent with data in a chronological study of Kilbourne Hole metapelites, in which a metamorphic age of 1.6 Gyr was obtained from Rb-Sr isochrons of adjacent layers and an age of 34 ($\pm$14) Myr from mineral isochrons[29].

We have attempted to unravel the cooling history of the xenoliths using data on the coarsening of exsolution lamellae in alkali feldspars[30], and the homogenization of plagioclases[31]. Data from coarsening experiments[30] indicate that lamellae of width 10-30 μm could be produced in 10^5 yr at 800 °C, and 10^{-3} yr at 1,100 °C (with an initial lamella width of 0 μm), but calculated homogenization rates[31] are orders of magnitude slower. At 1,100 °C, lamellae 10 μm wide would be homogenized in 10$^{4\pm1.5}$ yr, and ~10$^{10\pm1}$ yr are needed for 10-μm-wide lamellae at 800 °C. Although the homogenization rates, for which experiments involved coupled NaSi-CaAl diffusion[31], are consistent with the preservation of feldspar lamellae in the xenoliths, the coarsening estimates are in sharp disagreement with our hypothesis of slow cooling subsequent to a mid-Tertiary regional metamorphic event. Perhaps the strongest evidence against a mesoperthite origin related to the host basalt is the absence of coarse perthites in volcanic rocks; to our knowledge all volcanic perthite occurrences are cryptoperthites/microperthites with lamellae that are $\leqslant$1 μm wide. We believe that available experiments on lamellar coarsening are not relevant to ternary mesoperthites because the experiments were done on cryptoperthites with coherent structures at a pressure of 10^5 Pa (1 atm) and at temperatures <600 °C, and, most importantly, they were done on binary alkali feldspars. Although higher temperatures should enhance coarsening, coupled Al/Si diffusion, required for exsolution of ternary feldspars, will greatly hinder coarsening[30-32]. As the Mexican mesoperthites exsolved on the strain-free solvus with non-coherent structures, a mechanism involving nucleation and growth is required—a slower process than spinodal decomposition. Coarsening rates calculated from existing experimental data are inconsistent with

FIG. 2 Back-scattered electron image of a typical mesoperthite (sample ET24) showing the regular and continuous nature of exsolved plagioclase lamellae (darker bands). Quartz (dark) and rutile (light) are also present. Scale bar = 150 μm.

geological evidence for the growth rates of mesoperthites with strongly ternary compositions[33,34].

Using depths of 40-45 km (corresponding to 1.1-1.2 GPa) with temperatures of 1,100-1,150 °C, for the peak of regional metamorphism, and present-day temperatures of 800-950 °C for the partially cooled, basal crustal rocks, average geothermal gradients were 26-28 °C km^{-1} during the hypothesized basaltic underplating event and should be 20-21 °C km^{-1} in central Mexico today. Our gradients compare favourably with those estimated from measurements of heat flow obtained ~100 km to the north[35]. We believe that our conclusions apply for the region extending from the central Mexican plateau to at least as far north as southern New Mexico (USA), where similar metapelite xenoliths occur at Kilbourne Hole[36,37] and Engle Basin[38]. Furthermore, as basaltic magmatism is still occurring in this region, deep-crustal metamorphism may be happening in central Mexico today. □

1. Griffin, W. L. & O'Reilly, S. Y. in Mantle Xenoliths (ed. Nixon, P.) 413-432 (Wiley, New York, 1987).
2. Kay, R. W. & Kay, S. M. Rev. Geophys. Space Phys. 19, 271-297 (1981).
3. Roberts, S. J. & Ruiz, J. J. geophys. Res. 94, 7961-7974 (1989).
4. Ruiz, J., Roberts, S. J. & Patchett, P. J. Terra Cogn. 8, 271 (1988).
5. Bohlen, S. R. & Mezger, K. Science 244, 326-329 (1989).
6. Nixon, P. H. (ed.) Mantle Xenoliths (Wiley, New York, 1987).
7. Essene, E. J. in Evolution of Metamorphic Belts (eds Daly, J. S., Cliff, R. A. & Yardley, B. W. D.) (Geol. Soc. Spec. Publ. No. 41, 1989).
8. Koziol, A. M. & Newton, R. C. Am. Miner. 73, 216-223 (1988).
9. Bohlen, S. R. & Liotta, J. J. J. Petrol. 27, 1025-1034 (1986).
10. Bohlen, S. R., Wall, V. J. & Boettcher, A. L. Am. Miner. 68, 1049-1058 (1983).
11. Aranda-Gómez, J. J. thesis, Univ. Oregon (1982).
12. Aranda-Gómez, J. J. & Ortega-Gutiérrez, F. in Mantle Xenoliths (ed. Nixon, P. H.) 75-84 (Wiley, New York, 1987).
13. Luhr, J. F., Aranda-Gómez, J. J. & Pier, J. G. J. geophys. Res. 94, 7916-7940 (1989).
14. Stähle, V. Earth planet. Sci. Lett. 25, 71-81 (1975).
15. Padovani, E. L. R. & Carter, J. L. Oregon Dept Geol. Miner. Ind. Bull. 96, 43-57 (1977).
16. Bohlen, S. R. & Essene, E. J. Contr. Miner. Petrol. 62, 153-169 (1977).
17. Lindsley, D. H. & Nekvasil, H. Eos 70, 506 (1989).
18. Fuhrman, M. L. & Lindsley, D. H. Am. Miner. 73, 201-215 (1988).
19. Mora, C. I. & Valley, J. W. Contr. Miner. Petrol. 89, 215-225 (1985).
20. Powers, R. E. & Bohlen, S. R. Contr. Miner. Petrol. 90, 401-409 (1985).
21. Leyreloup, A., Bodinier, J. L., Dupuy, C. & Dostal, J. Contr. Miner. Petrol. 79, 68-75 (1982).
22. Robinson, J. V. thesis, Univ. Calif., Santa Cruz (1988).
23. Padovani, E. L. R. thesis, Univ. Texas, Dallas (1977).
24. Anovitz, L. M. & Essene, E. J. J. Geol. 95, 633-645 (1987).
25. Meyer, R. P., Steinhart, J. S. & Woollard, G. P. Carnegie Inst. Wash. Publ. No. 622, Ch. 5 (1961).
26. Hales, A. L., Helsley, C. E. & Nation, J. B. J. geophys. Res. 75, 7362-7381 (1970).
27. Rivera, J. & Ponce, L. Geofisica Int. 25, 383-402 (1986).
28. Ruiz, J., Patchett, P. J. & Arculus, R. J. Contr. Miner. Petrol. 99, 36-43 (1988).
29. Padovani, E. R. & Reid, M. R. New Mexico Bureau Mines Miner. Resources Mem. 46, 174-179 (1989).
30. Yund, R. A. & Davidson, P. Am. Miner. 63, 470-477 (1978).
31. Grove, T. L., Baker, M. B. & Kinzler, R. J. Geochim. cosmochim. Acta 48, 2113-2121 (1984).
32. Mardon, D. & Yund, R. A. Eos 62, 411 (1981).
33. Brown, W. L., Becker, S. M. & Parsons, I. Contr. Miner. Petrol. 82, 13-25 (1983).
34. Parsons, I. & Brown, W. L. Contr. Miner. Petrol. 82, 1-12 (1983).
35. Smith, D. L. & Jones, R. L. in Rio Grande Rift: Tectonics and Magmatism (ed. Riecker, R. E.) 269-278 (Am. Geophys. Union, Washington, DC, 1979).
36. Padovani, E. L. R. & Carter, J. L. Geophys. Monogr. Ser. 20, 19-55 (1977).
37. Bussod, G. Y. A. Terra Cogn. 2, 266-267 (1982).
38. Warren, R., Kudo, A. & Keil, K. in Rio Grande Rift: Tectonics and Magmatism (ed. Riecker, R. E.) 393-415 (Am. Geophys. Un., Washington, DC, 1979).

Genetic relatedness in primitively eusocial wasps

Joan E. Strassmann*, Colin R. Hughes*,
David C. Queller*, Stefano Turillazzi†,
Rita Cervo†, Scott K. Davis§ & Keith F. Goodnight*

* Department of Ecology and Evolutionary Biology, Rice University, Houston, Texas 77005, USA
† Dipartimento di Biologia Animale e Genetica, Università di Firenze, Via Romana 17, 50125 Firenze, Italy
§ Department of Animal Science, Texas A&M University, College Station, Texas 77843, USA

SOCIAL insects are characterized by indirect reproduction, in which most individuals achieve genetic success by helping to rear the offspring of colony mates. The evolution of such systems is expected to be sensitive to the genetic relatedness of colony mates. In general, reproductive altruism evolves most easily when relatedness is high, although it could be maintained under regimes of low relatedness after morphologically distinct castes have evolved[1,2]. Most social insects belong to the order Hymenoptera, and are therefore haplodiploid (males haploid, females diploid); this genetic system may favour the evolution of altruism because it makes rearing a full sister ($r = \frac{3}{4}$) genetically more valuable than rearing one's own offspring ($r = \frac{1}{2}$) (refs 1-3). Here we report new estimates of relatedness from 14 species of polistine wasps lacking morphological castes. Female colony mates are often not full sisters and therefore seldom realize the full advantage made possible by haplodiploidy. But relatedness is always fairly high, in striking contrast to the situation in some species with morphological castes.

Methods for using genetic markers to estimate relatedness, with standard errors, have been available for a decade[4-8]. But they have been applied to only three species of primitively eusocial insects (a halictid bee[9,10], an anthophorid bee[11] and a sphecid wasp[12]), whose lack of morphologically distinct castes makes them better than highly eusocial species as models for the early stages of social evolution. These methods have not been applied to primitively eusocial polistine wasps, which are the best-studied group. Colony mates in this group are known to be related from observational studies[13-16] and from early electrophoretic methods that did not permit estimation of standard errors[17,18]. The estimates reported here for 14 species of Polistes and Mischocyttarus confirm this finding, and in addition are sufficiently numerous and sufficiently well defined to allow some general tests of predictions about the role of relatedness in social insect societies.

Adult female wasps were collected from their nests at field sites in Texas, Yucatán (Mexico), Venezuela, and Italy. They were brought back to the laboratory and subjected to starch gel electrophoresis of proteins (see ref. 19 for methods). Between 1 and 6 variable proteins were found and used for estimation of relatedness[8]. The estimated relatedness values among female nestmates are generally high (Table 1), with a mean of 0.542 for the 15 populations (two geographically separated and genetically distinct poulations of Polistes exclamans were included). This is nearly the same as relatedness to offspring, so on average, these species cannot gain much of a relatedness advantage from helping on their natal nest. The highest point estimates are very near the full-sister value of $\frac{3}{4}$, and the lowest attain only about half that value. The 95% confidence intervals for eight species include $\frac{3}{4}$, while eleven include $\frac{1}{2}$ (Fig. 1). Only three species (P. gallicus, M. immarginatus, P. carolinus) should be viewed as being significantly higher than $\frac{1}{2}$, and one (P. annularis) is significantly lower.

Clearly, relatednesses higher than the offspring value of $\frac{1}{2}$ cannot provide the whole explanation for helping. First, few species have an average r significantly above $\frac{1}{2}$ and one is significantly below. Second, in species with an average r near $\frac{1}{2}$, some colonies must be below this average. Third, including males would presumably lower the average as haplodiploidy does not increase sister-brother relatedness. Finally, the relatedness values that are relevant to some altruistic behaviours should be lower than those reported here. For example, autumn females