

Key Points:

- A 9 mm/yr of oblique convergence, 4 mm/yr convergence and 8 mm/yr of strike slip, across the Eastern Cordillera
- Present-day GPS velocities and crustal thickness require ~50 Myrs to construct the present-day Eastern Cordillera
- GPS velocities are inconsistent with paleobotanical observations only allowing 3-6 Myrs to construct the Eastern Cordillera

Supporting Information:

- Supporting Information S1

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GPS velocities and the construction of the Eastern Cordillera of the Colombian Andes

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Abstract GPS velocities across the northeast trending Eastern Cordillera of Colombia show oblique convergence at 8.8 ± 1.7 mm/yr, consisting of 8.0 ± 1.7 mm/yr of right-lateral strike-slip shear along the mountain range and 3.7 ± 0.3 mm/yr of northwest southeast shortening. Faster convergence occurs only at the northeast end of the Cordillera, where its eastern edge trends northwest and the highest mountains lie. The strike-slip shear corroborates geologic work suggesting such movement southwest and northeast of the range. Given the ~200 km width of the Eastern Cordillera, the ~100–150 km of crustal shortening inferred from balanced cross sections and implied by recent estimates of crustal thickness would require ~25–40 Myr of shortening at ~4 mm/yr. The present-day GPS measurements, therefore, are inconsistent with the inference, based on paleobotanical observations that the entire Eastern Cordillera rose 1500–2500 m since 3–6 Ma and called for a different interpretation of those data.

1. Introduction

Many studies of fossil pollen from high terrain (>2500 m) of the Eastern Cordillera of Colombia suggest that between ~6 and ~3 Ma, vegetation resembled what today characterizes the tropical lowland regions adjacent to the Eastern Cordillera [e.g., Andriessen *et al.*, 1993; Helmens and Van der Hammen, 1994; Hooghiemstra, 1984; Hooghiemstra and Van der Hammen, 1998; Hooghiemstra *et al.*, 2006; Kroonenberg *et al.*, 1990; van der Hammen *et al.*, 1973; Wijninga, 1996; Wijninga and Kuhry, 1990]. This similarity, plus the difference between plants living in lowlands and highlands today, led to the deduction that the Sabana de Bogotá, and by extension the entire Eastern Cordillera (Figure 1) rose from low elevations, <1000 m, to their present-day heights since ~3 Ma. Subsequent studies of cooling ages of exhumed rock along the eastern flank of the Eastern Cordillera show an abrupt acceleration in cooling, suggesting rapid exhumation since ~3 Ma and again with the inference that the Eastern Cordillera rose substantially since ~3 Ma [Mora *et al.*, 2008, 2010a, 2010b, 2014]. These inferences of large, Pliocene or Quaternary surface uplift differ from most such inferences elsewhere, because either global cooling since ~3 Ma or accelerated erosion that might be due to global cooling, such by increased glaciation in elevated terrain, offer explanations for the apparent increases in surface elevations [e.g., Molnar and England, 1990; Zhang *et al.*, 2001]. Climate changes in the tropics since 3–5 Ma, however, do not seem to have been large, and certainly not large enough (~9–12°C) to account for the paleobotany-based 1500–2500 m differences between present-day and inferred past elevations. Thus, if the suggestion of recent surface uplift based on palynological and thermochronological observations were correct and applied to the entire Eastern Cordillera, it would require that the Eastern Cordillera has grown to its present dimensions in a remarkably short period of time. Recent work by Anderson *et al.* [2015] using biomarkers and stable isotopes, however, suggests that changes in elevation based on pollen spectra may be overestimated.

Two simply understood geodynamic processes can create high terrain. Horizontal shortening of crust in a state of isostatic equilibrium, whereby excess mass of high terrain is compensated by a deficit of mass in a crustal root (Airy isostasy), accounts for high terrain of most mountain belts. The time required for high terrain to develop by this process obviously scales with the rate that crust is shortened horizontally. Alternatively, many high plateaus are underlain by hot material in the upper mantle, as can occur if the mantle portion of the lithosphere is removed, either by peeling away from the crust as delamination [Bird, 1978, 1979] or by sinking as blobs of dense material during growth of convective instability [e.g., England and Houseman, 1989]. The speed with which such removal can occur remains controversial, but current ignorance allows

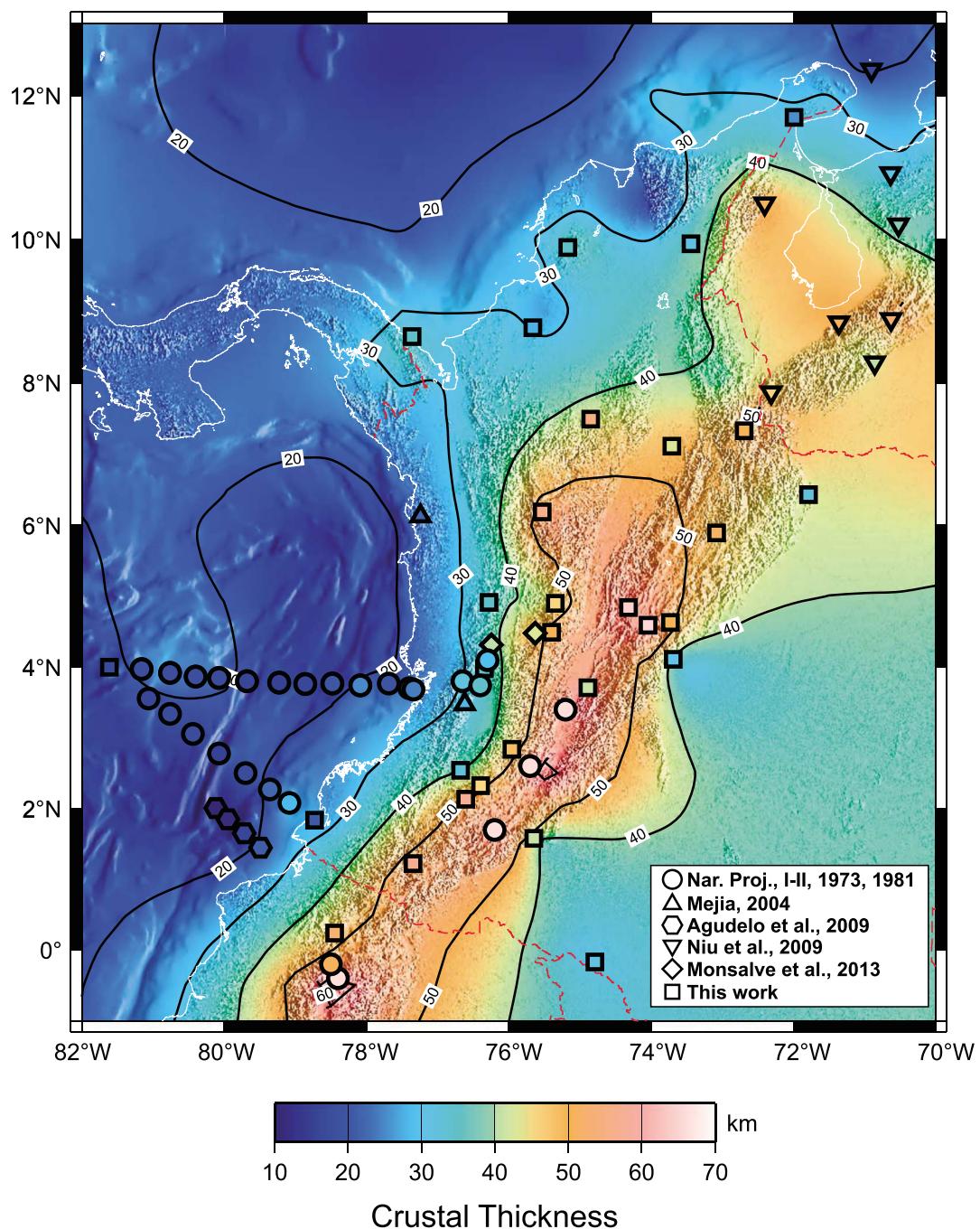


Figure 1. Map of topography of the Eastern Cordillera and adjacent regions, showing seismograph stations and estimates of crustal thickness from Poveda *et al.* [2015].

for removal of mantle lithosphere in periods as short as a few Myr [e.g., Houseman *et al.*, 1981; Houseman and Molnar, 1997]. Amounts of surface uplift that might isostatically balance the replacement of cold mantle lithosphere by hot asthenosphere, however, probably do not exceed 1000–2000 m.

Thus, the apparently recent surface uplift of the Eastern Cordillera inferred from paleobotanical observations seems to offer a test of possible processes that can build mountain belts rapidly. If these inferences of rapid uplift applied to the entire Eastern Cordillera, they would require that the current low rate of shortening apply only to the past few million years, and hence would indicate a remarkably abrupt recent change in rate. At the same time, however, because most mountain ranges have not been built in such short periods, the apparent

youth of the Eastern Cordillera would make it exceptional among mountain ranges around the world. Alternatively, such rapid surface uplift might refer only to the outer edges of the Cordillera where outward growth is taking place.

2. Geological and Seismological Constraints on the Deep Structure of the Eastern Cordillera

Abundant evidence shows that crustal shortening on the flanks of the Eastern Cordillera has occurred [e.g., *Bayona et al.*, 2008; *Cediel et al.*, 2003; *Colletta et al.*, 1990; *Cortés et al.*, 2006; *Dengo and Covey*, 1993; *Egbue and Kellogg*, 2012; *Mora et al.*, 2008, 2010a, 2010b, 2010c, 2014] and that therefore the high terrain is, at least in part, the result of crustal thickening and isostatic balance. This crustal shortening has been built, at least in part, on structures that initially developed during a Mesozoic stage of crustal extension when grabens and normal faults formed [e.g., *Cediel et al.*, 2003; *Jimenez et al.*, 2013; *Moreno et al.*, 2013; *Roeder and Chamberlain*, 1995; *Roure et al.*, 1997; *Sarmiento-Rojas et al.*, 2006; *Tesón et al.*, 2013]. Attempts to balance cross sections across the entire Cordillera have led to differing results. For example, *Colletta et al.* [1990] estimated more than 100 km of shortening, *Bayona et al.* [2008] estimated 110 km, *Dengo and Covey* [1993] suggested 150 km, and *Roeder and Chamberlain* [1995] inferred 170 km, but *Cooper et al.* [1995] argued for only 68 km and *Teixell et al.* [2015] for 82 km. Additionally, *Cortés et al.* [2006] argued for 70 km, though in the southern, relatively narrow part of the cordillera. For the eastern side of the Cordillera, *Mora et al.* [2008] inferred 58 km of shortening. *Tesón et al.* [2013] estimated between 62 and 80 km for four cross sections, and they concluded that shortening of the entire Eastern Cordillera must be less than 25%. Moreover, *Tesón et al.* [2013] argued that because the normal faults have been reactivated in oblique crustal shortening, amounts of shortening are less than the common values of 100–150 km assigned by others. We argue below that the opposite should hold, given that crust was thinned during the Mesozoic phase of crustal shortening.

Estimates of crustal thickness can also be used to estimate amounts of crustal shortening. If a high mountain range, of mean height h , is isostatically compensated by a crustal root of excess thickness ΔH , then crust beneath the range is thicker by $\Delta H + h$ than the crust that has not undergone crustal shortening (Figure 2). Suppose that crust of thickness H is shortened horizontally to build a range with crustal thickness $\Delta H + H + h$, over a width W . In a cross section, there is an excess crust given by $W(\Delta H + h)$. That extra cross-sectional area presumably was built by horizontal shortening of L , so that

$$L \cdot H = W \cdot (\Delta H + h)$$

With $\rho_c = 2.8 \times 10^3 \text{ kg/m}^3$ and $\rho_c - \rho_m = 0.4 \pm 0.1 \times 10^3 \text{ kg/m}^3$, for $\Delta H = 15, 20, \text{ or } 25 \text{ km}$, we would infer that $h = 2.1 \pm 0.7 \text{ km}, 2.9 \pm 0.9 \text{ km}, \text{ or } 3.6 \pm 1.2 \text{ km}$. With an observed mean height of $\sim 2.7 \text{ km}$, clearly a crustal root as thick as 15–25 km is plausible, as is a crustal thickness, $\Delta H + h$, thicker than that in surrounding regions by 18 to 28 km.

Using receiver functions, *Poveda et al.* [2015] estimated crustal thicknesses of $\sim 25\text{--}35 \text{ km}$ beneath the low area to the east of the Eastern Cordillera and thicknesses of $45\text{--}58 \text{ km}$ beneath the high terrain of the Cordillera (Figure 1). Thus, their receiver functions call for crust beneath the Eastern Cordillera 15–25 km thicker than that beneath surrounding regions (if possibly by larger or smaller amounts in subregions). Note that if the crustal thickness were initially $30 \pm 5 \text{ km}$, and only 25% shortening had occurred, as *Tesón et al.* [2013] inferred, the resulting thickening of $7.5 \pm 1.25 \text{ km}$ would account for only $\sim 1 \text{ km}$ to maybe 1.5 km of the current elevations. We presume that the balanced cross sections of *Tesón et al.* [2013] provide only minimum estimates of the total shortening across the belt. Moreover, if the crust were initially thin, as the evidence of Mesozoic graben formation implies [e.g., *Roeder and Chamberlain*, 1995], then for an initial crustal thickness of 30 km now to be 45–58 km, 50% to nearly 100% shortening or 150–300 km would be needed. This analysis shows that Airy isostatic compensation is a sensible assumption and that therefore the crust beneath the Eastern Cordillera is not unusually thin. Thus, the possibility that mantle lithosphere beneath the Eastern Cordillera was removed, with the high terrain resulting from isostatic compensation by a hot, low-density uppermost mantle, can be eliminated.

As noted above, some authors, particularly palynologists and paleobotanists cited above, have deduced that the Eastern Cordillera rose 1500–2500 m since $\sim 3\text{--}6 \text{ Ma}$, and some others, relying on young cooling ages of exhumed rock or evidence of more recent folding and faulting on the flanks of the Eastern Cordillera have

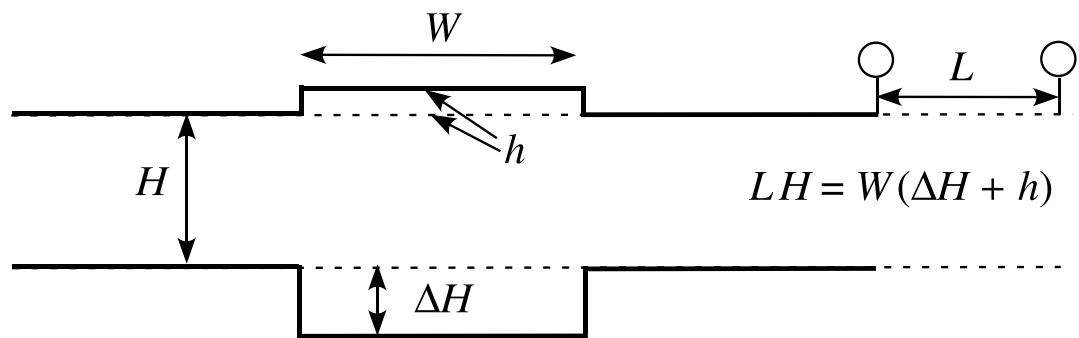


Figure 2. Cartoon showing budget of crust.

inferred that Plio-Quaternary deformation has played a key role in the construction of the high terrain [e.g., *Campbell and Bürgl, 1965; Gómez et al., 2003, 2005a; Horton et al., 2010; Mora et al., 2008, 2010a, 2010b*]. Most, however, suggest that crustal shortening responsible for the Eastern Cordillera began earlier. Some have concluded that initiation of important shortening began in Middle Miocene time [e.g., *Bayona et al., 2008; Colletta et al., 1990; Cooper et al., 1995; Dengo and Covey, 1993; Gómez et al., 2005b; Hoorn, 1993; Hoorn et al., 1995; Mora et al., 2014*], but a consensus suggests that a nonnegligible amount of shortening occurred earlier in Cenozoic time [e.g., *Babault et al., 2013; Bande et al., 2012; Bayona et al., 2013; Caballero et al., 2013; Campos and Mann, 2015; Cedié et al., 2003; Egbue and Kellogg, 2012; Gómez et al., 2003; Hoorn et al., 2010; Horton et al., 2010; Martinez, 2006; Mora et al., 2010b, 2010c; Ochoa et al., 2012; Parra et al., 2009a, 2009b, 2012; Sánchez et al., 2012; Saylor et al., 2011, 2012; Villamil, 1999*]. GPS velocities can be used to test whether crustal thickening in 3–6 Myr could build the Eastern Cordillera, or a longer duration is needed.

3. GPS Analysis and Velocities

GPS data collected in Colombia were obtained from the Global Navigation Satellite Systems GeoRED Project archive operated by the Colombian Geological Survey. Data were processed jointly by the Colombian Geological Survey and the University of Colorado Boulder with GOA 6.3 [Bertiger et al., 2010; Zumberge et al., 1997] using loosely constrained nonfiducial orbits and transformed into the IGS08 frame with orbit, clock, and Xfile products obtained from Jet Propulsion Laboratory (version 2.1) to produce daily positions. Tropospheric corrections were made with the Vienna mapping function products from the Vienna University of Technology [Nilsson et al., 2013] and ocean loading corrections were obtained from the Onsala Space Observatory. The South American frames are defined by methods of DeMets et al. [2010]. We estimate angular velocities and fixed velocities using methods described by DeMets et al. [1990]. Site velocities from the daily positions are estimated using maximum likelihood estimation fitting functions from Ward [1990] and Bos et al. [2013]. Annual and semiannual signals for the permanent stations with greater than 2.5 years of data are estimated and removed using the spectral methods described by Bos et al. [2013].

We processed data from nine cGPS sites (Figure 3) and 20 campaign sites located in the Eastern Cordillera with data obtained from 1996 to present. Velocities are shown in a frame of reference fixed to a stable South American (Table 1 and Figure 4a). Components of velocity perpendicular to the regional N45°E trend of the range represent shortening across it, and those parallel to the range (parallel to N45°E), indicate simple shear (Figures 4b and 4c). We note that although velocities derived from campaign data, in general, support the inferences drawn below, large residuals associated with annual signals limit their value. In addition, we include the velocity at cGPS site BOGT, because it is consistent with other data, but note that it is contaminated by anthropogenic ground water signals and also compaction of the zone [Rudenko et al., 2013]. We calculate, using cGPS data, horizontal shortening of 3.7 ± 0.3 mm/yr (~ 4 mm/yr) perpendicular to the range and a right-lateral strike-slip component of 8.0 ± 1.7 mm/yr. Spatial resolution of the cGPS stations prevents us from assigning either the shortening or dextral motion to any localized zone. Some shortening, however, is concentrated on the southeast margin, where geologic data show active faulting and localized convergence at 2.1 ± 1.2 (2σ) mm/yr [Veloza et al., 2015].

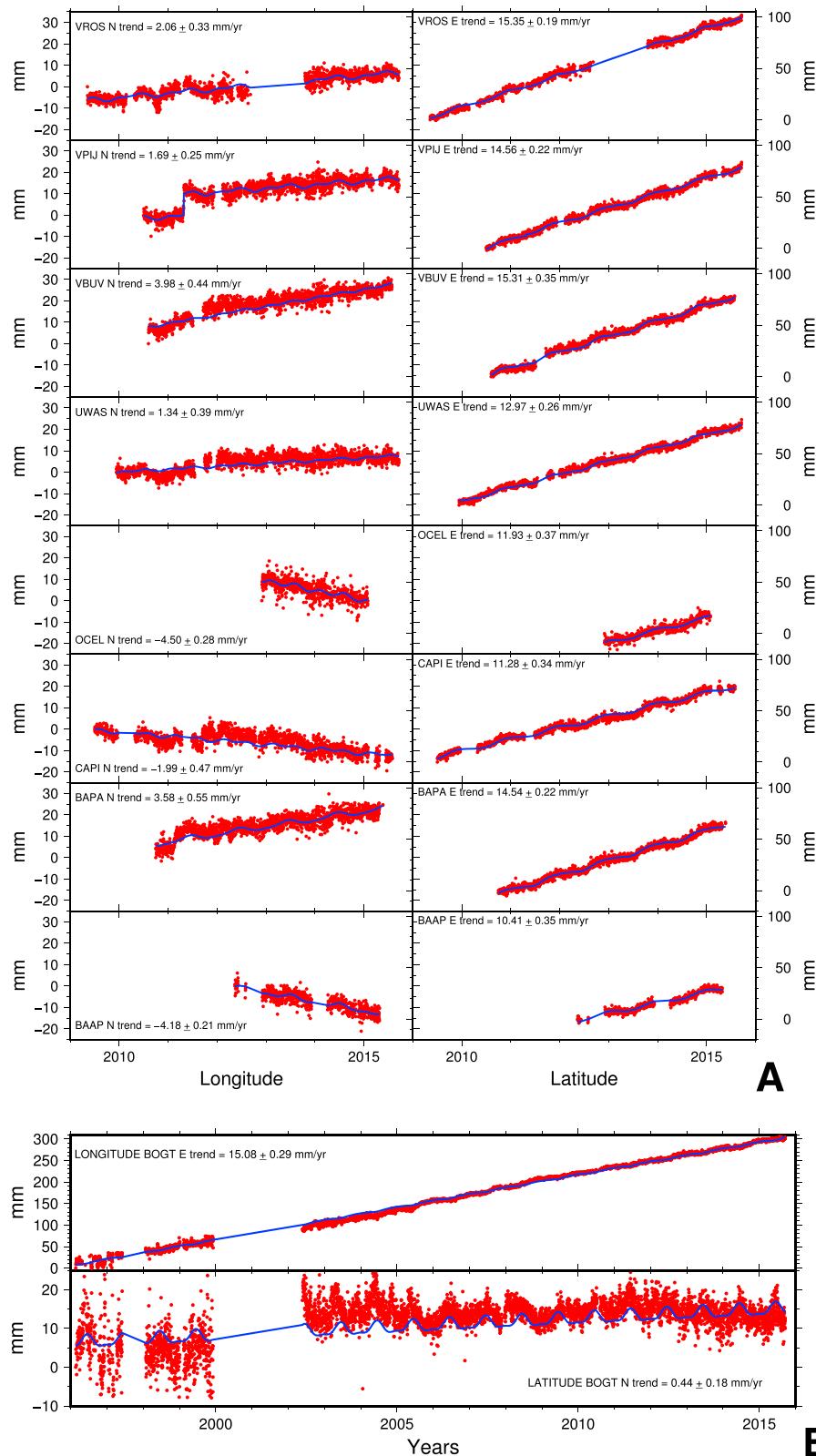


Figure 3. (a) Continuously recording GPS station time series of positions used in this study (Data truncated at 2009 in this figure) in the IGS08 frame of reference. Blue line includes the spectrally estimated annual and semiannual signal, which is removed when the velocity is estimated and the trend calculated. A single equipment-related offset at VPIJ in 2011 was removed. (b) BOGT is displayed with a separate time scale due to the long time series.

Table 1. GPS Site Locations and Calculated Velocities in a South America Fixed Frame and the Rotated 45°E and Projected Into Range Parallel and Perpendicular Components

PERM	South America Frame				All Distances Are Relative to LON 287.45 LAT 5.17 and Rotated 45°										
	LON	LAT	East	North	East Sig	North Sig	Corr	Name	NW-SE	SW-NE	Para	Perp	Para Sig	Perp Sig	Corr
288,38	4,27	0,09	1,19	0,32	0,63	-0,06	OCEL	2,12	129,18	0,91	0,78	0,49	0,51	-0,06	OCEL
285,68	4,85	6,81	5,10	0,36	0,62	-0,02	VROS	-147,54	-102,29	8,42	-1,21	0,51	0,52	-0,02	VROS
287,61	6,45	6,21	2,41	0,42	0,60	0,09	UWAS	101,59	-79,02	6,10	-2,69	0,54	0,49	0,09	UWAS
285,92	4,64	5,07	4,77	0,24	0,66	-0,05	BOGT	-145,42	-70,55	6,96	-0,21	0,48	0,50	-0,05	BOGT
286,14	5,53	8,80	4,93	0,47	0,68	0,02	VBUV	-67,05	-117,81	9,71	-2,74	0,59	0,58	0,02	VBUV
287,57	5,35	2,75	0,71	0,50	0,64	0,01	CAPI	21,17	-4,23	2,45	-1,44	0,57	0,57	0,01	CAPI
286,05	4,40	8,24	9,04	2,32	1,35	0,00	AMAR	-153,19	-44,45	12,22	0,57	1,89	1,90	0,00	AMAR
286,45	4,07	0,58	-0,12	0,52	0,73	-0,05	BAAP	-148,25	7,06	0,33	-0,49	0,62	0,64	-0,05	BAAP
285,34	5,47	8,41	4,26	0,74	0,68	0,01	BAPA	-127,77	-169,98	8,96	-2,93	0,71	0,71	0,01	BAPA
284,89	4,40	6,55	3,83	0,43	0,68	-0,05	VPIJ	-235,13	-126,27	7,34	-1,92	0,56	0,58	-0,05	VPIJ
												Perpendicular Gradient	3,71		
												Parallel Gradient	11,89		
CAMPAIGN															
287,72	4,82	-2,58	-2,64	1,73	0,82	0,00	MAN1	-5,65	43,76	-3,69	-0,04	1,36	1,35	0,00	MAN1
287,57	5,28	-0,02	4,88	1,05	2,52	0,00	VYOP	16,23	0,71	3,44	3,46	1,93	1,93	0,00	VYOP
287,45	5,17	0,87	-0,01	0,62	1,35	0,01	AZUL	0,00	0,00	0,61	-0,62	1,05	1,05	0,01	AZUL
288,11	5,88	-0,07	0,21	0,55	0,17	0,06	PAZA	96,65	-3,53	0,10	0,20	0,41	0,40	0,06	PAZA
287,23	6,16	1,98	-4,48	1,64	1,20	0,00	TUSA	54,33	-85,36	-1,77	-4,57	1,44	1,44	0,00	TUSA
286,67	6,18	8,60	-1,11	0,47	2,91	0,00	OIBA	16,23	-126,27	5,30	-6,87	2,09	2,08	0,00	OIBA
287,24	5,07	7,66	7,62	3,12	1,59	0,00	TAU1	-21,88	-7,76	10,80	-0,03	2,48	2,48	0,00	TAU1
286,33	5,90	6,37	6,13	2,18	1,88	0,00	PTNA	-27,52	-130,50	8,84	-0,17	2,04	2,04	0,00	PTNA
286,57	5,57	6,23	1,70	9,99	1,36	0,00	MOTA	-33,88	-90,30	5,61	-3,20	7,13	7,13	0,00	MOTA
286,65	5,65	6,33	5,99	3,05	2,61	0,00	ARCA	-22,58	-90,30	8,71	-0,24	2,84	2,84	0,00	ARCA
286,13	5,25	8,50	3,86	1,17	0,63	0,01	SUTA	-87,52	-98,77	8,74	-3,28	0,94	0,93	0,01	SUTA
286,01	5,02	6,17	8,97	1,06	1,63	0,00	VZIP	-112,23	-91,01	10,71	1,98	1,38	1,37	0,00	VZIP
286,07	4,90	5,86	5,46	1,27	3,01	0,00	GINA	-116,47	-78,31	8,00	-0,28	2,31	2,31	0,00	GINA
286,00	4,90	2,56	6,27	0,41	0,45	0,03	LANO	-121,41	-83,25	6,24	2,62	0,44	0,43	0,03	LANO
285,79	4,70	9,04	6,00	0,92	3,24	0,00	TIBA	-150,37	-83,95	10,63	-2,15	2,38	2,38	0,00	TIBA
286,04	4,40	4,20	5,67	2,47	3,27	0,00	CAQ1	-153,90	-45,16	6,98	1,04	2,90	2,90	0,00	CAQ1
286,12	4,31	9,78	9,66	2,15	2,13	0,00	QTME	-154,60	-33,16	13,75	-0,08	2,14	2,14	0,00	QTME
284,95	5,15	3,90	3,71	2,14	1,84	0,00	FRE1	-177,91	-174,91	5,38	-0,13	2,00	2,00	0,00	FRE1
286,10	5,10	2,78	3,56	0,26	0,69	0,03	NEM1	-100,23	-90,30	4,48	0,55	0,52	0,51	0,03	NEM1
284,54	5,53	7,96	6,56	0,94	1,13	0,01	PACO	-180,03	-230,59	10,27	-0,99	1,04	1,04	0,01	PACO
												Perpendicular Gradient	10,33		
												Parallel Gradient	17,44		

4. Discussion and Conclusions

Three aspects of the velocity field are noteworthy. First, relative movement of the regions east and west of the Eastern Cordillera includes a large fraction of right-lateral shear. Second, the convergence rate, the component of velocities west of the Eastern Cordillera relative to those east of it and perpendicular to the trend of the belt is only ~4 mm/yr. Third, at the northeast end of the Eastern Cordillera, shortening is essentially perpendicular to the local trend of the belt, and the highest mountains lie in this region.

Regarding the third aspect, among cGPS sites only UWAS defines movement in the northeastern part of the cordillera (Figure 4). The velocity of UWAS of 6.7 ± 0.7 mm/yr toward N69°E is essentially perpendicular to the trends of both the highest mountains of the Eastern Cordillera, the Sierra Nevada del Cocuy, and the boundary of the Eastern Cordillera and Llanos Basin to the east. Obviously, the correspondence of the highest shortening rate across the Eastern Cordillera with the highest mountains, which surely result from convergence in this area, makes sense.

Regarding the strike-slip component, although most discussions of the Eastern Cordillera have focused on the shortening across the belt, Montes *et al.* [2005] showed geological evidence for substantial right-lateral shear of the Eastern Cordillera. This evidence includes not only slip on strike-slip faults but also penetrative strain of cobbles in conglomerate layers. Thus, the shear that they found is distributed, not localized on one or a few major faults. This observation is consistent that the mapping of active faults in Colombia by Veloza *et al.* [2012], although they show relatively rapid right-lateral shear farther south, they depict no active

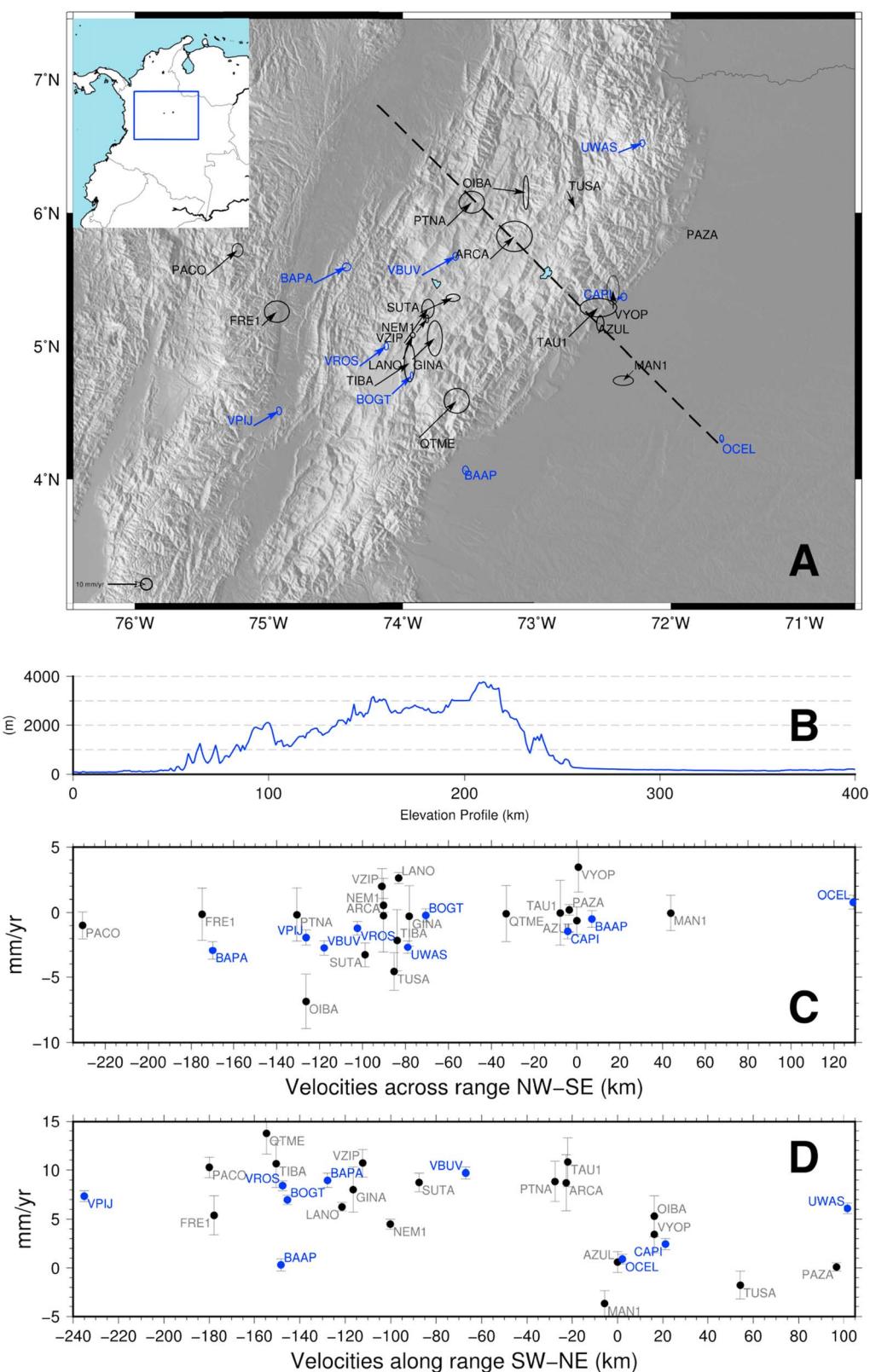


Figure 4. cGPS and campaign station velocities in a South American frame of reference plotted with 1 sigma uncertainties. (a) Map showing velocities: blue are cGPS and black are campaign sites; (b) elevation profile along dashed line in Figure 4a; (c) components of velocity perpendicular to the range plotted against distance from the southeast edge of the belt showing shortening across the range; (d) components of velocity parallel to the range plotted against distance from the southeast edge of the belt showing right-lateral motion.

strike-slip faults within the Eastern Cordillera in Colombia. Our GPS points are too few and too widely distributed to demonstrate localized strike slip.

Shortening across the Eastern Cordillera at only ~ 4 mm/yr could not build the Eastern Cordillera since as recently as 3–6 Ma. For amounts of shortening of 100–150 km, discussed above, if the range were built as recently as 3–6 Ma, we would expect shortening rates of 17–50 mm/yr, rates that the GPS data do not permit. Conversely, an average rate of ~ 4 mm/yr and 100–150 km of shortening require a duration ~ 25 –40 Myr. If convergence had occurred at a constant rate, such rates would require an initiation of crustal shortening that predates middle Miocene time but are consistent with Eocene or Oligocene time, as many have suggested [e.g., Babault *et al.*, 2013; Bande *et al.*, 2012; Cediel *et al.*, 2003; Egbue and Kellogg, 2012; Gómez *et al.*, 2003; Horton *et al.*, 2010; Martinez, 2006; Mora *et al.*, 2010b, 2010c; Ochoa *et al.*, 2012; Parra *et al.*, 2009a, 2009b, 2012; Sánchez *et al.*, 2012; Saylor *et al.*, 2011, 2012; Villamil, 1999]. Note too that if most of the ~ 70 –150 km of shortening occurred since only 12 Ma, as some suggest, the average rate of 5–12 mm/yr would require that the rate have slowed since that accelerated deformation began.

Thus, we should reconsider the implications of paleobotanical observations, which include (1) that vegetation currently living at high elevations of 2500–4000 m differs from that inferred from fossil plant organs at 3–6 Ma and (2) that 4–6 Ma fossil plant organs resemble those of plants currently living below $\sim 1500 \pm 500$ m [e.g., Hooghiemstra *et al.*, 2006]. First, the recent work by Anderson *et al.* [2015] suggests that the rise of the Sabana de Bogotá may have been slower than that inferred from fossil pollen. As important, the paleobotanical evidence comes from only a small part of the Eastern Cordillera. Thus, changes in elevations of that region ought not be generalized to the entire Cordillera. In particular, the oldest site of paleobotanical finds, Tequendama, with an age between ~ 6 and ~ 15 Ma [Wijninga, 1996], lies along the southwest end of the Eastern Cordillera, and it could have risen to its present-day elevation as the southwest margin of the Cordillera rose, without any concurrent surface uplift of the rest of the range. Finally, many of the plants that dominate high elevations today are immigrants from North America since ~ 3 Ma: *Myrica* at ~ 3 Ma, *Juglans* (walnut) at ~ 2.4 Ma, *Alnus* (alder) at ~ 1 Ma, and *Quercus* (oak) at ~ 400 ka [Andriessen *et al.*, 1993; Torres *et al.*, 2013; van der Hammen and Cleef, 1983; Van der Hammen and Hooghiemstra, 1997]. Perhaps we ought not to ignore the possibility that the differences in present-day floral assemblages from fossil assemblages are due less to recent uplift and more to invasive species from North America, which entered Colombia since 3–6 Ma, out-competed plants that had lived at high elevations and limited their habitats to lowlands.

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