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Kinematics of Late Paleozoic Continental Collision Between Laurentia and Gondwana

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In the Appalachians, late Paleozoic Alleghanian orogenesis is widely regarded as resulting from dextral oblique collision between irregular margins of Gondwana and Laurentia. However, this relative plate motion cannot account for coeval convergence in the Ouachitas and Variscides and is incompatible with some tectonic transport indicators in the Appalachians. An alternative kinematic model is proposed in which early sinistral transpression in the Appalachians is followed by counterclockwise rotation of Gondwana and the development of a system of dextral strike-slip faults extending from southern Europe to Alabama.

THE SUPER CONTINENT OF PANGEA formed during the late Paleozoic when Gondwana (which included South America and Africa) collided with North America (Laurentia) and Europe (1). The orogenic activity resulting from this collision is referred to as the Variscan and Hercynian orogenies in Europe and as Alleghanian orogeny in the Appalachian mountains of eastern North America. The Ouachita orogenic belt, along the southern margin of North America, also formed as a consequence of the above collision. A series of Carboniferous and Permian foreland basins (Fig. 1) related to crustal loading of the continental margin by advancing thrust sheets (2) formed on North America. Saliens and recesses in the orogen are at least

in part a consequence of collision of mismatched continental margins (3). A series of dextral strike-slip faults extends from southern Europe to Alabama (4–11) along the axis of the late Paleozoic orogen. Convergent motion between Gondwana and North America ceased before the end of the Paleozoic, and by Late Triassic, the continents had begun to separate, a process that eventually led to the opening of the present Atlantic Ocean (12).

There is widespread agreement among workers in the Appalachians and Ouachitas concerning most aspects of the scenario outlined in the preceding paragraph. However, there is uncertainty concerning the kinematic significance of the dextral strike-slip faulting in the internal parts of the orogen. Some workers (13) have interpreted the strike-slip faults to be a consequence of the operation of indentor or escape tectonic processes related to the convergence of mismatched continental margins. If this were the case, one would expect sinistral and dextral faults to be equally abundant. It is

difficult to account for the preponderance of dextral faults in connection with this interpretation. Other workers (14) have suggested that overall dextral-oblique convergence occurred between Gondwana and North America in the Appalachian region, and that displacement was coevally partitioned between thrust and dextral strike-slip faults. In this model, it is difficult to account for convergence along east or southeast trending segments of the orogen. One expects that dextral motion along northeast trending faults in the Appalachians would result in opening in the Ouachitas and perhaps in Europe. In this report, we propose a kinematic model that resolves the above contradictions. Discussion of this model follows an evaluation of relevant structural and geochronological data.

Rocks in the eastern Appalachian Piedmont of South Carolina and Georgia (Fig. 1) record three kinematically distinct phases of late Paleozoic deformation that are coeval with and considered to be a part of the Alleghanian orogeny observed in the Appalachian foreland (15–17). The earliest phase of Alleghanian deformation, called regional D₂ by Secor *et al.* (15), occurred along the Modoc fault, a 2- to 4-km-thick zone of mylonitic rocks that now dip steeply to the northwest and extend along the Fall Line in South Carolina and Georgia. The fault zone contains numerous map-scale sheets of synkinematically emplaced granitic orthogneiss and juxtaposes high-grade sillimanite-bearing schist and paragneiss of the Kiokee belt in the footwall against low-grade rocks of the Carolina slate belt in the hanging wall. Our evaluation of shear criteria in the mylonitic rocks indicates that, in its present orientation, the Modoc fault accommodated oblique-slip with dextral and normal components of at least 18 and 4 km, respectively (18). However, the present orientation of the fault is a consequence of F₃ folding (15). Regional geologic relationships (Fig. 1) (18, 19), seismic reflection data (20), and structural analysis of the D₃ Kiokee antiform (21) indicate that the Modoc fault originally had a low angle of dip. Recent ⁴⁰Ar/³⁹Ar geochronological data (22) and geothermobarometry calculations (23) suggest that as much as 15 km of crust has been omitted across the fault. We interpret the D₂ Modoc fault to be a low-angle normal fault associated with southward delamination of oceanic lithosphere from continental lithosphere at the onset of the Alleghanian orogeny (24) (Fig. 2).

Between 295 and 285 million years ago (Ma; during D₃) the Modoc fault zone was deformed by the development of northeast-trending, northwest-vergent folds (15–17, 21). These folds are interpreted to represent

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deformation in the upper plate above the midcrustal Alleghanian detachment associated with movement of the crystalline thrust sheet onto the edge of the North American craton (21). The age of this folding in the eastern Piedmont is estimated to be 285 to 295 Ma on the basis of $^{40}\text{Ar}/^{39}\text{Ar}$ age dates (17, 22) and is coeval with folding in the Appalachian foreland as inferred from stratigraphic (25) and geochronological (26) data.

The last Alleghanian tectonic event (D_4) to affect the eastern Piedmont of South Carolina and Georgia resulted in the development of the steeply dipping, northeast-trending Irmo shear zone (8, 15). This event occurred between 290 and 268 Ma (17). This shear zone overprints D_2 fabrics in the Modoc fault zone and is interpreted to have modified the shape of the F_3 Irmo antiform (15). The Irmo shear zone is a part of a system of late Alleghanian northeast-trending dextral shear zones in the Appalachian Piedmont (6, 8, 9, 11, 27).

Therefore, the three kinematically distinct phases of Alleghanian deformation in the eastern Piedmont represent an episode of low-angle normal faulting related to crustal delamination during northward directed convergence between Gondwana and North America, followed by northwest-vergent folding and overthrust faulting, and then by dextral motion along northeast trending strike-slip faults.

These observations of changing tectonic transport directions with time are not unique to the eastern Piedmont of South

Carolina and Georgia. Throughout the United States Appalachians there is a systematic change from north, to northwest, to west-directed transport during the Alleghanian orogeny. In southern New England, the Narragansett basin (Fig. 1) is interpreted to have formed during the early Carboniferous as a pull-apart basin in a northeast-trending, left-lateral, left-stepping strike-slip fault system on the basis of geophysical and geological data (28, 29). The Narragansett basin was filled with Pennsylvanian sediments and was contemporaneous with formation of the Alleghanian foreland basin along the west side of the central and southern Appalachians. Subsequent to its filling, the Narragansett basin underwent west directed compression and low- to medium-grade regional metamorphism (29). Subsequent deformation involving dextral motion along northeast-trending strike-slip faults (30) began at the time the Narragansett Pier Granite intruded the southwestern part of the Narragansett basin at 273 ± 2 Ma (31). The Narragansett basin therefore formed as a pull-apart basin associated with left-lateral strike-slip faulting during the early to mid-Carboniferous, then underwent west-directed compression, and then about 273 Ma, it began to be cut by northeast-trending dextral strike-slip faults.

Dean *et al.* (32) studied macroscopic- to mesoscopic-scale structures in the Valley and Ridge of West Virginia and concluded that there were two times and directions of shortening and thrusting in the foreland. There was an early episode of layer-parallel

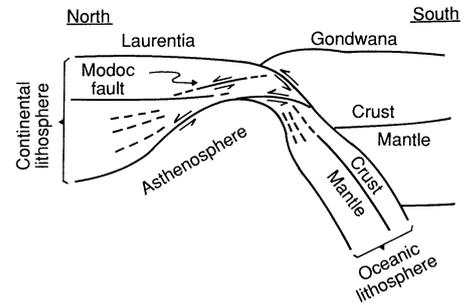


Fig. 2. Schematic cross section in an early stage of the Alleghanian orogeny, showing development of the Modoc fault as a low-angle normal fault during southward delamination of oceanic lithosphere beneath Gondwana. Modified from (24).

shortening in a $N10^\circ\text{W}$ to $N30^\circ\text{W}$ direction. This early deformation developed in association with folding and thrusting in the southern Appalachians. Superposed on these earlier structures are folds and thrust faults of the central Appalachians. These structures indicate that layer-parallel shortening was directed toward $N50^\circ\text{W}$ to $N70^\circ\text{W}$. Dean *et al.* (32) reported an even younger $N85^\circ\text{W}$ shortening direction superposed on the earlier trends. This analysis indicates that the southern Appalachian folds formed in response to north-northwest-directed shortening before a change to northwest- and then west-northwest-directed shortening recorded in the central Appalachians (32). Rodgers (33) reached a similar conclusion.

Two noncoaxial Alleghanian deformation phases are recorded by layer-parallel-shortening fabrics and joints in the Appalachian foreland of New York and Pennsylvania (34). The first (Lackawanna) phase was a north-northwest-directed episode of shortening, as early as Pennsylvanian, which we interpret to be cogenetic with the earliest deformation described above in the southern Appalachian foreland. Folds associated with the second or main phase of the Alleghanian orogeny change strike from west to south around the Pennsylvania salient (Fig. 1), and we interpret these folds to be cogenetic with the second Alleghanian phase of Dean *et al.* (32) in the southern Appalachians. We attribute the curvature of Main phase folds in the central Appalachians to the impingement of the Reguibat promontory (13) during northwest-directed convergence between Gondwana and North America. We interpret that the overall plate-convergence direction changed from north-northwest to northwest during the Alleghanian in the central Appalachians. However, transport directions locally rotated clockwise in Pennsylvania and New York because of the penetration of the Reguibat rigid indenter.

The Suwannee terrane of Gondwana was

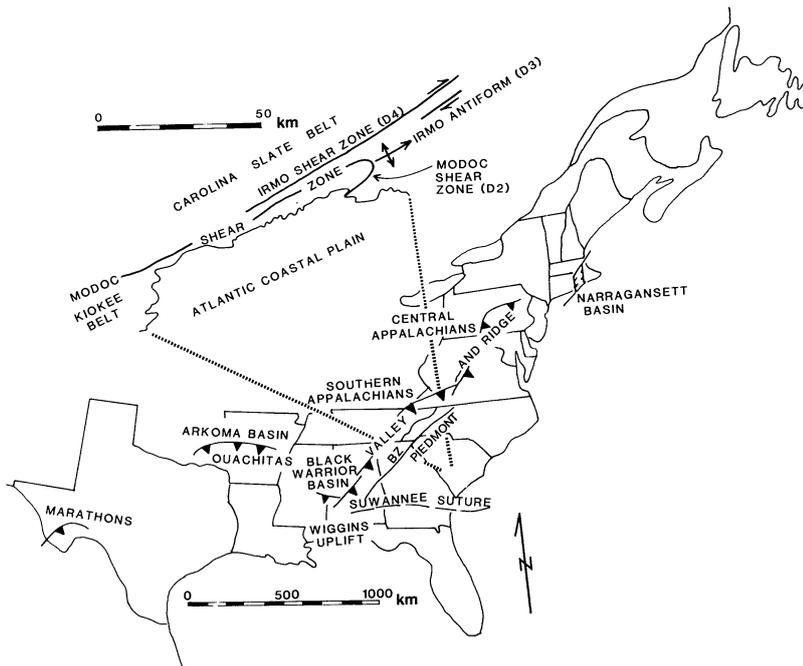


Fig. 1. Index map showing geologic and geographic features mentioned in the text; BZ is the Brevard fault zone.

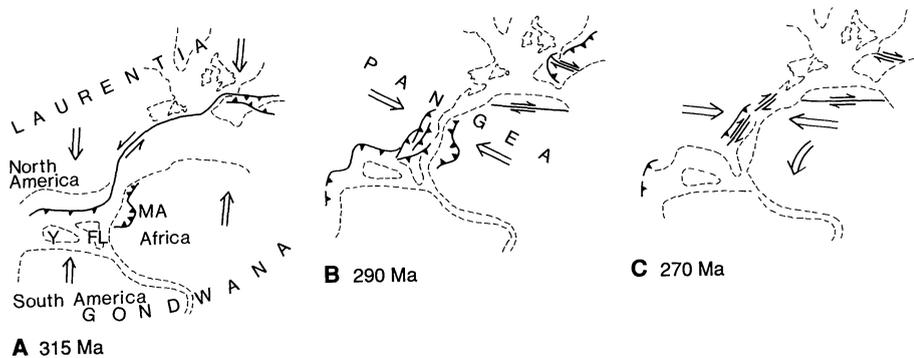


Fig. 3. Plate kinematic model: (A) Early to middle Carboniferous (~315 Ma) scheme showing relative northward motion of Gondwana toward Laurentia; (B) Late Carboniferous (~290 Ma) scheme showing northwestward motion of Gondwana toward Laurentia; (C) by Permian time (~270 Ma), relative motion of Gondwana was nearly due west; EU, Europe; Y, Yucatan; FL, Florida; MA, Mauritanides.

accreted to North America along an east-trending suture during the Alleghanian orogeny. Rocks in the Wiggins Uplift are interpreted to have been within the suture zone between the Suwannee terrane and North America, and they have yielded $^{40}\text{Ar}/^{39}\text{Ar}$ cooling ages of 292 to 315 Ma (35). These ages have been interpreted to indicate that uplift and cooling occurred during collision along the south dipping suture (35, 36).

To the west, the Ouachita orogen evolved as a collisional feature above a south- or southeast-dipping subduction zone during the Carboniferous (37). Stratigraphic studies show that sediments deposited in the Carboniferous Black Warrior basin, at the eastern end of the Ouachita foreland basin, had a source area located in the southwest of the basin and that the source area was a tectonically active continental arc or island arc consisting of low-grade metamorphosed sedimentary and volcanic rocks (38). The Ouachita and Black Warrior basins are coeval with the Alleghanian orogeny in the Appalachians and are probably genetically related.

In west Texas, the northeast-trending Marathon fold belt is interpreted to be a continuation of the Ouachita orogen (39). Deformation in the Marathons is thought to have continued for about 15 million years after deformation in the Ouachitas had ceased (40). These observations suggest that northwest-directed convergence in the Marathons followed or outlasted northward-directed convergence in the Ouachitas.

The above data indicate that systematic changes in the kinematics of the Alleghanian orogeny occurred along the entire length of the Appalachian-Ouachita-Marathon system (Fig. 3). We interpret this evolution to be a result of initial northward convergence and collision between Gondwana and Laurentia followed by a change to westward convergence by the end of orogenesis (Fig. 3). We

interpret that orthogonal head-on collision occurred over a south-dipping subduction zone on the southern margin of Laurentia, and oblique sinistral collision occurred along the northeast-trending eastern margin of Laurentia beginning during the late Mississippian and the earliest Pennsylvanian. This model fits with the interpretation of the Narragansett basin as a sinistral pull-apart basin. Extension along the Modoc fault (in its original subhorizontal orientation) is interpreted to be associated with delamination (41) of the subducted oceanic lithosphere from the southern margin of Laurentia at the onset of continental collision (16, 24) and may indicate a southerly direction of subduction. The numerous late Paleozoic synkinematic granites in the southern Appalachians are interpreted to be a consequence of delamination-related crustal heating (24). Folding and thrusting in the Ouachitas and the Lackawanna phase of deformation in the Appalachian Valley and Ridge were also a result of this early phase of collision. The overprint of a second or main phase (32, 34) of deformation, with northwest- and west-northwest-directed shortening indicates that convergence directions between Laurentia and Gondwana changed substantially. The closing of the Narragansett basin records this event in the New England Appalachians before 273 Ma, when there was a change to dextral strike-slip faulting (30). Similar age determinations from the Brevard zone [(27); 273 Ma] and the Irmo shear zone [(17); 268 Ma] demonstrate that late dextral strike-slip faulting was widespread in the Appalachians. This also corresponds to the time of strike-slip faulting in southern Europe (4, 42).

In a convergent orogen, it may be difficult to determine relative plate motion because of the operation of indentor and escape tectonic processes and because of coeval spatial partitioning of displacement among thrust, normal, and strike-slip faults. In spite

of the presence of the above complications in the Appalachian-Ouachita orogen, field and geochronological data indicate that convergence directions changed progressively counterclockwise from north to west during late Paleozoic orogenesis. This analysis is consistent with the available late Paleozoic paleomagnetic data from North America, Europe, and Gondwana (43, 44).

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Table 1. Schematic representation of the experimental treatments (4). All plots with kangaroo rats removed (-) were compared to all other plots (+), except those with *D. spectabilis* removed.

Treatment	Number of plots
Unmanipulated control	2 (+)
All rodents removed	2 (-)
All rodents and all ants removed	2 (-)
Kangaroo rats removed	2 (-)
Kangaroo rats and <i>Pogonomyrmex</i> ants removed	2 (-)
<i>Dipodomys spectabilis</i> removed	2
All ants removed	2 (+)
<i>Pogonomyrmex</i> ants removed	2 (+)
Seed addition	8 (+)

Control of a Desert-Grassland Transition by a Keystone Rodent Guild

JAMES H. BROWN AND EDWARD J. HESKE

Twelve years after three species of kangaroo rats (*Dipodomys* spp.) were removed from plots of Chihuahuan Desert shrub habitat, density of tall perennial and annual grasses had increased approximately threefold and rodent species typical of arid grassland had colonized. These were just the most recent and dramatic in a series of changes in plants and animals caused by experimental exclusion of *Dipodomys*. In this ecosystem kangaroo rats are a keystone guild: through seed predation and soil disturbance they have major effects on biological diversity and biogeochemical processes.

THE BIOLOGICAL DIVERSITY AND biogeochemical processes that characterize an ecosystem depend on interactions of the organisms with each other and with their abiotic environment. The presence or absence of certain kinds of organisms, called "keystone species" (1), can dramatically alter the structure and dynamics of ecological systems. In most ecosystems, vertebrate animals account for only a small fraction of the biomass and energy flow (2), but through predator-prey, competitive, and mutualistic interactions with other species and by causing physical disturbance they can have disproportionately large effects on habitat structure, species composition, and biogeochemical processes (2, 3). We show that long-term experimental removal of a guild of three kangaroo rat species from a desert ecosystem initiated changes that have led to the conversion of the habitat from shrubland to grassland.

In 1977, experiments were begun on an alluvial outwash plain with diverse desert shrub vegetation in the Chihuahuan Desert

of southeastern Arizona (4, 5). Twenty-four plots, each 0.25 ha in area (50 by 50 m), were fenced with fine wire mesh and assigned at random to experimental manipulations. Treatments included removal of some or all rodent or ant species and addition of millet seeds (Table 1). Access of different rodent species to appropriate plots was controlled by cutting holes of different sizes at ground level in the fences surrounding the plots. Populations of rodents, ants, birds, and plants were monitored systematically at a grid of permanent sample sites within each plot. Between 4 and 16 September 1989, in order to better characterize plant cover inside and immediately outside each plot, all plant species were counted at 10-cm intervals along eight 25-m transect lines: four inside transects began 8 m from the center of the plot and ran outward toward each corner; after a gap of 2 m on either side of the fence, the other four transects continued for another 25 m outside the fence.

In ten plots, one of three different combinations of desert rodent species was excluded (Table 1): all rodents; three species of kangaroo rats, *Dipodomys spectabilis*, *D. or-*

dii, and *D. merriami*; or just the largest and behaviorally dominant kangaroo rat, *D. spectabilis*. An initial analysis of variance (ANOVA), with plots as the sample units to avoid "pseudoreplication" (6), showed that treatments in which all rodents or all kangaroo rats had been removed were similar to each other in the plant variables analyzed below. They differed significantly from all other treatments, except *D. spectabilis* removal. In addition, there were no detectable effects of ant removal or seed addition treatments on these plant variables. Therefore, the eight plots where all kangaroo rats were absent were compared to the 14 plots where all kangaroo rats were present in the following analyses. The two plots from which just *D. spectabilis* had been removed were excluded from the analyses, because the vegetation parameters were often intermediate between the two treatment classes and the limited replication did not permit statistical resolution.

Long-term removal of kangaroo rats caused a dramatic change in habitat, from desert shrubland to grassland (Fig. 1). Effects of *Dipodomys* on vegetation were analyzed by ANOVA, not only comparing plots where kangaroo rats had been removed to plots where kangaroo rats were present, but also comparing transects inside and immediately outside the plots where kangaroo rats had been removed (Fig. 2). Tall-statured perennial and annual grasses colonized the open spaces between the shrubs and increased approximately threefold in the absence of kangaroo rats. Much of this response can be attributed to two species: the perennial *Eragrostis lehmanniana*, which increased more than 20-fold, and the annual *Aristida adscensionis*, which increased approximately threefold. There were complementary changes in two species of short

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