GR Focus Review

A greenhouse interval between icehouse times: Climate change, long-distance plant dispersal, and plate motion in the Mississippian (late Visean–earliest Serpukhovian) of Gondwana

Hermann W. Pfefferkorn [a,*], Vera Alleman [b], Roberto Iannuzzi [c]

[a] Department of Earth and Environmental Science, University of Pennsylvania, Philadelphia, PA 19104-6316, USA
[b] Facultad de Ciencias Biológicas, Universidad Ricardo Palma, Apartado 138, Lima 33, Peru
[c] Departmento de Paleontologia e Estratigrafia, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves, 9500, Porto Alegre, RS 91.509-900, Brazil

ARTICLE INFO

ABSTRACT

The late Paleozoic ice age (LPIA) is the closest example that can be compared with current climate conditions. Near the beginning of the LPIA fossil plants of Mississippian (late Visean to earliest Serpukhovian) age indicate a widespread frost-free climate in a wide belt on Gondwana indicating an interval of greenhouse conditions between the earlier Visean and later Serpukhovian icehouse times. This warm-temperate floral belt has been named the Paraca floral belt after the locality on the Peruvian coast where it was first recognized. The origin of this particular zono-biome was due to the interplay of (1) climate oscillations, (2) several kinds of long-distance plant dispersal within, between or through zono-biomes, and (3) plate motion. The Carboniferous age strata on the Paracas Peninsula in Peru serve as an example for an analysis of these large scale patterns through the analysis of local geology, paleobotany, and paleoecology. The processes observed during this time interval can serve as a model for long-distance plant dispersal at other times.

Contents

1. Introduction

The late Paleozoic ice age (LPIA) extended over approximately 100 Ma from late Devonian through mid Permian times and consists of icehouse and greenhouse climate intervals where each icehouse interval had a duration of one to ten million years (Montañez et al.,

2007; Fielding et al., 2008). In turn, each icehouse interval experienced much shorter Milankovitch scale glacial–interglacial oscillations (Heckel et al., 2007; Heckel, 2008; Birgenheier et al., 2009). At the same time plates were moving and the most significant motion was a clockwise rotation of Gondwana that moved western Gondwana away from the South-polar regions and eastern Gondwana towards it (Pfefferkorn, 1997; Iannuzzi and Rösler, 2000; Iannuzzi and Pfefferkorn, 2002). In addition, changes in elevation of mountains, cold coastal upwelling, and locally increased precipitation played a role in modifying the degree of ice cover locally and over time (Isbell et al., 2012). We are addressing here the interplay of continental motion

with worldwide temperature fluctuations and long-distance plant dispersal that is also known as "plant migration." Plant fossils are excellent climate proxies both through their autoecology as expressed in morphology and anatomy and their paleobiogeographic distribution. We are reviewing here the late Visean to earliest Serpukhovian Paraca Floral Belt as the expression of a relatively short greenhouse interval that occurs between the earlier Visean and the later Serpukhovian–Pennsylvanian icehouse intervals. This greenhouse time is best expressed at the type locality at Paracas, Peru. With this review we offer a synthesis of the current state of knowledge about geology, paleobotany, paleoclimatology and their Gondwana wide correlation and significance. In addition, six patterns of long distance plant dispersal (LDPD) were found that contributed to the formation of the warm-temperate Paraca zono-biome. These patterns of LDPD are important phenomena that can help in the understanding of modern biogeographic patterns (Lieberman, 2004; Nathan, 2006; Parenti and Ebach, 2009, p.103–113; Lomolino et al., 2010).

The Carboniferous of Paracas by itself is a small occurrence, but it has played a major role in Carboniferous paleobotany and over the decades has attracted scientists from Peru and many other countries, who have studied, either the site itself or material originating from the site. Plant fossils from Paracas are present in natural history collections in Peru itself and in many leading museums of the world. In addition the locality is in a nature preserve and park area that is easily accessible and has numerous visitors each year.

The Carboniferous beds of Paracas occur about 250 km south of Lima on the Pacific Coast (Fig. 1-A). The specific site is situated on the Paracas Peninsula (Fig. 1-B) south of Pisco in the province of Ica. The Carboniferous is bounded by normal faults and is overlain by Tertiary sediments (Fig. 1-C).

After the discovery of the Carboniferous rocks at Paracas (Fuchs, 1900) geologists and paleobotanists reported on the plant fossils found at Paracas mostly collected by others, during relatively short visits (Berry, 1922a,b; Seward, 1922; Gothan, 1928; Steinmann, 1929; Read, 1938; Jongmans, 1954; Doubinger and Alvarez-Ramis, 1980).

Fig. 1. Location of the Paracas Carboniferous. A — Position of Paracas area on the southern coast of Peru where the Nazca Ridge is being subducted. B — Paracas Peninsula showing the approximate boundary between the Cordillera de la Costa (CDLC) and the East Pisco Basin (EPB). C — Southeastern corner of Paracas Peninsula. Part underlain by Carboniferous stippled. Faults (F) shown by dashed lines. Location of exposures of Carboniferous beds marked by Roman numerals. I = La Mina section.

When one of the authors (V.A.) discovered excellently preserved material and suggested cooperative research to the other author (H.W.P.) a team of Peruvian, South and North American scientists and their students restudied the locality and collected fresh material. Based on this flora Alleman and Pfefferkorn (1988) recognized the Paraca warm temperate floral belt distinguished from the Amerosinian (Euramerican) realm to the north and the Gondwanan realm to the south. Iannuzzi and Pfefferkorn (2002) reinterpreted this belt and recognized its Mississippian age (late Visean to earliest Serpukhovian) on the basis of similarity to other Southern Hemisphere Mississippian floras. Alleman and Pfefferkorn (1991) and Alleman et al. (1995) presented paleoecological studies, Pfefferkorn (1995b, 1997) discussed the paleoclimatological significance, and Erwin et al. (1994) and Iannuzzi et al. (1998, 1999) described lycopsids and pteridosperms.

The La Mina section on the Paracas Peninsula is rich in plant fossils that occur as fragments in the float that comes down the slope and lies on the footpath winding along the cliff. This material is weathered even though this might not be obvious at first inspection. Fine features, as for instance ligules in lycopsids, are not preserved. Even within this material there are different degrees of weathering and one can see anything from nearly fresh material on the wave cut platform to highly weathered material higher up the slope, where fossils become ultimately unrecognizable as is the case on the desert floor. In addition there are differences in the grain sizes of the rocks in which the plant fossils are preserved, which ranges from fine-grained shales to medium-grained sandstones. It is obvious from the photographs in publications by earlier paleobotanists and from our inspection of specimens in various collections (Bonn, Heerlen, London, Washington, DC) that the majority of the specimens were collected from float.

While plant fossils are plentiful, most are preserved only as fragments. This fragmentation is in most cases primary, in other words it happened as part of taphonomic processes before the plant fragment was entombed in the sediment. Thus, one has to collect for significant amounts of time before specimens are brought together that show enough features and are well enough preserved to advance paleobotanical knowledge and allow a description of variability and the reconstruction of whole plants and paleoecological associations.

2. Geology of the Paracas Carboniferous

2.1. Geologic setting

The Carboniferous of the Paracas Peninsula occurs only in a small area (Fig. 1-C) and in four sites they form sea-cliffs that have developed along fault-lines. Due to the constant active erosion by the ocean fresh material is available in these cliffs that are labeled I through IV on the map (Fig. 1-C). However, only sections I and II are safely accessible. Section IV experiences constant rock falls and is therefore unsafe, even though it is accessible. Section I, called the La Mina Section, has also the advantage that the beds are dipping at a low angle and one can therefore walk the entire section with fresh material at sea-level (Figs. 2 and 3). The sections are safely accessible only during low tides and become inaccessible during the days of new moon and sometimes also during full moon.

The Paracas Peninsula is geologically part of the Cordillera da Costa that exists in this part of the Peruvian coast, because the fore-arc is lifted where the Nazca Ridge is being subducted (Fig. 1-A). The Cordillera da Costa and the area of the Paracas Peninsula are formed by tectonic horst and graben structures that are a few kilometers wide and largely, but not exclusively, arranged parallel to the trench. These horst and graben structures shape the larger part of the topography that is then modified by blowout basins and coastal erosion and deposition. Mississippian age rocks occur only in one small tectonic horst while the adjacent tectonic horsts consist under the Tertiary cover of either metamorphic rocks of Precambrian age or Jurassic–Cretaceous volcanics.
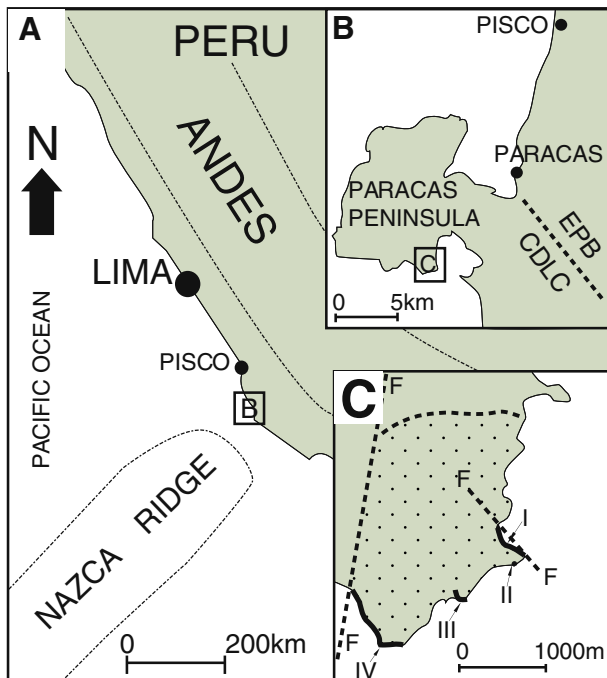
Fig. 2. View of La Mina section ("I" on map 1-C) from observation point above "La Mina" beach.

The Cordillera da Costa is underlain by basement rocks that collided with Gondwana in late Ordovician time (Ramos, 2008; Romero et al., 2013). This means that during the Carboniferous the area of Paracas was already part of the western edge of Gondwana. However, it was not as close to the ocean as it is now, because the direction of transport for the material that is deposited came from a mountain chain of some altitude towards the west that was being eroded and formed the actual edge of the continent, namely the volcanic arc suggested by Alemán and León (2002). On the other hand there is a beach-barrier-bar complex present in the Mississippian beds of Paracas, which means that an epicontinental sea or an intra-arc basin (Zapata et al., 2005) covered this part of the continent and the area of deposition of the Carboniferous sediments was at or very near sea level. In terms of regional geology the Paracas Carboniferous is part of the Madre de Dios Basin (Limarino and Spalletti, 2006).

The volcanic arc that developed during the Jurassic and Cretaceous influences the Mississippian strata only indirectly through dykes that are cutting through the Mississippian beds visible on the desert floor above La Mina beach and near the entrance to Puerto General San Martin (own observations). The volcanism contributed to the high rank of coalification in the Paracas area, which makes palynological investigation difficult and in some parts of the section impossible (own observations).

Thus, the Mississippian of Paracas is part of the long-term history of this area which has left traces only intermittently in (1) the Precambrian basement of the Arequipa Massif, (2) the Mississippian of Paracas, (3) the Jurassic–Cretaceous arc that developed over this area, (4) the Tertiary marine sediments, and (5) the Tertiary through Pleistocene uplift that is still continuing.

2.2. Litho- and sequence stratigraphy

For this project the section was measured and subdivided into 24 units for collecting purposes (Figs. 3, 4). If formalized, these collecting units would be members or beds in lithostratigraphic terms. Some of these units, namely units 1, 10, 14, 18, 20–22, and 24, are lithologically distinct from overlying and underlying beds because they represent thicker sandstone beds. Other units represent an inter-layering of thinner beds of sandstones, siltstones, shales, and coals. Some units represent sedimentary cycles and boundaries are formed by easily weathered fine-grained rocks, i.e. shales or coals. In other cases, as in units 15 through 17, there are lithologic or bedding differences between the units.

The La Mina section is only 170 m thick and contains only one marine incursion (units 20–22 and unit 24). Therefore, it seems to represent only part of one parasequence if we assume that no major part of the section is missing. That would limit the time represented in this section to maximally 1 to 1.5 Ma. An estimate for the minimum time required to deposit the rocks present is 300 k years (own estimates). Thus, the beds at Paracas will certainly not represent the entire greenhouse interval but rather a small part of it. The more extensive section reported from elsewhere (Pino et al., 2004; Zapata et al., 2005; Jacay et al., 2007) may add information in the future.

2.3. Environments of deposition

An investigation of the sedimentology resulted in a preliminary interpretation of the depositional environments (Nuñez del Prado, 1991a,b) that is used here with modifications. The lower 15 units represent three fluvial avulsion cycles (Fig. 4), units 16 through 19 a coastal plain with a channel in unit 18, units 20 through 22 a beach barrier sequence, unit 23 a return of a coastal plain, and unit 24 presumably a second beach barrier bar system. Unit 24 is not directly accessible because the covered interval is under the ocean and the exposed part forms cliffs in the ocean.

The lower part of the section, namely units 1–9, units 10–13, and units 14 and 15 can be interpreted as three avulsion cycles that begin in each case with a channel sandstone. Thus, the area of Paracas was
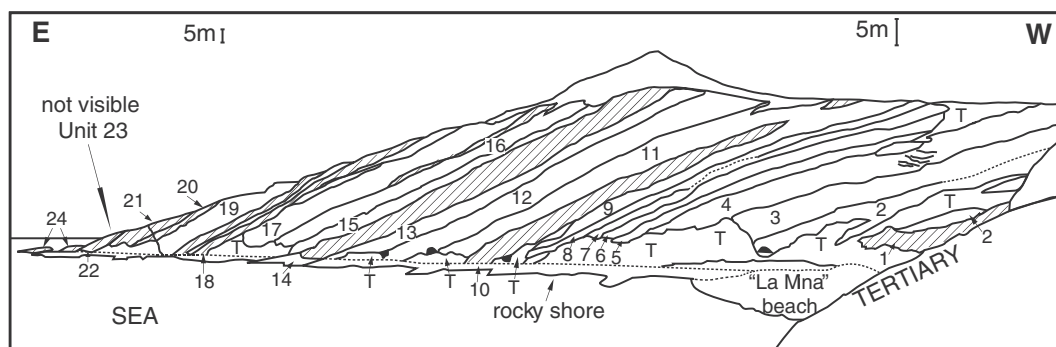

Fig. 3. Sketch of La Mina section from observation point above "La Mina" beach. The numbered beds represent the stratigraphic units distinguished for collecting purposes. Hatched units are thicker sandstones, while other units consist of interlayered beds of sandstones, siltstones, shales, and coals in various ratios. Four mine openings (tunnels or adits) marked in black. Scale changes along section as indicated. Talus slopes marked with T (after Alleman and Pfefferkorn, 1988).
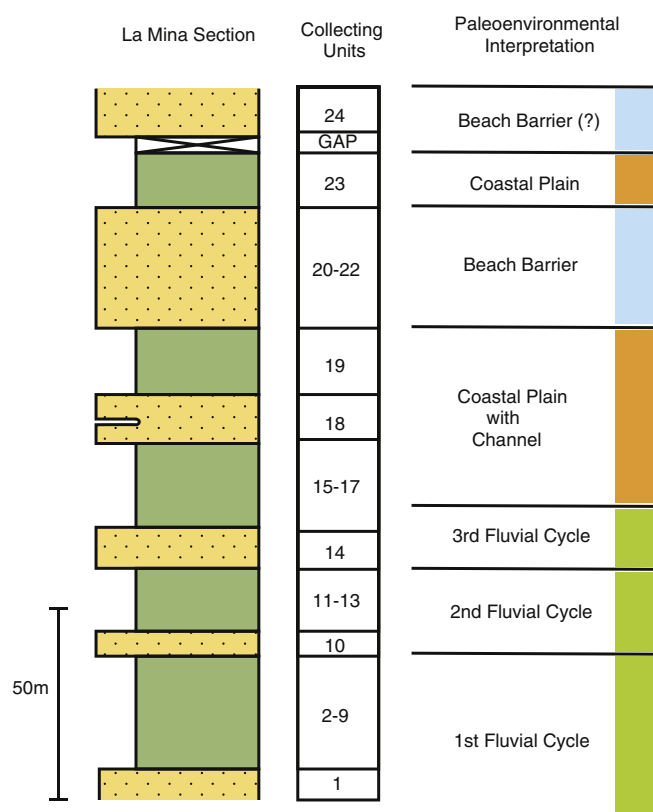
Fig. 4. Generalized geologic section at La Mina, Paracas, showing numbers of collecting unit and paleoenvironmental interpretations. Stippled, yellow intervals mark the thicker sandstone units; olive green intervals consist of interlayered sandstones, siltstone, shales, and coals. An interval covered by the ocean forms the base of unit 24. Paleoenvironmental interpretations modified after Nuñez del Prado (1991a) showing the change from fluvial to an alternation between coastal plain and beach barrier.

during this time interval in a fluvial part of a sedimentary basin and the style of the rivers was meandering.

The following units 16 through 19 represent different environments that occur in tidally influenced coastal plains. There are inter-distributary basins that contain fresh water clams (Alleman, 1991) and sedimentary couplets that indicate fill during flood events. Unit 18 consists of two channels that are separated by a sandy unit that represents some inter-channel beds. These sands are sedimentologically more mature than those in the fluvial units and allow the interpretation as tidally influenced lower reaches of rivers or distributaries. Unit 19 can be subdivided into 5 subunits that represent flood deposits in a fluvial plain that are quite heterogeneous in each of subunit and between subunits, even though the rhythmic structure is apparent. In each of the subunits only one of the layers is normally plant bearing and the lithology is distinct when studied in fresh material in the wave cut platform. In observing the units over the length of the outcrop it becomes apparent that they pinch out and are lenticular in nature. They represent the fill of local depressions during flooding events. This interpretation is upheld by observations of plant taphonomy in one unit where all the parts of a single plant occur except for the roots and all the stems are oriented parallel to each other (Erwin et al., 1994).

Unit 19.1 contains a fragmentary, extrabasinal flora in a highly indurated and dense matrix and the plant fossils appear in very low density. Parts of the rock are totally devoid of plant fossils. On the other hand, units 19.2 through 19.5 contain parautochthonous floras that grew just outside this depression and were moved by the flood into the depression.

This pattern is repeated in unit 23, where we see finer grained material, including some coal and large amounts of plant fossils. In unit 23 there are also three layers with standing *Tomiodendron* stems,

indicating that the flood/deposition events occurred interspersed with significant intervals of non-deposition that allowed mature forest to grow (Alleman and Pfefferkorn, 1991).

Units 20 to 22 are well-sorted sandstones that appear in part rather massive, in part extremely finely bedded that can be interpreted as a beach-barrier bar complex. The very finely bedded unit shows rhythmic bedding, probably laid down by tidal currents in filling a channel. No plant fossils occur in these sandstones.

Unit 23 dips into the ocean but at a short distance, even though un-reachable, there are cliffs of sandstones, very similar to those of unit 22. The interval covered by the ocean may represent either the top of unit 23 or the bottom of unit 24. The latter is interpreted here to be a possible repetition of the beach barrier system. Under the assumption that it is a continuation of the observed section and there is no fault hidden under water.

A filled channel exists in section II that can be reached from unit 23. Channel direction and other sedimentary features, especially current indicators, show that the currents in the entire system came from the Northwest and were flowing towards the Southeast, i.e. in present day orientation from the Pacific Ocean towards the continent.

According to Walther's Law environments that form a vertical succession existed side by side during the time of deposition moving laterally due to (a) geologic subsidence of the area, (b) filling with sediment, and (c) sea-level changes. This assumption is only correct within one parasequence and it appears that units 1 through 22 of the La Mina section represent one parasequence.

A block diagram of the resulting landscape (Fig. 5) includes the mountainous source area, the fluvial plain with meandering rivers, its transition to tidally influenced coastal plain with strait-channels, the beach-barrier-bar system, and the ocean. Both the mountains and the ocean have not left any direct trace in the small outcrop area but did exist in the general area during the time of deposition. This landscape that existed in Paracas in middle Mississippian times can be reconstructed using the data from stratigraphy, sedimentology, paleobotany, and paleoecology. The mountain chain itself and sedimentary environments in its vicinity are not preserved, but are either under the ocean in the continental margin or have been tectonically eroded (Romero et al., 2013).

3. Biostratigraphy, paleoclimate, and rotation of Gondwana

Biostratigraphic age determinations require the presence of species or genera with known ranges from well-studied areas with continuous sections elsewhere. There are four genera in the Paracas flora with known stratigraphic ranges in other climatic belts and another genus that has a close relative (Fig. 6). *Tomiodendron* occurs in the Angara floral realm from the Tournaisian through the Namurian. "*Triphyllopteris*" occurs in the Euramerican floral realm from late Tournaisian through early and middle Visean, while *Fryopsis* is known in the Euramerican floral realm from middle Tournaisian time into basal Namurian (Wagner, 1984). The first occurrences of *Nothorhacopteris* have been found in the Gondwana floral realm in the late Visean of Australia (Roberts et al., 1994) based on the radiometrically dated deposits. The lyginopterids are represented in the Paracas flora by the genus *Oclloa* (Erwin et al., 1994). The genus *Lyginopteris* is known in Europe from middle Visean to its well-defined last appearance datum (LAD) at the Langsettian–Duckmantian (Westphalian A–Westphalian B) boundary. Therefore, the late Visean is the unique stratigraphic interval where all six ranges overlap (box with dashed outline in Fig. 6).

Iannuzzi and Pfefferkorn (2002) determined the age as late Visean (including perhaps some basal Serpukhovian) through correlation within the Paraca Floral Realm through correlation with macrofloras, palynology, and comparison with numerical ages from Australia (Fig. 7). Fig. 7 also shows the relationship of the greenhouse interval represented by the Paracas flora in relationship to the larger scale warm and cold climate intervals.
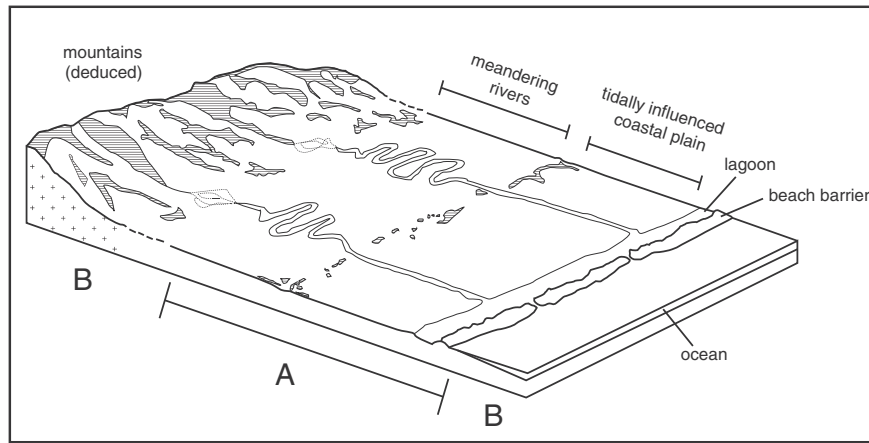
Fig. 5. Block diagram of the reconstructed late Visean age landscape at Paracas. A — area represented in outcrop; B — areas not preserved but deduced.

The geologic section at Paracas can be correlated biostratigraphically with other sections in Gondwana in northern South America (Brazil, Peru, and Bolivia), central Africa (Niger), the northern Indian Subcontinent (Kashmir), and eastern Australia (Fig. 8). Similar macrofloras and often coal deposits occur in each section only in the specific interval which is late Visean in age as in Paracas. However, indicators of either tropical or glacial conditions have quite a different distribution. Glacial deposits occur in older beds (Tournaisian, lower Visean) in western Gondwana in northern Bolivia, northeastern Brazil (sections 1 and 4 in Fig. 8), and northwestern Argentina while they occur in younger beds in eastern Gondwana in northern India and eastern Australia (sections 6–8 in Fig. 8) (Díaz-Martínez, 1995; Grader et al., 2008). Indicators of hot climate, like marine carbonates or aeolian deposits, show the opposite pattern occurring in younger beds in western Gondwana (sections 1, 3, and 4 in Fig. 8) and in older beds in eastern Gondwana (sections 6 and 7 in Fig. 8). This reversal in pattern is due to a clockwise rotation of Gondwana with western Gondwana moving north while eastern Gondwana moved south. Therefore, the Paraca Floral realm existed only during a geologically short time while the areas under consideration were at the same latitude and Earth experienced simultaneously a greenhouse climate interval (Iannuzzi and Pfefferkorn, 2002).

4. Long-distance plant dispersal (LDPD)

Plants are excellent proxies of climate if their fossils are found in or next to their place of growth, i.e. if they are found in autochthonous or parautochthonous occurrences (Pfefferkorn, 1995a; Gastaldo et al., 1996). Under these circumstances their morphology and/or anatomy reveal the environmental and climatic conditions that existed in that locality. For instance, certain growth forms like tuft trees with unbranched stems and large leaves can only survive in frost-free climates. The second important set of information comes from the paleobiogeographic distribution of fossil plants. In other words, paleophytogeographic realms track paleoclimate (Gastaldo et al., 1996) a statement that applies to the late Paleozoic as well as the more recent past and Recent (Williams et al., 2004). In these cases (Mississippian, Paleogene, or Recent) often a static view prevails because either a locality or a region is considered during a specific short time slice.

However, there is also a dynamic component to plant life. While rooted plants are immobile and are the "sessile benthos of terrestrial environments," their spores or seeds are distributed by different vectors, like gravity, wind, rivers, ocean currents, or animals. Thus, plants do "migrate" (= are dispersed) during their propagation phase

Fig. 6. Biostratigraphic correlation of the Paracas Carboniferous based on genera of plant macrofossils with known stratigraphic ranges in other climatic belts or other areas of Gondwana. The late Visean is the only time with greatest overlap if column 5 (range of *Nothorhacopteris* in Argentina) is excluded and the range of *Nothorhacopteris* in Australia substituted (column 6). The stratigraphic nomenclature used reflects the classical European terminology used for the larger part of this data set.
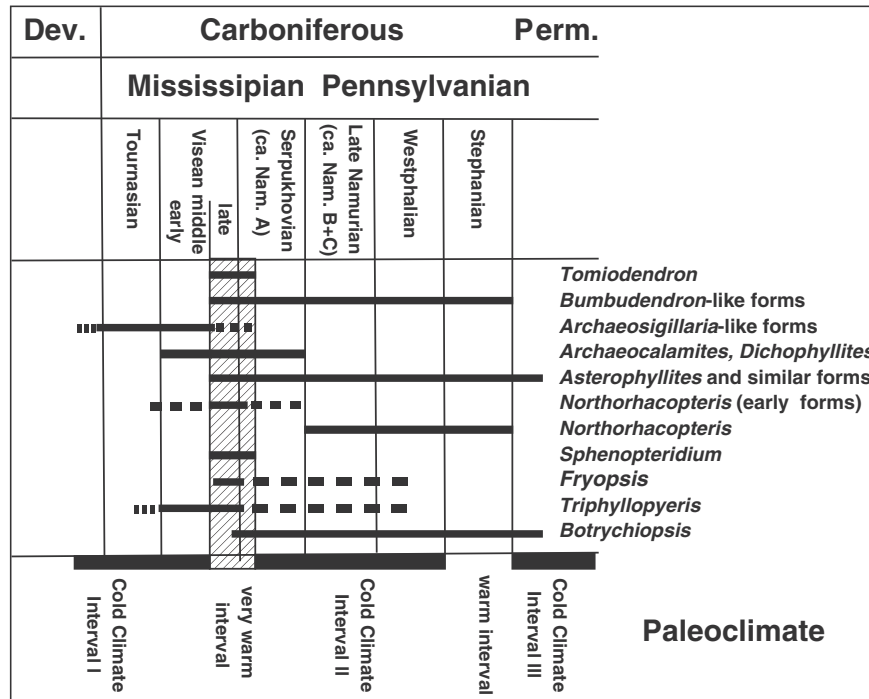
Fig. 7. Stratigraphic ranges of selected plant macrofossils in the middle part of the Carboniferous of Gondwana and their relationship to cold and warm climatic intervals. Hatched interval represents the Late Visean very warm climate interval characterized by the Paraca Floral Belt. This interval might have reached into the earliest Serpukhovian (slightly modified after Iannuzzi and Pfefferkorn, 2002).

and will become established in environments and climate zones that are suitable, can be reached, and are becoming available. Plants actually can be dispersed at astonishing speeds of 150 to 500 m per year (Clark et al., 1998). At these speeds a plant species could be dispersed across the North American continent in 7.8 k to 26 k years (New York to Los Angeles, approximately 3900 km) or across the Eurasian continent from Paris to Beijing (approximately 8600 km) in 17 k to 57 k years. Such a dispersal would fall within the duration of the shortest or second

shortest Milankovitch cycles and could be considered geologically speaking near instantaneous. All these considerations are valid only if there is a continuous belt of environmental and climatic conditions that allows such a dispersal.

In reality there are barriers such as mountain chains, deserts or oceans that prevent dispersal. These barriers can be breached by some plants and under rare circumstances. These possibilities have been called corridors or sweepstake routes depending on their degree of "openness"
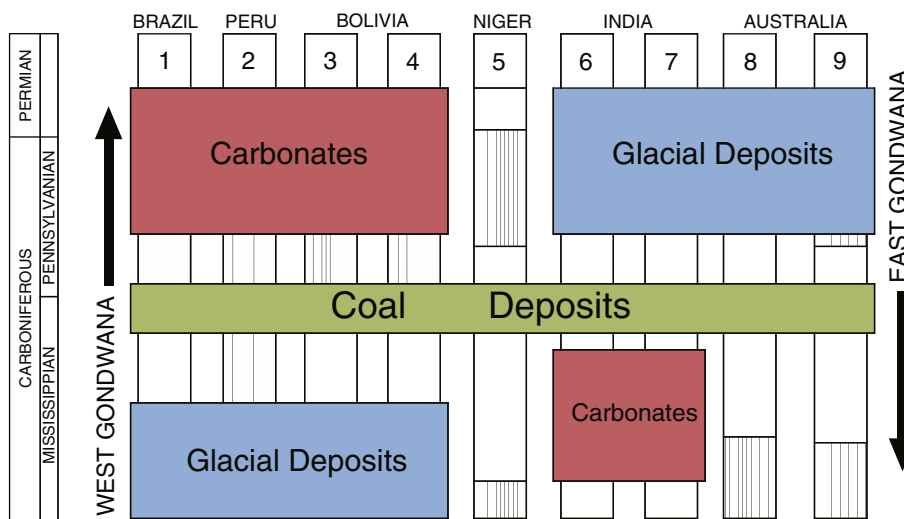

Fig. 8. Correlation of sections across Gondwana (i.e. northern South America, central Africa, northern Indian Subcontinent, and eastern Australia) showing the relationship of coal deposits as humid and temperate climate indicators, marine limestones (warm climate), and glacial deposits (cold climate). Because of the clockwise rotation of Gondwana during the time interval shown (which is indicated by the two arrows on either side), glacial deposits occur at the bases of sections 1–5 and the tops of sections 6–9. The coal deposits occurred when a relatively short greenhouse interval in the latest Visean and perhaps earliest Serpukhovian created a belt of frost-free climate reaching far south on Gondwana (modified after a figure by Iannuzzi and Pfefferkorn, 2002). Possible Pennsylvanian age glacial deposits in southern Bolivia (Anderson, 2011), northwestern Argentina, and southern Brazil (Iannuzzi and Rösler, 2000; Balseiro et al., 2009; Césari et al., 2011) are not shown. These deposits do not change the overall validity of this scheme but represent an overprint of climate oscillations that took place in contiguous areas located further south of the range of occurrence of the Paraca realm.

(Simpson, 1940). Sweepstake routes would be highly selective in which organisms could pass through only under unusual circumstances. An example for plants would be an extreme storm that could transport spores or small seeds across half the Pacific Ocean from Asia to Hawaii or tsunamis plus the existing gyres in the ocean as happened over the past two years. Such events brought plants to the Hawaiian island chain and only few events per million years were necessary to create the flora that existed before humans arrived (Cowie and Holland, 2006).

The main climatic limitation to plant dispersal is the temperature gradient between the equator and the poles. The resulting climate zones are modified through the shape of continents/ocean basins, ocean currents, atmospheric circulation, and topography. The resulting climatic areas are characterized by vegetation types that have similar appearances and adaptations even where evolutionary history, i.e. genetics is different. These climate-vegetation belts have been described as the major biomes or zono-biomes by Walter (1973) and a modern detailed treatment is presented by Breckle (2002). The ten zono-biomes reach from the ever-wet tropics (zono-biome 1) to the arctic (zono-biome 10). Most plants are adapted to one zono-biome while a few generalists can live in specific azonal environments in many areas. The Paraca floral belt is such a zono-biome but one that did not exist during icehouse times but formed during a greenhouse interval. It is important to recognize that biomes can form and disappear in geologic time (Williams et al., 2004).

Long-distance dispersal of plants has been recognized in the Carboniferous and six types of movement can be distinguished. Four of these types have a direct bearing on the late Visean Paraca floral belt. Type I is within zono-biome dispersal. During the late Visean greenhouse time plants spread throughout that belt on Gondwana from what is now Peru to what is now Australia and vice versa (Iannuzzi and Pfefferkorn, 2002). One has to express it this way because we see the results but there are not enough data yet to determine where the different plant groups originated.

The dispersal of plants in response to a moving continent (Iannuzzi and Rösler, 2000) is labeled here type II. Plants continued to propagate, i.e. "stayed," in the same latitudinal-climatic belt (= zono-biome) while the continent moved under them. Iannuzzi and Rösler (2000) demonstrated this for Carboniferous floras occurring in South America.

Type III of long-distance plant dispersal represents the response of plants to the effects of Milankovitch cycles, i.e. glacial–interglacial cycles, on one continent. This has been studied extensively for the Holocene and Pleistocene (Williams et al., 2004) where it represents the movement of biomes, too. An example from the Pennsylvanian of North America was presented by DiMichele et al. (1996) in which the long-distance plant dispersal occurred entirely within the tropical zono-biomes.

Another type (type IV) is the long-distance plant dispersal within one biome from continent to continent (Fig. 9). An example is the dispersal of the Paripteris-group of pteridosperms from their area of origin on one of the Chinese microcontinents to Kazakhstania, Europe, and finally North America (Laveine et al., 1992, 1994). Barriers played a major role and the dispersal over the full distance lasted approximately 10 Ma. The reason that this group was held up by barriers while other groups spread across them near instantaneously lies in the biology of the Paripteris-group and similar medullosan pteridosperms. They had very large prepollen grains about 2000 μm in diameter that were probably transported by insects that also fed on them. Their seeds were large and had a fleshy coat and it is likely that they were ingested and transported by amphibians and fishes similar to what happens today in the flooded forests of the Amazon basin (for instance: Lucas, 2008). Thus, not just seeds had to be moved but the animals, too, because otherwise the plants might get established after a transporting event for seeds but would not be able to propagate in the absence of the animal vectors.

Type V of long-distance plant dispersal represents between zono-biome migrations. These dispersals involve normally other evolutionary changes because the conditions in the other zono-biome are different. For this reason these dispersals are more difficult to recognize. An example is the suggested dispersal and evolution of Lesleya of a tropical zono-biome into Gangamopteris in a temperate zono-biome (Leary, 1993).

Type VI represents the migration of a plant from one zono-biome through another one into a third that is similar in character to the original one. The problem for the plant is to survive the conditions in the intermediate biome where they encounter different living conditions. An example is the dispersal of the tree-lycopsid Tomiodendron from the northern temperate zono-biome (Angara floral realm) through the tropics to the southern warm-temperate zono-biome, the Paraca belt (Alleman and Pfefferkorn, 1988; Iannuzzi and Pfefferkorn, 2002). These different kinds of long-distance plant dispersal help us to understand the formation of biomes and their dynamics (Lieberman, 2004; Nathan, 2006; Parenti and Ebach, 2009, p.103–113; Lomolino et al., 2010).

5. Discussion

Plants are proxies for paleoclimate but they are also dynamic participants through their long-distance dispersal/migration. This dynamic picture has to be combined with the motion of the continents and the oscillation of climate conditions. These three processes are superimposed over each other but happen with distinctly different speeds. Plate motion is measured in centimeters per year. Climate change happens at three scales, namely (1) the existence of warm climate intervals in Earth history that can last tens of millions to more than a hundred million years (see for instance Montañez et al., 2011, fig. 1.2 on p. 21), and (2) the alternation of warm and cold intervals on the scale of several million years (Montañez et al., 2007; Fielding et al., 2008). These two different time scales are today often lumped under the terms greenhouse versus icehouse intervals. A shorter time scale (3) is represented by the Milankovitch cycles created by astronomical forcing that have durations in descending length of approximately 400 k, 100 k, 41 k, and 26 k years. Long-distance plant dispersal on the other hand is the fastest of all these processes that happens at the speed or higher speeds than the shortest Milankovitch cycles.

These three processes (continental motion, climate oscillations at three different time scales, long-distance plant dispersal) are superimposed on each other and each interpretation has to tease these different processes apart. A major problem is that stratigraphic resolution is often not high enough yet to resolve the faster processes. The reason lies both in the fact that most of time is represented by gaps in any stratigraphic section and that the actual resolution achieved by the best data of current stratigraphic work often gives resolutions on the order of millions of years. For instance, the Visean has a duration of about 16 Ma (Menning and Deutsche Stratigraphische Kommission, 2002; Gradstein et al., 2004; International Commission on Stratigraphy, 2013). Palynologically it can be subdivided into two biozones that by inference have a mean duration of eight million years each. During any of these biozones numerous Milankovitch cycles could have happened as well as several greenhouse-icehouse oscillations. In other words, there is no contradiction if different working groups studying different areas find opposing types of climate conditions of the supposedly "same age." In reality they are not of the same age but rather fall into the same resolvable but very long time interval. Glacial deposits have been reported from the Visean of South America by various authors (Rocha Campos, 1985; Rocha Campos and Archangelsky, 1985; Anderson, 2011). However, these deposits are not coeval with the beds at Paracas.

Actually, Milankovitch cycles can be resolved so far in late Paleozoic rocks only under exceptional circumstances (see for instance DiMichele et al., 1996; Heckel et al., 2007; Heckel, 2008). Most of the time stratigraphy resolves the long-term and medium term greenhouse-icehouse oscillations and even those are often still difficult to date precisely, especially in Gondwana.
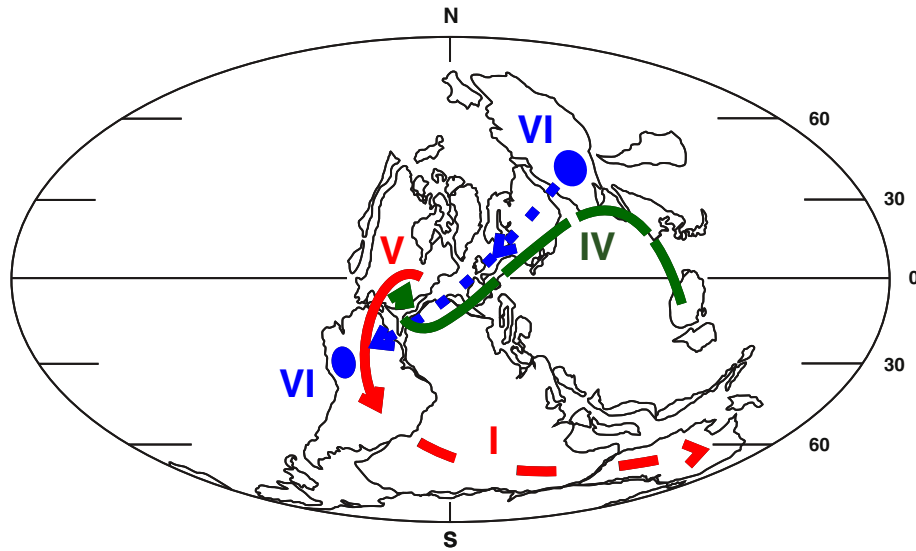
Fig. 9. World map showing four of the six types of major long-distance plant dispersal (LDPD) recognized during Carboniferous time. I (red, dashed line) — LDPD within one zono-biome across one continent; IV (green, long dashes) — LDPD within one zono-biome between continents crossing barriers; V (red arrow) — LDPD from one zono-biome to another which includes normally some evolutionary change in the organism; VI (blue, short dashes from large circle to large circle) — LDPD from one zono-biome to a similar one on the other hemisphere crossing one or several different zono-biomes. Base map from Scotese (2000) representing late Carboniferous plate configuration approximately 312 Ma. Not shown are type II dispersals triggered by a continent moving through climate belts and type III dispersals on one continent triggered by Milankovitch-scale climate oscillations.

In addition, there are other factors that can be deciphered and have to be taken into consideration like orogeny and erosion, and more intensive rainfall in certain areas due to ocean currents (Isbell et al., 2012). In other words, the complexities of the interplay of different factors are being better understood and are driving current research questions in stratigraphy and field geology.

Several authors have reported diamictites and other glacial features from the late Visean of South America (for instance Limarino and Spalletti, 2006; Césari et al., 2011) while the warm temperate Paraca floral belt of late Visean age has been reported by Alleman and Pfefferkorn (1988), Pfefferkorn and Alleman (1989), Pfefferkorn (1997), Iannuzzi and Pfefferkorn (2002), Balseiro et al. (2009) and Singh et al. (2013) from Kashmir (Fig. 10). Seemingly this is a contradiction. However, the warming in the late Visean is supported also by data from the marine realm (Raymond et al., 1990; Powell et al., 2009). The contradiction

is easily resolved when it is realized how long the "late" Visean lasted and that beds of that time interval are not very well resolved stratigraphically. The most recent stratigraphic treatment (Césari et al., 2011) actually shows glacial beds at 338 Ma (mid Visean) and at 325 Ma (later Serpukhovian) bracketing a 13 Ma long interval in which the Paraca flora (= FNC Flora of Césari et al., 2011) and the Paraca greenhouse interval occurred. Thus, this detailed stratigraphic study corroborates our results that a relatively short greenhouse time existed in the late Visean to early Serpukhovian.

The Carboniferous of Paracas has a long history of research and remarkable insights have been gained from this rather small outcrop. There are other occurrences of beds of the same age elsewhere in Peru and adjacent countries (Pino et al., 2004; Zapata et al., 2005; Jacay et al., 2007) and other important results can be expected from these and other outcrops still to be discovered.
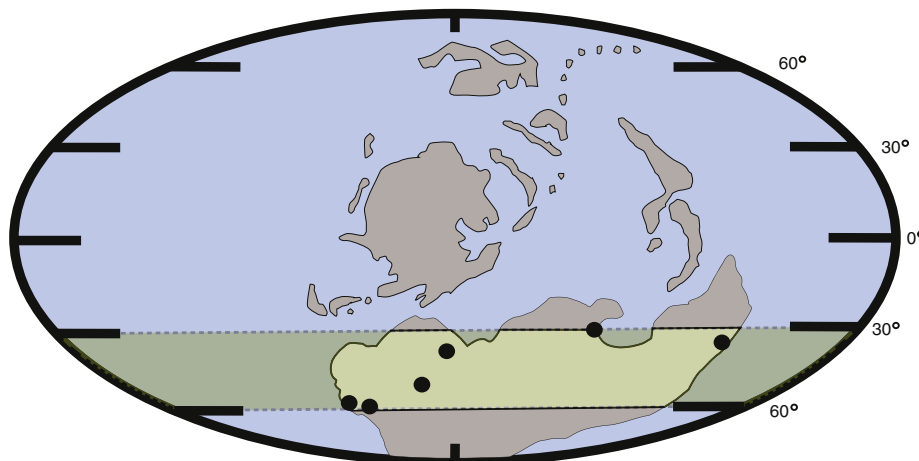

Fig. 10. World map of the late Visean (approximately 330 Ma) showing the position of the circum-Gondwana Paraca Floral Belt of late Visean age (modified after Iannuzzi and Pfefferkorn, 2002). Continental positions after the computer program "Plate Tracker" (Eldridge et al., 2000).

Acknowledgments

References

Alemán, A.M., León, W., 2002. A Carboniferous volcanic arc along the coastal cordillera? International Symposium on Andean Geodynamics (Toulouse), 5, pp. 23–26.

Alleman, V., 1991. Presencia de Myaliniidae (Mollusca, Bivalvia) en la serie Carbonífera de Paracas (Pisco, Dpto. De Ica). VII Congreso Peruano De Geología, Lima, 2, pp. 399–400.

Alleman, V., Pfefferkorn, H.W., 1988. Licopodos de Paracas: Significacion geologica y paleo-climatologica. Boletin de la Sociedad Geológica del Perú, 78 131–136.

Alleman, V., Pfefferkorn, H.W., 1991. Bosques en posicion de vida en el Carbonifero de Paracas. VII Congreso Peruano de Geología, Lima, pp. 395–398.

Alleman, V., Pfefferkorn, H.W., Erwin, D.M., 1995. Los contextos paleoecológicos variados de las floras Carboníferas de Paracas (Ica, Peru). Boletin de la Sociedad Geológico del Perú, 84 37–42.

Anderson, H., 2011. Glacial cycles of the late Paleozoic ice age; Tarija-Chaco Basin, southern Bolivia. Geological Society of America Abstracts with Programs 43.5, 603.

Balseiro, D., Rustán, J.J., Ezpeleta, M., Vaccari, N.E., 2009. A new Serpukhovian (Mississippian) fossil flora from western Argentina: paleoclimatic, paleobiogeographic and stratigraphic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 280, 517–531.

Berry, E.W., 1922a. Carboniferous plants from Peru. American Journal of Science 3 (Ser. 5), 189–194.

Berry, E.W., 1922b. Contributions to the paleobotany of Peru, Bolivia and Chile: Carboniferous plants from Peru. Johns Hopkins University Studies in Geology, 4 9–44.

Birgenheier, L.P., Fielding, C.R., Rygel, M.C., Frank, T.D., Roberts, J., 2009. Evidence for dynamic climate change on sub-10 (super 6)-year scales from the late Paleozoic glacial record, Tamworth Belt, New South Wales, Australia. Journal of Sedimentary Research 79, 56–82.

Breckle, S.-W., 2002. Walter's Vegetation of the Earth: The Ecological Systems of the Geo-Biosphere. Springer-Verlag, Berlin, Heidelberg, Germany.

Césari, S.N., Limarino, C.O., Gulbranson, E.L., 2011. An upper Paleozoic bio-chronostratigraphic scheme for the western margin of Gondwana. Earth Science Reviews 106, 149–160.

Clark, J.S., Fastie, C., Hurtt, G., Jackson, S.T., Johnson, C., King, G.A., Lewis, M., Jynch, J., Pacala, S., Prentice, C., Schupp, E.W., Webb III, T., Wyckoff, P., 1998. Reid's paradox of rapid plant migration. BioScience 48, 13–24.

Cowie, R.H., Holland, B.S., 2006. Dispersal is fundamental to biogeography and the evolution of biodiversity on oceanic islands. Journal of Biogeography 33, 193–198.

Díaz-Martínez, E., 1995. Devonico superior y Carbonífero del Altiplano de Bolivia: estratigrafia, sedimentologia y evolución paleogeografica. Informe ORSTOM Bolivia, 46 1–109.

DiMichele, W.A., Pfefferkorn, H.W., Phillips, T.L., 1996. Persistence of Late Carboniferous tropical vegetation during glacially driven climatic and sea-level fluctuations. Palaeogeography, Palaeoclimatology, Palaeoecology 125, 105–128.

Doubinger, J., Alvarez-Ramis, C., 1980. Nota sobre la flora de la Formacion Ambo, Carbonifero Inferior del Perú. Actas II Congreso Argentino de Paleontología y Bioestratigrafía y I Congreso Latinoamericano de Paleontología, Buenos Aires (1978), 4, pp. 89–101.

Eldridge, J., Scotese, C.R., Walsh, D.B., 2000. Plate Tracker for Windows, v. 1.0.19. Paleomap Project, Arlington, Texas.

Erwin, D.M., Pfefferkorn, H.W., Alleman, V., 1994. Early seed plants in the southern hemisphere: I. Associated ovulate and microsporangiate organs from the Carboniferous of Peru. Review of Palaeobotany and Palynology 80, 19–38.

Fielding, C.R., Frank, T.D., Birgenheier, L.P., Rygel, M.C., Jones, A.T., Roberts, J., 2008. Stratigraphic record and facies associations of the late Paleozoic ice age in eastern Australia (New South Wales and Queensland). In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the late Paleozoic ice age in time and space. Geological Society of America, Special Paper, 441, pp. 41–58.

Fuchs, F., 1900. Nota sobre el tereno Carbonífero de la Península de Paracas. Informes y Memorias de la Sociedad Ingenieros del Perú, 2 1–4.

Gastaldo, R.A., DiMichele, W.A., Pfefferkorn, H.W., 1996. Out of the icehouse into the greenhouse: a late Paleozoic analog for modern global vegetational change. GSA Today 6 (10), 1–7.

Gothan, W., 1928. Bemerkungen zur Alt-Carbonflora von Peru, besonders von Paracas. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie 59, 292–299.

Grader, G.W., Isaacson, P.E., Díaz-Martínez, Pope, M.C., 2008. Pennsylvanian and Permian sequences in Bolivia: direct responses to Gondwana glaciation. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the Late Paleozoic ice age in time and space. Geological Society of America Special Paper, 441, pp. 143–159. http://dx.doi.org/10.1130/2008.2441(10).

Gradstein, F.M., Ogg, J.G., Smith, A.G., Bleeker, W., Lourens, L.J., 2004. A new geologic time scale, with special reference to Precambrian and Neogene. Episodes 27, 83–100.

Heckel, P.H., 2008. Pennsylvanian cyclothems in Midcontinent North America as far-field effects of waxing and waning of Gondwana ice sheets. In: Fielding, C.R., Frank, T.D., Isbell, J.L. (Eds.), Resolving the late Paleozoic ice age in time and space. Geological Society of America, Special Paper, 441, pp. 275–289.

Heckel, P.H., Alekseev, A.S., Barrick, J.E., Boardman, D.R., Goreva, N.V., Nemyrovska, T.I., Ueno, K., Villa, E., Work, D.M., 2007. Cyclothem ("digital") correlation and biostratigraphy across the global Moscovian–Kasimovian–Gzhelian stage boundary interval (Middle-Upper Pennsylvanian) in North America and eastern Europe. Geology 35, 607–610.

Iannuzzi, R., Pfefferkorn, H.W., 2002. A pre-glacial, warm-temperate floral belt in Gondwana (late Visean, Early Carboniferous). Palaios 17, 571–590.

Iannuzzi, R., Rösler, O., 2000. Floristic migration in South America during the Carboniferous: phytogeographic and biostratigraphic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 161, 71–94.

Iannuzzi, R., Pfefferkorn, H.W., Díaz-Martínez, E., Alleman, V., Suárez-Soruco, R., 1998. La Flora Eocarbonífera de la Formación Siripaca (Grupo Ambo, Bolivia) y su Correlación con la Flora de Paracas (Grupo Ambo, Peru). Boletin Sociedad Geologica Perú, 88 39–51.

Iannuzzi, R., Díaz-Martínez, E., Suárez-Soruco, R., 1999. Los Elementos Florísticos de la Formación Siripaca (Grupo Ambo, Bolivia) y su Contexto Bioestratigráfico. Pesquisas 26 (1), 21–40.

International Commission on Stratigraphy, 2013. International Chronostratigraphic Chart v 2013/01. http://www.stratigraphy.org/CSchart/ChronostratChart2013-01.pdf (accessed on 04/16/2013).

Isbell, J.L., Henry, L.C., Gulbranson, E.L., Limarino, C.O., Fraiser, M.L., Koch, Z.J., Ciccioli, P.L., Dineen, A.A., 2012. Glacial paradoxes during the late Paleozoic ice age: evaluating the equilibrium line altitude as a control on glaciation. Gondwana Research 22, 1–19.

Jacay, J., Castillo, E., Güimac, K., 2007. Sedimentary evolution of Paleozoic lithostratigraphic units in central Peru (Ambo-Huánuco region). In: Díaz-Martínez, E., Rábano, I. (Eds.), 4th European Meeting on the Palaeontology and stratigraphy of Latin America. Cuadernos del Museo Geominero, 8, pp. 219–221.

Jongmans, W., 1954. The Carboniferous flora of Peru. Bulletin of the British Museum of Natural History 2, 189–224.

Laveine, J.P., Lemoigne, Y., Zhang, S.Z., 1992. Pangaea, Palaeotethys and Paripteris. Comptes Rendus de la Academie des Sciences Serie II 314, 1103–1110.

Laveine, J.P., Zhang, S.Z., Lemoigne, Y., 1994. The paleogeographic distribution of the Parispermaceae. Geobios 27, 395–401.

Leary, R.L., 1993. Comparison of the Early Pennsylvanian Euramerican fossil plant Lesleya with the Permian Glossopteris of South America. Comptes Rendus XII Congrès International de la Stratigraphie et Géologie du Carbonifère et Permien (Buenos Aires), 2, pp. 107–116.

Lieberman, B.S., 2004. Range expansion, extinction, and biogeographic congruence: a deep time perspective. In: Lomolino, M.V., Heaney, L.R. (Eds.), Frontiers of Biogeography, New Directions in the Geography of Nature. Sinauer Associates, Sunderland, Massachusetts, USA, pp. 11–124.

Limarino, C.O., Spalletti, L.A., 2006. Paleogeography of the upper Paleozoic basins of southern South America: an overview. Journal of South American Earth Sciences 22, 134–155.

Lomolino, M.V., Riddle, B.R., Whittaker, R.J., Brown, J.H., 2010. Biogeography, 4th ed. Sinauer Associates, Sunderland, Massachusetts, USA.

Lucas, C.M., 2008. Within flood season variation in fruit consumption and seed dispersal by two characin fishes of the Amazon. Biotropica 40, 581–589.

Menning, M., Deutsche Stratigraphische Kommission, 2002. A Geologic Time Scale 2002.

Montañez, I.P., Tabor, N.J., Niemeier, D., DiMichele, W.A., Frank, T.D., Fielding, C.R., Isbell, J.L., Birgenheier, L.P., Rygel, M.C., 2007. CO2-forced climate and vegetation instability during late Paleozoic deglaciation. Science 315, 87–91.

Montañez, I.P., Norris, R.D., Algeo, T., Chandler, M.A., Johnson, K.R., Kennedy, M.J., Kent, D.V., Kiehl, J.T., Kump, L.R., Ravelo, A.C., Turekian, K.K., 2011. Understanding Earth's Deep Past: Lessons for our Climate Future. National Academies Press, Washington, D.C.

Nathan, R., 2006. Long-distance dispersal of plants. Science 313, 786–788. http://dx.doi.org/10.1126/science.1124975.

Nuñez Del Prado, H., 1991a. Análisis sedimentológico preliminar y paleoambiente de sedimentación de la serie carbonífera de Paracas (Ica-Perú). VII Congreso Peruano de Geología, Lima, pp. 45–48.

Nuñez Del Prado, H., 1991b. Preliminary sedimentological analysis and depositional system of the Carboniferous at Paracas Peninsula, Peru. XII International Congress on Carboniferous and Permian Geology and Stratigraphy, Buenos Aires, pp. 63–64 (Abstracts).

Parenti, L.R., Ebach, M.C., 2009. Comparative Biogeography. University of California Press, Berkeley, California, USA.

Pfefferkorn, H.W., 1995a. We are temperate climate chauvinists. Palaios 10, 389–391.

Pfefferkorn, H.W., 1995b. Paleobotany and the evolution of climate. Actas Academia Nacional de Ciencia y Tecnologia 3 (2), 83–94.

Pfefferkorn, H.W., 1997. Paleoclimates of Peru during the late Paleozoic—fossil plants and moving continents. Sociedad Geológica del Perú, Lima, Volumen Especial, 1 671–673.

Pfefferkorn, H.W., Alleman, V., 1989. New climatic belt in Carboniferous of the Southern Hemisphere. 28th International Geological Congress, Washington, D.C., 2, p. 602.

Pino, A., Sempere, T., Jacay, J., Fornari, M., 2004. Estratigrafía, paleogeografía y paleotectónica del intervalo Paleozoico Superior — Cretáceo Inferior en el área de Mal Paso — Palca (Tacna). Sociedad Geológico del Perú, Publicación Especial, 5 15–44.

Powell, M.G., Schöne, B.R., Jacob, D.E., 2009. Tropical marine climate during the late Paleo-
    zoic ice age using trace element analyses of brachiopods. Palaeogeography,
    Palaeoclimatology, Palaeoecology 280, 143–149.
Ramos, V.A., 2008. The basement of the central Andes: the Arequipa and related terranes.
    Annual Review of Earth and Planetary Sciences 36, 289–324.
Raymond, A., Kelley, P.H., Lutken, C.B., 1990. Dead by degrees: articulate brachiopods,
    paleoclimate and the Mid-Carboniferous extinction event. Palaios 5, 111–123.
Read, C.B., 1938. The age of the Carboniferous strata of the Paracas Peninsula, Peru. Journal
    of the Washington Academy of Science 28, 396–404.
Roberts, J., Claque-Long, J., Jones, P.J., 1994. Revised correlation of Carboniferous and Early
    Permian units of the Southern New England Orogen, Australia. Newsletter on Car-
    boniferous Stratigraphy, 11 23–26.
Rocha Campos, A.C., 1985. Central Andean Area. In: Wagner, R.H., Winkler Prins, C.F.,
    Granados, L.F. (Eds.), The Carboniferous of the World II: Australia, Indian Subconti-
    nent, South Africa, South America & North Africa. Instituto Geológico y Minero de
    España, Madrid, Spain, pp. 188–196.
Rocha Campos, A.C., Archangelsky, S., 1985. Biostratigraphy and correlations. In: Wagner,
    R.H., Winkler Prins, C.F., Granados, L.F. (Eds.), The Carboniferous of the World II:
    Australia, Indian Subcontinent, South Africa, South America & North Africa. Instituto
    Geológico y Minero de España, Madrid, Spain, pp. 226–297.
Romero, D., Valencia, K., Alarcón, P., Peña, D., Ramos, V.A., 2013. The offshore basement of
    Perú: evidence for different igneous and metamorphic domains in the forearc. Journal
    of South American Earth Science 42, 47–60.
Scotese, C.R., 2000. Paleomap Project. http:www.scotese.com/bashclim.htm (accessed
    August 2012).
Seward, A.C., 1922. On a collection of Carboniferous plants from Peru. Quarterly Journal of
    Geological Society London 78, 278–284.
Simpson, G.G., 1940. Mammals and land bridges. Journal of the Washington Academy of
    Sciences 30, 137–163.
Singh, K.J., Singh, R., Cleal, C.J., Saxena, A., Chandra, S., 2013. Carboniferous floras in
    siliciclastic rocks of Kashmir Himalaya, India and the evolutionary history of the
    Tethyan Basin. Geological Magazine 150, 577–601.
Steinmann, G., 1929. Geologie von Peru. Carl Winters, Heidelberg, Germany.
Wagner, R.H., 1984. Megafloral zones of the Carboniferous. In: Sutherland, P.K., Manger, W.L.
    (Eds.), Neuvième Congrès International de Stratigraphie et de Géologie du Carbonifère,
    Washington and Champaign-Urbana (1979). Compte Rendu, 2, pp. 109–134.
Walter, H., 1973. Vegetation of the Earth, in Relation to Climate and the Eco-physiological
    Conditions. Springer-Verlag, New York, Heidelberg, Berlin.
Williams, J.W., Shuman, B.N., Webb III, T., Bartlein, P.J., Leduc, P.L., 2004. Late-Quaternary
    vegetation dynamics in North America: scaling from taxa to biomes. Ecological
    Monographs 74, 309–334.
Zapata, A., Sánchez, A., Carrasco, S., Cardona, A., Galdos, J., Cerrón, F., Sempere, T., 2005.
    The Mississippian of the western edge of Gondwana in Peru and Bolivia: distribution
    of sedimentary basins and associated magmatism. 6th International Symposium on
    Andean Geodynamics (Barcelona), pp. 817–820.

Hermann W. Pfefferkorn is a Professor of Earth and Envi-ronmental Sciences at the University of Pennsylvania in Philadelphia. He obtained his M.S. (1966) and Ph.D. degree (1968) from the University in Muenster (Germany) studying the stratigraphy, tectonics, and petrography of an area in southern Portugal while simultaneously specializing in pa-leobotany. He uses plant fossils to reconstruct paleoclimate and paleo-landscapes of the Carboniferous and Permian Pe-riods studying strata and fossil floras in North America, Peru, Poland, and China. This enables him to see patterns of climate change and vegetation dynamics of the past that have applications for the present and the future.

Vera Alleman graduated in Natural Sciences from the Uni-versity of Liège, Belgium, (1958) and received her master's (1993) and doctor's degrees (2005) in Lima, Peru. She is Prin-cipal Professor and Head of the Department of Paleontology of the Museum of Natural Sciences "Vera Alleman Haeghebaert" at the Ricardo Palma University in Lima, Peru, and was Presi-dent of the Association of Latin American Paleobotanists and Palynologists from 1996 to 2004. She studies and is interested in various aspects of Peruvian paleontology including plant and invertebrate fossils.

Roberto Iannuzzi is Associate Professor and Head of the De-partment of Paleontology and Stratigraphy of the Geosciences Institute of the Federal University of Rio Grande do Sul, and President of the Brazilian Society of Paleontology (2009–2011 and 2011–2013). He graduated in Biological Sciences (1990) and received a master's degree in Geosciences (1994) from the University of São Paulo and his Ph.D. in Geosciences (Paleontology) from the Federal University of Rio Grande do Sul (1999), Brazil. His research encompasses paleobotany, paleophytogeography, biostratigraphy, and plant paleoecol-ogy of Carboniferous–Permian plant fossils from Brazil, Bolivia and Peru. Recently, he has collaborated on studies of the Cretaceous–Paleogene floras from Antarctica and the Quaternary of central Brazil.