

Comparative Taphonomy and Paleoecology of a Glaciomarine Fauna, Carboniferous (Westphalian - Namurian) La Capilla Fm., Argentina.

**Rex Alan Hanger¹ and Mohutsiwa Gabadirwe², Department of
Geology, George Washington University, Washington, DC**

ABSTRACT

The Carboniferous La Capilla Fm. of the Calingasta-Uspallata basin of western Argentina contains a low diversity fauna inhabiting a continental shelf under glacial ice fronts advancing from the east. Distal glaciomarine sediments on these ice-influenced shelves of Gondwana are most commonly interpreted as being deposited under quiet, low-energy conditions. Taphonomic and paleoecologic analysis of a sample of the fauna reveals the following: low species richness, yet comparable equitability to coeval, tropical faunas; low articulation ratios and high pedicle valve dominance for brachiopods; diverse corrasion modes, about half relatively high categories; one hundred percent fracturing of brachiopod shells, with carinate fracture types dominant, and no evidence of epibiont coverage of brachiopod shells, despite presence of encrusting organisms in the fauna. Collectively, the data indicate long residence time on the seafloor, with strong episodes of reworking - contrary to the low-energy hypothesis. Modern analogues of continental shelves reworked by currents to depths of 250 meters exist in Antarctica. The existence of similarly preserved faunas in the coeval, marginal basins of southern Gondwana needs to be confirmed.

INTRODUCTION

Late Paleozoic glaciation is well-documented for the southern hemisphere (Crowell, 1978, 1983, and references therein). Fossiliferous strata are often associated with glacial sedimentary facies, allowing for the examination of paleoecologic and taphonomic relations. New fossil collections of the La Capilla Formation (Namurian - Westphalian) of the Calingasta-Uspallata (CU) Basin of western Argentina allow for the examination of paleoecologic and taphonomic relations in a basin dominated by glaciomarine sedimentation during a glacial to postglacial transition. Numerous basins along the southern coastline of Gondwana contain strata that record this transition (López-Gamundí, 1997). The bulk of the marine fossil record comes from tropical and warm-temperate environments (Blatt et al., 1991), and so the La Capilla fauna is significant, as it represents the first paleoecological and taphonomic description of these glaciomarine faunas.

1 Current Address: Department of Geology & Geophysics, 1215 West Dayton St., University of Wisconsin, Madison, WI 53706-1692.

2 Current Address: Botswana National Museum Post/Bag 00114, Gaborone, Botswana.

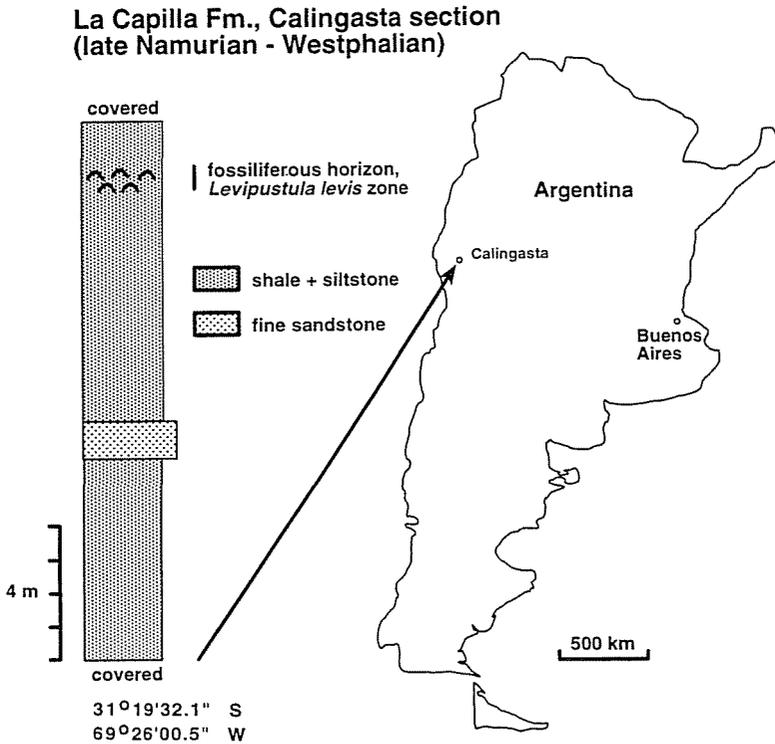


FIGURE 1. Stratigraphic section and location map for the fossil locality of the La Capilla Fm., Calingasta-Uspallata basin near the village of Calingasta, Argentina.

METHODS

A stratigraphic section of the La Capilla Formation was measured on the outcrops exposed through Quaternary alluvium a few kilometers north of the town of Calingasta (Figure 1). Testament to the continued uplift of the Andes is the fact that the outcrops described in Amos et al. (1963) are now covered completely by alluvium. Nevertheless, the fossiliferous zone noted in Amos et al. was rediscovered in outcrops nearby exposed since 1963. This single fossiliferous horizon, approximately 1.4 meters thick, was collected for fossil specimens. In addition to a bulk sample of 11.34 kg, large visible specimens were collected on the surface, a method suggested by Dennison and Hay (1967) and Stanton and Evans (1972) to improve sampling.

Bulk sample was broken down by rock splitter, and all evidence of skeletal material was saved. Fossils were counted as in Watkins (1973). Confidence intervals for both counts and proportions were completed using the methods of Buzas (1990). Diversity indices (S , S' , H , H_{\max} and E) were calculated using formulae outlined in Dodd and Stanton (1990). The taphonomic measures of articulated/disarticulated ratio, pedicle/brachial valve ratio, corrosion, fragmentation and epibiont coverage were tabulated (Brett and Baird, 1986; Brett and Bordeaux, 1991; Alexander and Gibson, 1993). Diversity indices and valve ratios were compared to the coeval communities described by Watkins (1973).

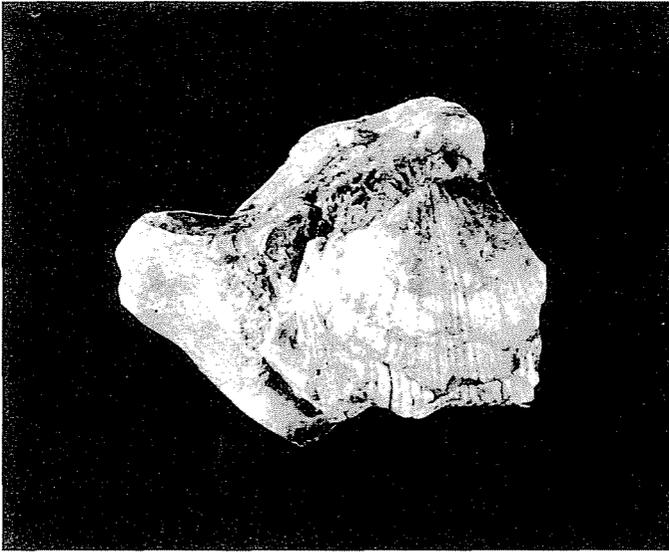


FIGURE 2. *Neospirifer leoncitensis* (Amos et al., 1963). A disarticulated pedicle valve that is characterized as corrosion category II, epibiont coverage category 1, with carinate fractures.

PALEOECOLOGY

Abundance

The La Capilla Fm. fauna near Calingasta is dominated by the large brachiopod, *Neospirifer leoncitensis* (Figure 2), which comprises approximately two thirds of all specimens (Table 1). Other taxa include the brachiopods: *Kitakamithyris septata*, *Levipustula levis*, and *Spiriferellina octoplicata*, the gastropod, *Peruvispira* sp., plus crinoid and fenestellid bryozoan remains. Amos et al. (1963) also recorded the terebratulid brachiopod, *Beecheria* sp. from this horizon, but the species was not recovered by us. Except for *Peruvispira*, the fauna is exclusively populated by sessile, epifaunal, suspension-feeders, as are most other Carboniferous shelf paleocommunities (Bambach, 1985).

Diversity

Diversity of fossil assemblages may be measured in numerous quantitative ways (Dodd and Stanton, 1990), and a fruitful avenue of research is to compare one location or fossil assemblage with others from different environments or times to assess the effects of variation in the primary causes of diversity: times, stability and resource. Calculations of S, S', H, H_{max} and E for the La Capilla Fm. are compared in Table 2 with those calculated from the data in Watkins (1973) for two different associations that are roughly coeval to the La Capilla Fm. These differ in that they are from tropical, deeper-water ramp environments surrounding islands originally isolated some unknown distance from northern Pangaea (Miller, 1987), and now outcrop as the Baird Formation in northern California. All three faunas are from argillaceous, silt to fine sands, so variation in substrate is minimized.

TABLE 1 - Relative abundance and paleoecologic characters of fossil taxa in the La Capilla Fm. L = life site, F = feeding type, M = mobility, E = epifaunal, S = suspension feeding, G = grazing, Ss = sessile, V = vagile.

Taxon	#	CI*	%	CI**	L	F	M
<i>Neospirifer leoncitensis</i>	181	155.6-209.4	66.30	0.60-0.72	E	S	Ss
<i>Kitakamithyris septata</i>	19	11.4-29.7	6.96	0.04-0.11	E	S	Ss
<i>Levipustula levis</i>	7	2.8-14.4	2.56	0.01-0.05	E	S	Ss
<i>Spiriferellina octoplicata</i>	1	0-5.6	0.37	0.00-0.02	E	S	Ss
<i>Peruvispira</i> sp.	2	0.2-7.2	0.73	0.00-0.03	E	G	V
crinoids	30	0.2-42.8	11.00	0.08-0.15	E	S	Ss
fenestellid sp. A	18	10.7-28.4	6.59	0.04-0.10	E	S	Ss
fenestellid sp. B	15	8.4-24.7	5.49	0.03-0.09	E	S	Ss
TOTAL	273		100.00				

*Confidence interval based on Poisson distribution for abundance.

**Confidence interval based on binomial distribution for proportion.

Simple species richness (S) for the La Capilla is low, and approximately 0.11 to 0.12 times less rich than both Baird associations. After making the correction for abundance, S' values for the La Capilla remain low in relation to the Baird, approximately 0.14 times less rich than both Baird associations. The effect of differing sample sizes between the La Capilla (273 specimens) versus the Baird (several thousand specimens each, see Table 10 in Watkins, 1973) associations is therefore minimal.

Shannon-Weaver diversity (H), is difficult to compare and interpret because values of H are determined by both richness of the association and the relative abundance of all the taxa present. The different possible values of H_{\max} shown in Table 2 are evidence of this. The ratio of H to H_{\max} , equitability (E), should be a comparable measure because for any association, E will vary from a value of 1 if all species are equally abundant, to 0 as the equitability decreases. The value of E for the La Capilla is less than that for the *Rugosoconetes* Association, and greater than that for the *Astartella* Association. Both of the Baird values fall within the 95% confidence interval for the La Capilla value of E (95% CI for H/H_{\max} proportion based on binomial distribution = 0.48 - 0.69), and thus, no statistically significant difference exists among all three. Again, this is true despite different sample sizes due to different collection effort.

Diversity is related to environment principally due to variations in time and stability (Dodd and Stanton, 1990). Two aspects of time are important here: geologic age of the three associations, and the time of accumulation of the associations, or, how time-averaged are the samples? Since the geologic age of all three are roughly coeval, diversity differences are not due to the variable numbers of possible species, or guilds through time (Bambach, 1985). The other time factor is more difficult to address. The La Capilla association comes from a single sample of 1.4 meters of strata exposed over less than ten meters of strike, while Watkins' (1973) samples come from multiple locations, sometimes over much thicker stratigraphic intervals. Data from Tables 2 and 3 are additive totals of all the localities in Watkins (1973), and so add another factor of time-averaging.

TABLE 2. Diversity measures of the La Capilla Fm. and the Baird Fm. of Northern California (*Rugosochonetes* association and *Astartella* association.)

index	La Capilla Fm.	Baird Fm. - <i>Rugosochonetes</i>	Baird Fm. - <i>Astartella</i>
S	8	70	65
S'	2.87	21.11	20.64
H	0.53	1.25	0.95
H _{max}	0.90	1.87	1.79
E	0.59	0.67	0.53

TABLE 3. Articulated/disarticulated ratio and pedicle/brachial valve ratio for La Capilla Fm. and Baird Fm. of northern California (*Rugosochonetes* association and *Astartella* association).

ratio	La Capilla Fm.	Baird Fm. - <i>Rugosochonetes</i>	Baird Fm. - <i>Astartella</i>
articulated/disarticulated	0.00	0.36	0.09
pedicle valve/brachial valve	68.33	1.08	1.10

TAPHONOMY

Valve Ratios

All brachiopod specimens of the La Capilla Fm. are disarticulated. Articulated/disarticulated ratios for the Baird Fm. are only slightly higher for the *Astartella* association, and much higher for the *Rugosochonetes* association (Table 2). Pedicle valves are dominant in the La Capilla Fm. This is due to the dominance of *N. leoncitensis* in the sample. Predominance of pedicle valves from large spiriferid brachiopod species has been noted before from inferred high-energy environments (Brett and Bordeaux, 1991). The extreme value of the pedicle/brachial valve ratio here indicates that the glaciomarine environment was particularly effective in disarticulating the brachiopod skeleton and then concentrating the thicker, larger pedicle valves, probably by mechanical destruction of the thinner, smaller brachial valves. Pedicle/brachial valve ratios from the Baird Fm. are much lower, with numbers of both valves being roughly equal, reflecting quieter environments on the deep island arc ramps.

Corrasion

Corrasion is the term used to describe all aspects of the mechanical abrasion, bioerosion and biogeochemical solution in worn fossils (Brett and Baird, 1986). Brett and Bordeaux (1991) devised a semi-quantitative method for corrasion description, recognizing four increasing levels of corrasion: I --uncorraded, II -- slightly corraded, with minor loss of micro-ornamentation, III - corraded, with intact costae, but loss of ornament, and IV -- highly corraded, for relatively smooth shells with costae removed. Higher corrasion values correspond to increased levels of exposure time at the sediment water interface. Figure 3A shows that corrasion level II predominates in the La Capilla fauna, but collectively, levels III and IV constitute just over 50% of all the brachiopod shells. Exposure time was relatively long in the low sedimentation environment distal to the glacial front.

Fractures

The fragmentation of brachiopod shells on the seafloor, and immediately post-burial, produces several discrete types of fractures that may be used to examine post-mortem taphonomic alteration, as well as life-position autecology (Alexander and Gibson, 1993). The anticipated life position of the large spiriferid, *N. leonicitensis* is an orientation with the anterior commissure held upright, roughly perpendicular to the sediment-water interface, with the weight of the animal resting on the long, wide interareas. Burial in life position should result in the telescoped fractures, figured in Alexander and Gibson (1991, p. 28). Instead, carinate and splayed type fractures predominate (Figure 3B), indicating toppling and transport of specimens. This is especially true for carinate fractures, indicating extensive transport and reworking of the La Capilla brachiopods.

Epibiont Coverage

Epibiont coverage is the surface area measure of the utilization of exposed brachiopod shells by encrusting organisms. The semi-quantitative method of epibiont coverage description (Brett and Bordeaux, 1991) divides coverage into 5 categories, from 1 = "clean" to 5 = greater than 15% coverage. For the La Capilla specimens, all shells are classed as category 1 (Figure 3C). Fenestellid bryozoans and crinoids, though common in the fauna, are never found attached to any brachiopod shell. If brachiopod shells had long exposure times on the seafloor, as suggested by corrasion data, then they should have been used by epibionts as encrusting surfaces. Probably, the high corrasion levels have removed evidence of attachment while leaving the skeletal remains of the epibiont taxa.

PALEOENVIRONMENTAL IMPLICATIONS

The La Capilla Fm. fauna is known from several localities in the Calingasta-Uspallata basin (González and Taboada, 1987) and the Tepuel basin to the south in Patagonia. The "Comunidad B" in both basins contain the brachiopods, molluscs, crinoids and bryozoans described here, though molluscs dominate in the Tepuel basin (Archangelisky, 1987). Presence of *L. levis* in this fauna allows for correlation with the *L. levis* zone in eastern Australia (Roberts, 1976, 1981; Roberts et al., 1976), where the zone also indicates glacial conditions. These other localities in Argentina and Australia indicate that the paleoenvironmental relations inferred here have extensive geographic

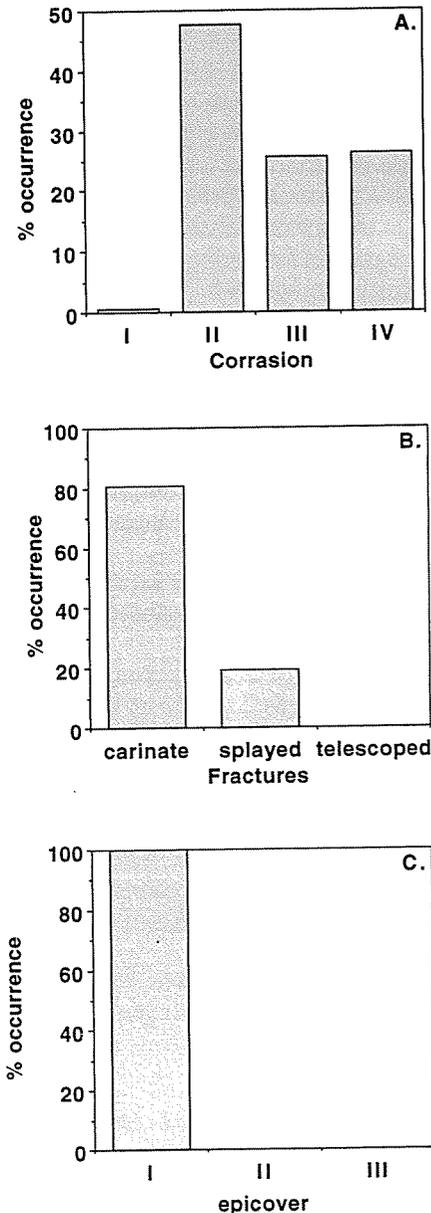


FIGURE 3. La Capilla Fm. fauna taphonomic measures as percent occurrence of all brachiopod shells. A. Corrasion B. Fractures C. Epibiont coverage

(and, paleogeographic) range. Correlative faunas have not been characterized in terms of the paleoecologic and taphonomic approach described here.

Carboniferous glaciomarine deposition in western Argentina formed as mountain glaciers entered foreland and back-arc basins on the active Panthalassan margin (López-Gamundí 1989). The areal extent of the outcrops of the mid-Carboniferous glaciomarine strata of the CU Basin, including the La Capilla Fm., suggested to López-Gamundí (1997) an apron-like glacial geometry along the eastern basin margin. As the glaciers receded, and sea level rose, a regular succession of strata was deposited from proximal, coarse sediment, including dropstones, with evidence of glacial abrasion; to distal, fine-grained mudstones and shales in open-marine areas.

A modern analogue for this environment (broad ice-shelf fed by alpine glaciers) is the Larsen Ice Shelf of Antarctica (Anderson and Molnia, 1989). Modern glaciomarine sediments of Antarctica (including the Larsen Ice Shelf) are predominantly compound sediments, characterized by: mud size predominance, minor presence of well-sorted, current-derived silts and fine sands, less than 10% ice-rafted material, rounded pebbles among the ice-rafted component, and diverse fauna (Chriss and Frakes, 1972). During interglacial/sea-level highstand periods, the remains of this shelly fauna (molluscs, bryozoans, echinoderms, corals and forams) may be extensively reworked into bioclastic debris by marine currents to depths ~250 meters (Anderson and Molina, 1989).

The data here support a high-energy, lower stability environment for the La Capilla Fm., similar to that below and adjacent to the modern Larsen Ice Shelf. Diversity is low for the La Capilla fauna relative to coeval tropical faunas, reflect-

tive of lower temperatures at higher latitudes in the presence of glacial ice. Long residence time on the seafloor is indicated by high disarticulation of brachiopod shells and high levels of corrosion. That this is due to at least temporary high-energy reworking and transport, and not exclusively slow sedimentation rate in a quiet environment of deposition as suggested by López-Gamundí (1987, 1889, 1997) is supported by the extreme predominance of pedicle valves with carinate and splayed fracturing, and low levels of bioerosion coupled with high corrosion.

The preliminary data presented here suggest that high-latitude, glaciomarine faunas of the Carboniferous had different paleoecologic structures and underwent different taphonomic alteration than coeval tropical faunas. Attribution of patterns and processes from the relatively well-known tropical faunas to the higher-latitudes is not justified. Comparative data from the remaining marginal basins of the southern coast of Gondwana should be collected to determine the regional significance of the paleoenvironmental implications discussed here. Further documentation of the coeval, warmer water faunas with the paleoecologic and taphonomic measures used here can be used to test the paleolatitudinal differences suggested here.

CONCLUSIONS

1) The La Capilla Fm. fauna is characterized by low diversity and moderate equitability as compared to the coeval Baird Fm. fauna of northern California. Lower diversity is reflective of decreased temperatures associated with adjacent glacial fronts. Epifaunal, sessile, suspension-feeders dominate the fauna.

2) Brachiopod articulation ratios are low, and pedicle valve / brachial valve ratios are extremely high as compared to the Baird Fm., indicating greater rates of taphonomic transport and reworking while on the seafloor.

3) Corrosion categories III and IV constitute over 50% of all brachiopod shells. All shells are fractured, with carinate fractures most common (80%). Epibiont coverage is absent, despite the presence of encrusting organisms in the collection. All three taphonomic measures suggest extended residence time on the seafloor, coupled with reworking by current activity.

4) Carboniferous glaciomarine environments of the southern marginal basins of Gondwana, though commonly described as low energy for the distal shelves, did in fact experience significant current reworking activity. The modern analogue for the Calingasta-Uspallata basin is the area below the Larsen Ice Shelf of Antarctica, which exhibits intensive reworking to water depths of 250 meters.

5) Paleoecologic and taphonomic structures for the Carboniferous high-latitude faunas are qualitatively and quantitatively different than their low-latitude counterparts.

ACKNOWLEDGEMENTS

G. C. Stephens invited R.A.H. to Argentina. F. Nullo provided valuable field assistance. P. Baldauf helped collect the fossils. M. G. prepared the fossils and calculated all paleoecologic and taphonomic measures. R. A. H. wrote the text. M. G. acknowledges the Government of Botswana and the Academy for Educational Development for a Botswana Development Training Project Scholarship.

LITERATURE CITED

- Alexander, R. R. and M. A. Gibson. 1993. Paleozoic brachiopod autecology based on taphonomy: example from the Devonian Ross Formation of Tennessee (USA). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 100: 25-35.
- Amos, A. J., 1979. *Guia Paleontologica Argentina, Parte I: Paleozoico*. Consejo Nacional de Investigaciones Cientificas y Tecnicas, Buenos Aires, Argentina, 151 p.
- Amos, A. J., Baldis, B., and Csaky, A., 1963. La fauna del Carbónico Medio de la Formación La Capilla y sus relaciones geológicas. *Ameghiniana* 3 (4), 123-134.
- Anderson, J. B. and Molnia, B. F., 1989. *Glacial-Marine Sedimentation*. Short Course in Geology, Volume 9. American Geophysical Union, Washington, DC, USA, 127 p.
- Archangelsky, S. (editor), 1987. *El Sistema Carbonifero en la Republica Argentina*. Academia Nacional de Ciencias, Cordoba, Argentina, 383 p.
- Bambach, R. K., 1985. Classes and adaptive variety: the ecology of diversification in marine faunas through the Phanerozoic. In: *Phanerozoic Diversity Patterns* (edited by J. W. Valentine), pp. 191-253. Princeton University Press, Princeton, New Jersey, 441 p.
- Blatt, H., W. B. N. Berry and S. Brande, 1991. *Principles of Stratigraphic Analysis*. Blackwell Scientific Publications, Boston, 512 p.
- Brett, C. E. and Baird, G. C., 1986. Comparative taphonomy: a key to paleoenvironmental interpretation based on fossil preservation. *PALAIOS* 1, 207-227.
- Brett, C. E. and Y. L. Bordeaux. 1991. Taphonomy of brachiopods from a Middle Devonian shell bed: implications for the genesis of skeletal accumulations, pp. 219-226. In MacKinnon, D. I., D. E. Lee and J. D. Campbell, (eds.), *Brachiopods Through Time*. A. A. Balkema, Rotterdam.
- Buzas, M. A. 1990. Another look at confidence limits for species proportions. *Journal of Paleontology*, 64: 842-843.
- Chriss, T. and Frakes, L. A., 1972. Glacial marine sedimentation in the Ross Sea. In: *Antarctic Geology and Geophysics* (edited by R. Adie), pp. 747-762. Commission on Antarctic Research, Oslo, Norway, 955 p.
- Crowell, J. C., 1978. Gondwanan glaciation, cyclothems, continental positioning and climate change. *American Journal of Science*, 278: 1345-1372.
- Crowell, J. C., 1983. Ice ages recorded on Gondwanan continents. *Geological Society of South Africa Transactions*, 86: 237-262.
- Dennison, J. M. and W. W. Hay. 1967. Estimating the needed sampling area for subaquatic ecologic studies. *Journal of Paleontology*, 41: 706-708.
- Dodd, J. R. and R. J. Stanton, Jr., 1990. *Paleoecology Concepts and Applications* 2nd Edition. John Wiley and Sons, New York.
- González, C. R. and A. C. Taboada. 1987. Nueva localidad fosilifera del Carbonico Marino en la Provincia de San Juan. *Decimo Congreso Geologico Argentino, San Miguel de Tucuman* 3: 103-105.
- Kottlowski, F. E. 1965. *Measuring Stratigraphic Sections*. Holt, Rinehart and Winston, New York.
- López-Gamundí, O. R., 1987. Depositional models for the glaciomarine sequences of Andean Late Paleozoic basins of Argentina. *Sedimentary Geology* 52 (1987), 109-126.

- López-Gamundí, O. R., 1989. Postglacial transgressions in late Paleozoic basins of Western Argentina: a record of glacioeustatic sea level rise. *Palaeogeography, Palaeoclimatology, Palaeoecology* 71 (1989), 257-270.
- López-Gamundí, O. R., 1997. Glacial-postglacial transition in the Late Paleozoic basins of southern South America. In: *Late Glacial and Postglacial Environmental Changes* (edited by I. P. Martin), pp. 147-168. Oxford University Press, New York, NY, USA, 485 p.
- Miller, M. M., 1987. Dispersed remnants of a northeast Pacific fringing arc; Upper Paleozoic terranes of Permian McCloud faunal affinity, western U.S. *Tectonics*, 6: 807-830.
- Polanski, J., 1978. *Carbónico y Pérmico de la Argentina*. Universitaria de Buenos Aires, Buenos Aires, Buenos Aires, Argentina, 216 p.
- Roberts, R. J., 1976. Carboniferous Chonetacean and Productacean Brachiopods from Eastern Australia. *Palaeontology* 19 (1), 17-77.
- Roberts, R. J., 1981. Control mechanisms of Carboniferous brachiopod zones in eastern Australia. *Lethaia* 14, 123-134.
- Roberts, R. J., Hunt, J. W., and Thompson, D. M., 1976. Late Carboniferous marine invertebrate zones of eastern Australia. *Alcheringa* 1, 197-225.
- Scott, R. W. 1978. Approaches to trophic analysis of paleocommunities. *Lethaia*, 11: 1-14.
- Stanton, R. J., Jr. and I. Evans. 1972. Community structure and sampling requirements in paleoecology. *Journal of Paleontology*, 46: 845-858.
- Watkins, R., 1973. Carboniferous faunal associations and stratigraphy, Shasta County, Northern California. *Bulletin of the American Association of Petroleum Geologists* 57 (9), 1743-1764.