Permian plants from the Chutani Formation
(Titicaca Group, northern Altiplano of Bolivia):
II. The morphogenus *Glossopteris*

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ABSTRACT

Fossil plants belonging to the morphogenera *Glossopteris*, *Pecopteris* and *Asterotheca* were collected from the upper part of the Chutani Formation (Titicaca Group), near the town of San Pablo de Tiquina, on the southeastern shore of Lake Titicaca (northern Altiplano, Bolivia). This paper presents the first description of specimens of the morphogenus *Glossopteris* from Bolivia. The Bolivian specimens of *Glossopteris* consist of poorly-preserved impressions, although they present the diagnostic features of this morphogenus. They are fragments of leaves with secondary veins of taeniopterid-type, typical of glossopterids from Late Permian deposits of Gondwana. The only species of *Pecopteris* confirmed in the first part of this study, i.e. *P. dolianitii* Rösler and Rohn (see Vieira et al. 2004), was previously reported from the Late Permian beds of the Rio do Rasto and Estrada Nova formations in the Paraná Basin (southern Brazil). Therefore, a Late Permian age is proposed for the fossil plant-bearing beds of the Chutani Formation based on the analyzed assemblage. The phytogeographic implications of this new find are briefly analyzed.

Key words: Altiplano of Bolivia, Permian, *Glossopteris*, phytogeography.

INTRODUCTION

The presence of the morphogenus *Glossopteris* in Bolivia had already been mentioned in the literature (Archangelsky 1984, 1986). However, none of the published syntheses on Bolivian Paleozoic floras mentions this floristic element (Suárez-Soruco 1974, Archangelsky 1993). Furthermore, the latest review affirms that, so far, there has not been any description of glossopterid plants from Bolivia (Archangelsky 1993). Consequently, this second part of the report on the fossil plants from the Chutani Formation presents, for the first time, a description of Bolivian specimens of the morphogenus *Glossopteris*. The new findings prove the floral connection and similarities between western Gondwana, represented by the Central Andean region (Peru-Bolivia basin), and other parts of the megacontinent.

MATERIALS AND METHODS

In 1996, three of the authors (RI, EDM, GWG) collected fossil plants belonging to the morphogenera

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Glossopteris, *Pecopteris* and *Asterotheca*. The fossils were found NE of San Pablo de Tiquina, a small town on the SE shore of Lake Titicaca (western Bolivia), where ferryboats cross the Strait of Tiquina to the Copacabana Peninsula. The fossil site is located approximately 80 m up-hill from the town's cemetery (for a location map see Vieira et al. 2004). The studied samples were collected from the upper part of the Chutani Formation (Titicaca Group – geological setting in Vieira et al. 2004). The fronds of *Pecopteris* and *Asterotheca* have been described by Vieira et al. (2004) and form the first part of this study. The leaves of *Glossopteris* were found as impressions on brownish yellow, hard, compact, silty dolostone. The specimens are fragmentary and stained by iron oxide. The impressions are usually unclear and we had difficulties to photograph them. All studied specimens are listed below and housed at the Museu de Paleontologia of the Departamento de Paleontologia e Estratigrafia of the Universidade Federal do Rio Grande do Sul (code prefix MP-Pb).

SYSTEMATIC RESULTS

Class GYMNOSPERMOPSIDA
Order GLOSSOPTERIDALES
Genus *Glossopteris* Brongniart 1828

Glossopteris cf. *G. occidentalis* White 1908
Figs. 1A, 2A, 3

Material: MP-Pb 3576A/B, 3579A/B

Description: The specimen MP-Pb 3576 is the best preserved and represents a middle portion of a fragmentary leaf. The incomplete specimen is 8.1 cm long and approximately 5.32 cm wide. The shape of the leaf cannot be deduced, but it shows parallel lateral margins. The midrib is distinct, about 6.7 mm wide, and composed of a bundle of thick parallel veins (at least 7 or 8), with rare connecting veins. The venation pattern is taeniopteroid: secondary veins arise from the midrib at acute angles (20-22˚), but they immediately take a sharp bend and follow a straight and parallel course at angles of 80-85˚ to the midrib, near the leaf margin they incline towards the apex, reaching the margin at angles

of 65-70˚. There are about 28-30 secondary veins per cm half way across the lamina. The pattern of meshes is not well preserved, but apparently the secondary veins show rare and irregularly distributed oblique anastomoses, dichotomizing few times (5 at least) to form short and fusiform meshes near midrib and narrow-elongate ones for the remainder of the lamina.

Comparison: The veining pattern agrees closely with the following species: *Glossopteris ampla* Dana as described by Archangelsky (1958); *G. damudica* Feistmantel by Maheshwari and Prakash (1965), Chandra and Singh (1992); *G. gigas* Pant and Singh by Chandra and Singh (1992); *G. occidentalis* White by White (1908); *G. taeniopteroides* Feistmantel by Feistmantel (1878), Maheshwari (1965) and Rohn and Rösler (1989); and *G. waginanus* (Rigby) Rigby, Chandra and Surange by Rigby (1966) and Rigby et al. (1988), respectively. Width of leaf and midrib, venation density (veins per cm), frequency of anastomoses (number of meshes between midrib and margin), and pattern of meshes, are comparatively more related to *G. occidentalis* and *G. damudica*. However, the latter differs from the Bolivian specimens in terms of general inclination of secondary veins which arise at obtuse angles. Further morphological details such as shape and size of leaf, and pattern of meshes along the complete leaf, are still required to obtain a more precise determination.

Glossopteris sp. 1
Figs. 1B, 2B, 2C, 4

Material: MP-Pb 3577A/B, 3578, 3580, 3581, 3582, 3583, 3584, 3585

Description: There are a few well-preserved specimens in the present collection. Amongst them, specimen MP-Pb 3577A is the most complete. This specimen represents a long (13.4 cm preserved) and narrow (1.74 cm maximum width) fragmentary leaf of unknown base, tapering gently and distally to an acute apex. Midrib strong, 4 mm broad (max.), persistent up to the leaf apex, composed initially of six
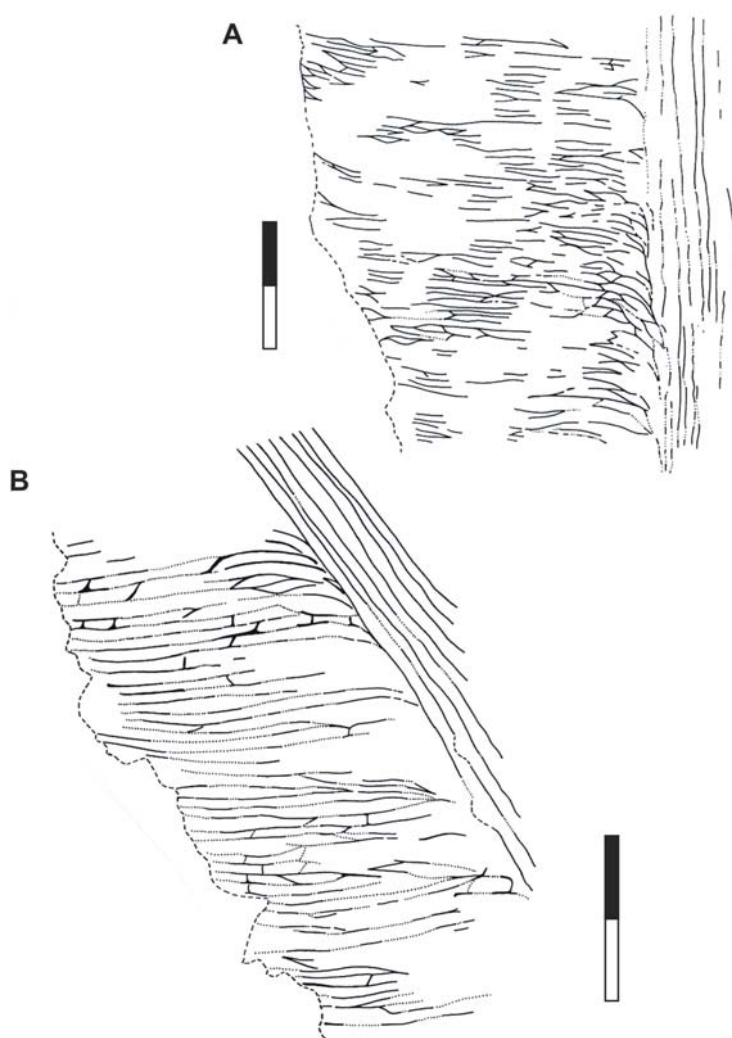
Fig. 1 – Drawings of described *Glossopteris* leaves: (A) specimens of *Glossopteris* cf. *G. occidentalis* White [MP-Pb 3576A] and (B) *Glossopteris* sp. 1 [MP-Pb 3577A] showing a middle portion of the leaf with prominent and thick midrib and taeniopteroid venation, respectively. Continuous line = outline preserved; dotted line = outline poorly preserved; chain line = outline broken. Scale bars: (A) = 1.0 cm; (B) = 0.5 cm.

thick parallel veins at the base, immediately reducing to four veins and gradually contracting towards the apex where it becomes resolved in finer veins. Taeniopteroid veining pattern, secondary veins leave the midrib at narrow (22-35°) to broad (55-65°) acute angles and, after a gentle arch, pass straight, parallel inclined at 55-65° to the midrib, reaching the margin at about 55°. The secondary veins often show irregularly distributed perpendicular and oblique anastomoses, dichotomizing several times (10 at least). The concentration of veins is approximately 25-30 per cm in the middle part of the lamina. The meshes vary from elongate to short, polygonal to fusiform in shape, alternating irregularly between long and short ones across the lamina.

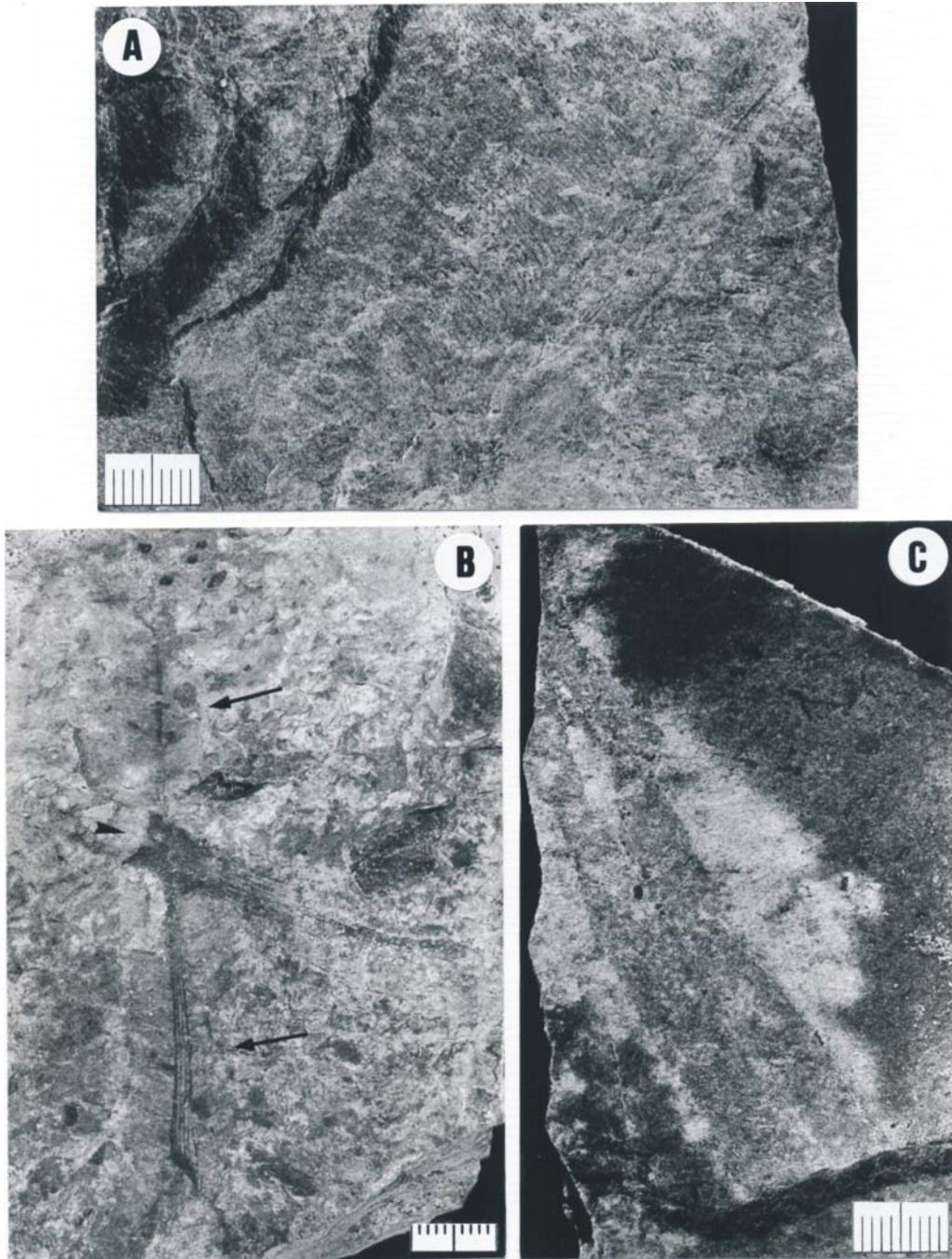The specimen MP-Pb 3580 represents a middle

Fig. 2 – Photos of *Glossopteris* leaves: (A) *Glossopteris* cf. *G. occidentalis* White [MP-Pb 3576A] showing a middle portion of the leaf; (B) specimens of *Glossopteris* sp. 1 showing almost a complete leaf [MP-Pb 3577A – two longest arrows] and base of the leaf [MP-Pb 3577B – shortened arrow]; (C) *Glossopteris* sp. 1 showing the middle part and top of the leaf [MP-Pb 3585A]. Scale bars: 1.0 cm.

Fig. 3 – Part of the leaf illustrated in Fig. 2 (A) [MP-Pb 3576A] enlarged to show details of taeniopteroid venation (arrow). Scale bars: 0.5 cm.

portion of the incomplete leaf and measures 3.4 cm in length and about 14.6 mm in width. The fragmentary leaf shows parallel lateral margins, a distinctive midrib with 2.6 mm in width, and is composed of a bundle of poorly preserved parallel veins. The veining pattern is taeniopteroid and equal to that of specimen MP-Pb 3577A. Secondary veins are not preserved near the midrib, in the remainder of the lamina they run at an angle of 60° to the midrib until they reach the margin.

Specimen MP-Pb 3577B corresponds to the base of a leaf. It is 6.7 cm long and 1.66 cm wide (max.), gradually contracting towards the base into a short and broad stalk (1 cm maximum width). The

stalk is composed of a bundle of thick parallel veins, which resolve in veins of secondary veining and midrib (about 4 mm wide) just above the beginning of the leaf lamina. Secondary veining is badly preserved, showing a similar general orientation to that verified in other specimens (about 60˚).

Comparison: The specimens under consideration resemble *Glossopteris dorizonenesis* Rohn, Oliveira-Babinski and Rösler, *G. leptoneura* Bunbury, and *G. stricta* Bunbury in possessing narrow leaf with acute apex, but all three species are distinct from them in venation pattern (Rohn et al. 1984, Chandra and Singh 1992). At first sight, the venation pattern reminds one of that of *G. taeniopteroides* Feismantel *sensu* Kovács-Endrödy (1976), who described these African leaves with less divergent secondary veins from the undivided midvein in comparison to the Indian representatives of the species. However, here the midrib is composed of longitudinal strands (her figures exhibit this feature too, fig. 17), the shape of the leaf is entirely different, and the number of secondary veins per cm is higher. In terms of venation pattern, specimens here described can also be compared with *G. damudica* Feistmantel and *G. nimishea* Chandra and Surange (Maheshwari and Prakash 1965, Kovács-Endrödy 1976, Chandra and Singh 1992). Both species, however, are different in leaf shape, and the secondary veins are almost perpendicular to the midrib and margin. In all characters, the leaves under consideration agree closely with specimens informally described and illustrated by Broutin et al. (1995) as *Glossopteris* sp. 1?, except for the greater density of secondary veins. However, on account of the incompleteness and poor preservation, the present specimens have not been classified under a new formal name.

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DISCUSSION

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AGE OF FLORA

Despite the relatively low taxonomic diversity, the floristic elements are useful for age assignment. The glossopterid leaves under consideration show some diagnostic features mostly found in leaves of West-ern Gondwana assemblages from the end of Early Permian (Kungurian) and younger ages. These features include small size, narrow shape and taeniopteroid venation pattern. In some cases, these kinds of leaves dominate Late Permian assemblages in South America (Rohn and Rösler 1989). In the Bolivian flora, the total absence of typical glossopterid leaves from both Gondwana Lower Permian (*Rubigea* sp. and *Gangamopteris* sp.) and Triassic (*Yabeiella* sp.; *Glossopteris* spp. from Pant and Pant 1987, Holmes 1992) is also remarkable. A very similar glossopterid leaf assemblage was collected in the uppermost part of the Gharif Formation, in the Arabian Peninsula (Broutin et al. 1995). This part of the Gharif Formation was dated as early Late Permian by palynology and marine fossils from underlying and overlying units. All these considerations about the glossopterid leaves studied indicate an end of Early Permian to Early Late Permian (middle through Late Permian) age for the deposition of the strata here analyzed.

The pecopterid foliage corresponds to taxa considered endemic of the Paraná Basin, in southern Brazil (see the first part of this report; Vieira et al. 2004). *Pecopteris* cf. *P. pedrasica* Read, and *Pecopteris* cf. *P. cadeadensis* Rohn and Rösler, are taxa identified with uncertainty, and will not be considered in this discussion. *Pecopteris dolianitii* Rohn and Rösler, the unique clearly identified species, has also been described from deposits of the Estrada Nova and Rio do Rasto formations in the Paraná Basin (Rohn and Rösler 1986). A Late Permian age (Kazanian-Tatarian) was proposed for these units based on the occurrence of: (a) Kungurian-Kazanian palynofloras in the underlying Irati and Palermo formations (Daemon and Quadros 1970, Arai 1980, Marques-Toigo 1991), and (b) Tatarian vertebrate terrestrial fauna at the top of the Rio do Rasto Formation (Barberena et al. 1985, Langer 2000). Besides *Sphenophyllum* spp. occurs in the lower part of the Rio do Rasto Formation (Serrinha Member – Rohn and Rösler 2000), while leaid conchostraceans are reported from the upper part. Both fossil groups are restricted to Pa-

Fig. 4 – Part of the leaf illustrated in Fig. 2 (B) [MP-Pb 3577A] enlarged to show details
of taeniopteroid venation (arrow). Scale bars in millimeters.

leozoic strata all over the world. In conclusion, a
Late Permian age for the Chutani Formation is here
proposed.

PHYTOGEOGRAPHY

Despite the relatively low taxonomic diversity, prob-
ably due to non-systematic and insufficient sam-
pling, the composition of the floral assemblage from
the Chutani Formation allows some phytogeo-
graphic discussion. The assemblage constitutes the
northernmost record of ''*Glossopteris* Flora'' at the
western edge of South America, considering
the known distribution of this flora in Permian de-
posits of South America (Rohn and Rösler 1987,
Archangelsky 1990). According to the current evi-
dence, the Bolivian assemblage was a typical Gond-

wana flora, without any Euramerican or Cathaysian elements. It includes glossopterid leaves associated with pecopterid fronds of Gondwana affinity, mostly related to endemic species from the Paraná Basin (see the first part of this report; Vieira et al. 2004). Hence, our observations suggest a shift of the northwestern boundary of the Gondwana Realm towards the tropics. The lack of information from northern South America hinders the determination of the northwestern boundary of this realm, which could be even further northwards.

An important fact is the link between Late Permian floras from the Paraná and Titicaca basins. The same type, and maybe even the same species, of glossopterid and pecopterid forms are found in both geographic areas (see Paleobotanical Results, and the first part of this report; Vieira et al. 2004), suggesting (a) the possibility of a direct dispersion route between them, and (b) the presence of similar paleoenvironmental and paleoclimatic conditions. We therefore propose that these two areas may be regarded as belonging to the same phytogeographic unit. The paleogeographic interpretation for this distribution depends on the continental configuration under consideration. In accordance with most paleomagnetic data, there are two basic Late Permian configurations proposed for Pangea: Scotese's model, the classical Pangea ''A'' (Scotese and McKerrow 1990, Golonka et al. 1994), and Pangea ''B'' model (Morel and Irving 1981). The model of Scotese places each basin at a different paleolatitude, and approximately 15° distant from each other. The Pangea ''B'' model assumes a paleolatitudinal proximity between both areas, more in accordance with the paleobotanic results obtained herein. The Pangea ''B'' configuration incorporates an anticlockwise rotation of Pangea during the Late Permian, displacing western Gondwana back to higher latitudes, and placing Bolivia and southeastern Brazil (Paraná Basin area) at a similar southern latitude (Díaz-Martínez et al. 1993, Broutin et al. 1995, Fluteau et al. 2001). The Pangea ''A'' model considers that most of this rotation took place later, in the Early Triassic (Golonka et al. 1994).

CONCLUSIONS

We confirm the presence of *Glossopteris* in the Bolivian Central Andes (west-central South America), as well as the phytogeographic extension of the Gondwana Realm towards northwestern Gondwana (northern South America). We also suggest a Late Permian age for the fossil-bearing beds of the Chutani Formation, although we do not discard the possibility of a younger (Early Triassic) age for the uppermost part of this unit, as suggested by Sempere et al. (1992). Broutin et al. (1995) suggest a wide extension of the *Glossopteris* Flora in the Late Permian for other regions of Gondwana (northern Africa and Arabian Peninsula) and southern Europe (Spain, Turkey). This could be due to paleoclimatic changes (more uniform global climate conditions, expansion of seasonal climates) and paleogeographic changes (anti-clockwise rotation and northward migration of Gondwana) that took place during the Late Permian (Díaz-Martínez et al. 1993, 2000, Broutin et al. 1995).

RESUMO

Plantas fósseis, pertencentes aos morfo-gêneros *Glossopteris*, *Pecopteris* e *Asterotheca*, foram coletadas na porção superior da seção aflorante da Formação Chutani,

próxima ao povoado de San Pablo de Tiquina, sudeste do lago Titicaca (Altiplano norte, Bolívia). Este trabalho apresenta a primeira descrição de espécimes do morfo-gênero *Glossopteris* provenientes da Bolívia. Os espéci-mes estudados de *Glossopteris* consistem em impressões foliares pobremente preservadas nas quais feições diag-nósticas estão presentes. Os fragmentos foliares apre-sentam venação secundária do tipo teniopteróide, uma característica típica de glossopterídeas encontradas em depósitos do Permiano Superior do Gondwana. Por sua vez, a única espécie de *Pecopteris* confirmada para estes níveis da Formação Chutani, i.e. *P. dolianitii* Rohn and Rösler (ver Vieira et al. 2004), foi previamente assi-nalada para estratos do Permiano Superior da Bacia do Paraná (formações Estrada Nova e Rio do Rasto). Por-tanto, uma idade neopermiana é tentativamente proposta para os níveis da Formação Chutani que contém a associa-ção estudada. As implicações fitogeográficas deste novo achado são brevemente analisadas.

Palavras-chave: Altiplano Boliviano, Permiano, *Glossopteris*, fitogeografia.

REFERENCES

ARAI M. 1980. Contribuição dos polens estriados na bioestratigrafia neopaleozóica da parte nordeste da Bacia do Paraná. Bol IG-USP 11: 98-105.

ARCHANGELSKY S. 1958. Estudio geológico y paleon-tológico del Bajo de la Leona (Santa Cruz). Acta Geol Lilloana 2: 5-133.

ARCHANGELSKY S. 1984. Floras Neopaleozóicas del Gondwana y su zonación estratigráfica – Aspectos paleogeográficos. Com Serv Geol Portugal 70: 135-150.

ARCHANGELSKY S. 1986. Late Paleozoic floras of the Southern Hemisphere: distribution, composition, pa-leoecology. In: GASTALDO RA (Org.), Land Plants: notes for a short course, Knoxville: University of Tennessee, p. 129-142. (University of Tennessee, Studies in Geology, 15).

ARCHANGELSKY S. 1990. Plant distribution in Gondwana during the late Paleozoic. In: TAYLOR TN AND TAY-LOR EL (Eds.), Antartic Paleobiology, its role in the reconstruction of Gondwana, New York: Springer-Verlag, p. 102-117.

ARCHANGELSKY S. 1993. Consideraciones sobre las flo-ras paleozoicas de Bolivia. Rev Téc YPFB (13/14): 167-172.

BARBERENA MC, ARAÚJO DC AND LAVINA EL. 1985. Late Permian and Triassic tetrapods of southern Brazil. Nat Geog Res 1: 5-20.

BROUTIN J, ROGER J, PLATEL JP, ANGIOLINI L, BAUD A, BUCHER H, MARCOUX J AND AL HASMI H. 1995. The Permian Pangea. Phytogeographic implications of new paleontological discoveries in Oman (Arabian Peninsula). C.R. Acad. Sci. Paris 321 (série IIa): 1069-1086.

CHANDRA S AND SINGH KJ. 1992. The genus *Glos-sopteris* from the Late Permian beds of Handapa, Orissa, India. Rev Palaeobot Palyn 75: 183-218.

DAEMON RF AND QUADROS LP. 1970. Bioestratigrafia do Neopaleozóico da Bacia do Paraná. In: XXIV CON-GRESSO BRASILEIRO DE GEOLOGIA, 24., Brasília. Anais..., Brasília: SBG, p. 359-412.

DÍAZ-MARTÍNEZ E, ISAACSON PE AND SABLOCK PE. 1993. Late Paleozoic latitudinal shift of Gondwana: stratigraphic/sedimentologic and biogeographic ev-idence from Bolivia. Doc Lab Géol Lyon 125: 119-138.

DÍAZ-MARTÍNEZ E, SEMPERE T, ISAACSON PE AND GRADER G. 2000. Paleozoic of western Gondwana active margin (Bolivian Andes). In: INTERNATIONAL GEOLOGICAL CONGRESS, 31., Rio de Janeiro. Pre-Congress Fieldtrip Bft 27..., Rio de Janeiro, 31p.

FEISTMANTEL O. 1878. Palaeozoische und mesozoiche Flora des östlichen Australiens. Palaeontographica suppl. 33: 55-130.

FLUTEAU F, BESSE J, BROUTIN J AND RAMSTEING G. 2001. The Late Permian climate. What can be in-ferred from climate modelling concerning Pangea scenarios and Hercynian range altitude. Paleogeog-raphy, Paleoclimatology, Paleoecology 167: 39-71.

GOLONKA J, ROSS MI AND SCOTESE CR. 1994. Phanero-zoic paleogeographic and paleoclimatic modeling maps. In: EMBRY AF, BEAUCHAMP B AND GLASS DJ (Eds.), Pangea: Global Environments and Resources: Canadian Society of Petroleum Geologists, p. 1-47. Memoir 17.

HOLMES WBK. 1992. *Glossopteris*-like leaves from the Triassic of eastern Australia. Geophytology 22: 119-125.

KOVÁCS-ENDRÖDY É. 1976. Notes on some *Glossopteris* species from Hammanskraal (Transvaal). Palaeont africana 19: 67-95.

LANGER MC. 2000. The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná Basin, Brazil. N Jb Geol Paläont Abh 215: 69-95.

MAHESHWARI HK. 1965. Studies in the *Glossopteris* Flora of India – 22. On some species of the genus *Glossopteris* from the Raniganj Stage of the Raniganj Coalfield, Bengal. The Palaeobotanist 13: 129-143.

MAHESHWARI HK AND PRAKASH G. 1965. Studies in the *Glossopteris* Flora of India – 21. Plant megafossils from the Lower Gondwana exposures along Bansloi River in Rajmahal Hills, Bihar. The Palaeobotanist 13: 115-128.

MARQUES-TOIGO M. 1991. Palynobiostratigraphy of the southern Brazilian Neopalaeozoic Gondwana Sequence. In: INTERNATIONAL GONDWANA SYMPOSIUM, 7., São Paulo. Proceedings..., São Paulo: IG-USP, p. 503-515.

MOREL P AND IRVING EC. 1981. Tentative paleocontinetal maps for the Early Phanerozoic and Proterozoic. J Geology 86: 195-198.

PANT DD AND PANT R. 1987. Some *Glossopteris* leaves from Indian Triassic beds. Palaeontographica Abt. B 205: 165-178.

RIGBY JF. 1966. The Lower Gondwana floras of the Perth and Collie basins, western Australia. Palaeontographica Abt. B 118: 113-152.

RIGBY JF, CHANDRA S AND SURANGE KR. 1988. Glossopterid plant remains in the Permian of western Australia. Mem Ass Australas Palaeontols 5: 73-78.

ROHN R AND RÖSLER O. 1986. Pteridófilas pecopteróides da Formação Rio do Rasto no Estado do Paraná e da Formação Estrada Nova no Estado de São Paulo (Bacia do Paraná, Permiano Superior). Bol IG-USP 17: 57-76.

ROHN R AND RÖSLER O. 1987. Relações entre a flora permiana do Gondvana e as floras das províncias setentrionais. In: CONGRESSO BRASILEIRO DE PALEONTOLOGIA, 10., Rio de Janeiro. Anais..., Rio de Janeiro: v. 2, p. 885-899.

ROHN R AND RÖSLER O. 1989. Novas ocorrências de *Glossopteris* na Formação Rio do Rasto (Bacia do Paraná, Permiano Superior). Bol IG-USP Publ Esp 7: 101-125.

ROHN R AND RÖSLER O. 2000. Middle to Upper Permian phytostratigraphy of the eastern Paraná Basin. Revista Universidade de Guarulhos, Geociências nº especial: 69-73.

ROHN R, BABINSKI MECBO AND RÖSLER O. 1984. *Glossopteris* da Formação Rio do Rasto no sul do estado do Paraná. In: CONGRESSO BRASILEIRO DE GEOLOGIA, 33., Rio de Janeiro. Anais..., Rio de Janeiro: SBG, v. 2, p. 1061-1074.

SCOTESE CR AND MCKERROW WS. 1990. Revised world maps an introduction. In: MCKERROW WS AND SCOTESE CR (Eds.) Paleozoic Paleogeography and Biogeography, London: Geol. Soc. London, p. 1-21. Memoir 12.

SEMPERE T, AGUILERA E, DOUBINGER J, JANVIER P, LOBO J, OLLER J AND WENZ S. 1992. La Formation de Vitiacua (Permien moyen à supérieur – Trias ?inférieur, Bolivie du Sud): stratigraphie, palynologie et paléontologie. N Jb Geol Paläont Abh 185: 239-253.

SUÁREZ-SORUCO R. 1974. Floras fósiles permocarboníferas presentes en Bolivia. Rev Téc YPFB 3: 97-102.

VIEIRA CEL, IANNUZZI R, GUERRA-SOMMER M, DÍAZ-MARTINEZ E AND GRADER G. 2004. Permian plants from the Chutani Formation (Titicaca Group, Northern Altiplano of Bolivia): I. genera *Pecopteris* and *Asterotheca*. An Acad Bras Cienc 76: 117-128.

WHITE D. 1908. Fossil Flora of the Coal Measures of Brazil. In: WHITE IC (Resp.), Comissão de Estudos das Minas de Carvão de Pedra do Brasil III – Relatório Final, Rio de Janeiro: Serviço Geológico do Brasil, p. 337-617.