

A new record of early Silurian land plant spores from the Paraná Basin, Paraguay (Malvinokaffric Realm)

JANE GRAY*, A. J. BOUCOT†, YNGVE GRAHN‡ & GREGORY HIMES¶

*Department of Biology, University of Oregon, Eugene, OR 97403, USA

†Department of Zoology, Oregon State University, Corvallis, OR 97331-2914, USA

‡Stockholm University, Department of Geology and Geochemistry, S-10691 Stockholm, Sweden

¶Texaco Overseas Holding Inc., c/o Amoseas, 237 Orchard Point, Post Office, Singapore, Republic of Singapore 9123

(Received 25 April 1991; revised version received and accepted 19 December 1991)

Abstract – The first conclusive evidence for Silurian rocks in the Paraná Basin, Brazil, was reported in 1985. This evidence was based on organic-walled microfossils, principally spore tetrads, and associated phytoplankton ('acritarchs' and prasinophytes), the first recovered from the Vila Maria Formation on the northeastern rim of the Basin. The spore assemblage was typical of Gray's Microfossil Assemblage Zone I; size-frequency data for the tetrads suggested an early Silurian (early Llandovery; Rhuddanian) age. We now document a new MA Zone I occurrence of spore tetrads together with a few single trilete spores, from the southwestern rim of the Paraná Basin, Paraguay. The single spores are among the earliest known to have normally dissociated from a tetrahedral tetrad. Size-frequency data for the tetrads suggest a late Llandovery, pre-C₅ (mid-Telychian) age. These spores, together with phytoplankton and chitinozoans, were recovered from beds laterally equivalent to the Vargas Peña Shale at the type locality from which Llandovery diplograptids and monograptids are known. Llandovery age rocks on the southwestern and northeastern borders of the Paraná Basin, c. 1400 km apart, suggest that early Silurian rocks were extensively distributed throughout southern Brazil and adjacent Paraguay. Close conformity between the age reference obtained with graptolites and spore tetrads again demonstrates the stratigraphic utility of early Silurian spores in providing reliable age determinations for otherwise unfossiliferous rocks. Spore tetrad assemblages available from the Malvinokaffric Realm (South America, Africa, Arabia) represent a distinct phytogeographic unit contrasted with spore tetrad assemblages from the North Silurian Realm of North America and parts of Europe.

1. Introduction

The presence of Silurian rocks in the Paraná Basin (see Gray *et al.* 1985, fig. 1) of southern Brazil was not settled until 1985. At that time conclusive evidence for the early Silurian age of the Vila Maria Formation on the northeastern margin of the Basin, State of Goiás, was provided by spore and phytoplankton assemblages (Gray *et al.* 1985). Chitinozoans recently identified by Grahn in the southern extension of the Vila Maria Formation in the northeastern Paraná Basin likewise indicate an early Silurian (early to middle Llandovery (Rhuddanian–Aeronian)) age.

Silurian rocks previously recognized on the northwestern rim of the Basin were based on a single brachiopod from the State of Mato Grosso do Sul, Brazil. The specimen, originally regarded as consistent with an early Silurian age determination (Caster, 1947), was later shown to be of early Devonian age (Boucot & Caster, 1984).

On the southwestern rim of the Basin in eastern Paraguay, early Silurian taxa have also been recognized among the fauna of the Itacurubí Group that

includes the Vargas Peña Shale exposed in the Vargas Peña Clay Pit (used in brick making) also known as the 'Quarry' (Fig. 1) (Wolfart, 1961; Harrington, 1972).

In both Vila Maria and Vargas Peña formations, benthic invertebrates, including sometimes abundant bivalves and brachiopods, have proved inconclusive for restricted age determination (Harrington, 1972; Gray *et al.* 1985; Babcock *et al.* 1990; Melo & Boucot, 1990; Boucot *et al.* 1991). Chitinozoans recently recovered from the Vargas Peña Shale collected at the Quarry (Wood *et al.* 1989, p. 288) are consistent with an early Silurian age with taxa 'similar to the ancyrochitinids and pterochitinids... previously reported from the Lower Silurian from North Africa and Florida', but, as reported, inconclusive with regard to a more restrictive age.

Consequently, the early Silurian age of the Itacurubí Group has rested on *Diplograptus modestus* Lapworth subsp. and *Climacograptus innotatus* Nicholson cf. *C. innotatus brasiliensis* Ruedemann collected from the Vargas Peña Quarry by Harrington (*in* Harrington, 1972). Both taxa previously were regarded as indicating an early Llandovery (Rhuddanian) age (Wolfart, 1961; Harrington, 1972) because of their

‡ Present address: Swedish Museum of Natural History, Section of Paleozoology, Box 50007, S-10405 Stockholm, Sweden.

occurrence in the European and North American early Silurian sequences. However, climacograptids of the *innotatus* group are now known in the late Llandovery (late Aeronian–Telychian) of Spain and North Africa (the Sahara). Jaeger (pers. comm. 1991) has recovered *C. innotatus brasiliensis* Ruedemann, 1929, from the Zone of *Monograptus gregarius* (Zone 19 of Elles & Wood (1901–1918); early Aeronian) to the Zone of *Monograptus griestoniensis* (Zone 24 of Elles & Wood; mid-Telychian), and possibly from *cyphus* Zone (Zone 18 of Elles & Wood; late Rhuddanian) to *spiralis* Zone (Zone 25 of Elles & Wood; late Telychian), i.e. from later early Llandovery through late, if not latest, late Llandovery. But in Brazil its only dated record is its occurrence with *M. cf. gregarius* at Cachoeira Vira-Mundo (Jaeger, 1976).

In Europe, climacograptids *sensu lato* can occur as late as early Devonian time (Jaeger *in* Boucot, 1988). Consequently climacograptids no longer are definitive of the early Silurian, although climacograptid-bearing units of the Trombetas Group, Brazil, yield Llandovery age chitinozoans and a single monograptid species (Jaeger, 1976). *Diplograptus modestus*, including all subspecies, is globally still restricted to the early Llandovery (Rhuddanian) with a possible extension into the latest Ordovician (Rickards, pers. comm. 1991; Jaeger, pers. comm. 1991). According to Jaeger (pers. comm. 1991), all subspecies of *D. modestus* disappear before *Climacograptus innotatus brasiliensis* makes its first appearance.

Newly recovered organic-walled microfossils (spores, phytoplankton, chitinozoans) reported on herein appear to provide the most restrictive age determination for the Vargas Peña Shale. These microfossils have been recovered from boreholes that intersect the shale horizon to the east of the outcrop in the Quarry and its vicinity (see additional discussion below). These organic-walled microfossils, together with restudied monograptids, confirm the Llandovery age originally attached to the Itacurubí Group by Wolfart (1961). Collectively, however, they suggest a latest middle to late (late Aeronian to mid-Telychian), rather than early Llandovery (Rhuddanian) age for the Vargas Peña Shale.

Organic-walled microfossils, including spore tetrads produced by pre-tracheophytic land plants (Gray *et al.* 1985; Gray *in* Babcock *et al.* 1990), the first reported from Paraguay, plus diplograptids and monograptids from Paraguay (Rickards, pers. comm. 1989), thus confirm the presence of early Silurian beds on the northeastern side of the Paraná Basin in the State of Goiás, Brazil (Gray *et al.* 1985), and some 1400 km to the south on the southwestern rim of the Basin in eastern Paraguay.

2. The spore-bearing beds

2.a. Location and extraction

The Vargas Peña Quarry (= Vargas Peña Clay Pit), the type locality of the Vargas Peña Shale from which most of the marine megafossils have been collected, is located on the west side of the valley (Ypacaraí Graben) 2 km northwest of Ypacaraí, Central Department (Fig. 1; see Degraff, Franco & Orue, 1981, for discussion of the local geology of the type area).

Land-plant spores, marine phytoplankton and chitinozoans, reported on herein, were recovered from cores obtained from the Vargas Peña Shale in wells 269-R4 (Santa Elena) and 269-R3 (Jhugua Poi), both in the San José area, Paraguay (Fig. 1). The two wells intersect an eastwardly dipping sequence about 45 km to the east of the Ypacaraí Valley.

A total of eight well-core samples were available (Tables 1, 2, 3). These were extracted according to procedures outlined by Gray (1965). No oxidation or other chemical procedures were used that might lead to a differential alteration of spore tetrad size, and comparative spore-bearing material has been treated by identical procedures to minimize the possibility of chemical size alteration. We have no control, however, over the effects of natural oxidation with regard to changes in spore tetrad size. The excellent preservation of organic-walled microfossils suggests that oxidation is probably minimal in the core samples. There is no evidence of coalification, as shown by the light, straw-colored fossils.

2.b. The spore assemblage

2.b.1. Assemblage characteristics

The spore assemblage from the Vargas Peña Shale can be assigned to Microfossil Assemblage (MA) Zone I (Gray, 1985). MA Zone I assemblages, as defined elsewhere (Gray, 1985), consist predominantly of obligate spore tetrads, those permanently conjoined at maturity (Fig. 2). In the upper part of MA Zone I a small percentage of single, trilete spores (Fig. 2) appears for the first time, although locally these may be absent. These are single spores normally dissociated at maturity from tetrahedral tetrads, not single spores obviously torn out of obligate tetrads. 'Trilete' spores in the latter category can occur much earlier in time (Gray, unpub. data). Dissociated trilete spores do not become common until later C₅ (mid-Telychian), late Llandovery time, when they first dominate pre-Devonian spore assemblages. The change in dominance from obligate tetrads to single trilete spores defines the beginning of MA Zone II; locally, obligate tetrads may remain common.

MA Zone I as recently redefined (Gray, 1989), extends from the mid-Ordovician (Llanvirn, beneath the Zone of *D. murchisoni*; Gray *et al.* unpub. data)

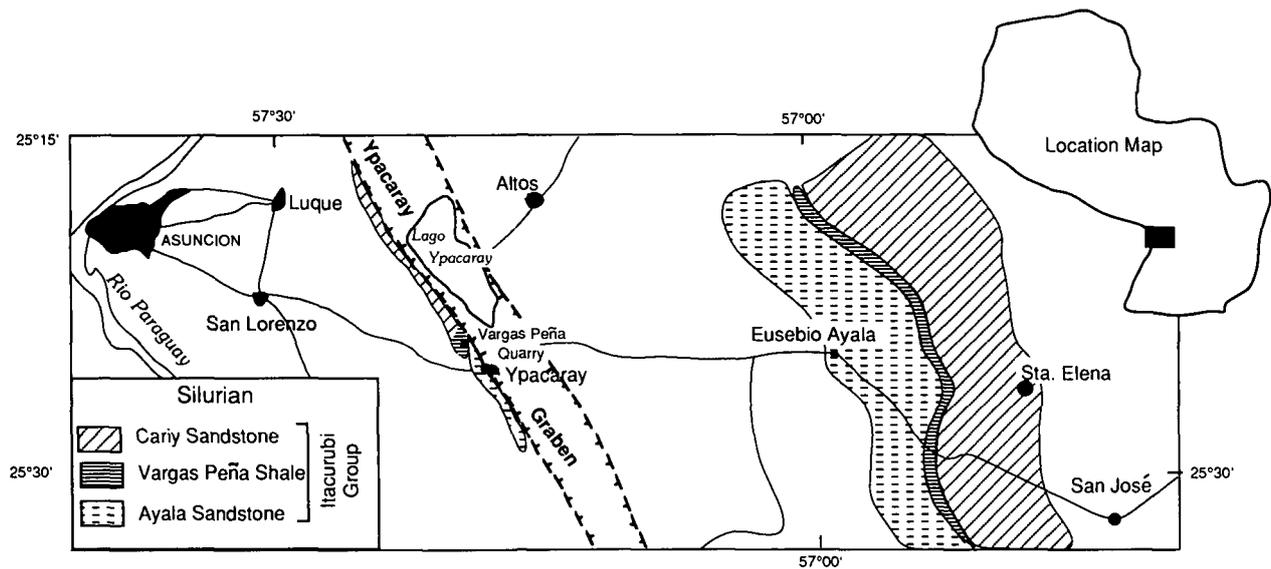


Figure 1. Locality map of central Paraguay showing distribution of the Itacurubí Group, the Vargas Peña Quarry at Ypacaray and the area to the east in the vicinity of Sta Elena and San José (see text for additional details (after Harrington, 1972)).

into the lower C_5 (mid-Telychian) zone of the late Llandovery. The upper age limit of MA Zone I (lower limit of MA Zone II), fixed on the last appearance of dominant tetrads and first dominant appearance of single trilete spores, is based on the C_5 (mid-Telychian) ostracode *Mastigobolbina lata* (Berdan, pers. comm., 1982), co-occurring in beds dominated by obligate spore tetrads in the Middle Shale Member of the Rose Hill Formation at Millerstown, Pennsylvania. Overlying beds belonging to MA Zone II, dominated by trilete spores, yield the C_5 (mid-Telychian) brachiopod *Eocoelia curtisi* from the Upper Shale Member of the Rose Hill Formation.

Characteristics of spore tetrads from the Vargas Peña Shale have been discussed in detail elsewhere (Gray, 1991; and unpub. data). Some of the scarce trilete spores, that occur in a frequency of about 1 per 25–30 tetrads, and that provide evidence of normal dissociation from meiotic tetrahedral tetrads (Fig. 2), are reminiscent of *Ambitosporites* Hoffmeister with a well-defined equatorial crassitude (4–5 μm thick), simple, mostly straight, laesura arms (or rays) and similar size (11 measured specimens have a size range of 35 to 68.5 μm and an average size of 51.9 μm). Others (Fig. 2) appear to lack crassitudes and the laesura arms, while well-defined, are undulating rather than straight (the two illustrated specimens have diameters of 15 and 30 μm). Trilete spores from the Vargas Peña Shale are uniformly smooth-walled; as apparent from the SEM micrographs (Fig. 2) at least some bear a thin, closely adherent perispore that covers the sutures (or germinal scars) of the laesura arms. The presence of a perispore has not been determined for the *Ambitosporites*-type trilete spores nor for *Ambitosporites* Hoffmeister. Perispore in modern embryophyte spores is a supraexinous sporo-

pollenin-bearing layer formed by a *tapetum* (Pacini, 1990). The presence of perispore is incontrovertible evidence for an embryophytic origin for these trilete spores.

These single trilete spores could have dissociated from some of the co-occurring tetrads, some of whose individual spores display equatorial thickening (crassitudes) similar to spores of the *Ambitosporites*-type and are of similar size. Occasional, still-conjoined trilete spores provide direct evidence of some tetrad dissociation.

Spore assemblages from the Vargas Peña Shale include rare dyads perhaps in a ratio of 1 per 100 tetrads and occasional scraps of cuticle.

2.b.2. Phytogeographical implications

Within MA Zone I, tetrad assemblages available from Malvinokaffric and extra-Malvinokaffric realms show significant differences. Within the Malvinokaffric Realm, all tetrads from the Paraná Basin are smooth without external ornamentation like those illustrated (Fig. 2). Tetrads from Africa (Ghana, Libya, South Africa) and Arabia, like those from both sides of the Paraná Basin in Brazil and Paraguay and the Amazon Basin, in Brazil, South America, also lack external ornamentation. No MA Zone I tetrads throughout this vast area of the Malvinokaffric Realm have been seen with reticulate and rugose ornamentation like those of spore tetrads from extra-Malvinokaffric Realm Ordovician–Silurian boundary rocks and early Silurian rocks from Eastern North America (Gray, 1985, 1988, 1991), and equivalent age beds in Britain (Burgess, 1991). Specimens belonging to MA Zone I from Libya alleged by Richardson (1988) to show ornamentation are dealt with elsewhere (Gray, unpub.

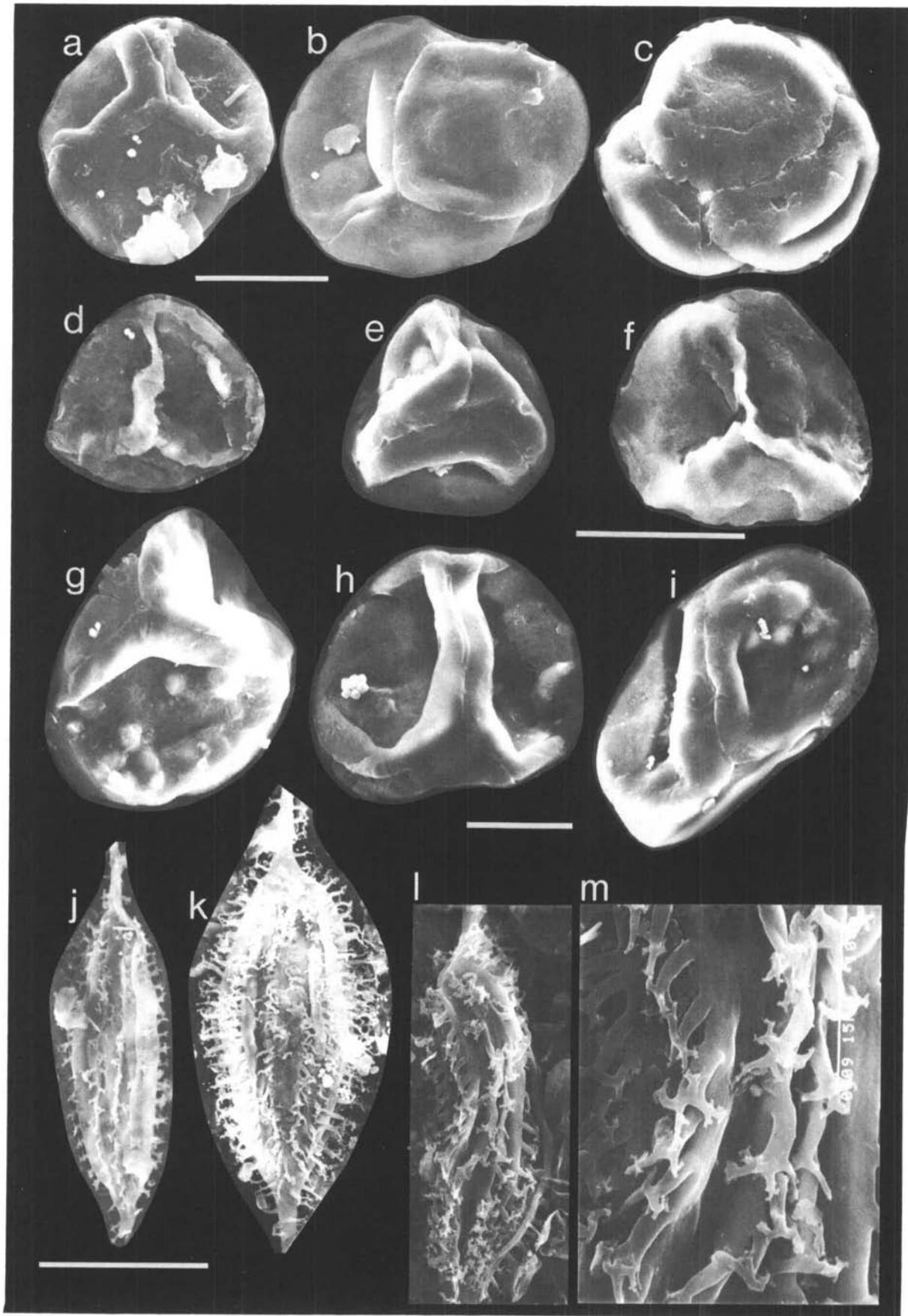


Figure 2. For legend see facing page.

Table 1. Distribution of phytoplankton and *Cyathochitina* in Core 269-R3 and spore tetrad size data

Gray Laboratory Sample No. Depth (m)	1590 35	1591 37	1592 ¹ 50	1593 57	1594 76	1595 80
Phytoplankton²						
<i>Ammonidium microcladum</i>	x	—	.	x	—	—
<i>A. waldronense</i>	x	—	.	x	—	—
<i>Dactylofusa maranhensis</i>	x	—	.	x	x	x
<i>Diexallophasis denticulata</i>	x	x	.	x	x	x
<i>Domasia limaciforme</i>	x	x	.	—	x	—
<i>Electroriskos aurora</i>	—	x	.	—	—	x
<i>Eupoikilofusa striatifera</i>	x	x	.	—	x	x
' <i>Fissilisphaeridium dischides</i> '	x	—	.	x	—	—
<i>Leprotolypa aniae</i>	—	—	.	—	—	x
<i>Oppilatala eoplanktonica s.l.</i>	x	—	.	x	—	—
<i>Psenotopus chondrocheus</i>	x	—	.	—	—	—
<i>Sol radiofurcata</i>	x	x	.	—	—	—
<i>Veryhachium carminae</i>	x	x	.	x	x	x
<i>V. europaeum</i>	x	—	.	x	—	—
Chitinozoans						
<i>Cyathochitina</i> spp.	—	—	.	x	x	—
Spores³						
Number	100	100	100	100	99	100
Average diameter (µm)	42.3	42.8	47.0	42.7	46.8	47.7
Standard deviation	7.66	6.67	9.43	9.54	9.65	10.01
Range (µm)	25–61	27–70	25–69	26–62	25–71	25–73

¹ Sample 1592 not examined for phytoplankton. ² Compiled by Colbath. ³ Measurements by Gray.

Table 2. Distribution of phytoplankton and *Cyathochitina* and *Sphaerochitina* in Core 269-R4 and spore tetrad size data

Gray Laboratory Sample No. Depth (m)	1596 195.5	1597 200
Phytoplankton¹		
<i>Dactylofusa maranhensis</i>	—	x
<i>Diexallophasis denticulata</i>	x	x
<i>Eupoikilofusa striatifera</i>	x	—
<i>Oppilatala eoplanktonica s.l.</i>	—	x
Chitinozoans		
<i>Cyathochitina</i> spp.	x	x
<i>Sphaerochitina</i> 'sp. B'	—	x
Spores²		
Number	15	100
Average diameter (µm)	51.7	42.0
Standard deviation	7.44	5.79
Range (µm)	38–66	23–60

¹ Compiled by Colbath. ² Measurements by Gray. Acritarchs recognized by Colbath (in Gray *et al.* 1985): *Leiosphaeridia* spp.; *Dictyotidium* sp.; *Diexallophasis* sp.; *Multiplicisphaeridium* sp.; *Visbysphaera* n.sp.; *Veryhachium* sp.; *Electroriskos pogonius*; *Pterospermella* sp.

data). The tetrad status of a number of these is problematic and a number of problems relate to Richardson's interpretation of ornamentation.

This significant difference in tetrad ornamentation is the first clue to a major phylogeographical differentiation in pre-Devonian land plants from the Malvinokaffric and North Silurian realms (Gray & Boucot, unpub. data). All normally dissociated tri-radiate spores in these assemblages are smooth-walled in conformity with the smooth-walled trilete spores that dominate Microfossil Assemblage Zone II (Gray, 1985).

2.b.3. Spore, phytoplankton and chitinozoan biostratigraphy

Two approaches to biostratigraphy have been used with Ordovician–early Silurian spore tetrads. At this juncture, ranges of individual taxa have not provided the basis for this biostratigraphy, in part because presently named taxa have been so confusingly and inadequately defined (Gray, unpub. data) and taxa used to establish regional biostratigraphies are not always present in local sections other than those on which such zonations were originally based. Instead, the principal approach to biostratigraphic zonation is based on gross spore assemblage features. The primary assemblage feature that provides the backbone to the

Figure 2. Scanning electron photomicrographs of organic-walled microfossils from the Vargas Peña Shale, Paraná Basin, Paraguay (see text for specific locality information). Items (a–c), (e), (g–i), tetrahedral tetrads of spores. Items (d, f), single trilete spores that have normally dissociated from tetrahedral tetrads (note perispore that covers the triradiate 'suture' – a hallmark of a normally dissociated spore: Gray, 1991). Items (j–m), *Dactylofusa maranhensis* Brito and Santos. Items (l, m) are of a single specimen. Items (a, d): G1597; (b, l, m): G1590; (c, e, f, j): G1593; (g, h): G1592; (i): G1594; (k): G1595. The 'G' numbers are the same as those of Figure 3. Upper left scale bar (20 microns): (a–e, g, h). Upper right scale bar (10 microns): (f, m). Lower left scale bar (50 microns): (j). Lower right scale bar (20 microns): (i, k, l).

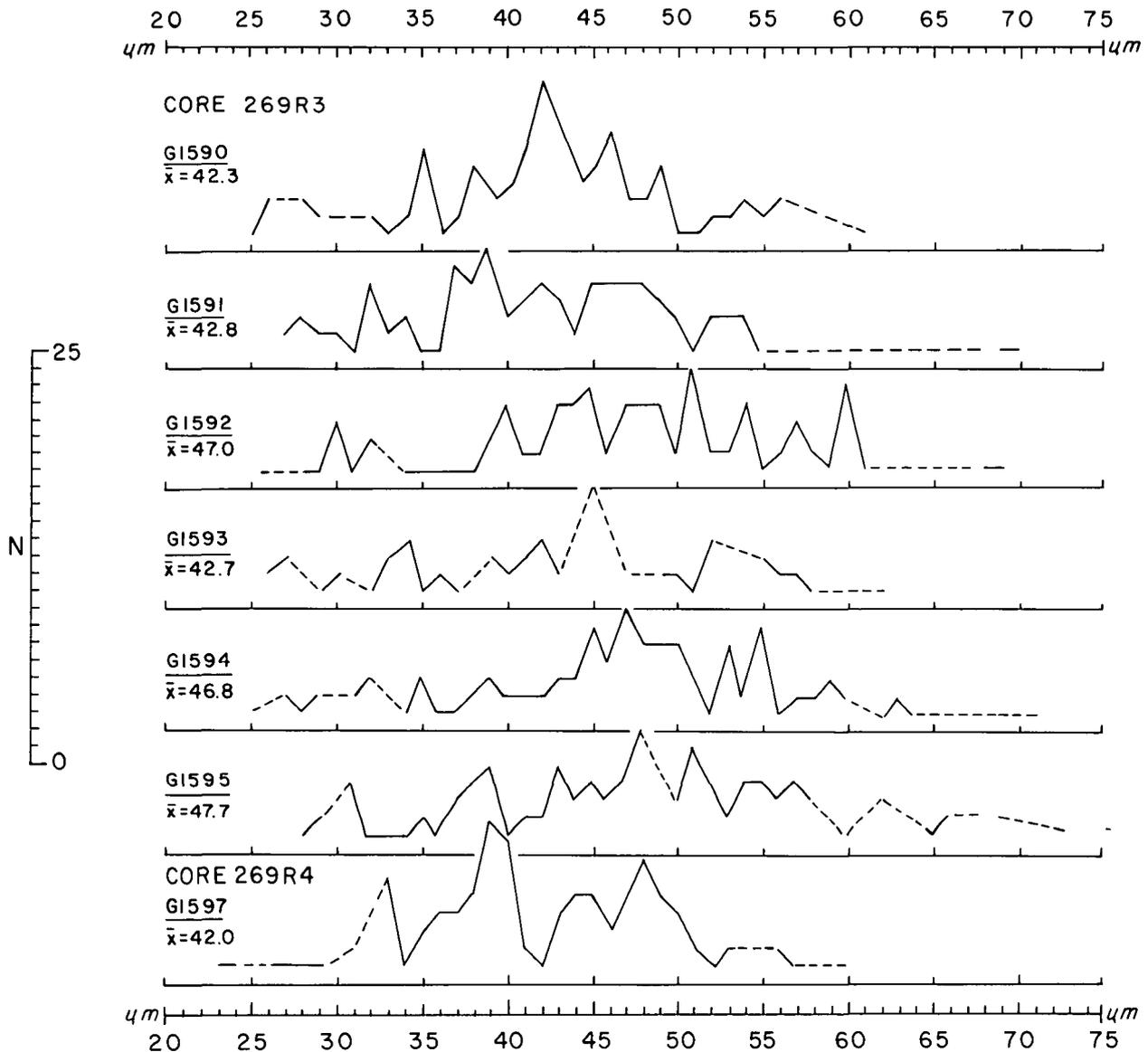


Figure 3. Distribution of spore tetrad size from the Vargas Peña Shale (Core 269-R3, Gray Samples 1590, 1591, 1592, 1593, 1594, 1595, and Core 269-R4, Gray Sample 1597). The sample means are listed below the sample numbers. All measurements are in microns (scale at bottom and top of figure). These measured specimens are all from near the top of Microfossil Assemblage Zone I (see text for age discussion). There is no significant age difference in the spore-bearing samples from either core. Samples from Core 269R3 are in stratigraphic sequence, youngest at top. Vertical bar is the scale for counting numbers of specimens. The dashed lines indicate size intervals for which there were no measured specimens.

biostratigraphy is the change from spore tetrad dominated (MA Zone I) to single trilete spore dominated (MA Zone II) microfloras (Gray, 1985).

In the most closely examined continuous sequence of spore assemblages that includes the entire Llandovery (Millerstown, Pennsylvania, U.S.A.), change from tetrad dominated to single trilete spore dominated assemblages occurs in the lower part of Zone C₅ (mid-Telychian) over a time span estimated at no more than 500 000 years (Gray, 1989, 1991). Numerous other samples have confirmed the time of change as a late Llandovery (Telychian) evolutionary event. The spore assemblage type from Paraguay (compact spore tetrads with a small percentage of single, trilete spores) is consistent with a mid-

Llandovery (late Aeronian) to pre-later C₅ (mid-Telychian) age determination.

The second principal biostratigraphic approach with the spore tetrads is a morphometric one that takes advantage of a consistent increase in tetrad size (Gray, Theron & Boucot, 1986, fig. 5, with an adjustment of the MA Zone I–II boundary upwards into mid-C₅) over time in the pre-C₅ (mid-Telychian) Llandovery. The average diameter of the more than seven hundred spore tetrads measured from the Vargas Peña Shale was 44.5 microns (Tables 1, 2, Fig. 3). In comparison with previously measured spore tetrads from reasonably well-dated Llandovery sections from the extra-Malvinokaffric Realm (Gray, Theron & Boucot, 1986, fig. 5; Gray, 1988, appendix), Vargas

Table 3. Stratigraphic distribution of phytoplankton and identified chitinozoans used to establish age relations of the Vargas Peña well core samples

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
Devonian		.	.	.	x	.	.	x	x	x	.	.
		-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
Silurian	Pridoli	.	.	.	x	.	.	x	x	x	.	.
		-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	Ludlow	.	x	.	x	.	x	x	x	x	x	.	.
		-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	Wenlock	x	x	.	x	x	x	x	?	.	.	x	x	x	x	.	.
		-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----
	Llandovery	U	x	x	x	x	x	x	x	x	x	x	.	x	x	x	x
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
	M	x	.	x	x	x	x	x	x	x	x	.	x	x	x	x	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
	L	.	.	x	x	.	.	x	x	x	.	x	
	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	-----	
Ordovician		.	.	x	x	.	.	x	x	

1 *Ammonidium microcladum*; 2 *A. waldronense*; 3 *Dactylofusa maranhensis*; 4 *Diexallophasis denticulata*; 5 *Domasia limaciforme*; 6 *Electroriskos aurora*; 7 *Eupoikilofusa striatifera*; 8 *Fissilisphaeridium dischides*; 9 *Leptrolypa aniae*; 10 *Oppilatala eoplanktonica s.l.*; 11 *Psenotopus chondrocheus*; 12 *Sol radiofurcata*; 13 *Veryhachium carminae*; 14 *V. europaeum*; 15 *Cyathochitina* spp.; 16 *Sphaerochitina* 'sp. B'.

Peña tetrad size is similar to that of tetrads from Member 3, Jupiter Formation, Anticosti Island, Québec (see Gray, Theron & Boucot, 1986, fig. 5). Brachiopods and conodonts are rare in spore-bearing Member 3, but *Eocoelia hemisphaerica* from the lower Jupiter Formation and *Monograptus sedgwickii* Zone graptolites in overlying Member 4 are consistent with a Llandovery C₂ (late Aeronian) age for Jupiter Member 3 (Duffield, 1985).

At present, less control is available from tetrad size measurements for stratigraphic placement, than for the shift in assemblage type from tetrads to single trilete spores, an apparently geologically synchronous event. Nevertheless, size-frequency data for the Vargas Peña spore tetrads (Tables 1, 2, Fig. 3) is wholly consistent with the assemblage type in suggesting an age of from late middle Llandovery–earlier late Llandovery or about C₂–C₃ (late Aeronian–early Telychian) in the late Llandovery or a pre-latest late Llandovery (i.e. mid-Telychian) age.

Chitinozoans from the spore-bearing borehole samples (G1590, G1591 (Core 269-R3) and G1597 (Core 269-R4)) were all roughly of the same age. The chitinozoan fauna yielded, among others, *Cyathochitina* sp. B, *Cingulochitina* cf. *C. serrata* and some *Angochitina* and *Ancyrochitina* species similar to those of the lower Pitinga Formation in the Amazonas Basin. The fauna cannot be younger than early Telychian (C₄). However, the absence of species belonging to the genus *Pogonochitina*, which is very common in the Telychian of Brazil, Guinea and North Africa, could indicate a somewhat older age.

Colbath concluded (pers. comm. 1989) from the phytoplankton assemblage from the same borehole samples (Tables 1–3 that also include in Table 2 comparative phytoplankton data from the early Silurian Vila Maria Formation (Colbath in Gray *et al.*

1985)) that the Vargas Peña Shale can be no older than middle Llandovery (Aeronian).

The combined chitinozoan and phytoplankton data establish upper and lower age limits, respectively, independent of the spore data, for the Vargas Peña Shale. These are consistent with the spore tetrad assemblage type and size-frequency data in suggesting a late middle Llandovery–early late Llandovery age (late Aeronian–early Telychian) for the shale beds.

3. Marine megafossil biostratigraphy

Shelly fossils from the Vargas Peña Shale, such as *Tentaculites* (Ciguel, 1988), *Anabaia* (Melo & Boucot, 1990) and *Conularia* (Babcock *et al.* 1990) provide little precise help for zonation either because of restricted geographical distribution and/or extended stratigraphic ranges. The brachiopod *Anabaia*, for example, is presently known only from the Malvinokaffric Realm of South America including the mid-Andean region and the central Amazon Basin, where it occurs throughout the early and late Silurian sequences. *Anabaia paraguayensis* is known only from the Itacurubí Group and its three formations (Melo & Boucot, 1990).

Potentially more age-diagnostic are graptolites collected by Helge L. Hansen (*in* Cocks, 1972, p. 626) from Paraguay (locality unspecified). These were found associated with 'ribbed atrypoid or rhynchonellide' brachiopods (probably *Anabaia paraguayensis*) and *Tentaculites* (abundant in outcrop in the Vargas Peña Quarry) in a deeply weathered, pinkish siltstone reminiscent of the lithology exposed in the Quarry (Rickards, pers. comm. 1989). Cocks (pers. comm. 1989) has now confirmed that these graptolites come from the Vargas Peña Quarry. Rickards (*in* Cocks, 1972, p. 626) identified them as *convolutus* or *sedgwickii*

Zone graptolites (*M. lobiferus* and *M. aff. sedgwickii*). After re-examining the monograptids Rickards (pers. comm. 1989) has concluded that they are more likely of *convolutus* Zone, latest middle Llandovery (Aeronian), age.

Diplograptus modestus, on the other hand, collected from the Vargas Peña Quarry by Harrington and identified by Turner (1959 in Harrington, 1972, p. 46), was regarded as early Llandovery (Rhuddanian) in age. Rickards (pers. comm. 1991) has examined Turner's illustration (his fig. 6) of *Diplograptus modestus*, and states 'I wouldn't like to say what his fig. 6 is – the photographic reproduction is poor. It could be *modestus s. l.*, but it could also be an *extraordinarius* type of thing, or a deformed *persculptus*...' Disregarding the possibility of a *persculptus* identification, and a late Ordovician age (*D. modestus* also occurs in the *persculptus* Zone), an early Silurian (early Llandovery; Rhuddanian) age is indicated by Harrington's graptolites from the Vargas Peña Quarry.

The spore tetrad assemblage type, with its few dissociated trilete spores, is consistent with a latest middle Llandovery (Aeronian) age. A latest middle Llandovery age is also consistent with a lower, or maximal, age limit of middle Llandovery for the co-occurring phytoplankton assemblage (Table 3). Latest middle Llandovery is slightly older, however, than would have been predicted from the spore tetrad measurements alone. An early Llandovery (Rhuddanian) age, based on '*D. modestus*', is still older than would have been predicted from either the spore assemblage or tetrad measurements or from the monograptids collected by Hansen from the Vargas Peña Shale and re-examined by Rickards. But because of the uncertainty regarding the assignment of this taxon expressed by Rickards, less reliance is placed on its stratigraphic significance than on the monograptid re-examined by Rickards.

Discordance between the age reference suggested by tetrad size and monograptids may have several alternative interpretations: (1) it may reflect an inadequate graptolite sample; (2) it may reflect a need to recalibrate the extra-Malvinokaffric Realm spore tetrad size-age scale; (3) it may reflect the limited number of presently available size-frequency spore measurements for the late middle Llandovery (Aeronian) and for the pre-younger C₅ (mid-Telychian) late Llandovery; or (4) it may reflect biogeographically parallel size increase trends in which equivalent age Malvinokaffric Realm tetrads average larger diameters than tetrads from the North Silurian Realm. This last possibility accords with the phytogeographical differentiation, noted above, that suggests different vegetational assemblages in the Malvinokaffric and North Silurian realms albeit both producing tetrad disseminules. Inadequate information is presently available to resolve this apparent age discrepancy.

In view of the age anomaly involving the independent graptolite collections and the spores, it might be that an early through early late Llandovery age range is in accord with the disparate fossil assemblages represented in the Vargas Peña Shale. Depending on the ultimate assignment of graptolites now called *Diplograptus modestus* and the ultimate interpretation of the tetrad data, the age of the Vargas Peña sequence might be extended into the Ordovician at its base, and, at its top, contracted further down into the mid-Llandovery or even the early Llandovery (Rhuddanian), or extended higher in the late Llandovery (Telychian).

4. Regional and environmental implications

4.a. Paraná Basin, southern Brazil

The Vargas Peña and Vila Maria faunas both occur in fine-grained marine shales. Nevertheless, it is clear that the Vargas Peña fauna from the southwestern rim of the Basin represents more offshore marine conditions than the Vila Maria fauna from the Basin's northeastern boundary. Marine phytoplankton and land plant spores support these environmental interpretations.

The Vila Maria fauna lacks articulate brachiopods, graptolites and trilobites; all are abundant in the Vargas Peña. The Vila Maria, contrariwise, abounds in the nearshore bellerophontid gastropod *Plectonotus* (*Plectonotus*) (Boucot *et al.* 1986) and nuculoid bivalves. Both are uncommon in the Vargas Peña. Marine phytoplankton from the Vila Maria, though badly coalified as contrasted with the superb preservation of the Vargas Peña material, include a taxonomically less diverse assemblage than the Vargas Peña. The absence of chitinozoans in the type area of the Vila Maria in Goiás, their presence in the southern extension of the formation, and their abundance in the Vargas Peña, are all in accord with an offshore deepening to the south and southwest in the Basin away from the type area of the Vila Maria. Relatively greater abundance of land-derived spore tetrads compared with marine phytoplankton in the Vila Maria Formation than in the Vargas Peña Shale is consistent with the relatively shallow-water, nearshore deposition of the Vila Maria in the type area (Gray & Boucot, 1972, 1977; Gray, Laufeld & Boucot, 1974).

The Vila Maria fauna can be viewed ecologically as a boundary mixture of *Plectonotus* Community and a nuculoid bivalve community, both suggesting Benthic Assemblage 1 conditions. The Vargas Peña fauna indicates Benthic Assemblage 2, and includes the *Anabaia* (= *Harringtonina*) Community (for community definitions see Wang *et al.* 1987).

These faunal conclusions do not appear to be related to sampling artifacts: in their respective type areas considerable section is exposed above and below the abundantly fossiliferous beds that supports similar

environmental conclusions. The Vila Maria is overlain and underlain by units lacking unequivocal marine invertebrates. However, the trace fossil *Arthropycus* (*Arthropycus* Community) (Burjack & Popp, 1981), in beds above the shelly fauna of the Vila Maria, is equally consistent with a more shallow-water, near-shore or Benthic Assemblage 1 position for the beds containing it. The Vargas Peña Shale is overlain (Cariy Sandstone) and underlain (Ayala Sandstone) by units containing a varied marine megafauna that includes trilobites and articulate brachiopods (Harrington, 1972; Boucot *et al.* 1991); environmental interpretation of their depositional environments is similar to that of the Vargas Peña.

4.b. Parnaíba (Maranhão) Basin, northeastern Brazil

Brito (1967) correlated the Itaim Formation from the Parnaíba Basin with the Trombetas Formation of the Amazon Basin on the basis of a few shared acritarchs. He (Brito, 1967, p. 480) regarded his Palynological Zones S and T as 'together the equivalent of the Itaim Formation'. He suggested the age of Zone T to be 'probably Lower Silurian in its upper part and Upper Ordovician in its lower part'. Lange (1972) concluded that the Itaim Formation should be assigned to the Serra Grande Formation. He (1972) believed the Serra Grande Formation represented lower Llandovery and part of the middle Llandovery.

The Serra Grande Formation now has group status. The Ipu and Tianguá formations are of Silurian age and have yielded possible late Llandovery chitinozoans in the Ipu Shale interbeds and middle Llandovery to earliest Wenlock chitinozoans in the Tianguá. The basal Jaicós contains transitional Llandovery–Wenlock chitinozoans. Early Devonian (Emsian) microfossils are found in much of the Jaicós, and middle Devonian (Eifelian) microfossils in the Itaim Formation. While the name 'Itaim' was attached to the unit from which Brito (1967) described Silurian acritarchs, including the taxon *Dactylofusa maranhensis* originally described by Brito & Santos (1965 *in* Brito, 1967) from borehole samples, the acritarchs could not have come from the presently named Devonian Itaim Formation. In 1967, the Itaim Formation had a much broader concept than that applied to the 'true' Itaim now restricted to units well above those studied by Brito. Brito provided no information on the source beds used in his study but Brito & Santos (1965 *in* Brito, 1967) referred to cores 76 and 77 of well 2-SL-1-MA and core 53 of well 2-PM-1-MA. According to Melo (pers. comm. 1990, 1991) these cores are undoubtedly within the presently named Tianguá Formation: Brito's 'former palynological zone T...to which *D. maranhensis* seems to be confined, roughly corresponds to the Tianguá Fm. only'.

However, certain of the marine phytoplankton of

Brito's 'Itaim' (now Tianguá Formation) are similar to those known from the later Llandovery age Elmina Sandstone of Ghana, West Africa (Gray, 1988, p. 352). These provided the age reference for the Elmina as straddling the Ordovician–Silurian boundary (Bär & Riegel, 1980). The Silurian acritarch *Dactylofusa maranhensis* (Fig. 2), for example, is now known in the Elmina Sandstone (Gray, 1988); in the Tianguá Formation; and in the Vargas Peña Shale from which late Llandovery spore tetrads and diplograptids and monograptids are known. *Dactylofusa maranhensis* has yet to be reported from the Trombetas Group. Consequently, *D. maranhensis* has a range of middle Llandovery–earliest Wenlock (Tianguá Formation) and also occurs in the late Llandovery Vargas Peña Shale.

4.c. Amazon Basin, north central Brazil

The Trombetas Formation, as originally defined in the type section in the State of Pará, was correlated with the Elmina Sandstone, Ghana, West Africa. The Elmina was believed to straddle the Ordovician–Silurian boundary (for discussion of these correlations based on spore assemblages and other organic-walled microfossils see Gray, 1988). As now recognized, the Trombetas has group status (Caputo, 1984) and is known to be partly of Ordovician and Llandovery age and partly of post-Llandovery age. The Llandovery age reference is based on the presence of spore tetrads (Gray, 1988, p. 352) in the lower Pitinga shales (referred to by Gray as 'the lower Trombetas'), the lateral facies of the unfossiliferous upper Nhamundá sandstones with which the Pitinga interfingers or overlies. Grahn has recovered late Llandovery (early Telychian, C₄) chitinozoans from Pitinga shales corresponding to the spore-bearing sample. These spore- and chitinozoan-bearing samples are well down in the section from the post-Llandovery Trombetas–upper Pitinga shale with marine fossils of late Wenlock to Ludlow age and the Manacapuru Formation with latest Ludlow–earliest Pridoli to early Lochkov age fossils.

Jaeger (1976, p. 293) found *Monograptus* cf. *gregarius* together with *Climacograptus innotatus brasiliensis* in basal-most Pitinga at the type locality (Cachoeira Vira-Mundo) of the Trombetas Group. He suggested the presence of the *gregarius* Zone in what is now considered to be regionally the lowermost Pitinga, i.e. in beds straddling the lower–middle Llandovery boundary. Grahn (unpubl. PETROBRÁS report, 1988) has found middle Llandovery (Aeronian) to earliest Wenlock chitinozoans in the lower Pitinga. He has also found Rawtheyan, earlier Ashgill, age chitinozoans in the upper Autás-Mirim Formation that underlies the Nhamundá Formation, and puts the Ordovician–Silurian boundary at approximately the base of the Nhamundá Formation. Consequently,

the oldest recorded age for the lower Pitinga (*gregarius* Zone) provides a maximal age limit for the Pitinga spore tetrads of late early or early middle Llandovery (Rhuddanian–Aeronian) age.

The nearshore depositional environment of the Vila Maria at the northern rim of the Paraná Basin and the apparent onlap over basement in a northerly direction, with more marine conditions to the south, suggest that the Paraná and Amazon basins were probably not linked together directly during early Silurian time (Caputo, pers. comm. 1989).

4.d. South Africa

In South Africa, varied palaeontological remains from the Disa Siltstone and underlying Soom Shale members of the Cedarberg Formation, Table Mountain Group, are consistent with an age for these units near the Ordovician–Silurian boundary.

The Disa Siltstone contains a marine invertebrate fauna which Cocks *et al.* (1970), Cocks (1972) and Cocks & Fortey (1986) concluded is of Hirnantian, later Ashgill, age. Berry & Boucot (1973) regarded the same fauna as basal Llandovery age. A few spore tetrads have been recovered by Gray from the Disa Siltstone.

The trilobite *Mucronaspis olini* from the Soom Shale is presently in accord with an Ordovician age assignment for the Cedarberg (Cocks & Fortey, 1986). *M. olini* occurs in Gaspé, Québec, with *Glyptograptus persculptus*. An Ordovician or Silurian age assignment for the trilobite thus ‘depends on whether one accepts the zone of *G. persculptus* as latest Ordovician [as presently assigned] or earliest Silurian [to which it was previously assigned]’ (Gray, Theron & Boucot, 1986, p. 450). Spore tetrads from the Soom Shale (Gray, Theron & Boucot, 1986; Gray, 1988) are consistent with an age assignment near the Ordovician–Silurian boundary but cannot be more precisely placed than either latest Ordovician or earliest Silurian.

4.e. Regional and environmental conclusions

The biostratigraphic relations of these units and the character of their fossil assemblages combine to provide some significant regional implications with regard to latest Ordovician–earliest Silurian sedimentation patterns in the Malvinokaffric Realm. Together they indicate the presence of one or more areas of earlier Silurian non-marine sedimentation in the present South Atlantic region. This inference is based on: (1) the non-marine aspect of the lower to middle Nhamundá Formation that lacks marine fossils, including organic-walled microfossils, but which is underlain by the Autás-Mirim Formation (Caputo, 1984) with a chitinozoan assemblage in its upper beds of Rawtheyan, older Ashgill, age, possibly similar in age to the Soom Shale; (2) the shallowing

trend seen from the Paraná Basin, eastern Paraguay, northeasterly to Goiás, and to the Parnaíba Basin, Brazil, that indicates an approach toward non-marine conditions in a northeasterly direction; and (3) the possible presence of non-marine, certainly unfossiliferous, earlier Silurian above the Disa Siltstone Member of the Cedarberg Formation with its marine fauna.

In addition, there is the presence from Ghana on the southwest to Libya and Arabia on the northeast of a major earlier Silurian African landmass to the south of the Silurian outcrop and subcrop belt (Boucot, 1985, fig. D1, where the lowermost line needs to be shifted to the east of Paraguay). Seilacher & Alidou’s (1988) recognition of early Silurian, Benthic Assemblage 2 trace fossils, including *Cruziana* and *Arthropycus*, in the Kandi area of northeastern Benin, northeast of a point midway between Accra and Takoradi in Ghana, lends additional support to the positioning of the shoreline shown in Boucot’s figure D1. Presently available data are compatible with the conclusion that marine late Silurian is absent within the Paraná Basin, and that a major disconformity exists between the Silurian and the earliest Devonian beds.

Acknowledgements. We are grateful to Texaco for making the borehole samples available and for permitting publication of this paper. Kent Colbath generously identified phytoplankton from the Vargas Peña Shale and provided an age for the Shale. Hermann Jaeger and Barrie Rickards answered questions about graptolites and Robin Cocks about the Vargas Peña Quarry. Gray is responsible for the spore data, Grahn for chitinozoan information for Brazil and Boucot for brachiopod data. All of us cooperated on regional and environmental conclusions. We are grateful to L. P. Quadros, M. V. Caputo and J. H. Gonçalves de Melo, all PETROBRÁS, Brazil, for their comments on various drafts of this paper. Gray and Boucot both thank the Earth Science Division of the National Science Foundation for support of this research. Grahn gratefully acknowledges a grant from the Swedish National Science Research Council (NFR G-GU 8811-302) that made his work possible.

References

- BABCOCK, L. E., GRAY, J., BOUCOT, A. J., HIMES, G. T. & SIEGELE, P. K. 1990. First Silurian conulariids from Paraguay. *Journal of Paleontology* **64**, 897–902.
- BÄR, P. & RIEGEL, W. 1980. Mikrofloren des höchsten Ordovizium bis tiefen Silurs aus der unteren Sekondier-Serie von Ghana (Westafrika) und ihre Beziehung zu den Itaim-Schichten des Maranhão-Beckens in NE-Brasilien. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **160**, 42–60.
- BERRY, W. B. N. & BOUCOT, A. J. 1973. Correlation of the African Silurian rocks. *Geological Society of America Special Paper* **147**, 1–83.
- BOUCOT, A. J. 1985. Late Silurian–Early Devonian biogeography, provincialism, evolution and extinction.

- Philosophical Transactions of the Royal Society of London* **B309**, 323–39.
- BOUCOT, A. J. 1988. Ordovician–Silurian boundary in South America. In *A Global Analysis of the Ordovician–Silurian Boundary* (eds L. R. M. Cocks and R. B. Rickards), pp. 285–90. *Bulletin, British Museum (Natural History)*, *Geology* **43**.
- BOUCOT, A. J. & CASTER, K. E. 1984. First occurrence of *Scaphiocoelia* (Brachiopoda; Terebratulida) in the early Devonian of the Paraná Basin, Brazil. *Journal of Paleontology* **58**, 1354–9.
- BOUCOT, A. J., ROHR, D. M., GRAY, J., FARIA, A. DE & COLBATH, G. K. 1986. *Plectonotus* and *Plectonotoides*, new subgenus of *Plectononotus* (Bellerophonacea: Gastropoda) and their biogeographic significance. *Neues Jahrbuch für Geologie und Paläontologie Abhandlungen* **173**, 167–80.
- BOUCOT, A. J., MELO, J. H. G. DE, SANTOS NETO, E. V. & WOLFF, S. 1991. First *Clarkeia* and *Heterorthella* (Brachiopoda; Lower Silurian) occurrence from the Paraná Basin, in eastern Paraguay. *Journal of Paleontology* **65**, 512–14.
- BRITO, I. M. 1967. Silurian and Devonian Acritarcha from Maranhão Basin, Brazil. *Micropaleontology* **13**, 473–82.
- BURGESS, N. D. 1991. Silurian cryptospores and miospores from the type Llandovery area, south-west Wales. *Palaeontology* **34**, 575–99.
- BURJACK, M. I. A. & POPP, M. T. B. 1981. A ocorrência do icnogênero *Arthropycus* no Paleozóico da Bacia do Paraná. *Pesquisas, Porto Alegre* **14**, 163–8.
- CAPUTO, M. V. 1984. Glaciação neodevoniana no continente Gondwana ocidental. *Anais do XXXIII Congresso Brasileiro de Geologia* **2**, 725–39.
- CASTER, K. E. 1947. Expedição geológica em Goiás e Mato Grosso. *Mineração e Metalurgia* **12**, 126–7.
- CIGUEL, J. H. G. 1988. *Tentaculites itacurubiensis* n. sp., dos depósitos regressivos do Paraguai oriental, Siluriano inferior da bacia do Paraná. *Revista Brasileira de Geociências* **18**, 86–92.
- COCKS, L. R. M. 1972. The origin of the Silurian *Clarkeia* shelly fauna of South America, and its extension to west Africa. *Palaeontology* **15**, 623–30.
- COCKS, L. R. M., BRUNTON, C. H. C., ROWELL, A. J. & RUST, I. C. 1970. The first lower Palaeozoic fauna from South Africa. *Quarterly Journal of the Geological Society of London* **125**, 583–603.
- COCKS, L. R. M. & FORTEY, R. A. 1986. New evidence on the South African Lower Palaeozoic: age and fossils reviewed. *Geological Magazine* **123**, 437–44.
- DEGRAFF, J. M., FRANCO, F. & ORUE, D. 1981. Interpretación geofísica y geológica del Valle de Ypacaraí (Paraguay) y su formación. *Revista Asociación Geológica Argentina* **36**, 240–56.
- DUFFIELD, S. L. 1985. Land-derived microfossils from the Jupiter Formation (Upper Llandoveryan), Anticosti Island, Quebec. *Journal of Paleontology* **59**, 1005–10.
- ELLES, B. L. & WOOD, E. M. R. 1901–1918. *A Monograph of British graptolites*, parts I–XI. London: Palaeontographical Society, 539 pp.
- GRAY, J. 1965. Extraction techniques. In *Handbook of Paleontological Techniques* (eds B. Kummel and D. Raup), pp. 530–87. San Francisco: W. H. Freeman.
- GRAY, J. 1985. The microfossil record of early land plants: advances in understanding of early terrestrialization, 1970–1984. *Philosophical Transactions of the Royal Society of London* **B309**, 167–95.
- GRAY, J. 1988. Land plant spores and the Ordovician–Silurian boundary. In *A Global Analysis of the Ordovician–Silurian Boundary* (eds L. R. M. Cocks and R. B. Rickards), pp. 351–8. *Bulletin, British Museum (Natural History)*, *Geology* **43**.
- GRAY, J. 1989. Adaptive radiation of early land plants. *28th International Geological Congress, Abstract Volume 1*, I-582–I-583.
- GRAY, J. 1991. *Tetraedraletes*, *Nodospora* and the ‘cross’ tetrad: an accretion of myth. In *Pollen and Spores: Patterns of Diversification* (eds S. Blackmore and S. Barnes), pp. 49–87. Oxford: Clarendon Press.
- GRAY, J. & BOUCOT, A. J. 1972. Palynological evidence bearing on the Ordovician–Silurian paraconformity in Ohio. *Bulletin, Geological Society of America* **83**, 1299–314.
- GRAY, J. & BOUCOT, A. J. 1977. Early vascular land plants: proof and conjecture. *Lethaia* **10**, 145–74.
- GRAY, J., COLBATH, G. K., FARIA, A. DE, BOUCOT, A. J. & ROHR, D. M. 1985. Silurian-age fossils from the Paleozoic Paraná Basin, southern Brazil. *Geology* **13**, 521–5.
- GRAY, J., LAUFELD, S. & BOUCOT, A. J. 1974. Silurian trilete spores and spore tetrads from Gotland: their implications for land plant evolution. *Science* **185**, 260–3.
- GRAY, J., THERON, J. N. & BOUCOT, A. J. 1986. Age of the Cedarberg Formation, South Africa and early land plant evolution. *Geological Magazine* **123**, 445–54.
- HARRINGTON, H. J. 1972. Silurian of Paraguay. In *Correlation of the South American Silurian Rocks* (eds W. B. N. Berry and A. J. Boucot), pp. 41–50. *Geological Society of America Special Paper* **133**.
- JAEGER, H. 1976. Das Silur und Unterdevon vom thüringischen Typ in Sardinien und seine regional-geologische Bedeutung. *Nova Acta Leopoldina* n. s. **45** (224), 263–99.
- LANGE, F. W. 1972. Silurian of Brazil. In *Correlation of the South American Silurian Rocks* (eds W. B. N. Berry and A. J. Boucot), pp. 33–9. *Geological Society of America Special Paper* **133**.
- MELO, J. H. G. DE & BOUCOT, A. J. 1990. *Harringtonina* is *Anabaia* (Brachiopoda, Silurian, Malvinokaffric Realm). *Journal of Paleontology* **64**, 363–6.
- PACINI, E. 1990. Tapetum and microspore function. In *Microspores: Evolution and Ontogeny* (eds S. Blackmore and R. B. Knox), pp. 213–37. Academic Press.
- RICHARDSON, J. B. 1988. Late Ordovician and Early Silurian cryptospores and miospores from north-east Libya. In *Subsurface Palynostratigraphy of North-east Libya* (eds A. El-Arnauti, B. Owens and B. Thusu), pp. 89–109. Benghazi: Garyounis University Publications.
- RUEDEMANN, R. 1929. *Climacograptus innotatus* var. *brasilensis*. In *Una zone de Graptolitos do Llandovery inferior no Rio Trombetas, Estado do Para, Brasil* (C. J. Maury) *Monographias do Serviço Geológico e Mineralógico do Brasil, Ministerio da Agricultura, Industria e Commercio* no. 7, 21–4, 27–9, 47–53.
- SEILACHER, A. & ALIDOU, S. 1988. Ordovician and Silurian trace fossils from northern Benin (W-Africa). *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte*, 431–9.
- TURNER, J. C. M. 1959. Faunas graptolíticas de América

- del Sur. *Revista Asociación Geológica Argentina* **14**, 1–180.
- WANG YU, BOUCOT, A. J., RONG JIA-YU & YANG XUE-CHANG 1987. Community paleoecology as a geologic tool: the Chinese Ashgillian–Eifelian (latest Ordovician through early Middle Devonian) as an example. *Geological Society of America Special Paper* **211**, 100 pp.
- WOLFART, R. 1961. Stratigraphie und Fauna des älteren Paläozoikums (Silur, Devon) in Paraguay. *Geologische Jahrbuch* **78**, 29–102.
- WOOD, G. D., MILLER, M. A., SAWICKI, D. A. & SHINEL-DECKER, C. L. 1989. Chitinozoans and microplankton from the Silurian Vargas Peña Shale (Itacurubí Group), Chaco Basin, Paraguay. *Paly-nology* **13**, 288.