# DIVERSE DEVONIAN PLANT ASSEMBLAGES FROM VENEZUELA

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**Résumé**

**Assemblages divers de plantes du Dévonien du Vénézuéla.**

Onze localités dans le membre inférieur de la formation Campo Chico, Vénézuéla occidental, présentent les assemblages les plus divers de plantes fossiles constatés à l'époque dévonienne en Amérique du sud. Ceux-ci renferment *Haskinsia* (2 espèces), *Colpodexylon* (3 espèces), *Leclercqia* cf. *complexa*, *Archaeosigillaria*, *Pseudosporochnus*, *Serrulacaulis*, "*Taeniocrada*", trimerophytes et progymnospermes. Les assemblages sont tout à fait comparables à ceux du Dévonien moyen de l'État de New York. Les fossiles suggèrent un âge entre l'Eifelien supérieur et le Frasnien inférieur, bien qu'un âge givétien soit préférable par comparaison avec d'autres flores. La géologie des localités fossiles examinées indiquent un environnement de dépôt marin marginal/deltaïque.
MOTS-CLÉS : Dévonien, Plantes fossiles, Sédiments, Gondwana, Amérique du Sud.

**Resumen**

**Varios conjuntos de plantas del Devónico de Venezuela.**

Once localidades en el Miembro Inferior de la Formación Campo Chico, Venezuela Occidental, suministran los conjuntos de plantas Devónicas de Suramérica que hasta ahora han sido reportados. Incluyen : lycophytes *Haskinsia* (2 especies), *Colpodexylon* (3 especies), *Leclercqia* cf. *complexa*, *Archaeo-sigillaria*, *Pseudo-sporochnus*, *Serrulacaulis*, '*Taeniocrada*', trimerophytes y progymnosperms. Los fósiles de plantas sugieren que proceden de una edad entre lo más alto Eifeliano y bajo Frasniano, aunque una edad Givetiano se prefiere - conclusión basada en la comparación con otras floras. Los conjuntos se relacionan más claramente con el Devónico Medio del Estado de Nueva York. La geología de las localidades fosiliferas examinadas es determinante de un ambiente deposicional marino marginal/deltáico.
PALABRAS CLAVE : Devónico, Plantas fósiles, Sedímentos, Gondwana, América del Sur.

**Abstract**

**Diverse Devonian plant assemblages from Venezuela.**

Eleven localities in the Lower Member of the Campo Chico Formation, Western Venezuela, provide the most diverse assemblages of plant fossils yet reported from the Devonian of South America. These include lycophytes (*Haskinsia* (2 species), *Colpodexylon* (3 species), *Leclercqia* cf. *complexa*, *Archaeosigillaria*), *Pseudosporochnus*, *Serrulacaulis*, '*Taeniocrada*', trimerophytes and progymnosperms. The plant fossils suggest an age between uppermost Eifelian and lower Frasnian, although a Givetian age is preferred on the basis of comparison with other floras. The assemblages are most closely related to those of the Middle Devonian of New York States. The geology of the plant-bearing localities is reviewed, and a marginal marine/deltaic depositional environment proposed.
KEYWORDS : Devonian, Plant fossils, Sediments, Gondwana, South America.

# INTRODUCTION

In comparison with the extensive Devonian floras of Laurussia, Kazakhstan and China, those of Gondwana are (with the exception of Australia) usually sparse and poorly preserved. The discovery of abundant and diverse megafossils in Venezuela, which received their first taxonomic treatment by Edwards & Benedetto (1985), hinted at the presence of an assemblage "more diverse and better preserved than hitherto recorded from the Devonian of South America" (p. 599). Subsequent collection by Edwards confirmed the potential of the outcrops and a large number of specimens was obtained. Fieldwork in March 1990 by the present authors enlarged the collection and expanded the number of plant-bearing localities. Detailed descriptions of the individual taxa will be published as a series of papers (CMB, work in progress). We attempt here to put the plant fossils into their geological and stratigraphic context, and to discuss their diversity and palaeobiogeographic implications.

## HISTORICAL, GEOGRAPHICAL AND GEOLOGICAL CONTEXT

A number of Devonian inliers occur in the area of the western Venezuela/Colombia border (fig. 1). Earliest studies of Devonian invertebrate fossils in the Venezuela/Colombia basin were published by Weisbord (1926) and Liddle *et al.* (1943). More recently work by Bowen (1972) and Benedetto (1980b) has contributed to our knowledge of the Devonian strata. Scrutton (1973) has investigated collections of corals, and Benedetto (1984 and papers therein) has provided analysis of the brachiopod, mollusc and arthropod faunas.

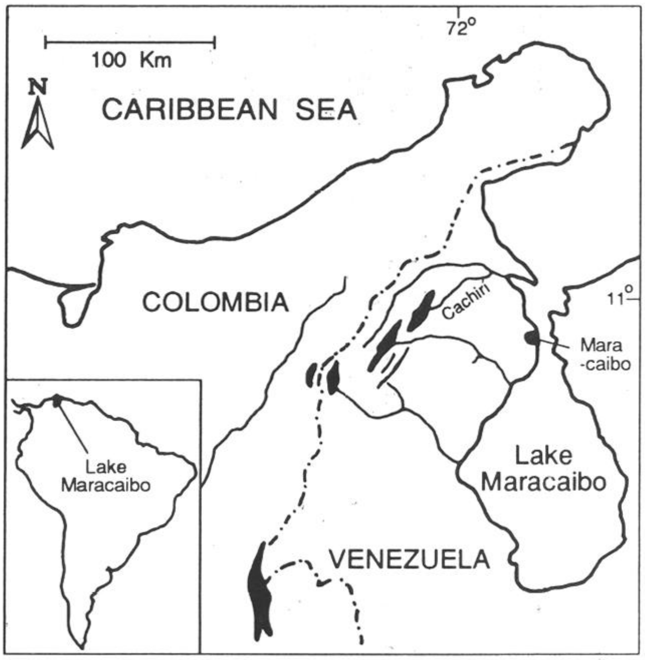


Fig. 1 - **The area of the northern Venezuela/ Colombia border showing Devonian outcrops (black).**

The fieldwork for this study was based in the Sierra de Perijá on the most northerly of the Devonian outcrops (fig. 1) on the hill marking the watershed between the head-waters of Río Cachirí and Río Pescado (fig. 2a), found on the Tulé topographic map (Dirección de Cartografiá Nacional, Republica de Venezuela Ministerio de Obras Publicas, Hoja 5748, 1:100,000 - 1970) grid reference approximately 780E, 1184N, in Zulia State, about 80 km west of Maracaibo.

One significant modification has been made to the topographic base map. On the base map the hacienda "El Reposo" is not positioned in the same place as the hacienda known by that name to the local inhabitants. It is not clear if the original map was wrong, or whether the hacienda has moved. The position of "El Reposo" on our map is therefore approximately 1.5 km NNW of its position on the base map and also on the maps of Bowen (1972) and Benedetto (1984).

Since the fieldwork of Benedetto the erosion of the old road (Route au Río Socuy of Benedetto 1984) and the subsequent construction of a new lower track has led to spectacular new exposure and made considerable reinterpretation of the geology in this immediate area possible.

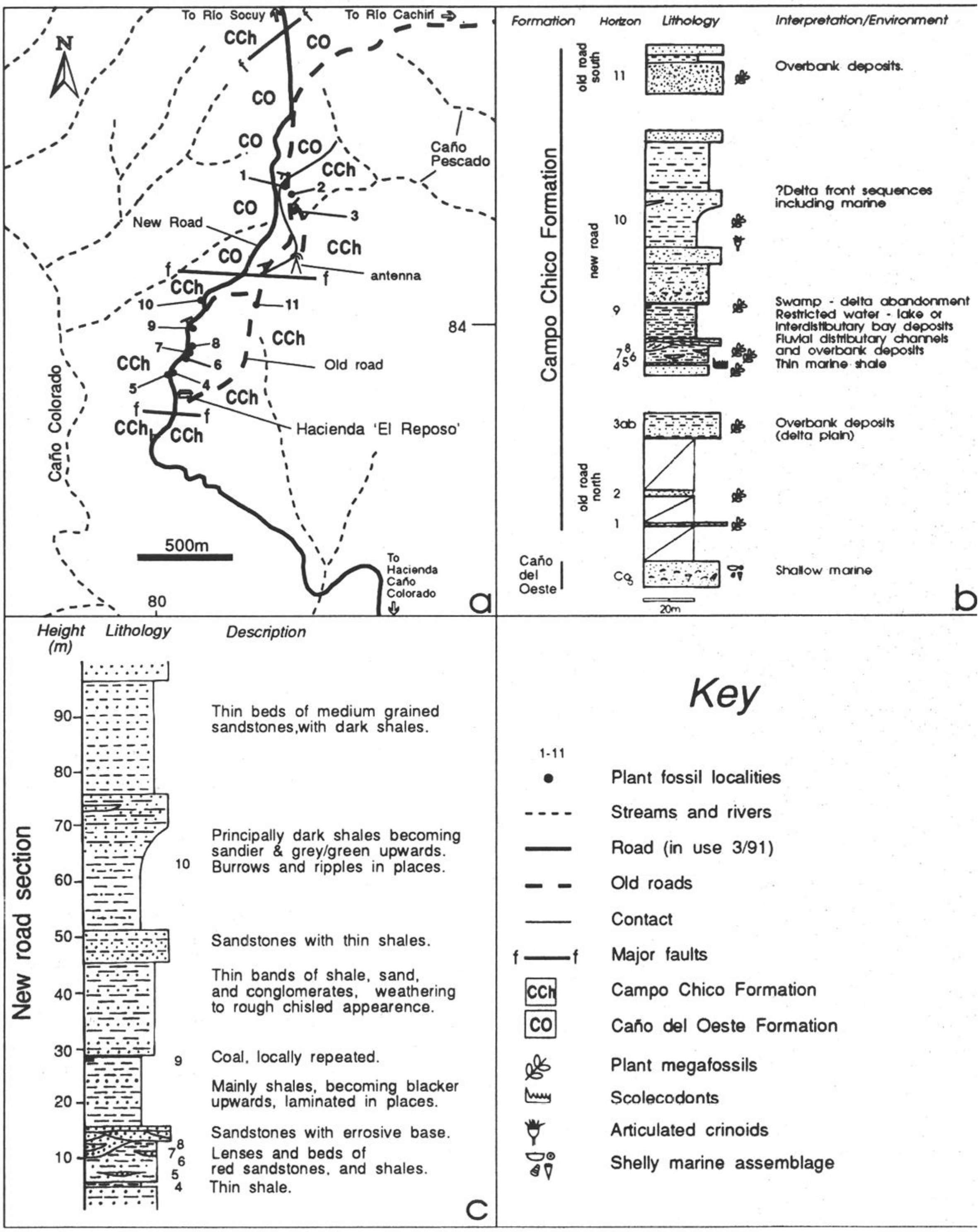


**Fig. 2a - Map of fieldwork area, showing plant fossil localities.**
**2b - Sequence of fossil bearing sections and interpretation of depositional environments.**
**2c - Logged section along new road.**
**(After Casas *et al.* 1990)**

## NORTHERN LOCALITIES

Figure 2a shows the roads, tracks and streams in the fieldwork area, together with the plant fossil localities.

About 600 m south of the convergence of the old and new roads and the track to Río Cachirí, a jeep track leaves the old road and climbs steeply southwards to a radio antenna site on the hilltop. In the angle of the junction a mound three metres high has bare rock exposed on the east side of the old road. Here the relationship between the marine Caño del Oeste Formation and the overlying mostly non-marine Campo Chico Formation can be demonstrated.

Figure 3c shows a section of the exposure in this vicinity. To the north orange/brown sandstones typical of the Caño del Oeste Formation contain internal and external moulds of solitary corals, crinoids, brachiopods and gastropods. In the roadside exposure, c100 m to the south, green and orange sandstones and shales occur (locality 3a). Here the harder sandstones are barren whereas the interbedded softer sandstones and shales contain abundant, diverse, well preserved plants including monospecific accumulations of axes of the lycophyte *Haskinsia sagittata*. The productive horizon, perhaps 1 m thick, continues into the road-bed (locality 3b). Between the marine horizon and locality 3 poor exposure in the road-bed yielded narrow naked branching plant axes badly preserved in white medium and coarse grained sandstones and grey mudstones (localities 1 and 2).

The section of Benedetto (1984, fig. 4) shows in this vicinity his fossil assemblages $Co_5$ and $Co_8$ which are assumed to correspond to the marine shelly assemblage and locality 3 of this work. We arbitrarily draw the boundary between the Caño del Oeste and Campo Chico Formations at the base of the exposure containing locality 1 as the overlying rocks contain exclusively plant fossils, although sediments containing plant remains are commonly interbedded with units with marine fossils in the highest beds of the Caño del Oeste Formation (Benedetto 1984).

## SOUTHERN LOCALITIES

The southern localities are shown in figures 3a and 3b. North of the entrance to "El Reposo" the new road emerges on to a ledge cut into the hillside, with a steep drop from the road into Caño Colorado to the west while spectacular exposure cut to the east allowed the recording of a logged section (fig. 2c).

The lowest horizon exposed, in the gutter to the east of the road, is a thin dark shale which contains abundant axes of "*Taeniocrada*" and rarer lycophytes (locality 4). Palynological preparations from this horizon demonstrate a high organic carbon content and rare scolecodonts.

The overlying 10 m of predominantly red and grey sandstones occur mostly as lenses and bodies with erosive bases and internal lateral accretion surfaces interbedded with clay drapes and plugs, although some more continuous thin sandstone horizons are present. This unit is topped by a more massive sandstone bed ("main sandstone bed") 2-3 m thick which extends laterally across the exposure. This bed cuts down into the underlying sediments towards the south of the exposure to form a channel some 4 m deep and 20 m across. The entire unit contains abundant plant fragments. Locality 5 occurs in an exposure to the west and 2 m above the level of the road, containing a predominantly lycophyte assemblage. Locality 6, in the cliff face about 7 m below the main sandstone, contained well preserved but fragmentary plants. Locality 7, in the road-bed some 4 m below the main sandstone contained stems up to 10 cm wide of as yet unidentified plants, together with fragments of other axes. At the place where the main sandstone crops out in the road-bed a small lens of fine grey sandstone containing well preserved plant remains was found immediately below it (locality 8).

Above the sandstone beds the next 13 m of section contains mainly weathered, fissile shales, sometimes laminated on a millimetre scale, which are for the most part barren containing only rare fragmentary and badly preserved plant fossils. At the top of this unit a grey mudstone contains abundant fertile axes of a small trimerophyte (locality 9). The unit is capped by a powdery black coal layer which varies in thickness between a few cm and 20-30 cm. More than one coal bed is visible in places, the lower being probably eroded away for most of its original lateral extent.

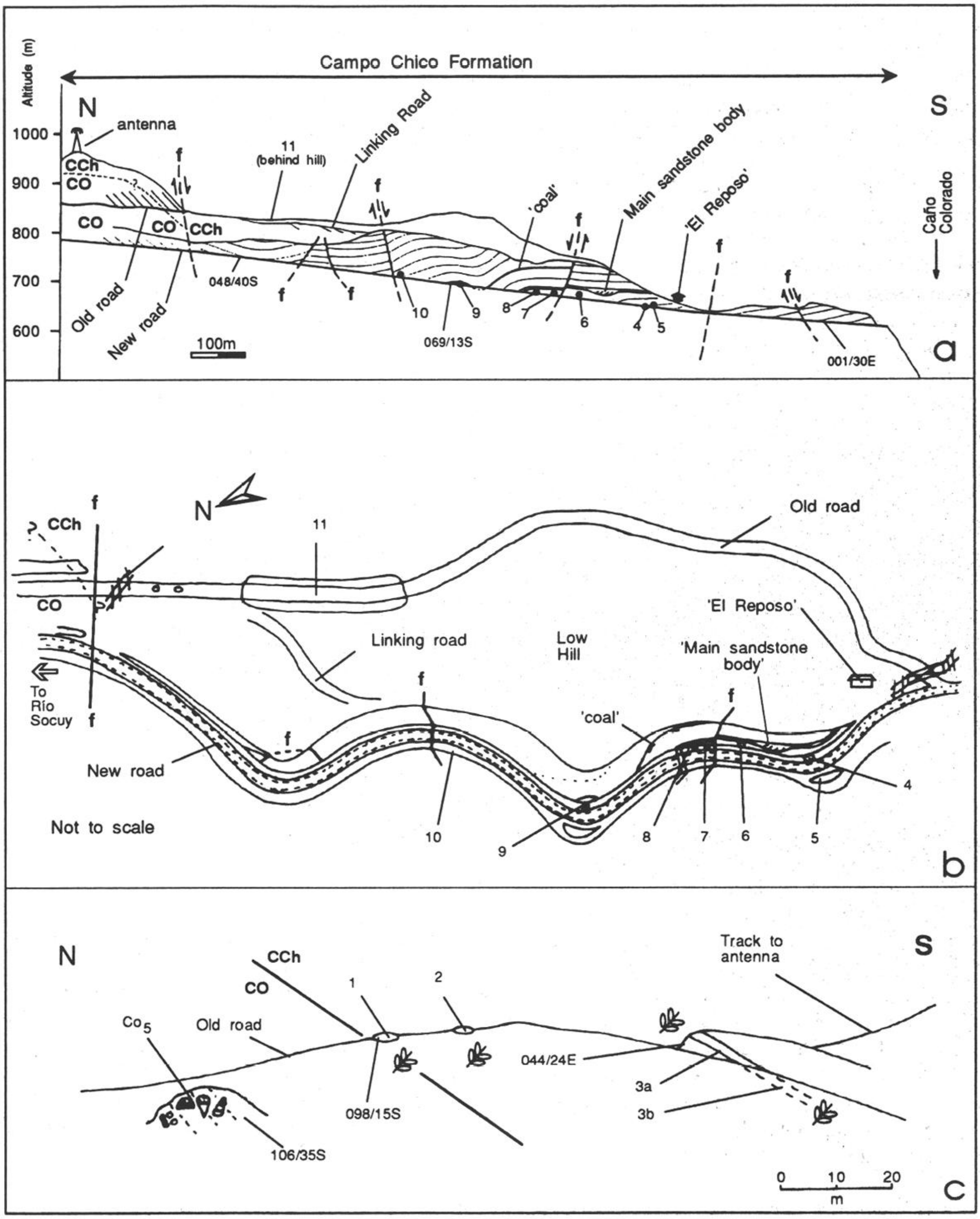


Fig. 3a - **Section along new road, showing fossil localities.**
3b - **Sketch plan of southern localities (compare with 3a).**
3c - **Section along old road showing northern localities.**
(After Casas *et al.* 1990, symbols as fig. 2)

The remainder of the new road section consists of cycles of shales and sandstones. One horizon has yielded articulated crinoid material. Other features are rippled surfaces in sandstone beds and both vertical and horizontal burrows. Locality 10 yielded poor plants preserved as black films of carbon on the grey/green shales. To the north, beyond a small fault, a second coal horizon is present.

The outcrop can be followed upwards via the linking road to the old road. Although exposure is not complete there is no evidence of large scale faulting in the immediate area. The pink and grey fine-grained sandstones of locality 11 have been uncovered by a water channel eroded into the old road bed which runs southwards towards "El Reposo". It is not possible to see bedding in these exposures. The preservation of the diverse compression fossils is again of high quality.

The more southerly of the two plant fossil localities of Edwards & Benedetto (1985) is thought to be in the southern part of the old road, perhaps nearer to "El Reposo" than locality 11 of this work. This is supported by the presence of a single pink slab among the green and buff slabs (presumably derived from the similar green rocks found at and around locality 3) of the original collection from which their two species of lycophyte were described. Their southern locality is not believed to lie at the base of the Campo Chico Formation (as Edwards & Benedetto 1985, fig. 1b) but at a horizon approximately equivalent to locality 11 of this work. Our geological map (fig. 2a) is therefore modified accordingly.

The exposure on the new road allows the demonstration of a fault with considerable displacement between the northern and southern localities. To the north of locality 10 the bedding is almost horizontal, and some 300 m north of the road corner the exposure becomes poor and fades out altogether (fig. 3b). Thirty metres further north orange weathered shales contain a marine fauna of corals and brachiopods clearly belonging to the Caño del Oeste Formation. Thus a horizon high in the Campo Chico Formation is in close horizontal proximity to rocks of the formation stratigraphically below it, and a fault of some considerable throw (150 m+?) is deduced. Similarly, on the old road above and to the east, about 100 m north of locality 11, beyond scrappy exposure, a cliff section dipping southeast also contains marine assemblages in some lower horizons. Indeed, this section may incorporate the progressional Caño del Oeste/Campo Chico boundary, although no plant fossil have yet been found. Extension of the fault between these two roads coincides with the steep southern front of the "antenna hill", and thus adds weight to the stratigraphic sequence of localities presented here.

In addition to the recorded localities loose material from unknown horizons was collected from along the new road.

## ENVIRONMENTS OF DEPOSITION

Bowen (1972) considered the Campo Chico Formation to have been deposited in "restricted water" [restringido de aguas llanas (salobres?), p. 744] and Benedetto considered it to represent a predominantly continental cycle of sedimentation lying between two fossiliferous marine cycles. Sanchez and Benedetto (1983) described the depositional environment as being continental, the lower horizons bearing plant remains as being alluvial plain, saltmarsh and swamp deposits lying above delta plain deposits of the top of the Caño del Oeste Formation. In this preliminary study we are able to offer more detailed interpretations for that part of the Campo Chico Formation exposed along the new road (fig. 2b).

The lower levels of the new road exposure, including localities 5-8, show sandstones with cross bedding, lateral accretion surfaces, channels and lenses with erosive bases and clay plugs and drapes. This part of the Formation is therefore interpreted as being deposited in an alluvial environment, including distributary channel and overbank deposits. This interpretation is supported by the presence in several horizons of well preserved plant remains, including lycophytes with delicate microphylls which show no sign of long distance transportation, and the lack of a marine or brackish water fauna.

Below this predominantly sandstone unit the thin horizon of dark organic rich shales (locality 4) may represent a marine horizon based upon the presence of rare scolecodonts, although these may have been reworked. Above the sandstone unit the succeeding unit of shales contains neither channel structures, sandstone bodies or marine fossils, but shows signs of small scale laminations in places. Therefore it is interpreted as a deposit formed in a lacustrine, lagoonal, or possibly interdistributary bay environment. The presence of abundant plant fossils in the upper horizons together with the overlying coal imply shallowing of the water and the development of a swamp. Overlying sediments containing shale and sandstone units include evidence of fully marine sedimentation (articulated crinoid) and are probably cyclic coarsening upwards sequences which could be interpreted as representing repeated advances of a delta front in a subsiding basin or a sea of fluctuating level. Stratigraphically above and below the new road outcrop the two localities on the old road (3 and 11) which contain abundant well preserved plant remains are interpreted as river channel and overbank deposits based on this evidence only, there being no recognisable sedimentary structures.

As a whole these parts of the Campo Chico Formation are interpreted as marginal marine and terrestrial sediments, deposited at the interface between a mobile fluvial system and the sea, and represent the establishment of a delta or coastal plain environment, its local abandonment and re-establishment. Such a sedimentary sequence may well include marine invertebrates of biostratigraphic use, although none have yet been found.

## FOSSILS

### PLANT MEGAFOSSILS

Plant fossils occur mainly as coalified compressions (devolatilised adpressions *sensu* Bateman 1991) although at two horizons (3 & 4) there is some limonite permineralisation of the xylem of zosterophylls and "*Taeniocrada*". The occurrence of some of the fossils in relation to the localities is summarised in table 1.

The lycophytes are represented by presumed herbaceous forms, dominated by *Haskinsia* (at least 2 species) and *Colpodexylon* (3 species). *Haskinsia sagittata* and *Colpodexylon cachiriense* were described from material collected from the vicinity of locality 3 by Edwards & Benedetto (1985). In the course of the present study the former species was found at several horizons, but only a single trifurcate leaf, most closely resembling *C. cachiriense*, was discovered at locality 3 (*C.* cf. *cachiriense* in tabl. 1). A single unequivocal specimen of *Leclercqia*, with leaf morphology similar to *L. complexa* Banks *et al.* was found at locality 4. This is the first time this important genus has been demonstrated from the Devonian of South America. *Archaeosigillaria* and *Lycopodites* are also present.

| | |
|---|---|
| 11 | *Colpodexylon sp. 1, C. sp., Archaeosigillaria sp., Pseudosporochnus sp.,* progymnosperms. |
| 9 | Trimerophyte, *Haskinsia Sagittata.* |
| 8 | *Haskinsia sp., Pseudosporochnus sp.,* progymnosperms. |
| 7 | Large axes. |
| 5 | *Colpodexylon sp. 2, Haskinsia sagittata, H. sp. 1, Lycopodites sp., Pseudosporochnus sp..* |
| 4 | *Leclercqia cf. complexa, Haskinsia sagittata, 'Taeniocrada'.* |
| 3 | *Colpodexylon cf. cachiriense, Haskinsia sagittata, Serrulacaulis sp., Pseudosporochnus sp. 1,* spiny zosterophyll, progymnosperms. |
| 1, 2 | Naked branching axes. |

Tabl. 1 - **Plant fossil occurrences in relation to localities.**

Two species are attributed to the zosterophylls. These are *Serrulacaulis* and a new spiny plant similar to *Sawdonia*. Two species are believed to belong to the trimerophytes. The Cladoxylales are represented by digitate branches and terminal trusses of *Pseudosporochnus*. There are a number of species of progymnosperms present, but these have yet to receive any detailed attention. Axes of "*Taeniocrada*" have S-type xylem cells (Kenrick *et al.* 1991) and their affinities have yet to be determined. This is the first record of the S-type cell in sediments younger than Lower Devonian. In addition there are at least two additional species which remain *incertae sedis*, as well as a number of distinguishable types of sterile axes which cannot be identified even to order level.

In total composition the current collections probably contain more than 20 species, by far the most diverse Devonian assemblages yet reported from Gondwana.

### SPORES

Spore assemblages have been recovered from matrix from several plant-bearing localities and the crinoid and coal horizons using standard palynological techniques. The majority of the spores obtained were found to be moderately to badly corroded, therefore making identification to specific level difficult. The most productive horizon was found to be locality 4, which includes forms approaching such taxa as *Grandispora (Calyptospora) libyensis*, *Rhabdosporites langii*, *Spinozonotriletes* cf. *naumovae*, cf. *Calyptosporites velatus*, ?*Lophozonotriletes scurrus* and *Acinosporites lindlarensis* (J.B. Richardson, pers.comm.).

## AGE OF THE CAMPO CHICO FORMATION

### INVERTEBRATES

Building on the terminology of Liddle (1928) and Sutton (1946), Bowen (1972) defined the Campo Chico Formation as lying unconformably below the Caño del Noroeste Formation of Pennsylvanian age. Benedetto (1980b) reviewed the evidence and provided new field information to combine these two formations as one essentially continental deposit lying beneath the marine Caño Indio Formation. The Caño del Noroeste Formation of Bowen became the Upper Member of the Campo Chico Formation of Benedetto (1980b), whereas the Campo Chico Formation became the Lower Member.

Benedetto (1980a) regarded the earliest horizons in the Caño Indio Formation dated by marine bivalves as Pennsylvanian, and this is at present the closest independent constraint on the upper range of the likely ages of the present plant assemblages. Other biostratigraphic evidence within the Upper Member of the Campo Chico Formation is as yet scanty and unsubstantiated. The age of the brachiopod faunas ($Co_{5-7}$) in the Caño del Oeste Formation which lie some 50 m below the lowest plant rich horizon in the Campo Chico Formation were determined by Benedetto (1984) as being lower or middle Givetian. These dates were suggested by comparison with Appalachian faunas. Edwards & Benedetto (1985, p. 616), however, quote a "Givetian (probably middle to late Givetian)" age for the $Co_6$ horizon but provide no new evidence to support this.

Benedetto (1980b), supported by very limited plant macrofossil evidence, tentatively suggested a Frasnian/Famennian (i.e. Upper Devonian) age for the Lower Member of the Campo Chico Formation, although the published evidence summarised above suggests that the base of the Formation may be as old as lower Givetian.

### PLANT MACROFOSSIL STRATIGRAPHY

Figure 4 gives the approximate known ranges of genera so far recognised in the assemblages and closely related forms (see table 1), these ranges being biased towards Laurentian records (Edwards & Berry 1991). In New York State, whence derives one of the best documented successions of Eifelian to Frasnian plant assemblages, the fossils occur in mainly terrestrial sediments. Many of these cannot yet be accurately correlated with European successions, hence these ranges can only be regarded as approximate.

Banks (1980) suggested a succession of 7 floral zones for the late Silurian and Devonian which have stratigraphic implications. However, using plant megafossils is currently of only limited accuracy because of the dependence on the presence of key taxa and the long stratigraphic ranges of many genera (Edwards & Berry 1991).

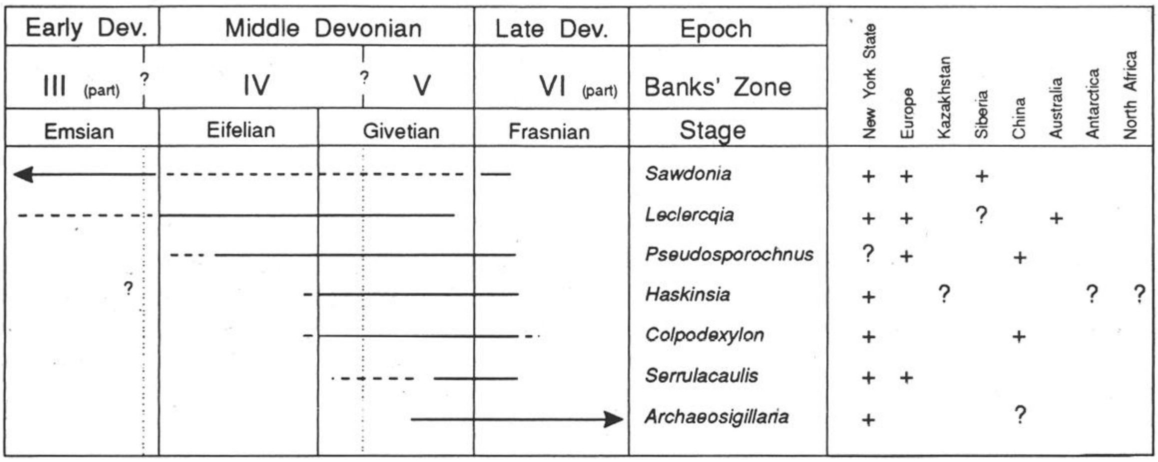


Fig. 4 - **Approximate stratigraphic occurrence and geographic occurrence of genera so far recognised in the Venezuelan assemblages and related plants** (see text). Dashed lines represent uncertain dating or no recorded occurrence during a long time interval (*Sawdonia*), question marks represent uncertain identification.

Banks' zone IV (topmost Emsian to low Givetian) is one of the most eventful in terms of the appearance of genera - some 17 of the 59 non-endemic genera of pre-Carboniferous vascular plants analysed by Edwards & Berry (1991) are first recorded in this zone, many of them appearing later than at the base. The zone ends with the arrival of *Actinoxylon* and slightly later *Svalbardia* towards the base of the Givetian. Neither of these genera are yet present in the Venezuelan assemblages, nor are the larger, probably arborescent lycophytes which are also typical of zone V (low Givetian to top of Givetian) elsewhere. Many of the genera (e.g. *Pseudosporochnus*, *Colpodexylon*, *Haskinsia*, *Serrulacaulis*) extend into the base of zone VI (Frasnian to mid Famennian). However *Leclercqia* has yet to be proven in strata younger than Givetian. *Archaeopteris*, the most characteristic genus of zone VI and a plant of widespread occurrence, is notably lacking from the Venezuelan assemblages. Taken overall the plant megafossil evidence suggests a Givetian age as most likely for the assemblages, although a latest Eifelian or early Frasnian age cannot be completely ruled out on current evidence. It is possible that the assemblages may straddle stage or zone boundaries.

## SPORES

Bowen (1972) proposed that palynomorphs within the top of the Campo Chico Formation (i.e. the top of the Lower Member of Benedetto 1980b) suggest a "Middle to Upper Devonian (probably Frasnian) age" although none of the evidence was published.

Spores examined from horizon 4 suggest a late Eifelian or lowest Givetian age (J. B. Richardson, pers comm). However it was noted that many of the taxa present have long stratigraphic ranges, and that this estimate is in part based on the absence of *Geminospora* which in European assemblages is found to become abundant in the lower part of the Givetian close to the beginning of Banks' zone VI. However *Geminospora* might be difficult to recognise as the material so far recovered is poorly preserved. A reliable age based on spores may be possible only if a greater thickness of strata is sampled in more detail, or if better preserved material can be isolated.

CONCLUSION OF AGE

The evidence suggests that the most likely age for the assemblages is Givetian, with the plant megafossils perhaps favouring a Middle-Late Givetian age, and the spores favouring an Early Givetian age for at least the lower horizons. None of the evidence is yet conclusive and a late Eifelian or early Frasnian age cannot be dismissed entirely. This contrasts with the Frasnian date for the lower half of the Lower Member of the Campo Chico Formation as suggested by Benedetto (1980b). The plant assemblages are thought to range through up to about half of the 400 m thickness of the Lower Member in this area, and so these rocks are likely to be of an older age than so far believed.

## PALAEOPHYTOGEOGRAPHY

Previous authors (e.g. Meyen 1987 ; Scheckler 1986 ; Allen & Dineley 1988) have remarked upon the apparent uniformity of Middle Devonian and early Frasnian floras, although some have emphasised the distinct nature of the Siberian and Kazakhstan assemblages (e.g. Scheckler 1986 ; Petrosyan 1968). A preliminary survey of the phytogeographical affinities of the Venezuelan fossils is now possible, although a full evaluation will not be possible until all the plant groups have been worked on in detail. Figure 4 shows occurrences of some of the Venezuelan plant genera in other geographical areas.

Regarding the Venezuelan lycophyte flora, the most common genera, *Haskinsia* and *Colpodexylon*, are also common in New York State, although represented by fewer species. *Haskinsia* is recorded in Givetian to early Frasnian strata, and *Colpodexylon* has much the same range although perhaps surviving into slightly younger rocks. *Colpodexylon* is also represented by a distinctive species from South China (Schweitzer & Cai 1987) and poorly preserved material referred to *C.* cf. *deatsii* from Vietnam (Janvier *et al.* 1989). *Haskinsia*, like *Colpodexylon*, has not been recorded from European or Baltic assemblages. However material referred to *Artschaliphyton* (Senkevich 1971) from Kazakhstan needs reinvestigation since it possesses oval leaf attachments and petiolate leaves with a broad approximately deltoid lamina. It is therefore more likely to be referable to *Haskinsia* than to *Archaeosigillaria vanuxemii* as suggested by Fairon-Demaret & Banks (1978). The close similarity between New York State *H. collophylla* and Venezuelan *H. sagittata* has been remarked upon before (Bonamo *et al.*, 1988). In Gondwana, material from Antarctica previously referred to *Drepanophycus schopfii* may belong in *Haskinsia* (Edwards 1990). In addition, cf. *Haskinsia* reported by Fairon-Demaret & Regnault (1986) from the ?Emsian of Morocco suggests that the full stratigraphic range of the genus has yet to be determined.

The occurrence of *Leclercqia* cf. *complexa* further extends the biogeographic range of this well known genus. *Leclercqia* is well known in Laurussia from New York State and Maine as well as Belgium and Germany (Bonamo *et al.* 1988). Material referred to *Protolepidodendron scharyanum* from Siberia bears a close resemblance to unprepared *Leclercqia* in the published illustrations (Ananiev 1960) and requires further investigation. In Gondwana *Leclercqia* has been reported from Australia (Fairon-Demaret 1974). *Leclercqia* can therefore be regarded as a more or less cosmopolitan genus. It should also be recorded that a newly redescribed lycophyte with some similarity to *Leclercqia* is known from the Carboniferous of Argentina (Arrondo *et al.* 1991).

Specimens of *Archaeosigillaria* sp. from Venezuela are essentially identical in stem and leaf morphology to some specimens referred to *A. vanuxemii* from Honk Falls, New York State by Grierson & Banks (1963, their locality 10). Their specimens share with the Venezuelan examples a leaf morphology which is distinct from that of specimens from Riverside Quarry, New York State, referred to *A. vanuxemii* by Fairon-Demaret and Banks (1978). The morphology of the leaves of the holotype of *A. vanuxemii* is unknown. The detailed reinvestigation of this genus is currently being undertaken (CMB, work in progress).

Of the meagre vascular plant occurrences so far described from the Middle/Upper Devonian from other parts of South America, most of the material is badly preserved and of little biogeographic use. Decorticated and defoliated axes apparently of lycophytes, referred to such genera as *Haplostigma* and *Palaeostigma*, occur in Brazil and Argentina as well as Africa and Antarctica (see discussion *in* Edwards 1990) but these are of little taxonomic value compared with axes bearing leaves (Bonamo *et al.*, 1988). An exception is *Protolepidoden-*

*dron kegeli* (Kräusel & Dolianiti 1957) from Brazil. The single specimen bears dense long curved leaves, reconstructed as being tuning-fork shaped. However it is often overlooked that the authors did not discount the possibility that the leaves are infact trifurcate, and hence the possibility that the plant belongs to *Colpodexylon*. Indeed, there is an uncanny similarity between their illustration, if inverted, and the abaxially recurved leaves of one of the new *Colpodexylon* species from Venezuela. *Archaeosigillaria picosensis* is also represented from Brazil by a single specimen (Kräusel & Dolianiti 1957) although its affinities to other *Archaeosigillaria* species is unclear.

*Serrulacaulis* has been reported from upper Givetian and lowest Frasnian strata in New York State (Hueber & Banks 1979), and also from older (probably Gi a-b) rocks in Belgium (Lessuise & Fairon-Demaret 1980). *Sawdonia*, the closest genus to the new spiny zosterophyll, is characteristic of Lower Devonian assemblages across Laurussia, but also occurs in Siberia, and in the low Frasnian of New York State. It is as yet unknown from Gondwana. *Pseudosporochnus* is known from the Middle Devonian of Belgium, and also occurs in other Laurussian localities, as well as China (Schweitzer & Cai 1987). In New York State it has been recorded, although not described, from the Upper Devonian (Banks 1966) and some other specimens have been attributed to this genus on anatomical evidence only (Stein & Hueber 1991).

In conclusion, the Venezuelan flora so far analysed bears closest resemblance to that of New York State, particularly in respect of the herbaceous lycophytes, where *Haskinsia*, *Colpodexylon*, *Archaeosigillaria* and *Leclercqia* are all present. European assemblages lack the first two, but contain *Leclercqia*, and among the other groups *Pseudosporochnus* and *Serrulacaulis*. Some of the genera are even more widespread. The Venezuelan assemblage adds weight to the concept of a single world-wide flora during these times, although there are some hints at a low level of regionalism. For instance among the herbaceous lycophytes we find high diversity in New York State and Venezuela, more moderate diversity in Europe and Asia, poorly preserved forms in the higher latitudes of Gondwana (Edwards 1990), and an apparent lack of herbaceous forms in Ellesmere Island (Scheckler *et al.* 1990). In contrast larger, probably arborescent forms are present in Kazakhstan, Spitzbergen, North Africa, New York State and China (Meyen 1987). It will be of interest to see whether such generalisations stand up to the continued sampling of coming years or if such distributions can be accounted for by taphonomic arguments or collection failure.

Conclusions as to the significance of the similarity of the Venezuelan and New York State floras are confused by the lack of consensus on a Middle Devonian palaeocontinental reconstruction. For instance, the interpretation of Heckel & Witzke (1979) shows the two areas in very close proximity. The more recent maps of Scotese & McKerrow (1990) show the localities separated by a wide ocean and about 30° latitude. The tightening and enlargement of the global database of Devonian plant fossil occurrences and ages may be one step towards a better understanding of the geography and climatology of these times.

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## REFERENCES CITED

Allen K. C. & Dineley D. L. (1988) - Mid Devonian to mid-Permian floral and faunal regions and provinces. *In* Harris A. L. & Fettes D. J. (eds.). The Caledonian-Appalachian Orogeny. *Geol. Soc. Lond. Special Publication*, 38, p. 531-548.

Ananiev A. R. (1960) - Studies in the Middle Devonian flora of the Altai-Sayan mountain region. *Bot. Zh*, 45 , p. 649-666 (in Russian with English summary).

Arrondo O., Cesari S. N. & Gutierrez P. R (1991) - *Frenguellia* a new genus of lycopods from the Early Carboniferous of Argentina. *Rev. Palaeobot. Palynol.*, 70, p. 187-197.

BANKS H. P. (1966) - Devonian Flora of New York State. *Empire State Geogram*, 4, p. 10-24.

BANKS H. P. (1980) - Floral assemblages in the Siluro-Devonian. *In* DILCHER D. L. & TAYLOR T. N. (eds.). Biostratigraphy of fossil plants. Dowden, Hutchinson and Ross, Stroudsberg.

BANKS H. P., BONAMO P. M. & GRIERSON J. D. (1972 ) - *Leclercqia complexa* gen. et sp. nov., a new lycopod from the late Middle Devonian of eastern New York. *Rev. Palaeobot. Palynol.*, 14, p. 19-40.

BATEMAN R. M. (1991) - Palaeoecology. *In* CLEAL, C. J. (ed.). Plant fossils in geological investigation : the Palaeozoic, Ellis Horwood, Chichester, UK, p. 34-116.

BENEDETTO G. (1980a) - Bivalvos Pensilvanianos de la Formacion Caño Indio, Sierra de Perijá, Venezuela. *Boletín de Geología*, 14, 26, p. 197-245, Caracas.

BENEDETTO G. (1980b) - Síntesis biostratigráfica del Paleozoico tardío de la Sierra de Perijá, Venezuela. *Anais Acad. Brasil. Ciencias*, 52, p. 827-839.

BENEDETTO G. (1984) - Les Brachiopodes devonicus de la Sierra de Perijá (Venezuela). *Biostratigraphie du Paléozoique (Brest)*, 1, p. 1-191.

BONAMO P. M., BANKS H. P. & GRIERSON J. D. (1988) - *Leclercqia, Haskinsia*, and the role of leaves in the delineation of Devonian lycopod genera. *Bot. Gaz.*, 149, p. 222-239.

BOWEN J. M. (1972) - Estratigrafia del pre-Cretáceao en la parte Norte de la Sierra de Perijá. *Mem. IV Congr. Geol. Venezolano*, II, p. 729-760.

CASAS J. E., MOODY J. M. & BERRY C. M. (1990) - Estudio palaeontologico de la Formacion Campo Chico (Devonico Medio-Superior). *Informes Tecnicos*, IT-10905, Maraven S.A., Caracas.

EDWARDS D. (1990) - Silurian-Devonian palaeobotany : Problems, progress and potential. *In* TAYLOR T. N. & TAYLOR E. L. (eds.) Antarctic Palaeobiology. Its role in the reconstruction of Gondwana. *Springer Verlag*, New York. p. 89-101.

EDWARDS D. & BENEDETTO G. (1985) - Two new species of herbaceous lycopods from the Devonian of Venezuela with comments on their taphonomy. *Palaeontology*, 28, 3, p. 599-618.

EDWARDS D. & BERRY C. M. (1991) - Silurian and Devonian. *In* CLEAL C. J (ed.). Plant fossils in geological investigation : the Palaeozoic, Ellis Horwood, Chichester, p. 117-153

FAIRON-DEMARET M. (1974) - Nouveaux specimens du genre *Leclercqia* Banks H. P., Bonamo P. M. & Grierson J. D (1972) du Givetian (?) du Queensland (Australia). *Bull. Inst. R. Sci. Nat.* Belg., 50, p. 1-4.

FAIRON-DEMARET M. (1980) - A propos des specimens déterminés *Protolepidodendron scharianum* par Kräusel et Weyland, 1932. *Rev. Palaeobot. Palynol.*, 29, p. 201-220.

FAIRON-DEMARET M. & BANKS H. P. (1978) - Leaves of *Archaeosigillaria vanuxemii*, a Devonian lycopod from New York. *Amer. J. Bot.*, 65 (2), p. 246-249.

FAIRON-DEMARET M. & REGNAULT S. (1986) - Macroflores dévoniennes dans le Nord du Maroc. *Ann. Soc. Geol. Belg.*, 109, p. 499-513.

GRIERSON J. D. & BANKS H. P. (1963) - Lycopods of the Devonian of New York State. *Palaeontogr. Am.*, 4, p. 220-295.

HECKEL P. H. & WITZKE B. J. (1979) - Devonian world geography determined from distribution of carbonates and related lithic palaeoclimatic indicators. *Sp. Pap. Palaeontology*, 23, p. 99-123.

HUEBER F. M. & BANKS H. P. (1979) - *Serrulacaulis furcatus* gen. et sp. nov., a new zosterophyll from the lower Upper Devonian of New York State. *Rev. Palaeobot. Palynol.*, 28, p. 169-189.

JANVIER P., THANH T. D. & GERRIENNE P. (1989) - Les placodermes, arthropodes et lycophytes des grès Dévoniens de Dô Son (Haïphong, Viêtnam). *Geobios*, 22 (5), p. 625-639.

KENRICK P., EDWARDS D. & DALES R. C. (1991) - Novel ultrastructure in the water-conducting cells of the Lower Devonian plant *Sennicaulis hippocrepiformis*. *Palaeontology*, 34, 4, p. 751-766.

KRÄUSEL R. & DOLIANITI E. (1957) - Restos vegetais das camadas Picos Devoniano Inferior do Piauí. *Minest. Agr. Dep. Nac. Prod. Miner. Div. Geol. Miner. Bull.*, 173, p. 7-19.

LESSUISE A. & FAIRON-DEMARET M. (1980) - Le gisement à plantes de Niaster (Aywaille, Belgique) : repère biostratigraphique nouveau aux bords de la limite Couvinien-Givetian. *Ann. Soc. Geol. Belg.*, 103, p. 157-181.

LIDDLE R.A. (1928) - The geology of Venezuela and Trinidad. *J. P. MacGowan*, Fort Worth. 552 pp.

LIDDLE R. A., HARRIS G. D. & WELLS J. W. (1943) - The Río Cachirí section in the Sierra de Perijá, Venezuela. *Bull. Amer. Palaeont.*, 27 (108), p. 269-375.

MEYEN S.V. (1987) - Fundamentals of palaeobotany. *Chapman and Hall*, London.

PETROSIAN N. M. (1968) - Stratigraphic importance of the Devonian flora of the USSR. *In* OSWALD D. H. (ed.). International Symposium on the Devonian System, Calgary, 1967. *Alberta Soc. Petro.Geol.*, Calgary, p. 579-586.

SANCHEZ T. M. & BENEDETTO G. (1983) - Paleoecologia, comunidades bentonicas y sucesion paleoambiental en el grupo Río Cachirí, Devonica, Sierra de Perijá, Venczuela. *Ameghiniana*, 20, 3-4, p. 163-198.

SCHECKLER S. E. (1986) - Floras of the Devonian-Mississippian transition. *In* BROADHEAD T.W. (ed.) Land Plants: notes for a short course, 15, University of Tennessee, p. 81-96

SCHECKLER S. E., BASINGER J. F. & HILL S. A. (1990) - Floristic evolution in the Devonian Okșe Bay Group of Ellesmere, Arctic Canada. *Amer. J. Bot.*, 77 (supplement), p. 93.

SCHWEITZER H.-J. & CAI C.-Y. (1987) - Beitrage zur Mittledevon-flora Sudchinas. *Palaeontogr. Abt. B*, 207, p. 1-109.

SCOTESE C. R. & MCKERROW W. S. (1990) - Revised world maps and introduction. *In* MCKERROW W. S. & SCOTESE C. R. (eds.) Palaeozoic palaeogeography and biogeography. *Geol. Soc. Lond. Mem.*, 12, p. 1-21.

SCRUTTON C. T. (1973) - Paleozoic coral faunas from Venezuela, II : Devonian and Carboniferous corals from the Sierra de Perijá. *Bull. Brit. Mus. Natur. Hist. Geol.*, 23, 4, p. 223-281.

SENKEVICH M. A. (1971) - New Devonian Lycopodiales. Materials on the Geology and Minerals of South Kazakhstan, 4, (29), *«Nauka» Kazakhskoi SSR*, p. 88-92.

STEIN W. E. & HUEBER F. M. (1989) - The anatomy of *Pseudosporochnus* : *P. hueberi* from the Devonian of New York. *Rev. Palaeobot. Palynol.*, 60, p. 311-359.

SUTTON F. A. (1946) - Geology of Maracaibo Basin, Venezuela. *Bull. Amer. Assoc. Petr. Geol.*, 30 (10), p. 1621-1741.

WEISBORD N. E. (1926) - Venezuelan Devonian fossils. *Bull. Amer. Paleont.*, 11 (46), p. 221-272.