Diversity and distribution of Devonian Protolepidodendrales (Lycopsida)

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A review of recent literature regarding Devonian Protolepidodendrales (Lycopsida) emphasises the progress that has been made in the understanding of this group of common fossils. They share complex microphylls, undifferentiated sporophylls and a presumed herbaceous habit. Maximum diversity occurred in the Middle and lowermost Upper Devonian. Usually only relatively well preserved material can yield determinative characters. The genera *Protolepidodendron, Colpodexylon, Haskinsia, Artschaliphyton, Minerodendron, Leclercqia, Archaeosigillaria* and a new genus are discussed. A regional survey demonstrates that *Leclercqia, Haskinsia* and *Colpodexylon* are widely distributed across Laurussia, Siberia and Kazakhstan with more sporadic occurrences in Gondwana. Endemic forms may be found in South China and South Africa during the Middle and early Late Devonian.

Key-words—Protolepidodendrales, Diversity, Lycopsida, Devonian.

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सारांश

डिवोनियन प्रोटोलेपिडोडेन्ड्रेल्स (लाइकॉप्साइडा) की विभिन्नता एवं वितरण

क्रिस्टोफर एम. बेरी

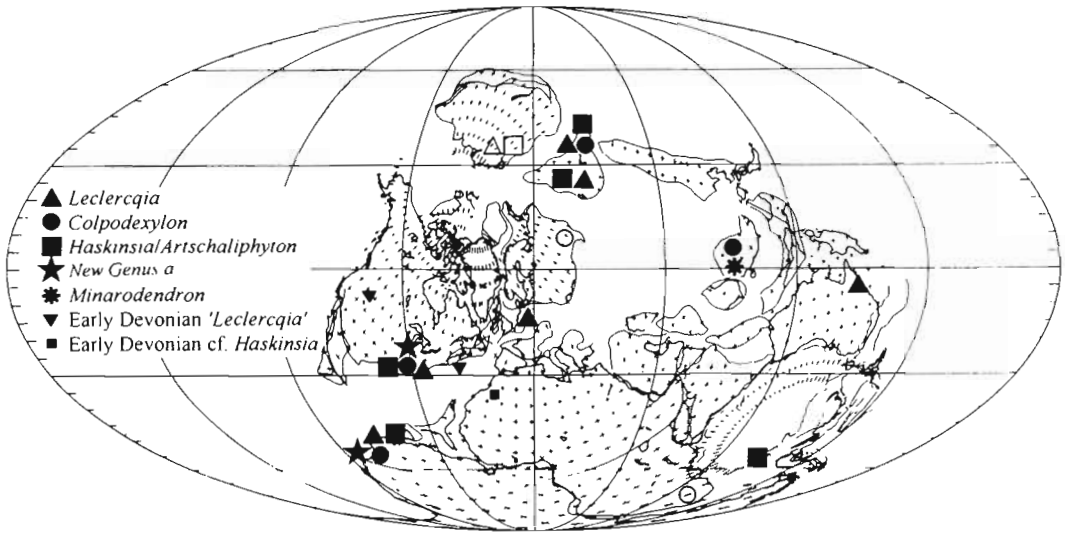
डिवोनियन प्रोटोलेपिडोडेन्ड्रेल्स से सम्बद्ध साहित्य की विशेष समीक्षा की गई है। इस समूह के अश्मित पौधों में जटिल सूक्ष्मपर्ण और एक जैसी स्पोरोफिल विद्यमान है तथा ये शाखीय स्वभाव के हैं। इनमें सबसे अधिक विभिन्नता मध्य एवं अधरितम् उपरि डिवोनी कल्प में हुई है। *प्रोटोलेपिडोडेन्ड्रॉन, कॉल्पोडेक्सीलॉन, हास्किन्सिआ, आर्टसचालिफाइटन, मिनरोडेन्ड्रॉन, लैकलर्किआ, आर्कियोसिजिलेरिया* एवं एक नई प्रजाति की इस शोध-पत्र में विवेचना की गई है। क्षेत्रीय सर्वेक्षण से प्रदर्शित होता है कि *लैकलर्किआ, हास्किन्सिआ* एवं *कॉल्पोडेक्सीलॉन* लॉरुसीआ, साइबेरिया एवं कजाखस्तान में दूर-दूर तक वितरित हैं।

IN 1960, Banks presented a summary of progress in research on Devonian lycopsids. The literature on this topic has grown considerably in the past thirty five years. This summary will focus on Protolepidodendrales Pichi-Sermoli. In addition, I include Archaeosigillariaceae Kräusel and Weyland because although fertile organs have not been demonstrated, and anatomically they may be more advanced, this family has similar morphological attributes (particularly complex leaf morphology — Berry & Edwards, in press b) which allow similar treatment. Members of the 'pre-lycopods' (Gensel & Andrews, 1984) and small 'arborescent' forms (neither of which category having complex leaf morphologies) are not taken into account. It will also pay attention to the palaeogeographic situation of the localities.

Stratigraphically well documented reports of Protolepidodendrales range from Emsian to Lower Frasnian. Other more uncertain reports, particularly those of *Frenguellia* (see below) reported from the Lower Carboniferous, require further examination.

PROGRESS ON TAXONOMY

Since 1944, a number of new genera and species have been described, many based on material originally attributed to genera such as *Protolepidodendron* and *Drepanophycus*. Attention has progressively focused on leaf morphology as a way of delimiting genera and species (Bonamo,



Text-figure 1—Localities of genera of herbaceous lycopsids. Hollow shapes indicate uncertain occurrences.

Banks & Grierson 1988), although aspects of the anatomy of the plants has not escaped attention (e.g., Grierson & Banks, 1983; Li, 1990). Protolepidodendrales (Pichi-Sermoli, 1958) are now believed to be made up of plants with helically arranged or pseudowhorled divided laminate or broad petiolate microphylls, undifferentiated sporophylls bearing globose or ellipsoidal sporangia in an adaxial position, and stems with an exarch coronate or lobed xylem strand.

Currently two families are recognised within the Protolepidodendrales. Protolepidodendraceae Kräusel & Weyland 1949 contains those members with a completely divided leaf, and Haskinsiaceae Grierson & Banks 1983 those with a broad blade attached to the stem by a petiole. Archaeosigillariaceae Kräusel & Weyland 1949 is currently regarded as a satellite taxon of Protolepidodendrales (Berry & Edwards, in press).

CONTRIBUTIONS TO INDIVIDUAL GENERA

Protolepidodendraceae

Protolepidodendron Kräusel & Weyland 1932

Protolepidodendron scharyanum was recognised on the basis of stem morphology and bifurcated leaves recorded by Krejci (1880). The name was validated by Kräusel and Weyland in 1932 (Bonamo, Banks & Grierson, 1988). With the discovery of the morphology of *Leclercqia complexa* from New York State, the leaf morphology has been questioned. Subsequent examinations have failed to confirm the presence of more complex leaves, and probably never will because of the poor preservation of the type specimen. Schweitzer and Cai (1987) considered that *Leclercqia* is a junior synonym of *Protolepidodendron*. However, given that *Protolepidodendron* is based on such a poor type specimen which fails to demonstrate distinctive characters, and *Leclercqia* is based on material for which both anatomy and morphology are understood in astonishing detail, such a viewpoint is unprovable, and defies the progress of the science. It is the consensus of the majority of workers that *Protolepidodendron* as a genus should be restricted to the type specimen (Fairon-Demaret, 1980; Bonamo, Banks & Grierson, 1988). *P. gilboensis* (Grierson & Banks, 1963) has yet to be re-examined in the light of present-day knowledge of the group. The original description of *P. kegeli* (Kräusel & Dolianiti, 1957), based on a single specimen, is inconclusive about the morphology of the leaf and therefore cannot be attributed to a genus using current methodology.

Leclercqia Banks, Bonamo & Grierson 1972

This genus was originally differentiated on the basis of the three dimensional five-tipped leaves (Banks, Bonamo & Grierson, 1972) of the type

species, *L. complexa*. Subsequently more details of its anatomy, and leaf morphology have emerged, particularly in respect of the possession of a ligule, and leaf segments have also been shown to divide occasionally to give up to seven tips (Grierson, 1976; Grierson & Bonamo, 1979; Bonamo, Banks & Grierson, 1988). Anatomically it possesses a xylem column with peripheral ridges of protoxylem. Spores of *Leclercqia* are the only examples well studied from a protolepidodendrid (Richardson *et al.*, 1993). This body of knowledge makes this the most completely known Devonian herbaceous lycopsid. Its geographic range has also extended considerably over the years (see palaeogeographic synthesis).

A number of other Lower Devonian specimens have assigned to this genus which have flat dining-fork shaped division of the five-tipped leaves rather than the three-dimensional trichotomy and two lateral dichotomies of *L. complexa* (Kasper, 1977; Kasper & Forbes, 1979). These plants certainly belong in a different species, and probably a different genus.

Colpodexylon Banks 1944

This genus was first recorded as two species from New York State. It is recognised by its leaves which divide in a flat trifurcation to give three segments, the middle one being the longest. There are presently two distinct forms of *Colpodexylon*. The first includes the type species *C. deatsii, C. trifurcatum* (Banks, 1944), *C. cachiriense* (Edwards & Benedetto, 1985), and *C. camptophyllum* (Berry & Edwards, 1995). The leaves of these species are difficult to tell apart, and it has been suggested that these species represent various samples in space and time from a population which was variable in time and geographical space rather than strictly defined biological entities (Berry & Edwards, 1995). Any observed 'leaf bases' or 'leaf cushions' are likely to represent differential compaction of stem tissues during preservation rather than life stem morphology. The second form has leaves in which the segments distal to the trifurcation are proportionally shorter than those in the first and also have more distinctly developed leaf bases. These include *Colpodexylon variabile* (Schweitzer & Cai, 1987) and *Colpodexylon coloradoense* (Berry & Edwards, 1995). Neither of these species has yet revealed gross anatomy and it will be interesting to discover if the anatomical characteristics of the type species, a deeply lobed primary xylem column, will be confirmed from this second group too.

Minarodendron Li 1990

Initially attributed to Protolepidodendron by Halle (1936) and Schweitzer and Cai (1987), Li created the new genus on the basis of the distinctive leaf morphology and details of the anatomy. The only presently recognised species, *M. cathaysiense*, has a leaf with serrate margins, and a trifurcate tip. The middle segment is angled downwards from the trifurcation, giving a three-dimensional structure rather than the typically flattened example of *Colpodexylon*. Anatomically, the plant contains tracheids with mainly scalariform multiperforate bordered pits which had not previously been recognised in Middle Devonian herbaceous lycophytes.

Haskinsiaceae

Haskinsia Grierson & Banks 1983

Drepanophycus colophyllus was transferred to be the type of *Haskinsia* on the discovery that leaves were petiolate with a broad lamina (Grierson & Banks, 1983). On the discovery of sagittate leaves in *H. sagittata* (Edwards & Benedetto, 1985) the type species was re-examined and also shown to have sagittate leaves (Bonamo *et al.*, 1988). *H. sagitatta* and *H. colophylla* may well be conspecific. A new species, *H. hastata*, has recently been described with hastate leaves (Edwards & Berry, a). Berry and Edwards also illustrated specimens of *Haskinsia* sp. which has larger leaves than any yet attributed to the genus. Anatomically the type species has a solid cylinder of metaxylem surrounded by longitudinal ridges of protoxylem. *Haskinsia* was regarded as a satellite taxon of the Protolepidodendrales by Thomas and Brack-Hanes (1984) and the family was not recognised. Following the description of fertile species from Venezuela (Berry & Edwards, in press) Haskinsiaceae can now be included within the order with certainty.

Artschaliphyton Senkevich 1971

Although the leaves of this species have not been illustrated photographically the original diagnosis allows this genus to be recognised to be very similar to *Haskinsia* (Berry & Edwards, in press). Leaves were broadly sagittate and petiolate. It has been suggested

that these two genera are synonymous, with *Artschaliphyton* having priority, but formal action must await examination of the type specimens (Berry *et al.,* 1993; Berry & Edwards, in press a). Indeed, specimens from Xinjiang, northern China, probably from the same continental plate as the type specimens of *A. unicum* from Kazakhstan, have been identified as *Haskinsia sagittata* by Cai and Wang (1995), reinforcing the ambiguity of delimitation of these genera.

Archaeosigillaria (Goppert) Kidston 1901

Like *Protolepidodendron, Archaeosigillaria* is based on a type specimen for which the leaf morphology is not understood. In a recent analysis of this problem, Berry and Edwards (in press b) have suggested that the genus be restricted to the type specimen. They have, however, made progress with the understanding of the nature of the hexagonal pattern which is recognised by most authors as the typical feature of the genus. It is essentially similar to that of *new genus a* (see below). In consequence, they can not confirm the assignation of any of the many species reported from around the world to this genus, and suggest that from the point of view of palaeogeographic analysis at least, this genus is redundant at present.

New genus a Berry and Edwards (in press b)

This genus was erected on the discovery of lycophytes with a hexagonal stem pattern and leaves which arise from a broad thick base to form a long tapering lamina with two small lateral teeth. Berry and Edwards were also able to recognise the basis of the hexagonal pattern, which is recognised at various levels in the stem. On the stem surface a pattern of hexagonal grooves delimits the adjoining swollen leaf bases. Within the outer cortical regions of the stem there are also parenchymatous ovals beneath each leaf base which can give the appearance of a hexagonal pattern in various preservational states. The specimens attributed to *Archaeosigillaria vanuxemii* by Fairon-Demaret and Banks (1978) may belong to this genus.

REGIONAL SYNTHESIS

Laurussia-North America

Herbaceous Devonian lycopsids have been most intensively studied in North America, and particularly New York State. Lower Devonian specimens of *Leclercqia* have been reported from New Brunswick and Maine (Kasper, 1977; Kasper & Forbes, 1979) but require reassessment before realistic taxonomic assignment (see above). *Leclercqia complexa, Haskinsia colophylla, Colpodexylon deatsii* and *C. trifurcatum* have all been described in detail from Givetian to lower Frasnian strata (see references above). *New genus a* was reported from the Givetian (Berry & Edwards, in press b). Extensive plant assemblages of Eifelian to Frasnian age from Ellesmere Island, Arctic Canada, have failed to yield herbaceous lycophytes (Scheckler *et al.,* 1990).

Laurussia-Europe and Russian Platform

The lack of a diverse herbaceous lycophyte flora in the Middle Devonian deposits of Europe is notable. *Leclercqia* has been reported from Germany and Belgium (Fairon-Demaret, 1980, 1981). From the lower Frasnian of the Ural Mountains (Russian Platform) Tchirkova-Zalesskaa (1957) reported *Lepidodendropsis priscus* which from the line drawing appears to have trifurcate leaves and stem characteristics similar to *Colpodexylon cachiriense* Edwards and Benedetto. A leafless protolepidodendroid stem was reported from Scotland by Lang (1926). Neither *Lycopodites runcariana* Stockmans 1965 nor *L. lindlarensis* Schweitzer 1974 has distinctive characters, lacking divided leaves. Neither is likely to be a member of Protolepidodendraceae.

Siberia

Pictures attributed to *P. scharyanum* (Ananiev, 1960) from the Altai-Sayan mountains bear a strong similarity to unprepared *Leclercqia*. *Artschaliphyton* has been reported from the North West Siberian platform (Iurina, 1988).

Kazakhstan

The only lycophytes reported from Kazakhstan which bear complex microphylls are the type material of *Artschaliphyton* (Senkevich, 1971) and specimens of *P. scharyanum* again bearing a

similarity to *Leclercqia* (and have indeed been identified as such; M. Fairon-Demaret - pers. com).

Collections from Xingxiang, northern China, probably belong with this palaeocontinent, in the same way that Pridoli assemblages from the same area are believed to originate from the Kazachstan plate (Cai *et al.*, 1993, 1995). The Middle Devonian fossils include *Haskinsia sagittata, Colpodexylon* sp. (Cai & Wang, 1995), and probable *Leclercqia (P. scharyanum* of Sze, 1960, *P. falcatum* of Dou & Sun, 1983).

South China

The south China assemblages include the 'short-tipped' *Colpodexylon variabile,* with its well defined expanded leaf bases otherwise uncharacteristic of the genus, and the endemic *Minarodendron. Leclercqia* and *Haskinsia/Artschaliphyton* have not yet been recorded there. Janvier *et al.* (1989) reported badly preserved fossils from north eastern Vietnam which bear a strong resemblance to more conventional *Colpodexylon* specimens, although leaf morphology is not well enough preserved to be completely certain of the generic assignment. This locality lies in complex terranes between the South China and Indochina plates.

Gondwana-South America

With the exception of Venezuela little progress has been made in South America in terms of the discovery of herbaceous lycophyte material. One interesting plant to be discovered in recent times is *Frenguellia* (Arrondo *et al.*, 1991). This plant shows all the characters of being a Devonian herbaceous lycophyte. It has a typical protolepidodendroid stem, divided leaves, and sporangia adaxially mounted on apparently unmodified leaves. It is based on a number of specimens from several localities, some of which are regarded to be Lower Carboniferous in age, usually based on lithological correlation. Specimens from the type locality demonstrate trifurcate leaves, and other specimens appear to have 5-divided leaves with the more proximal lateral tips pointing back towards the leaf base (Arrondo *et al.*, 1991). The apparent complexity of these leaves may result from overlap of adjacent leaves and fortuitous fracture. Yet further specimens (Morel *et al.*, 1993), which I have been able to study, demonstrate very clear protolepidodendroid-type sporangia attached in the adaxial position. The distal parts of the leaf, although undoubtedly divided, are not well preserved in the coarse matrix. It is possible that a number of different plants of different ages have been given the name *Frenguellia*. However, due to the tectonic complexities of the region and the indirect basis of the age determinations it is altogether possible that some of these plants might be Middle Devonian in age.

Gondwana - South Africa

Anderson and Anderson (1985) produced a useful summary of the Devonian lycophytes. Due to the typical coarse sediments of this region, none has proven leaf morphology, although some appear to have preserved leaves. Some species illustrated may not indeed be lycopsid. None can be placed in any of the genera mentioned above with certainty at present, including all those many formerly attributed to *Archaeosigillaria* (Berry & Edwards, in press b). Specimens of *Archaeosigillaria* cf. *A. picosensis* (Chaloner *et al.*, 1980) are distinctive, the only similar specimens reported are those of Kräusel and Dolianiti (1957) from Brasil. Together with *Archaeosigillaria devreisii* these may indicate a distinctive lycophyte assemblage for high southern latitudes. *Palaeostigma sewardii,* which is probably not a lycophyte, is also known only from South Africa and Brazil.

One specimen which has been reported many times is British Museum V. 236. Its original illustration by Seward (1903) shows typical lycopsid stem with long leaves, which was therefore regarded to be a "Lepidodendrid stem". It has been until present regarded as a paratype of *Haplostigma irregulare* (Seward, 1932; Plumstead, 1967). In uncovering the leaves, I was able to show that they are considerably longer than illustrated (up to 20 x 0.9 mm). Some fold back at the limit as shown by Seward, and thin abruptly at the same time. This suggests that these leaves were divided, and are folded back at the point of division, but the specimen is too poorly preserved to be conclusive. I refered this specimen to cf. *Colpodexylon* (Berry, 1993).

Such diversity of lycophyte axes suggests that when leafy specimens in finer sediments are found a number of genera and species will be shown to have made up the herbaceous lycophyte element of the South African flora.

Gondwana-North Africa

Lejal-Nicol (e.g., 1975) and Lejal-Nicol and Massa (1980) reported diverse assemblages of lycopsid stems impressions and compressions attributed to both herbaceous forms (e.g., *Protolepidodendron*) as well as larger types from the Lower Devonian of Libya. None of the identities of the herbaceous forms can be confirmed using leaf morphology, and the dates have now been shown to be incorrect or unsupported (Streel *et al.*, 1990).

Fairon-Demaret and Regnault (1986) reported cf. *Haskinsia* from sediments dated as Emsian on the basis of conodont ages from North Marocco.

Saudi Arabia

Forey *et al.* (1992) mention a small leafless indeterminate lycopsid stem which I suggested might derive from an *Haskinsia* or *Colpodexylon (cachiriense)*-like plant. It could equally well derive from *Leclercqia, Minarodendron* or an as yet unidentified genus. However as the Jubah Sandstone is considered Emsian in age, it demonstrates with the Moroccan example (above) the presence of probable early Protolepidodendrales in northern Gondwana matching the Lower Devonian occurrence of *Leclercqia* in North America.

Gondwana-Australia

The only record from Australia remains that of *Leclercqia complexa* from the Givetian of the Burdekin Basin, Queensland (Fairon-Demaret, 1974).

Gondwana-Antarctica

Most of the lycophytes reported from the Devonian of Antarctica are leafless (Edwards, 1990; McLoughlin & Long, 1994). However Edwards (1990) suggested that leafy specimens named *Drepanophycus schopfii* by Grindley *et al.* (1980) are deltoid and petiolate and more likely to be attributable to *Haskinsia*.

Venezuela

The diverse assemblages of western Venezuela (Berry *et al.*, 1993) have yielded *Colpodexylon cachiriense, C. camptophyllum* and *C. coloradoense* (Edwards & Benedetto, 1985; Berry & Edwards, 1995), *Haskinsia sagittata, H. hastata, H.* sp. (Edwards & Benedetto, 1985; Berry & Edwards, in press a), *Leclercqia* cf. *complexa* (Berry, 1994) and *new genus a* (Berry & Edwards, in press b).

PALAEOGEOGRAPHIC SYNTHESIS

There is growing evidence for a widespread *Leclercqia/Colpodexylon/Haskinsia (Artschaliphyton)* lycopsid flora throughout much of Laurussia, Kazachstan, Siberia, and elements of this in eastern Gondwana.

The only markedly different assemblage is that in South China, where *Minarodendron* and as yet unpublished lycopsids (Li Chengsen pers. comm.) are endemic and the only specimens of a Laurussian lycopsid (*Colpodexylon*) are the most different from the original concept of the genus. The lack of diverse herbaceous lycopsid assemblages in Europe (especially Belgium and Germany where Middle Devonian assemblages are otherwise well developed), Spitzbergen and Arctic Canada is noteworthy. The reason for their absence is not readily apparent, but may be some sort of facies control — this must await a separate study. The lack of well preserved material from South Africa may also hide some regional differentiation.

New genus a is presently restricted to New York State and Venezuela, although this may be due to its recent recognition, and it may "spread" in the future.

Previous authors have not been able to recognise marked provincialism in Middle and early Late Devonian floras (e.g., Meyen, 1987; Allen & Dinely, 1988; Edwards & Berry, 1991). On close inspection of the evidence it is tempting to suspect that this may be due to 'shoehorning' of fossils into pre-existing taxa. Certainly the example of the Lower Devonian Posongchong Formation in South China is informative where many species originally placed in originally Laurussian taxa such as *Zosterophyllum* have on closer inspection turned out to represent new and sometimes bizarre endemic forms (see Cai & Wang, 1995 for a summary). Certainly new discoveries from China demonstrate the presence of endemics in the Middle Devonian (e.g., Li & Hs, 1987). Herbaceous lycophytes are an interesting test of phytogeography because over the last few years a 'modus operandi' has been established which makes it very easy to verify well presented reports. This involves the detailed preparation, photography and publication of details of leaf and stem morphologies. Although this method of working and publication has yet to be

adopted world-wide, the present impression is that a more-or-less uniform flora of Protolepidodendrales characterised the majority of the palaeocontinents. It is a major challenge for the future to raise this level of confidence in taxonomic assignment in other major groups of Middle and Upper Devonian plants.

Edwards and Benedetto (1985) suggested that herbaceous lycophytes may have been tolerant of a range of climates. Edwards (1990) further 'very tentatively' suggested that high-latitude vegetation was dominated by herbaceous lycopsids in the Middle to early Late Devonian and was of lower diversity than the vegetation of lower latitudes. The majority of occurrences from high southern palaeolatitudes do not have preserved leaves (when they do they suggest affinities to Laurussian taxa such as the Antarctic *Haskinsia* and South African cf. *Colpodexylon*). The preservation of the fossils is therefore not as good as at the best of the Laurussian sites, where the tendency is to ignore lycopsids with no preserved leaves. In my mind it is unresolved as to whether this apparent palaeogeographical distribution of lycopsids is caused by taphonomy, the lack of suitable deposits, the low number of discovered high latitude sites, or a genuine pattern.

Finally the palaeogeographic situation of the Venezuela assemblage remains problematical. The assemblages of Venezuela and New York State are similar at the generic level, and even contain species in common. This similarity can be considered to either reflect expression in the fossil record of a widespread flora, or because of close geographical proximity. The latter possibility is supported by geophysical evidence suggesting that the localities in Venezuela are located within an area of displaced terranes accreted to the Guyana shield probably during the collision of north and south America during the formation of Pangea (Restropo & Toussaint, 1988), and might therefore have a Laurussian rather than Gondwanan origin. On the other hand, the widespread distribution of many elements of the Venezuelan assemblages might otherwise suggest that the taxonomic similarities of assemblages is not of significance. Only a detailed analysis of the geological and palaeontological (plant, invertebrate and fish) evidence is likely to give a convincing answer to this question.

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