Three dwarf lycophytes from the Carboniferous of Argentina*)

S. Archangelsky, C. L. Azcuy and R. H. Wagner

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Impressions of the bark of two small lycophytes, *Bumbudendron paganzianum* gen. et sp. nov. and *Bumbudendron nitidum* sp. nov., are described from middle Carboniferous shales in the Sierra de Paganzo. Lepidodendroid leaf cushions with a well-developed leaf scar showing a single trace, and the presence of a fertile branch structure, invite comparison with *Bodeodendron/Sporangiostrobus* of the contemporaneous equatorial belt. The presence of an infrafoliar bladder provides the main distinguishing character. Small stem impressions with a thick cuticle are recorded of the simple lycophyte *Malanzania nana* gen. et sp. nov. which has false leaf scars corresponding to spiny excrescences. These remains have been found in the middle Carboniferous of Malanzán in the Sierra de los Llanos. They are comparable to *Palaeostigma* of Brazil and South Africa. The cuticle shows approximately isodiametric cells flanking the holes corresponding to false leaf scars, and more elongate cells in a fan-shaped disposition occupying the wide areas separating these scars.

The rather poor record of Pennsylvanian lycophytes in western South America is analysed, the result being that there may be two additional elements, viz. *'Lepidodendropsis' peruviana* (Gothan) Jongmans and *'Cyclostigma' pacifica* (Steinmann) Jongmans. The generic names of these taxa have been misapplied and a revision of these two species is recommended.

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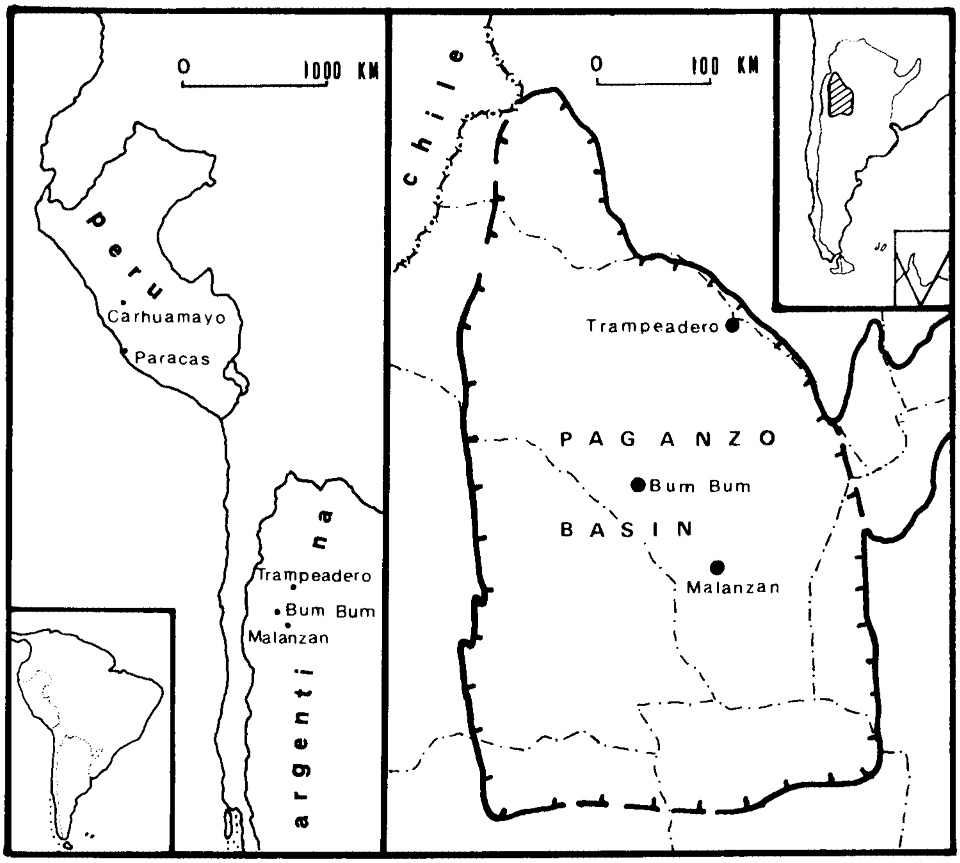

Fig. A. Maps showing the position of the South American localities discussed. New species are described from Bum Bum and Malanzán localities in the Paganzo Basin. All localities are in La Rioja Province (provincial boundary shown). Inset shows location of Paganzo Basin.

Introduction

Carboniferous lycophytes have been recorded only occasionally from Gondwanaland, and this is particularly true of Pennsylvanian material. A recent summary of Pennsylvanian floras from Australia (Morris, 1975) lists only three lycophyte species from the so-called *Rhacopteris* Flora, viz. *Cyclostigma australe* Feistmantel, *Lepidodendropsis steinmanni* Jongmans and *Sigillaria (Clathraria)* sp. nov. The latter has been figured and described by Morris, and refers to the imprint of the bark of a small lycophyte with spirally arranged, transversely oval leaf scars showing a double leaf trace and a pair of parichnos scars. It is clearly not a species of *Sigillaria* and probably represents a new genus. Lycophyte remains were also described from the Carboniferous of Perú (Jongmans, 1954; Doubinger & Alvarez-Ramis, 1980), viz. *Cyclostigma pacifica* (Steinmann) Jongmans, *?Lepidodendropsis (Lepidodendron) lissoni* (Steinmann) Jongmans, *Lepidodendropsis devoogdi* Jongmans, and *Lepidodendropsis steinmanni* Jongmans. Although the age of this flora has been given as Mississippian, there is still an element of doubt as to whether it should not rather be attributed to the early Pennsylvanian. The number of taxa present may also be subject to discussion and the generic names employed are subject to reservation (compare p. 31).

There have been occasional records of Pennsylvanian lycophytes from Argentina, but their preservation is generally poor and the identifications are questionable (compare p. 28).

The new material described in the following pages has been obtained almost exclusively from two localities in the eastern part of the Paganzo Basin, corresponding to the Sierras Pampeanas of west-central Argentina (Fig. A). A preliminary report on this material has been given by the writers in 1978. Specimens described as *Bumbudendron paganzianum* gen. et sp. nov. and *Bumbudendron nitidum* sp. nov. were collected by the second and third authors, in company with J. Morelli of the University of Buenos Aires, from the locality of Bum Bum in the Sierra de Paganzo, near the town of Patquía, La Rioja Province. These remains occur together with abundant *Rhacopteris ovata* auct. (non McCoy) and rarer *Paracalamites* sp., *Cordaites* sp., *Cordaicarpus* sp., and *Sphenopteris* sp. They are found as imprints on thinly bedded shales which are partially haematized. The plant bed is 7 cm thick. The haematization has allowed relatively large pieces to be collected from a fine-grained rock which would otherwise have disintegrated into small fragments in this area of desert weathering. The shales are interpreted as a lacustrine deposit representing the flooding of an area of local vegetation as indicated by the discovery of a small lycophyte stump standing upright in the shales and infilled by a coarser overlying deposit. This stump, a few centimetres in diameter (Fig. 1), is that of a small plant, probably not in excess of a few metres tall. The floated lycophyte remains occur as imprints of the outer bark. Little decortication seems to have taken place before these remains were imprinted on the fine mud of the lake bottom, and the inference is that these formed part of the local vegetation. The outline of the leaf cushions is almost invariably well-preserved, whereas the leaf scars are sometimes preserved and sometimes only partially visible or almost entirely effaced. Where the outline of the leaf scar is only partly visible, the shape of an infrafoliar bladder appears. This apparent-

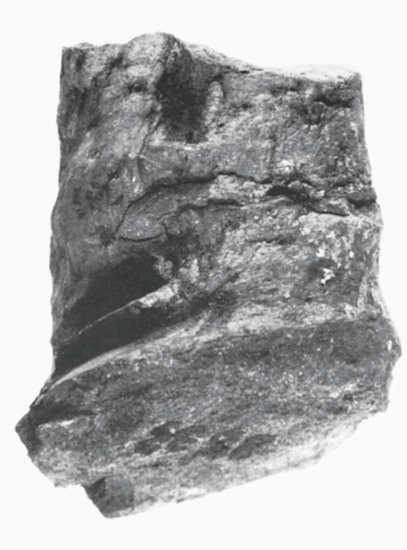

Fig. 1. Lycophyte stump standing upright in the shales, infilled by coarser overlying sediments, approximately natural size.

ly marks a subepidermal level. The grain of the rock is sufficiently fine to show the imprint of cellular tissue which displays larger, almost isodiametric cells for the leaf scar area and narrower, more elongate cells for the leaf cushions as well as for the infrafoliar bladders. No organised vegetable matter has been preserved.

The second generic category of lycophyte described in the present paper, i.e. *Malanzania nana* gen. et sp. nov., has been collected by the first author and his colleague, R. Leguizamón, from siltstones belonging to a lake fill of Pennsylvanian age in the vicinity of Malanzán, in the Sierra de los Llanos, near the eastern margin of the Paganzo Basin. This locality is also in the province of La Rioja. *Malanzania nana* occurs as imprints of the outer bark together with a thick cuticle. The imprints show a smooth bark with widely spaced, subcircular, small false leaf scars. This lycophyte is one of the less common elements in a drifted assemblage which comprises also *Botrychiopsis weissiana* Kurtz, *Bergiopteris insignis* Kurtz, *Fedekurtzia argentina* (Kurtz) Archangelsky, *Vojnovskia argentina* Archangelsky & Leguizamón, *Paulophyton* sp., *Ginkgophyllum diazii* Archangelsky & Arrondo, *Cordaites riojanus* Archangelsky & Leguizamón, *Cordaites* spp. (2 species).

The material has been lodged in the collections of the Centro de Investigaciones en Recursos Geológicos (CIRGEO) in Buenos Aires. All numbers are prefixed PB which identifies the palaeobotanical collection. Duplicate material has been donated to the Rijksmuseum van Geologie en Mineralogie, Leiden, The Netherlands.

Acknowledgements

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Systematic descriptions

Bumbudendron gen. nov.

Type species — *Bumbudendron paganzianum* sp. nov.
Derivatio nominis — Bum Bum section in the Sierra de Paganzo, La Rioja, Argentina.

Diagnosis — Small lycophytes with fusiform, spirally disposed leaf cushions separated by shallow furrows showing a fine, irregular, longitudinal ornament. Phyllotaxis lepidodendroid. Leaf scars in the upper third of leaf cushions. A single leaf trace occurs in a nearly central position in the scar. Infrafoliar bladder situated below the leaf trace, and underlying the lower part of the leaf scar as well as the adjacent part of the leaf cushion. Sporophylls inserted perpendicularly on the stem, reflexed in c. 90^0 and carrying a relatively small, sessile sporangium in proximal position.

Bumbudendron paganzianum sp. nov.
Figs. 2 - 6.

Derivatio nominis — The Paganzo Basin in west-central Argentina.
Syntypes — CIRGEO PB 205, 207, 208, 209, 211, 211bis.
Additional specimens — CIRGEO PB 206, 210.
Type locality — La Rioja province (Argentina), Bum Bum section, Lagares (= Tupe) Formation, locality 33.

Diagnosis — Stems at least up to 3.4 cm wide, with fusiform leaf cushions in a low spiral, at an angle of c. 35^0 (lepidodendroid phyllotaxis); intervening furrows shaped as relatively wide and flat interareas showing a clearly marked ornament consisting of small, longitudinal wrinkles. Leaf cushions sharply delimited at the apex and along the sides but merging into the interarea at the base. Leaf cushions smooth, with a nearly pentagonal leaf scar showing a rounded arch for the three upper sides and two convergent lower sides. Leaf scar in subapical position and occupying the entire width of the cushion. Leaf trace simple and situated just below the centre of the leaf scar. Lanceolate infrafoliar bladder overlaps the leaf scar area up to the leaf trace, and extends downwards almost to the base of the leaf cushion. The infrafoliar bladder has a keeled appearance. It shows up as a faint outline in the upper part which overlaps the lower half of the leaf scar, and is more clearly visible in the adjacent area of the leaf cushion, particularly with regard to the 'keel'. Where decortication has advanced to the extent of effacing the lower part of the leaf

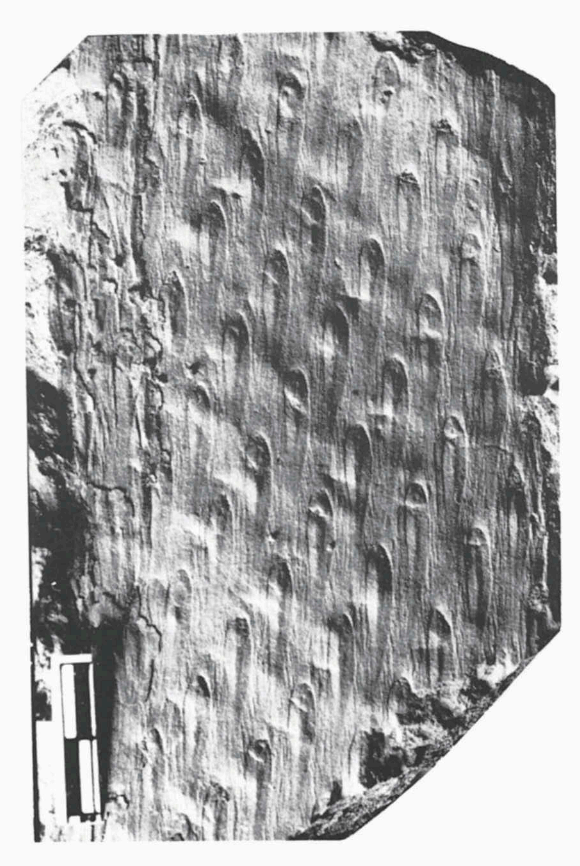


Fig. 2. *Bumbudendron paganzianum* gen. & sp. nov., CIRGEO PB 211 (syntype), stem fragment, × 2.

scar (up to the position of the vascular bundle), the upper part of the leaf scar is marked as a subtriangular area which is somewhat smaller than the original top half of the leaf scar. The infrafoliar bladder shows up more clearly in these somewhat decorticated leaf cushions. The presence of both complete leaf scars and incomplete ones has been noted on single specimens of bark, and it may be assumed that even slight decortication has been capable of largely effacing the leaf scar. No ligule pit has been observed.

Cellular tissue of the leaf scars shows almost isodiametric cells without apparent organisation (i.e. cells below the level of an abscission layer), whilst the leaf cushions show rather narrower, more elongate cells, at least twice as long as they are wide.

Single-veined sporophylls are inserted at approximate right angles to some of the stem (or branch) fragments; they are reflexed in c. 90^0 to form a distal lamina which overlaps those above. Sporophylls are keeled and show a slight spur in downward direction where the distal lamina projects upwards. Single, relatively small sporangia (approximately 3/4 length of the horizontal lamina), which are oval in longitudinal compression, are found sessile on the adaxial part of the sporophyll.

Description of syntypes — The most complete specimen (PB 211) is 3.4 cm wide. It shows a lepidodendroid phyllotaxis with regular parastichies (orthostichies are not apparent) (Fig. 2). The leaf cushions are elongate fusiform with the maximum width in the top half and sometimes near the apex. There is a gradual narrowing downwards, but the width is sometimes maintained a little beyond halfway down the length. The outline of the leaf cushion is clearly marked in the top half but fades in the lower half where it merges into the ornamented interarea separating it from the adjacent leaf cushions. However, the areas of leaf cushion are always distinguished by the absence of ornament and the presence of a cell pattern imprinted on the shale. The leaf scar is in a subapical position and shows subpentagonal, subtriangular or subcircular shapes in successive stages of decortication. The leaf trace is almost in the centre of the complete leaf scar. An infrafoliar bladder is visible as an elongate triangular, 'keeled' area, with the base of the triangle occupying the lower half of the leaf scar (up to the vascular bundle). The interarea between leaf cushions shows small longitudinal wrinkles which sometimes appear anastomosed and which generally converge upon the apices of leaf scars. These interareas, which follow the spiral of phyllotaxis, are rarely of the same width as the leaf cushions and generally a little narrower.

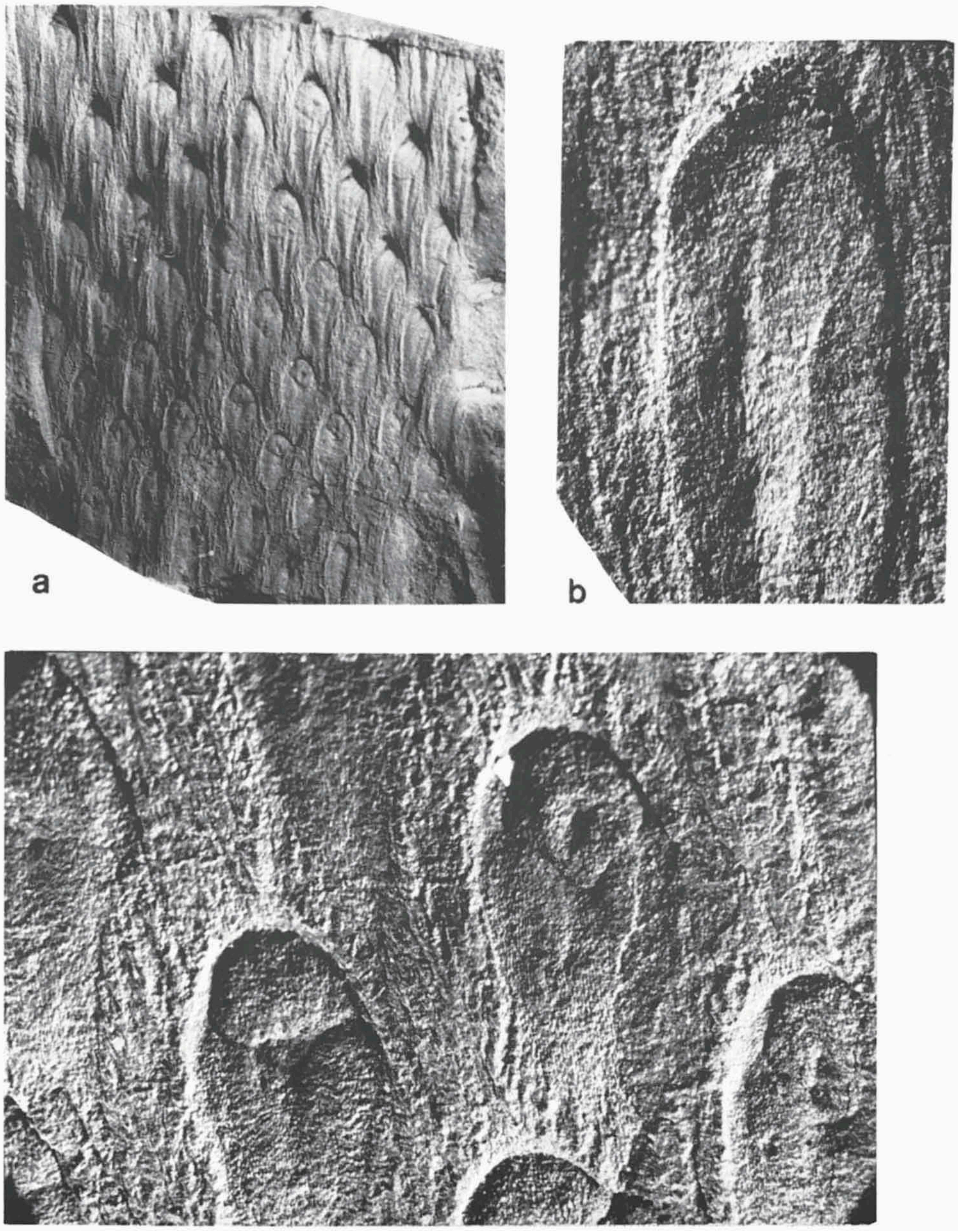
This specimen, in conjunction with some additional, more fragmentary pieces (PB 205, 207, 208, 209), shows the relatively flat nature of the surface of the *Bumbudendron paganzianum* stem on which only the upper parts of the leaf cushions formed slightly elevated areas (Figs. 3a - d).

All these specimens show a clearly marked cellular texture on both the leaf cushions and scars, but rarely on the interarea where the ornament prevails. The relatively large, almost isodiametric cells in the area of the leaf scar contrast with the narrower, more elongate cells visible on the remainder of the leaf cushion. The infrafoliar bladder also shows elongate cells which are most clearly marked in the central part of the bladder and which are only slightly different to those of the adjacent leaf cushion area. Among the rugosities of the interarea between leaf cushions it is possible to discern elongate cells of the same kind as occur in the cushions. These cells are all regarded as subepidermal.

Specimen PB 209 shows the same shape and separation of leaf cushions as well as adherent sporophylls on what appears to be a fertile branch or stem (Fig. 4a). The sporophylls are inserted at angles of 70^0 to almost 90^0 on a relatively wide stem. They are slightly decurrent at the point of insertion and possess an arcuate shape as a result of reflexing. The limb seems rather fleshy, with a minimum width of 2.5 mm which is certainly less than the real width since it occurs in longitudinal compression. The imprint of the vein is not clearly marked, but this is probably a matter of preservation. The imprint of sessile sporangia (Fig. 4b) shows that there is a single sporangium per sporophyll and that the length of the sporangium is appreciably less than that of the horizontal lamina. In longitudinal compression the sporangium is 3 mm long and 1 mm high. It has an oval shape. The distal lamina is longer than the proximal part of the sporophyll and its maximum length, as measured on this specimen, is 11 mm. The distal lamina appears to be broken and its real length is therefore regarded as being in excess of 11 mm. It is clear that the distal laminae of successive sporophylls overlapped. A compression border has been observed along the stem of the specimen in hand.

Another specimen (Figs. 5a - d) with attached sporophylls (PB 205) shows various successive laminae with a vertical separation of about 5 mm. These sporophylls are inserted perpendicularly and are reflexed in 90^0, the distal laminae overlapping each other slightly (Figs. 5c, d). There is one sporangium per sporophyll, 4 mm long and 1.5 mm high, whilst the proximal part of the sporophyll, on which the sporangium rests, is 5 mm long. The sporophyll lamina is at least 2 mm wide and apparently possesses a single vein, although this cannot be observed clearly. The distal lamina is curved, tongue-shaped.

Specimen PB 210, with a stem 3.4 cm wide, also shows some sporophylls with a limb of at least 1 mm width and possessing a simple vein. The interarea between the leaf cushions of this specimen is as wide as or even wider than the

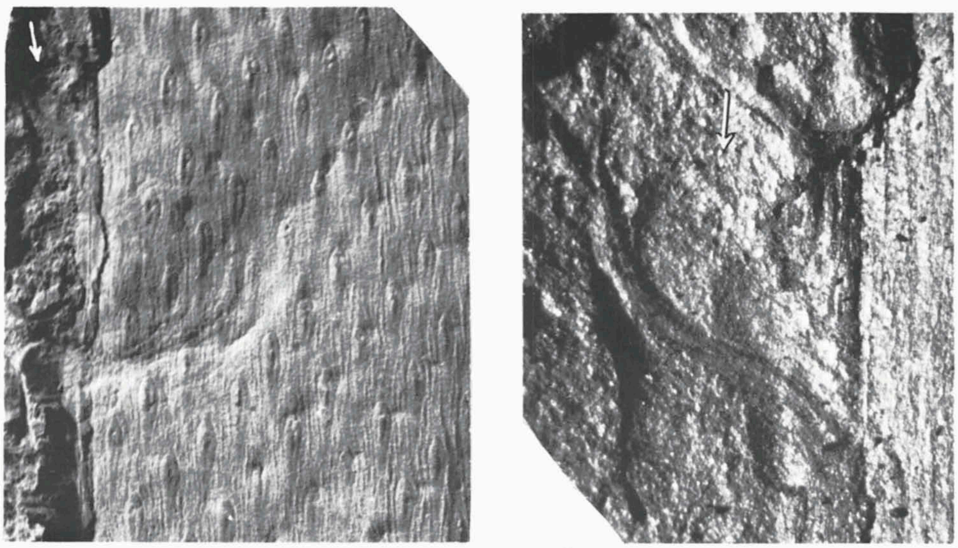


a b

c

d

Fig. 3. *Bumbudendron paganzianum* gen. & sp. nov., CIRGEO PB 207 (syntype); a: latex replica showing distribution of leaf cushions and interareas, × 3; b - d : details of leaf scars, × 20.



a b

Fig. 4. *Bumbudendron paganzianum* gen. & sp. nov., CIRGEO PB 209 (syntype); a: general aspect, × 2; b: detail of sporophyll bearing a sporangium, × 7. Arrows point to sporangium.

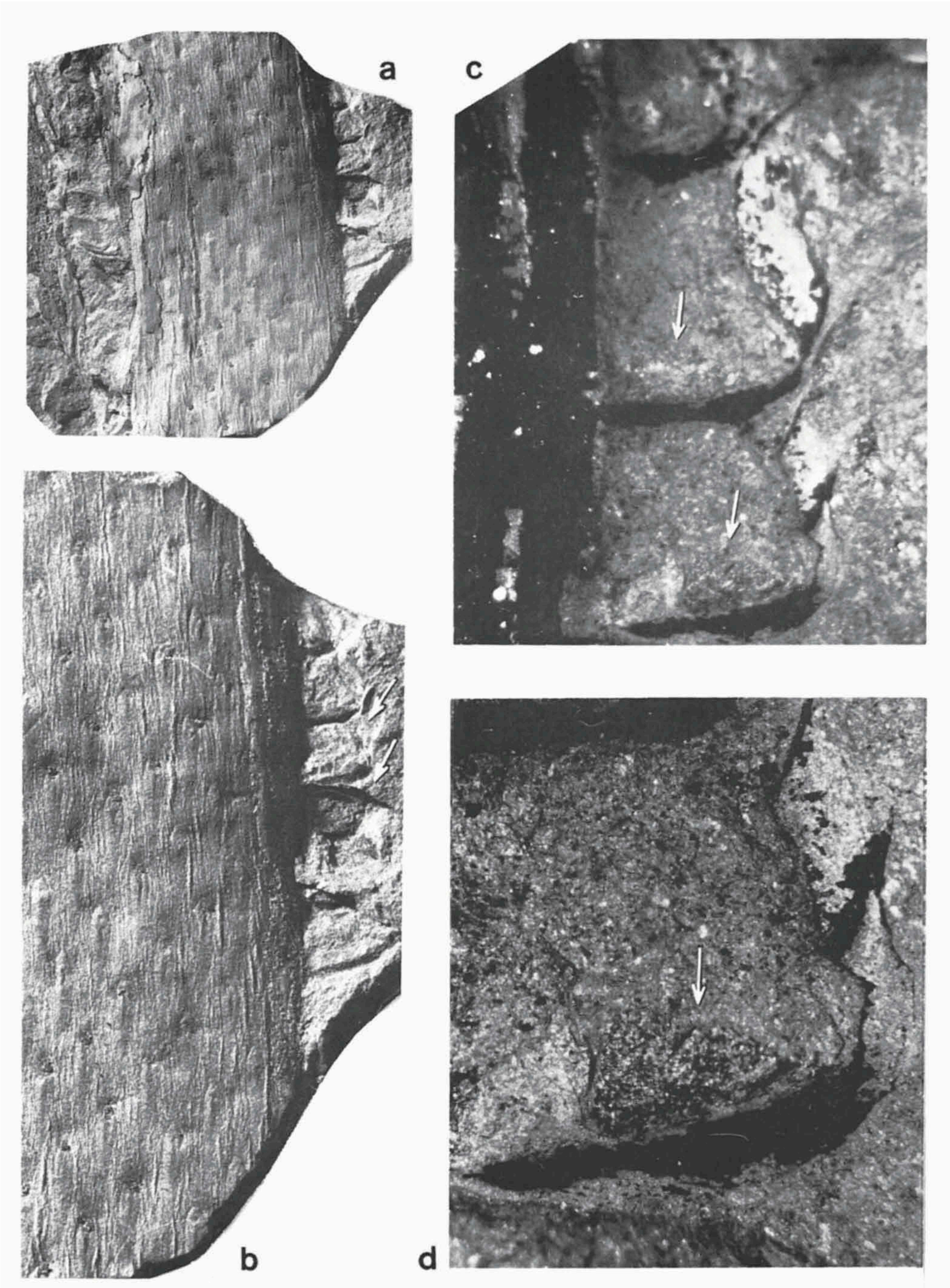


Fig. 5. *Bumbudendron paganzianum* gen. & sp. nov., CIRGEO PB 205 (syntype); a: general aspect, × 1; b: disposition of sporophylls, × 2; c: detail showing sporophyll shape, × 7; d: detail showing sporangium, × 14. The photographs of Fig. 5 c, d were taken of a specimen covered with xylol. Arrows point to sporangia.

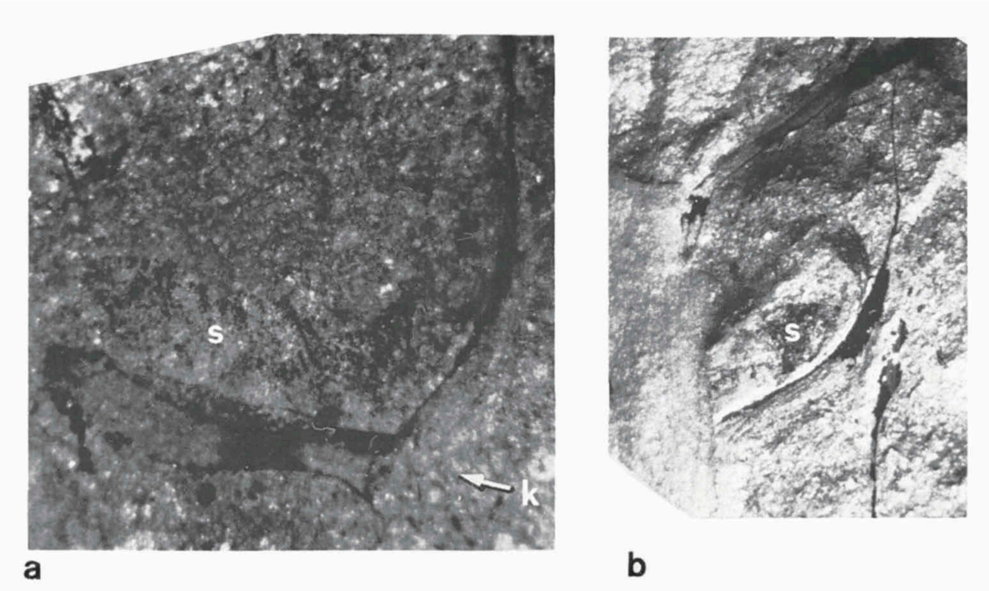


Fig. 6. *Bumbudendron paganzianum* gen. & sp. nov., CIRGEO PB 208 (syntype); a: cross section of sporophyll with an oval sporangium in the proximal part; note the well developed heel on the abaxial side (arrow), × 14; b: another sporophyll with sporangium, × 7; s = sporangium, k = heel.

cushions. The ornament of these interareas is relatively prominent.

Specimen PB 207 is more decorticated and shows well-marked infrafoliar bladders. Specimen PB 208 (Figs. 6a, b) shows a sporophyll in cross section with an oval sporangium on the proximal part. This sporophyll displays a well-developed heel on the abaxial side (Fig. 6a). It coincides with the reflexing in 90^0 of the distal lamina and clearly represents the minor branch of a fundamental dichotomy.

In all these fertile specimens it is extremely difficult to establish the exact width of the sporophyll, since the longitudinal compression is likely to simulate a narrower lamina than is actually present. The longitudinal compression of the sporangia also makes it impossible to determine their width. The thickness of the sporophyll lamina may also be subject to modifications as a result of compression. However, it appears that the lamina is approximately one third as thick as the vertical dimension of a sporangium.

	CIRGEO coll. nos		
Measurements in mm	PB 211	PB 209	PB 210
maximum width of leaf cushion	1.5 - 2	1.4	1.5
maximum length of leaf cushion	7.8	5	5 - 6
width of leaf scar	2.5 - 3	2	1.5

Bumbudendron nitidum sp. nov.
Figs. 7 - 8

Derivatio nominis — nitidus (Lat.) = handsome.
Holotype — CIRGEO PB 201.
Additional specimens — CIRGEO PB 192-200, 202.
Type locality — as for *Bumbudendron paganzianum* (Bum Bum loc.33).

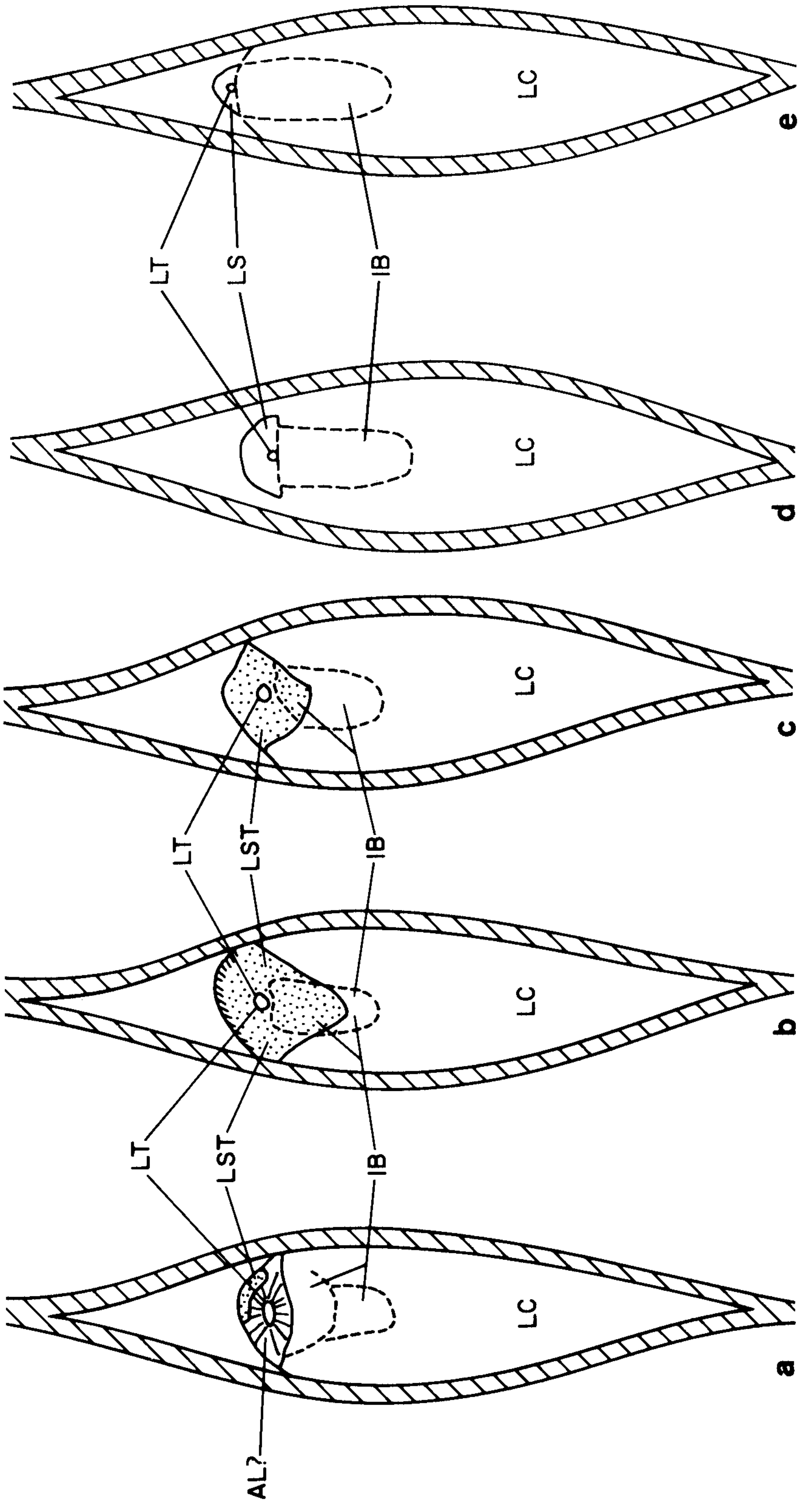
Diagnosis — Stems at least up to 3.4 cm wide in compression; showing elongate fusiform leaf cushions in a fairly steep spiral (c. 40^0), with lepidodendroid phyllotaxis. Leaf cushions sharply delimited by narrow furrows of constant width (equalling about ¼ of the width of leaf cushion) and showing a fine ornament of tiny longitudinal wrinkles. Leaf cushions smooth, with an approximately hexagonal leaf scar in subapical position and occupying nearly the entire width of the cushion. A single leaf trace occurs a little above the centre of the leaf scar. Linguiform infrafoliar bladder underlying the lower part of the leaf scar (up to the leaf trace) and extending downwards to a little less than halfway the leaf cushion. Width of bladder is about one third of the maximum width of leaf cushion. The infrafoliar bladder shows up on even the slightest decortication when the outline of the leaf scar is still visible (Fig. 7a); further decortication first effaces the lower part of the leaf scar (bringing up the outline of the infrafoliar bladder most clearly) and then the upper part of the scar, leaving a slightly expanded leaf trace visible in a small area which may represent a less decayed part of the original leaf scar area (Fig. 7b).

Almost isodiametric cells appear in the leaf scar area; generally, they lack any apparent organisation, but in one case a radial pattern has been observed. The latter possibly corresponds to an abscission layer, whereas the cells without apparent organisation are likely to show a level below the abscission layer. More narrowly elongate cells are found in the general area of the leaf cushion (and including the infrafoliar bladder).

Fructification unknown.

Comparison — This species differs from *B. paganzianum* in the constant width of the much narrower furrows (interareas) separating the leaf cushions. The latter are clearly delimited around the entire cushion, whereas the basal parts of leaf cushions in *B. paganzianum* merge into the interareas. The shape of the infrafoliar bladder is also very different in these two species. It is linguiform and smaller in *B. nitidum,* whereas it is lanceolate, apparently keeled, and larger in *B. paganzianum.* There is also an apparent difference in the shape of

Fig. 7. *Bumbudendron nitidum* gen. & sp. nov., sketches illustrating the relationship between leaf scar and infrafoliar bladder, based on CIRGEO PB 201 (holotype), approximately × 20. LC = leaf cushion, LT = leaf trace, LST = leaf scar tissue, IB = infrafoliar bladder, AL? = possible abscission layer; a: leaf cushion on the left with radial cell pattern interpreted as a possible abscission layer, leaf trace in the centre, infrafoliar bladder vaguely discernible; b, c: slightly decorticated leaf cushions with infrafoliar bladder discernible up to leaf trace and overlapping in part with the leaf scar, random cell tissue in the leaf scar area represents a layer below the abscission layer, shape of leaf scars varies with decortication; d, e: strongly decorticated leaf cushions whereby the lower part of the leaf scar disappears (d) and, eventually, only the area surrounding the leaf trace remains visible (e). Outline of the infrafoliar bladder visible in its entirety at stages d, e. Interareas (furrows) indicated by shading.


LT
LS
IB
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e
d
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AL?
a

the leaf scars. The top of the leaf scar in *B. paganzianum* is shaped like a rounded arch, whereas it is more angular in *B. nitidum*. Furthermore, the vascular bundle occurs slightly above the centre of the scar in *B. nitidum* and a little below the centre in *B. paganzianum*.

Lycopodiopsis millani Arrondo & Petriella (1979), a lycophyte from Mina La Clelia in the same Lagares Formation at a relatively short distance west of the Sierra de Paganzo, shows a superficial resemblance to *Bumbudendron nitidum*. Four specimens were illustrated, three of which appear rather decorticated. The fourth specimen (op. cit., lám. II, fig. 5: holotype) displays elongate fusiform leaf cushions with a lepidodendroid phyllotaxis in a steep spiral (65^0 to 70^0). Narrow furrows delimit these leaf cushions quite sharply at all sides. Although a subtriangular leaf scar is mentioned by Arrondo and Petriella, the published photograph does not allow the latter to be discerned clearly. It seems possible that the specimen has been slightly decorticated and that the leaf scar is not entirely visible. A single leaf trace has been recorded as well as the absence of parichnos and ligule. The attribution to *Lycopodiopsis* cannot be maintained since Chaloner et al. (1979) restricted this genus to petrified material showing the anatomy. *Brasilodendron*, the name for material showing the outer morphology, may or may not be the correct name to be applied. The possibility that the species described by Arrondo and Petriella may belong to *Bumbudendron*, follows not only from the stratigraphic occurrence which is the same as that of *B. paganzianum* and *B. nitidum*, but, more particularly, from the drawing of an elongate structure below the putative leaf scar (op. cit., p. 123, fig 1 D), which possibly represents an infrafoliar bladder. This structure has been mentioned as a keel by Arrondo and Petriella, but has not been drawn as such. Unfortunately, the photograph of the holotype, figured at less than natural size, does not show sufficient detail to allow the matter of a possible infrafoliar bladder to be determined.

Bumbudendron? millani differs from *Bumbudendron nitidum* in the following characteristics: (1) a steeper phyllotaxis (65^0-70^0 as against c. 40^0 in the latter); (2) the leaf cushions appear to be smaller as well as less elongate in *B.?millani* (maximum length of cushion is 8 mm as against 14 mm in *B. nitidum;* and the length/breadth ratio is 4:1 as against a ratio of 5:1 to 7:1 in *B. nitidum);* (3) the intervening furrows are less markedly developed in *B.? millani;* (4) the shape of the possible infrafoliar bladder of *B.? millani* is different to that of *B. nitidum* which has a less elongate, more linguiform bladder.

Description — The type of *Bumbudendron nitidum* shows clearly the fusiform, rather elongate leaf cushions which are surrounded entirely by the narrow intervening furrows, of constant width. The leaf cushions thus appear sharply delimited. They appear very constant in shape, with the widest part just halfway up the cushion. The specimen PB 201 shows different degrees of decortication (Figs. 8 a - g), i.e. some cushions with a well-developed leaf scar (one of which displays a radial cell pattern centred on the leaf trace, and thus quite suggestive of an abscission layer), some with the lower half of the leaf scar effaced and showing the upper part of the infrafoliar bladder in its place, and some with only a small part of the upper part of the leaf scar remaining around a slightly expanded leaf trace. Apparently, the small punctiform leaf trace in leaf scars with a well-marked outline changes into a slightly larger print of the vascular bundle with progressive decortication. Finally, the expanded leaf trace appears surrounded by a small area of remaining leaf scar area, probably as the result of differential decay with the parenchymatic cells in the immediate vicinity of the vascular bundle remaining a little longer and forming a slight protrusion with the leaf trace on the somewhat decorticated stem. This protrusion has sometimes been squashed sideways. At this level of decortication there is such a complete loss of leaf scar outline that a false leaf scar is simulated.

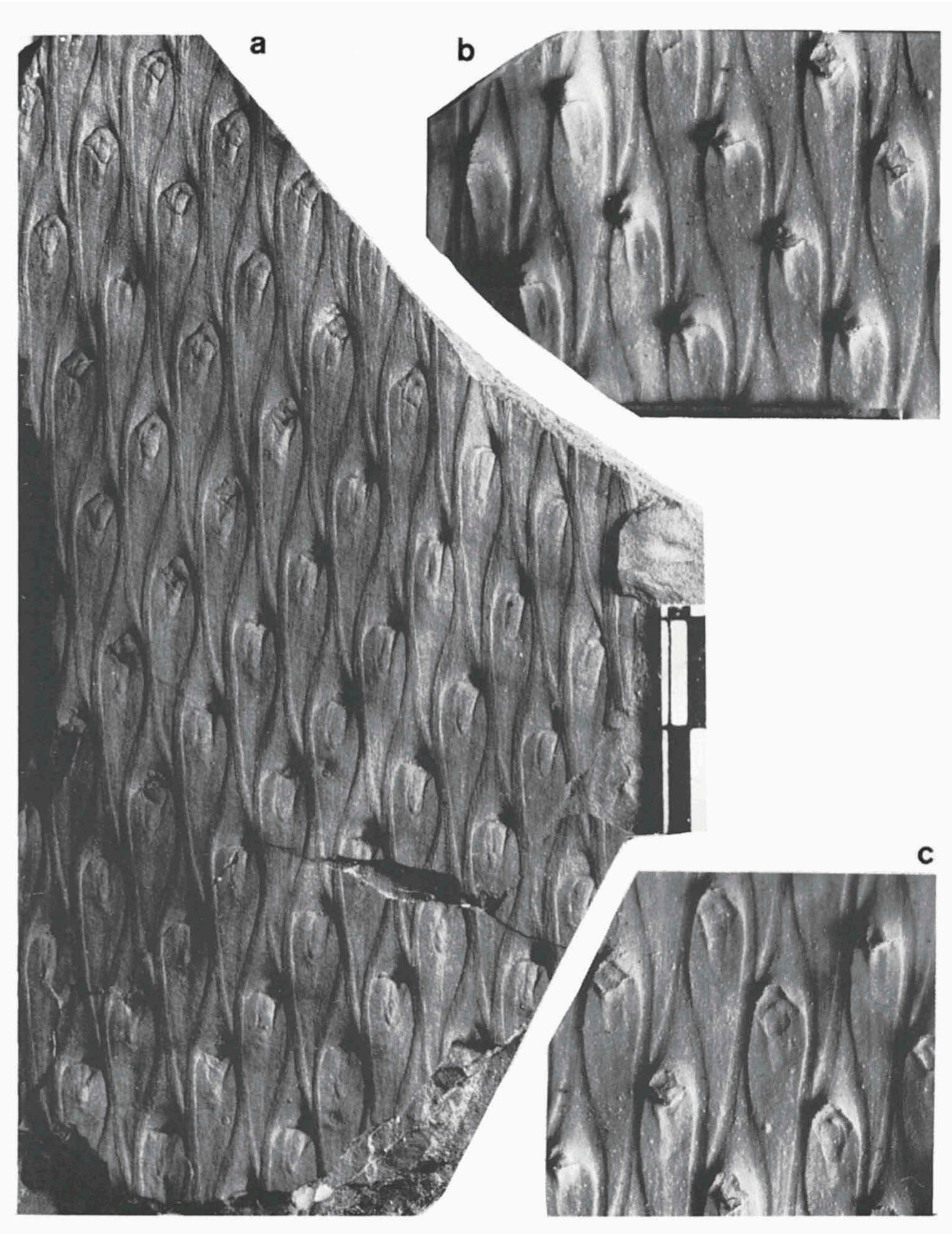


Fig. 8. *Bumbudendron nitidum* gen. & sp. nov., CIRGEO PB 201 (holotype), replicas, a - c: × 4.

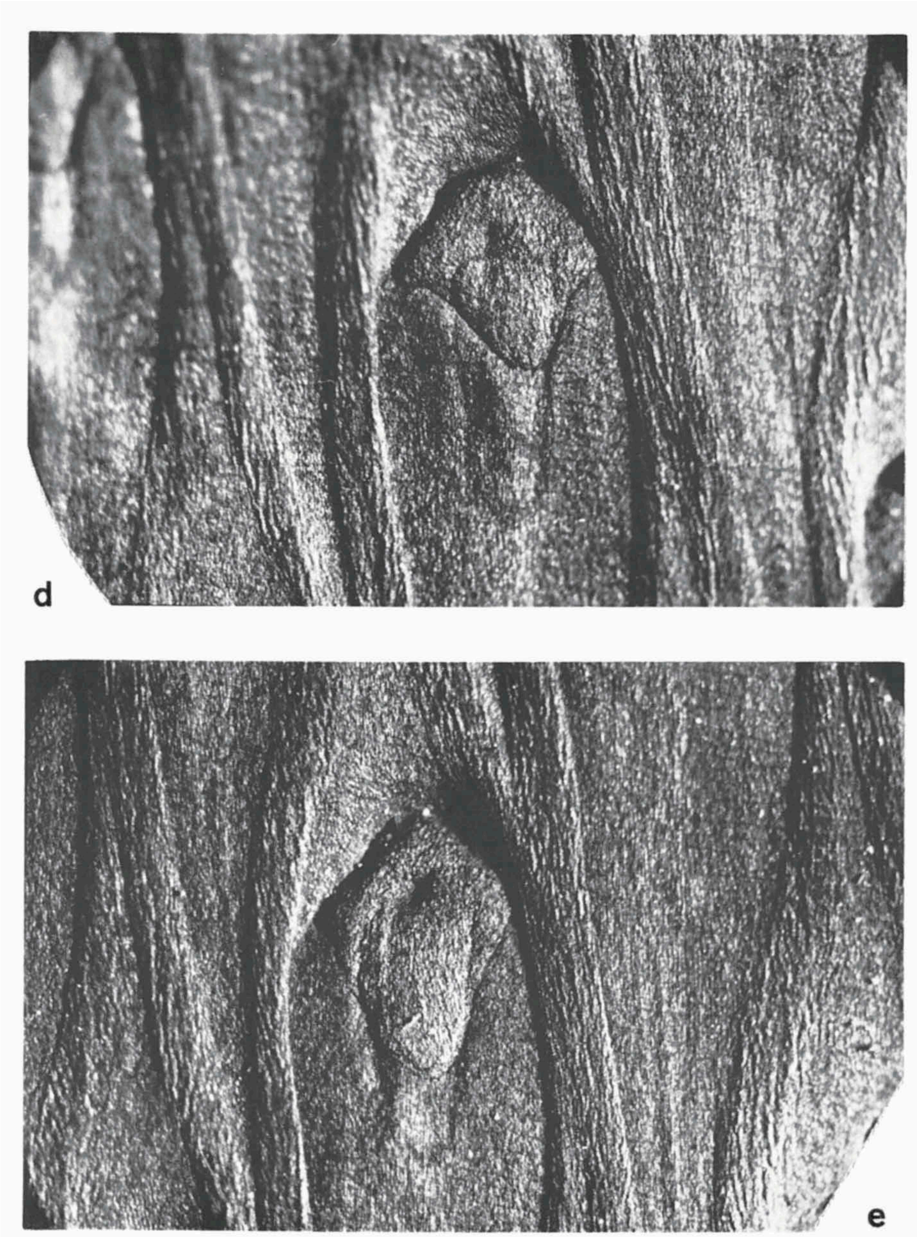


Fig. 8 d, e. Details of leaf cushions, × 20, for explanation see Fig. 7 b, c.

The infrafoliar bladder is clearly marked on all the cushions, even where the leaf scar is visible. In some cases the outline of the lower part of the leaf scar is visible as well as the outline of the upper part of the infrafoliar bladder and the two areas are found to be clearly overlapping. Where the leaf scar is predominant the area is marked by almost isodiametric cells, but where the outline of the lower part of the leaf scar has become fainter the narrower, elongate cells of the region of the infrafoliar bladder are found. This seems to suggest that the leaf scar at and just below the abscission layer shows the cells

Fig. 8 f, g. Details of leaf cushions, × 20, for explanation see Fig. 7 d, e.

of the leaf base, whereas cells of the outermost cortex show themselves just underneath after only a little decortication. It is most unlikely that the elongate cells visible within the outline of the infrafoliar bladder, and which are very similar to those of the leaf cushion in general, may be regarded as representing the tissue of the bladder. Although this can be no more than an assumption, the experience gained with petrified lycophyte stems shows that the infrafoliar bladders probably contained aerenchyme. As such, they may be regarded as replacing the parichnos strands of other Carboniferous lycophytes.

The positioning of the infrafoliar bladder in *Bumbudendron,* which partly underlies the lower half of the leaf scar area, and partly extends further downwards in the leaf cushion, coincides with that of the different parichnos canals of *Lepidodendron* which shows one pair of parichnos on the leaf scar and another pair on the leaf cushion immediately below.

The holotype of *Bumbudendron nitidum* shows fragments of leaves next to the bark impression. These leaves seem to have been fairly long, with a single vein and parallel margins to a blade of 1.5 mm width in one case and 0.6 mm in another. It also shows two possible sporophyll bases, inserted perpendicularly on the stem or branch, and decurrent on the abaxial side.

The additional specimens are more poorly preserved, apparently as the result of more advanced decortication. They display somewhat wider interareas (furrows) separating the leaf cushions (up to one half the width of adjacent cushions).

Bumbudendron nitidum has also been found with a single specimen in the type section of the Tupe Formation in the Quebrada del Tupe in the Sierra de Maz, well over a hundred kilometres westwards in the Paganzo Basin. This specimen comes from loc. Tu 3 in the unpublished type section measured by the third author in collaboration with Dr A. J. Cuerda of the University of La Plata.

	CIRGEO coll. nos				La Plata coll. no.
Measurements in mm	201	192	194	195	8714
maximum width of leaf cushion	2	2	2	1.5	2.2
maximum length of leaf cushion	13	10	14	13	13
width of leaf scar	0.5 - 1	1	1.2	—	—

General comparisons

The fertile specimens of *Bumbudendron paganzianum* invariably show the insertion of sporophylls on wide axes with leaf cushions. Although there is no information on the anatomical structure of these axes, it appears that these are fertile branches rather than specialised strobili. This invites comparison with *Sporangiostrobus,* a fertile branch structure of the equatorial belt of Carboniferous times. There is evidence to show that *Sporangiostrobus* constituted the terminal parts of the stem or major branches of the lycophyte tree *Bodeodendron* (Wagner & Spinner, 1976). Like *Bumbudendron,* it shows leaf cushions of lepidodendroid aspect and phyllotaxis. Its leaf scars are also without parichnos and display a single leaf trace near the centre. The comparison ends here however, since *Bodeodendron* does not possess an infrafoliar bladder (as follows from a somewhat decorticated specimen in the possession of the third author). There is also a difference in size. *Bodeodendron/Sporangiostrobus* was a much larger plant than *Bumbudendron.* Widths of up to 10 cm have been observed in flattened *Sporangiostrobus* and there are terminal parts of fertile branches with a width of 7 cm. Only half this width has been observed in the fertile specimen PB 210 of *Bumbudendron paganzianum.*

Lycophytes with fertile branches rather than strobili seem to have been relatively common in the Gondwana Realm. Jongmans (1954) figured fertile branches from the Carboniferous of Perú under the names of *Cyclostigma pacifica* (Steinmann) Jongmans (his pl. 24, figs. 30, 30a) and *Lepidodendropsis* *devoogdi* Jongmans (his pl. 21, figs. 20, 22, in particular). He clearly stated that the fructification of *L. devoogdi* did not constitute a true strobilus, and compared in this respect with *Lepidodendropsis vandergrachtii* Jongmans, Gothan & Darrah. It is not quite clear from the illustrations presented by Jongmans that the different taxa recognised should not, in fact, be assigned to a single species. The material figured by Jongmans seems to present different degrees of decortication, but at least one specimen (figured as *Cyclostigma pacifica* — Jongmans, 1954, pl. 20, fig. 14b2) shows leaf scars with a single leaf trace near the centre of the scar. The leaf cushions are poorly developed in this specimen which also lacks an infrafoliar bladder as occurs in *Bumbudendron.*

The small lycophytes *Lepidodendropsis* Lutz, *Sublepidodendron* Nathorst and *Prelepidodendron* Danzé-Corsin, all from the Mississippian of the equatorial belt, differ from *Bumbudendron* in the absence of an infrafoliar bladder. *Lepidodendropsis* and *Sublepidodendron* are also characterised by false leaf scars (compare Chaloner & Boureau, 1967). *Prelepidodendron* has been defined as a lepidodendroid plant with leaf cushions disposed in alternating verticils (i.e. with clear orthostichies sensu Meyen, 1976), and showing leaf scars with a leaf trace (Danzé-Corsin, 1958; Cogney & Danzé-Corsin, 1960). The phyllotaxis of *Bumbudendron* is more like that of *Lepidodendropsis* and *Sublepidodendron.*

The Permian Gondwana lycophyte *Brasilodendron* (Chaloner, Leistikow & Hill, 1979) also shows a suggestion of fertile branch structure as indicated by a rather wide axis with almost perpendicularly inserted, presumed sporophylls with a reflexed distal lamina (op. cit., pl. II, figs. 1 - 4; text-fig. 2). No sporangia have been recorded with these presumed sporophylls, but the orientation and reflexing of these limbs are strongly suggestive. Also, the presence of non-reflexed leaves attached to the lectotype of *Brasilodendron pedroanum* (Carruthers) Chaloner, Leistikow & Hill (op. cit., pl. I, fig. 1) suggests two different kinds of leaf-like structures which probably served different functions. Likewise, the long distal laminae of the sporophylls of *Sporangiostrobus* bear a marked resemblance to the leaves of *Bodeodendron,* the difference being found in the presence of sporangia and the reflexing in 90^0 of the sporophyll as it passes into the distal lamina. The lycophyte branches from Perú, as figured by Jongmans (1954), show similar differences and resemblances with regard to fertile and vegetative leaves.

Brasilodendron also shows lepidodendroid leaf cushions and phyllotaxis. The leaf cushions have been described as lacking a proper leaf scar and the attachment of the (permanent?) leaves is shown as subapical. The specimen figured on Chaloner et al.'s pl. I, fig. 4 shows apparent leaf scars with a possible leaf trace, as well as a leaf cushion without a scar. This is somewhat similar to *Bumbudendron* specimens (e.g. our Figs. 8a - g) showing a mixture of well developed leaf scars and remnants of the upper parts of scars which have been interpreted as different levels of decortication. *Brasilodendron* also lacks parichnos and has no recorded ligule (as is the case in *Bumbudendron).* The two genera differ, however, in the absence of an infrafoliar bladder in *Brasilodendron.* The single species, *Brasilodendron pedroanum,* has associated megaspores of the *Lagenoisporites brasiliensis* type. Poorly preserved imprints of megaspores associated with *Bumbudendron* at loc. 33 of the Bum Bum section, show apparently smooth contact faces, curvaturae and raised laesurae of

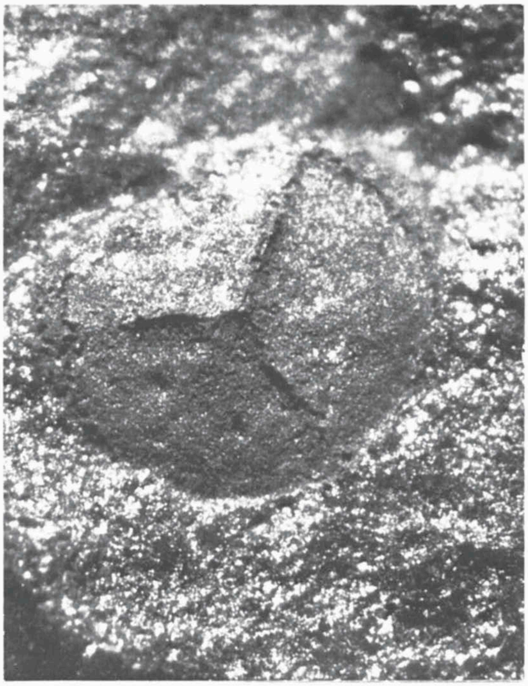


Fig. 9. Megaspore associated with *Bumbudendron* at loc. 33 of the Bum Bum section, × 56.

a well-developed trilete mark (Fig. 9). The possible attribution to *Lagenoisporites* (or *Lagenicula* — see Spinner, 1969) has to be kept in abeyance in view of the deficient preservation of the megaspores found associated with *Bumbudendron*. It is noted that Spinner recorded *Lagenicula brasiliensis* from middle Carboniferous strata of the Tupe Formation in the Sierra de Maz.

The presence of an infrafoliar bladder in the Gondwana lycophyte *Bumbudendron* invites comparison with some of the lycophytes from Angaraland described most recently by Meyen (1976). There is a marked resemblance between somewhat decorticated specimens of *Bumbudendron paganzianum* and *Tomiodendron kemeroviense* (Chachlov) Radczenko as figured by Meyen (1976, pls 4 - 5, pl. 6, figs. 43 - 45). The latter shows a long, narrowly triangular infrafoliar bladder similar to that of *B. paganzianum*. It is also characterised by fusiform leaf cushions with lepidodendroid parastichies, and shows the slightly raised leaf cushions to merge at the base into a fairly substantial interarea with a wrinkled ornament. The leaves of *Tomiodendron kemeroviense* were inserted near the apex of the leaf cushions. However, this species has been regarded by Meyen as lacking a proper leaf scar such as occurs in *Bumbudendron paganzianum*. Knowing that even the slightest decortication may remove the evidence for a leaf scar and observing the clear outline of infrafoliar bladders in Meyen's specimens which also display the imprint of cortical fibres, it is obvious that his *Tomiodendron kemeroviense* material is decorticated to the extent where leaf scars may no longer be visible. Although this reinforces the suspicion that *Tomiodendron kemeroviense* and *Bumbudendron paganzianum* may have to be regarded as one and the same taxon, it seems unwise to identify the latter with the Angara species in the absence of information about the leaf scar in *Tomiodendron kemeroviense*. The wide geographical separation of the two species also imposes an element of caution. The genus

Tomiodendron is diagnosed by Meyen as being characterised by false leaf cushions. Unfortunately, the illustrations provided for the different species show stems in various stages of decortication.

Comparison can be made also with *Lophiodendron tyrganense* Zalessky. Meyen (1976) mentions that the infrafoliar bladder of this Angara lycophyte shows up in the first stage of decortication, just like it does in *Bumbudendron*. *Lophiodendron tyrganense* also shows lepidodendroid parastichies, but it differs from *Bumbudendron* in having relatively broader leaf cushions and in not possessing well-developed leaf scars. In view of the possibility that even slight decortication may remove the evidence for a leaf scar, this may perhaps be an unreliable character for generic distinction. It has to be taken into account however. *Lophiodendron variabile* Meyen, as figured on Meyen's pl. 2, figs. 12 - 13, shows strongly curved leaves which might be interpreted as sporophylls on a fertile branch from which the sporangia were shed.

An infrafoliar bladder also seems to be present in the case of *Lepidodendropsis fenestrata* Jongmans & Koopmans from the Carboniferous of Egypt (Jongmans & van der Heide, 1955, pl. 7, figs. 1a - b, particularly). This species shows fusiform leaf cushions in lepidodendroid parastichies. The insertion of the leaves was in the apical part of the cushions and no leaf scar seems to have been present. The infrafoliar bladder is small, linguiform, and occurs characteristically just below the apparent position of the vascular bundle. There is no mention of the infrafoliar bladder in the description of *Lepidodendropsis fenestrata,* but it shows up clearly in the type specimen as illustrated by Jongmans and Koopmans (1940, pl. II) and by Jongmans (loc. cit.). This character suggests that the Egyptian species ought to be removed from *Lepidodendropsis* (which has no infrafoliar bladders) and placed either in *Tomiodendron* or in *Bumbudendron,* in case a leaf scar could be demonstrated in less decorticated material. It is noted that the Egyptian plant comes from the northern edge of Gondwanaland.

Malanzania gen. nov.

Type species — *Malanzania nana* sp. nov.
Derivatio nominis — Malanzán, the nearest village to the type locality in the Sierra de los Llanos, La Rioja province, Argentina.

Diagnosis — Small stems with widely spaced, spiny excrescences in spiral arrangement. False leaf scars irregularly subcircular. Outer bark smooth with thick cuticle.

Comparisons — *Palaeostigma* Kräusel & Dolianiti (1957) differs in the irregular positioning of the spinous excrescences. It may be a matter of debate whether or not this character, mentioned in the diagnosis of *Palaeostigma,* should be regarded as significant for a generic distinction.

Haplostigma Seward, as restricted by Kräusel & Dolianiti (1957), shows protruding false leaf scars in spiral arrangement. The size of the protrusions and the likelihood that these are merely bases of larger leaf-like structures, both suggest a rather different aspect for this plant. Its age is also rather different, i.e. Devonian.

Archaeosigillaria Kidston shows closely spaced sigillarioid orthostichies with (false?) leaf scars of nearly hexagonal outline and containing a central leaf trace. Small, curved, rather fleshy leaves have been found attached to dichotomising small branches. There is virtually no comparison with the almost smooth outer bark of *Malanzania* and *Palaeostigma,* on which tiny spinose excrescences occur.

Cyclostigma Haughton is a much larger plant with spaced out, subcircular leaf scars showing a leaf trace and paired parichnos (Chaloner, 1968). Long leaves have been found attached to this arborescent lycophyte which is obviously very different to *Malanzania* and *Palaeostigma.*

Malanzania nana sp. nov.
Figs. 10 - 15.

?1941 *Bothrodendron australe* (Feistmantel) Seward — Frenguelli, p. 473, lám. I, fig. 3.

Derivatio nominis — nana (Lat.) = a female dwarf.
Holotype — CIRGEO PB 107.
Type locality — Cuestita de la Herradura section in Malanzán Formation, near Malanzán, Sierra de los Llanos, La Rioja province, Argentina.
Additional material — CIRGEO PB 105, 106, 108 - 119 (Malanzán); Museo de La Plata LP PB 8632 (Trampeadero section, Quebrada La Cébila, Sierra de Ambato, La Rioja province); LP PB 4390 (Agua de los Jejenes, Precordillera, San Juan province.)

Diagnosis — Small stems, up to 13 mm wide in compression (based on 10 specimens from Malanzán), possibly unbranched (longest stem fragment observed measures 10 cm); with widely spaced, small, false leaf scars (separation between scars at least the width of a scar and generally in excess of this dimension); shape of false leaf scars subcircular to subrhombic; phyllotaxis lepidodendroid, with fairly regular disposition in a steep spiral (c. 60^0); leaf scars up to 1 mm in diameter, without clear evidence of a leaf trace, and apparently due to shearing off at the base of small, spiny excrescences, up to 1 mm long. Area between false leaf scars apparently smooth.

Thick cuticle, thinning in the area surrounding each false leaf scar. No stomata, and with two different kinds of cells: (1) narrow, elongate cells, up to 90 µm long, which are found in the upper and lower parts adjoining the opening of the leaf scar, and forming fan-shaped rows; (2) more isodiametric cells, c. 30 µm long, which occur on the lateral sides of the false leaf scar. Anticlinal walls up to 7 µm thick.

Description — The most complete specimen (CIRGEO PB 107), 10 cm long and 1 cm wide, is the imprint of a stem and its counterpart, together with a thick cuticle preserving the outline of epidermal tissue. The specimen is broken at both extremes (Fig. 10a). False leaf scars in lepidodendroid phyllotaxis, without apparent orthostichies, although there is a hint of sigillarioid vertical disposition. However, the spiral disposition predominates, with two possible parastichies, viz. a low spiral at c. 10^0 angle and a steep spiral at c. 60^0. When observing the apparent rows, it seems clear that these are not parallel but at a slight angle to the stem margin.

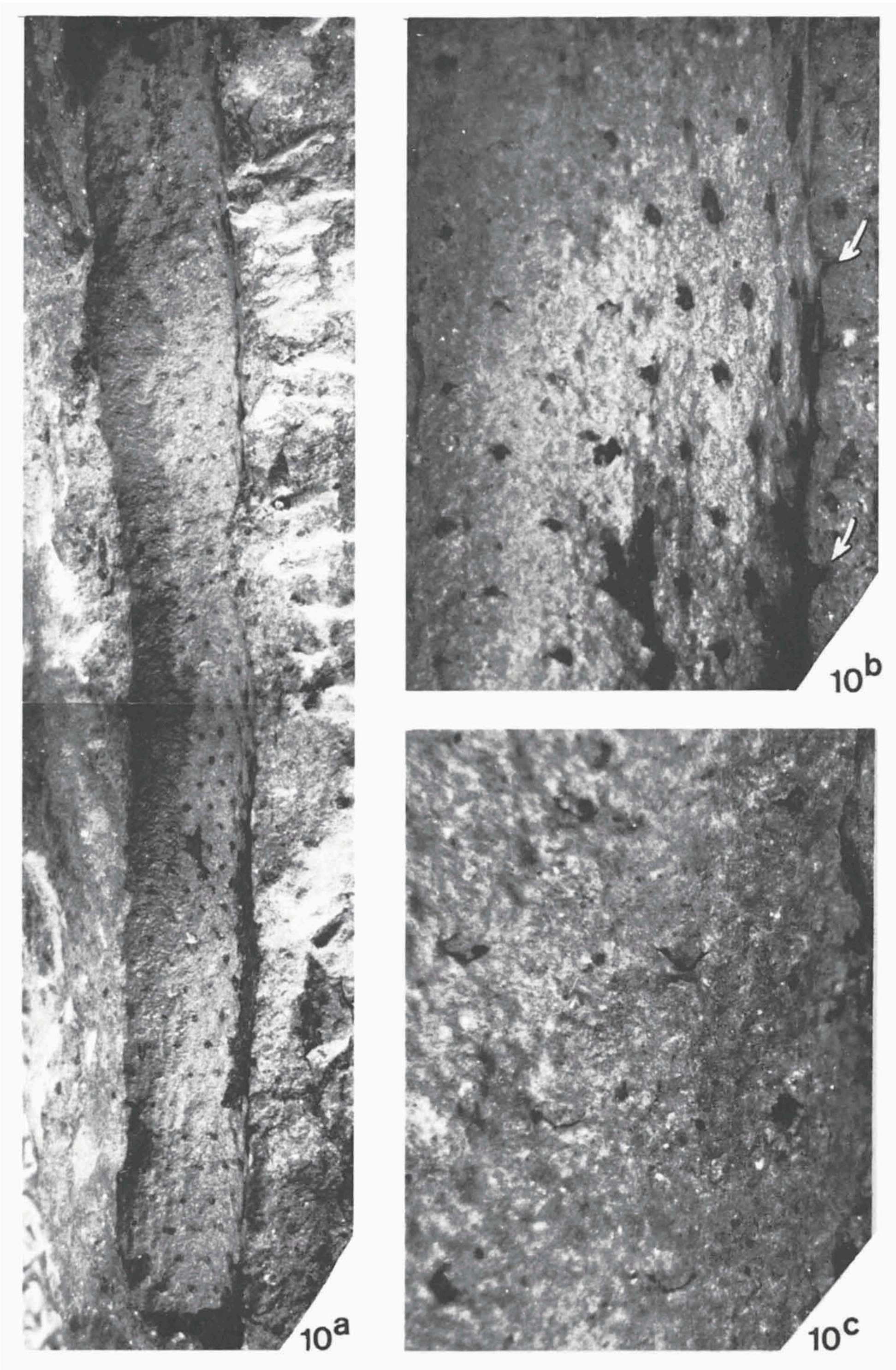
The scars appear subrhombic, with 0.5 - 1 mm in maximum diameter, which is subhorizontal; lower border rounded (Fig. 10c). They are slightly in relief, forming minor mamelons, without clear borders with the general surface area of the stem which is smooth (it is noted that the silty nature of the rock would prevent the preservation of a fine ornament). Scars separated by distances of about 2.5 to 3.5 times their diameter. Some faint longitudinal wrinkles near the margin of the stem are probably compression features unrelated to the stem surface. However, there is some longitudinal alignment of the scars which may be due to the linking of scar bases into very faint ribs. Small, spiny excrescences with expanded bases are seen along the margin of the stem and relate to the scars which are obviously due to shearing off at the stem surface on splitting the rock. These small excrescences (enations?) are approximately 1 mm long (i.e. about as long as the maximum diameter of their base). They are somewhat inclined towards the stem on the adaxial side, with a curved, acuminate apex (Figs. 10b, d - f).

The specimen PB 112 (Fig. 11), which is a fragment 12.5 mm wide (incomplete), also shows a lepidodendroid phyllotaxis without orthostichies. False leaf scars are equidistant vertically and subhorizontally, and widely spaced (at distances 4 to 5 times the scar diameter). The disposition of the scars in the horizontal sense is a very low spiral, at about 5 - 10^0 angle. Vertically, it approximates to an angle of c. 45^0.

PB 119 (Fig. 12), which is 13 mm wide, shows the faint imprint of a cellular structure within the scars. No organisational details can be discerned.

Practically all the specimens from Malanzán show the presence of a thick cuticle with the stem impressions. These cuticles are easily detached, but need a long period of oxidation. Only a single layer of cuticle occurs with the imprints which apparently represent partially decayed stem fragments consisting of sheets of cuticle with epidermal cells adhering and, perhaps, also some part of the outer cortex. Generally, there is only a thin layer of coal between the cuticle and the imprint on the rock, so it does not apear that much tissue was left with the cuticle prior to fossilisation. This is consistent with the lacustrine facies of the sediment. A minor proportion of the specimens from Malanzán are casts with an oval cross section (due, mainly, to compaction) and not merely bits of cuticle with partially decayed tissue. These rare specimens (Fig. 10a) allow the shape of the spiny excrescences to be determined. These specimens floated into position as entire stem fragments and decayed in the sediment. The thin pellicle of coal attached to the cast shows that the impression on the sediment was produced after substantial decay. Unfortunately, the rather coarse grain of the siltstone seems to have prevented the finer details of cell structure to become imprinted on the rock. Only in some very occasional specimens is there any hint of cellular structure visible on the cast, and these are not susceptible to interpretation.

The cuticles show marked thinning around the false leaf scars which appear as holes in the cuticle (Figs. 13, 14a). Two kinds of epidermal cells are visible on the cuticle, viz. (1) elongate cells, up to 90 μm long and 9 μm wide, which occur in the upper and lower parts of the area surrounding a leaf scar opening, and (2) more isodiametric cells (approx. 30 μm diameter) flanking the scars laterally. The elongate cells form fan-shaped rows. They diminish in length and finally grade into the more isodiametric kind of cells away from the scars (Figs. 14a, b). The anticlinal walls are thick, about 5 - 7 μm wide. There is no evidence for stomata, and the occasional holes in the cuticle (not corresponding to the leaf scars) are apparently due to decay. Trichomes also ap-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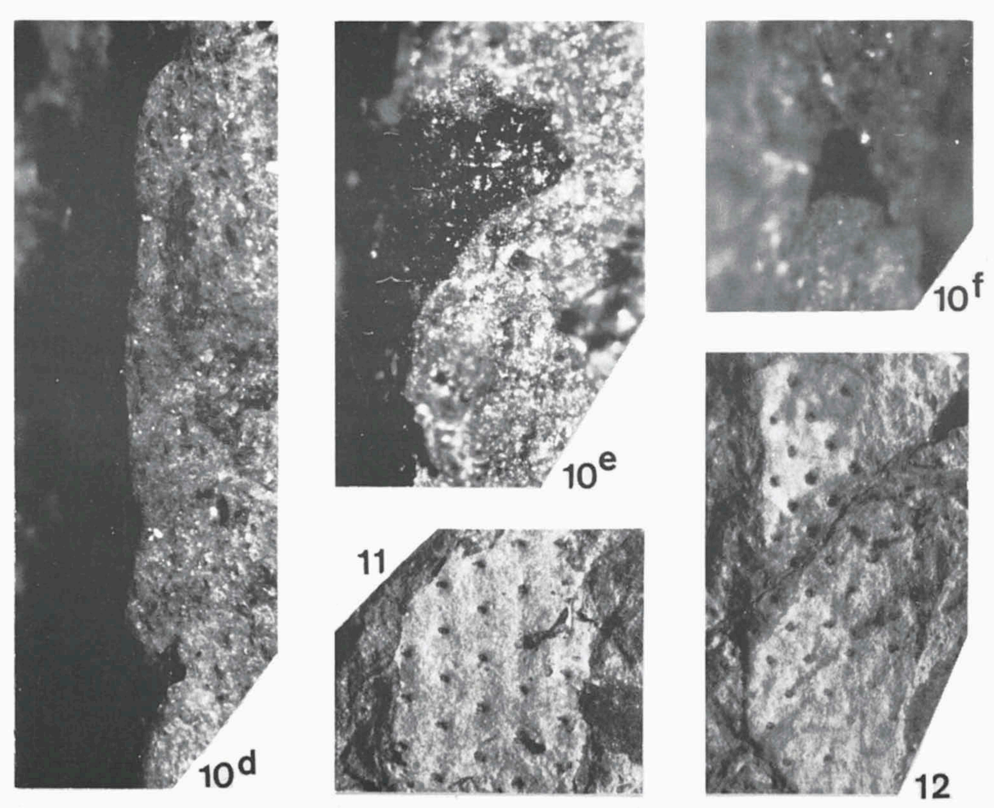


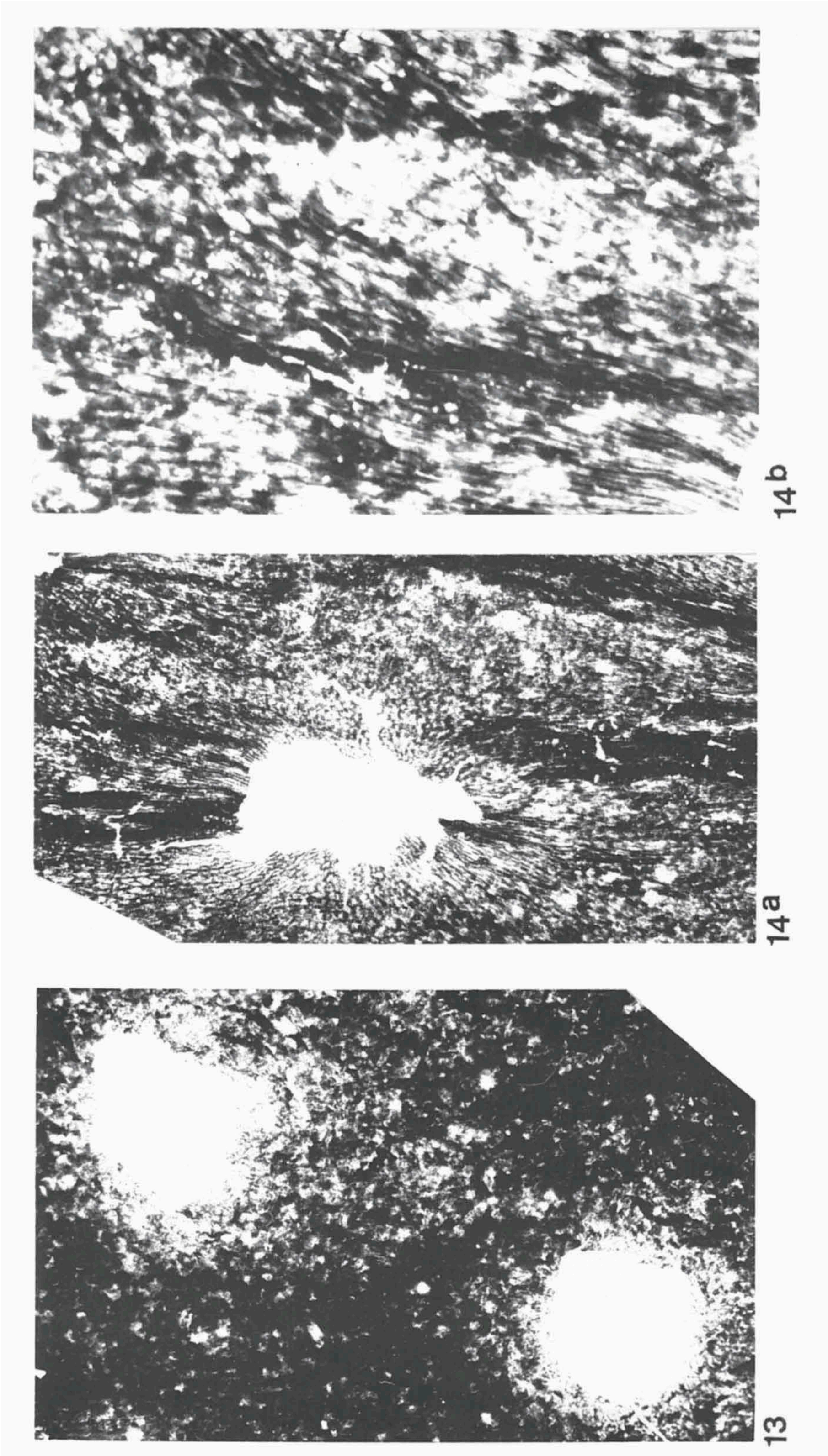
Fig. 10. *Malanzania nana* gen. & sp. nov., CIRGEO PB 107 (holotype); a: stem with cuticular remains (black) still attached, × 2; b: marks of false leaf scars, small spiny excrescences (arrows) on the right edge and remnants of cuticles (black), × 7; c: distribution and shape of false leaf scars, × 14; d: two small truncated excrescences on the edge of the stem, × 14; e: detail of one truncated excrescence, × 28; f: spine-like excrescence, × 28.

Fig. 11. *Malanziana nana* gen. & sp. nov., CIRGEO PB 112, showing distribution of false leaf scars, × 2.

Fig. 12. *Malanziana nana* gen. & sp. nov., CIRGEO PB 119, showing phyllotaxis and distribution of false leaf scars, × 2.

pear to be absent. The anticlinal walls are often deep and thickened in places, leaving a small lumen. The cuticles often appear folded longitudinally.

Malanzania nana is one of the rarer elements of the flora collected from the Cuestita de la Herradura locality near Malanzán. Two fragments attributable to the same species have been found in the Trampeadero Formation of the La Cébila section near the provincial boundary between La Rioja and Catamarca. They occur on a single piece of rock (LP PB 8632, Figs. 15a, b). The larger stem fragment is 16 mm long and 6 mm wide, and shows spirally disposed false leaf scars (at an angle of c. 50^0) which are about 1 mm apart. These scars, which are approximately isodiametric, appear as small mamelons, without a leaf trace. The entire surface is covered by almost isodiametric to slightly elongate cells (in the direction of the length of the stem, Fig. 15b). The anticlinal walls are weakly carbonised. Cell structure is also found on the surface of


13
14a
14b

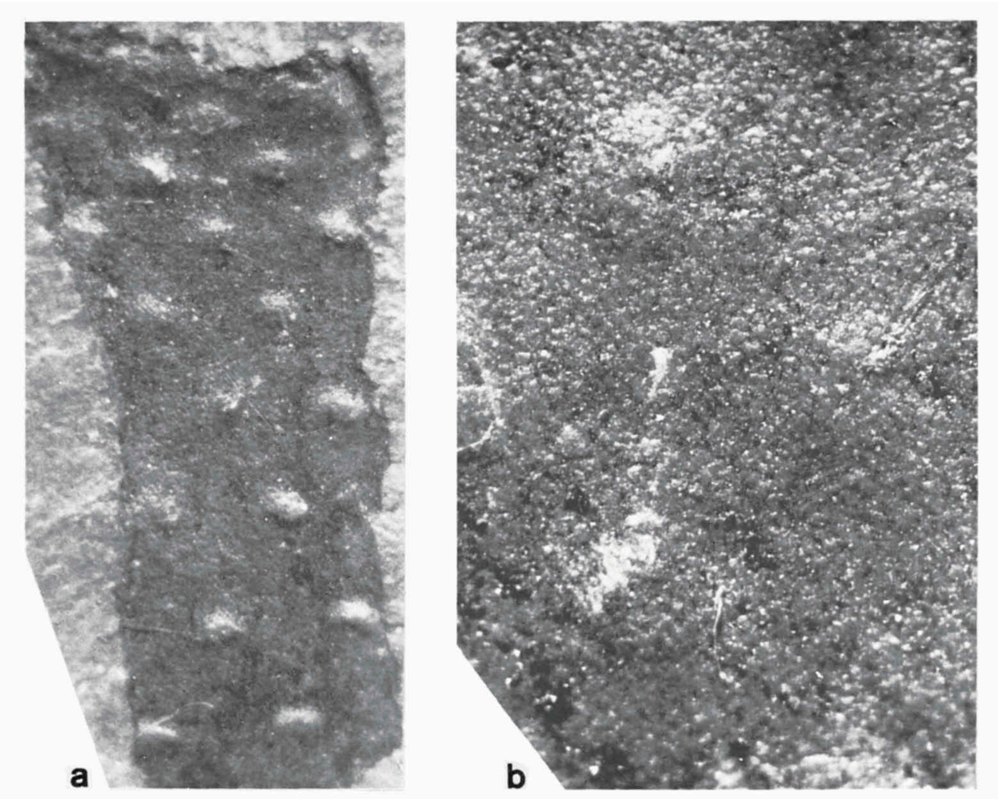


Fig. 15. *Malanzania nana* gen. & sp. nov., LP PB 4390, from Quebrada de la Cébila, Trampeadero Formation; a: fragment of stem with false leaf scars, × 7; b: detail of surface with cell markings, × 20.

the mamelons. These cells are regarded as subepidermal and probably represent the outer cortex.

The second fragment is even smaller. It shows two scars , one of which is subcircular whereas the other is transversally elongate, with a rounded lower border. It is 5 mm long and shows the remains of a cuticle. The area in between the false leaf scars shows the imprint of rows of cells forming longitudinal, fan-shaped bands above and below the scars. These bands are less well developed lateral to the scars. One of the scars shows a central marking which possibly corresponds to a leaf trace. In spite of the fragmentary nature of these two specimens from Trampeadero, they seem to be characteristic for *Malanzania nana.*

Fig. 13. *Malanzania nana* gen. & sp. nov., CIRGEO PB pm 19, cuticle showing two false leaf scars and thin edges with cellular detail, × 40.

Fig. 14. *Malanzania nana* gen. & sp. nov., CIRGEO PB pm 17; a: detail of one false leaf scar, showing surrounding epidermal cells of two different types, × 40; b: detail of cuticle on upper sector of false leaf scar, showing transition of elongated-narrow cells to short, almost isodiametric cells in interarea, × 110.

Comparison — It seems likely that the specimen figured as *Bothrodendron australe* (Feistmantel) by Frenguelli (1941, p. 473, lám. I, fig. 3) corresponds to *Malanzania nana.* However, its leaf scars are bigger (2 - 2.5 mm as against 1 mm) and the width of Frenguelli's specimen (25 mm) is in excess of that found in the specimens from Malanzán. This means that this specimen cannot be attributed without reservation to *Malanzania nana.* Like the latter, its shows a lepidodendroid disposition of scars which are widely apart, i.e. about 5 mm separation between leaf scars. The preservation of the scars is rather poor.

Cyclostigma sp., which Frenguelli (1949, p. 323, fig. 16) figured from Barreal in the Precordillera of San Juan, is too poorly preserved for an adequate comparison. It apparently differs from *Malanzania nana* in the much closer spacing of its leaf scars which are separated by less than the diameter of the scars.

Bothrodendron(?) sp., as described by Seward (1922, pl. XIII, fig. 9, and textfigure), also resembles *Malanzania nana* in the general shape and separation of false leaf scars. However, the scars appear more prominently on Seward's specimen, and they also show a central leaf trace. Moreover, the size of the stem fragment indicates a larger plant than *Malanzania nana.* Jongmans (1954) referred Seward's specimen to *Cyclostigma pacifica* (Steinmann), but it seems preferable to us to keep it separate from that species.

Cyclostigma pacifica (Steinmann) Jongmans, as figured by Jongmans from Perú, is rather different in that it possesses stems of larger size which show more prominent leaf scar mamelons with a well marked leaf trace. The striate ornament on some of Jongmans's specimens probably represents a cortical layer which is not apparent on any remains of *Malanzania.*

The disposition of leaf scars in some of the specimens of *Malanzania nana,* which tends towards vertical rows, suggests a comparison with certain remains of *Archaeosigillaria.* The most comparable species is *Archaeosigillaria essiponensis* Mensah & Chaloner (1971), of the lower Carboniferous of Ghana. This species shows similar spiny excrescences of comparable size to those of *Malanzania nana.* However, the plant fom Ghana has larger stems, with an even thicker cuticle showing much bigger epidermal cells. The cuticle is very similar in all other respects however; the disposition of the cells is identical, there are no stomata, and the false leaf scars correspond to marked gaps in the cuticle. The main difference is in the markings between the leaf scars, which are clearly bordered in a way that corresponds to *Archaeosigillaria* and not to *Malanzania,* and also in the disposition of the scars which are more clearly in vertical rows. The false leaf scars of *A. essiponensis* also show a clearly marked leaf.

Some species described as *Cyclostigma* are also quite comparable, e.g. *Cyclostigma asiatica* Radczenko of the lower Carboniferous of Siberia. The attribution to *Cyclostigma* may not always be correct in these cases.

A critical review of the middle Carboniferous lycophytes recorded from Argentina

There are only sparse records of lycophytes in the Pennsylvanian strata of Argentina, and these are often rather doubtful as a result of poor preservation and inadequate description. Fortunately, most of the relevant specimens are in the Palaeontology Department, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad de Córdoba (Kurtz Collection) and in the Museo de Ciencias Naturales at La Plata (Frenguelli Collection). These have been re-examined by the first author, whose observations are as follows. A survey of the literature is added as required.

Szajnocha (1891) figured and described specimens referred to *Lepidodendron* ex gr. *L. nothum* Unger and to *Lepidodendron pedroanum* Carruthers. They came from Retamito in the Precordillera of San Juan province. This locality is presently considered as middle Carboniferous. The specimens, though possibly in the University of Córdoba, have not been available for re-examination. Szajnocha's illustration of *Lepidodendron* ex gr. *nothum* (loc. cit., pl. II, fig. 1) shows closely spaced, regularly rhombic leaf cushions without any detail allowing a proper identification. The specimen figured as *Lepidodendron pedroanum* (Szajnocha, 1891, pl. II, figs. 2 - 3) shows the following characteristics (despite a diagrammatic representation): (1) lepidodendroid phyllotaxis and shape of the leaf cushions; (2) the separation of leaf cushions by interareas; (3) the apparently apical position of the leaf scar; (4) the merging of the lower parts of leaf cushions with interarea; (5) a height of leaf cushions in the order of 5 to 6 mm. These characteristics suggest a possible identity with *Bumbudendron paganzianum,* as described in the present paper. However, the leaf cushions are a little too wide for this species and the interareas too narrow. Also, Szajnocha's material apparently shows a subcircular infrafoliar bladder (his pl. II, fig. 3), whereas this bladder is more lanceolate in *Bumbudendron paganzianum.* It should be noted that Kräusel (1961) was prepared to accept Szajnocha's identification.

Kurtz (1921) figured a number of lycophyte remains in his Atlas and additional specimens appear on the missing plates which will be published in the near future as part of the annotated version of this classical work on Argentine palaeobotany. The following remarks are based on a re-examination of the actual specimens (quoted with the catalogue numbers of the collection in Córdoba).

A) Material from Sierra de los Llanos, La Rioja province:
Lepidodendron sp. (loc. cit., pl. XII, fig. L; CORD PB 854) is the poorly preserved imprint of a possible lycophyte.

B) Material from Saladillo, La Rioja:
Lepidodendron sternbergii var. *aculeatum* Brongniart (loc. cit., pl. XIV, fig. P; CORD PB 862) is in fact a sedimentary structure with small ripplemarks which, in one part of the specimen, provides a suggestion of poorly defined leaf cushions. This name ought to be struck from the list of Argentine plant fossils.
Lepidodendron pedroanum (Carruthers) Zeiller (loc. cit., pl. XIV, fig. O; CORD PB 861) is a specimen with lepidodendroid leaf cushions separated by narrow interareas with longitudinal markings. Its leaf cushions are oval to subrhombic, with a rounded apex and poorly defined base (as in *Bumbudendron paganzianum).* There are no clearly marked leaf scars but the insertion of the leaf seems to have been subapical. Some of the leaf cushions show a faint linguiform outline in the central part which possibly represents an infrafoliar bladder. The shape of the leaf cushion is somewhat different to that of

Bumbudendron paganzianum, but there seems to be generic identity.
Lepidodendron selaginoides Sternberg (loc. cit., pl. XIV, fig. N; CORD PB 858) refers to a specimen which may be regarded as conspecific with PB 861.
Lepidodendron sp. (unpublished pl. XXXVIII, fig. 1; CORD PB 860) is a poorly preserved specimen referable to Lycophyta in general. The same applies to PB 859, an unfigured specimen of the Kurtz Collection.

C) Material from Trapiche, San Juan province, Department of Jáchal (Precordillera):
Lepidophloios laricinus Sternberg (loc. cit., pl. XV, figs. 144, 144a) refers to a tabulate coral specimen. Another specimen (pl. XV, fig. 144b), also identified as *Lepidophloios laricinus,* is a poorly preserved lycophyte which shows leaf cushions of different shape to that of *Bumbudendron* (CORD PB 144).

D) Material from Retamito, San Juan province:
Lepidodendron sp. (unpublished pl. XXXVIII, fig. 2; CORD PB 396) is similar to *'Lepidodendropsis' peruviana* (Gothan) Jongmans. It shows an infrafoliar bladder and the subapical insertion of the leaf trace. The interareas display coarse markings which anastomose in places. It is possible that this specimen should be referred to *Bumbudendron,* but not to one of the species described in this paper. Kurtz's specimen is not well enough preserved to merit description as a new species.
Lepidodendron australe McCoy (unpublished pl. XXXVIII, fig. 3; CORD PB 395a - name as stated on the label) is an incomplete fragment of 10 cm width, with closely spaced leaf cushions of lepidodendroid shape and phyllotaxis, 10 mm high at 5 mm maximum width (which occurs halfway up the leaf cushion or slightly above this position). There is virtually no interarea between leaf cushions. The specimen appears slightly decorticated and shows an infrafoliar bladder but no leaf scar. The insertion of the leaf seems to have been in the apical part of the leaf cushion. It is possible that this specimen belongs to the same new (?) species of *Bumbudendron* as PB 396.

E) Material from Cruz de Caña, La Carpintería, San Juan province:
The specimen CORD PB 412 (unpublished pl. XXIX, fig. 412) is an unidentifiable lycophyte impression.

It thus appears that the specimens figured in Kurtz's Atlas are either indeterminable or belong to a species of *Bumbudendron* close to *'Lepidodendropsis' peruviana* (Gothan) Jongmans.

Frenguelli (1944), when dealing with the Retamito locality, discussed *Lepidodendron pedroanum* at some length and suggested that the lycophytes recorded by Szajnocha (1891) and those figured by Kurtz (1921) as *Lepidodendron pedroanum* (and including the specimens listed as *Lepidodendron veltheimianum* and *L. sternbergii* by Kurtz, in Bodenbender, 1897) should all be referred to *Lepidodendron peruvianum* Gothan.

Frenguelli (1944, pl. X, figs. 1, 2) figured and described from Retamito decorticated specimens of *Lepidodendron peruvianum.* Despite its rather poor preservation, his fig. 1 shows characteristics similar to those of *Bumbudendron paganzianum.* The fairly large leaf cushions, of lepidodendroid phyllotaxis, are elongate, widely spaced, and poorly delimited, the interareas being smooth to faintly striate in longitudinal direction. There are indications of a keel which possibly represents the lanceolate infrafoliar bladder of *B. paganzianum.* The leaf trace is positioned in the extreme apex of the leaf cushion. Frenguelli's fig. 2 represents a heavily decorticated fragment of a lycophyte which cannot be identified generically.

Frenguelli (1941) also figured and described *Lepidodendron* cf. *veltheimianum* Sternberg and *Lepidodendron* sp. from the locality of Agua de los Jejenes in San Juan province. These specimens are so poorly preserved that the former can only be called a lycophyte branch fragment with attached leaves, whilst the latter is totally unidentifiable. Frenguelli (1941) also figured a specimen attributed to *Bothrodendron australe* Feistmantel. This has been compared with *Malanzania nana* gen. et sp. nov.

Frenguelli (1946, pl. I) figured a *Lepidodendron australe* McCoy from the Quebrada de la Herradura in the Precordillera of San Juan province. This specimen shows closely spaced, subrhombic, sub-isodiametric false(?) leaf cushions which suggest a comparison with *Archaeosigillaria.*

Remarks on the Carboniferous lycophytes from Paracas and Carhuamayo, Perú

The Carboniferous of Perú has yielded well-preserved impression floras from the Paracas Peninsula and, about 450 km to the North, from the region of Ambó and Carhuamayo, north of Cerro de Pasco. These floras, which have been described by numerous authors (most recently by Doubinger & Alvarez-Ramis, 1980), are generally attributed to the Mississippian. However, there is an obvious resemblance to middle Carboniferous elements from Argentina (e.g. *Rhacopteris ovata* auct.) and the age may still be regarded as subject to discussion.

Lycophyte remains form an important part of the Paracas and Carhuamayo floras. Berry (1922) figured and described two lycophytes from Perú, viz. *Lepidodendron rimosum* Sternberg (his pl. VIII, figs. 1 - 3) and *Lepidodendron obovatum* Sternberg (his pl. I, fig. 5). These illustrations show the apparent absence of a proper leaf scar and indicate the position of the leaf insertion as apical to subapical. However, this may be a matter of partial decortication comparable to that shown by *Bumbudendron* as described in the present paper. The specimen figured by Berry on his pl. VIII, fig. 2, and which shows a subapical leaf insertion, has been separated as a different taxon by Gothan (1928). It shows comparable characteristics to those of *Bumbudendron nitidum* in possessing elongate leaf cushions with little separation, an infrafoliar bladder of similar though not quite as linguiform shape, a leaf scar in the upper third of the cushion, and a single leaf trace. The other illustrations provided by Berry suggest a comparison with *Bumbudendron paganzianum* since they show a 'keel' which may be a lanceolate infrafoliar bladder as occurs characteristically in the latter species. The interareas between leaf cushions seem variable in width and display longitudinal markings. Jongmans (1954, p. 196) mentioned that Berry's pl. VIII, fig. 3, showing the reconstruction of a leaf scar, may have been interpretative without factual basis. This may well be the case since it shows characters which do not show up in the other illustrations.

Gothan (1928) established a new species, *Lepidodendron peruvianum* (loc. cit., p. 294, pl. XIII, fig. 2), in which he included some of the material figured by Berry (1922, pl. I, fig. 5; pl. VIII, fig. 1 - non fig. 2). He consequently disallowed the original identifications. Read (1938, fig. 4) figured another example of Gothan's species and accepted the latter's interpretation of Berry's material. The leaf cushions of *Lepidodendron peruvianum* are obovate and the type specimen shows them to be a little longer than they are wide. The leaf scar is poorly delimited but occurs clearly in the apical part of the cushion. There are clear infrafoliar bladders (which explains the lack of a well-defined leaf scar); they are elongate in the long axis of the leaf cushion. The interarea between leaf cushions is narrow and apparently smooth. The lower part of the leaf cushions merges into the interarea. *Bumbudendron paganzianum* is quite similar with regard to merging of the lower parts of the leaf cushions with the interarea, and it also shows a similar shape and position of the infrafoliar bladder. However, the shape of the leaf cushions is quite different, and the Peruvian specimens are much larger than the Argentine representatives of *Bumbudendron*. It is likely, however, that *Lepidodendron peruvianum* should be referred to the new genus *Bumbudendron*.

The most exhaustive work on the Peruvian material is that of Jongmans (1954). He included Gothan's species with *Lepidodendropsis,* and defined two additional species, viz. *Lepidodendropsis steinmanni* Jongmans and *Lepidodendropsis devoogdi* Jongmans. He also figured and described *Cyclostigma pacifica* (Steinmann) Jongmans. It is difficult to see from Jongmans' illustrations that different taxa would in fact be present, since decortication could account for many of the apparent differences. However, the material kept in the British Museum (Natural History) and which represents the smaller part of the collection described by Jongmans (the larger part is in the Geologisch Bureau at Heerlen, the Netherlands), clearly shows the presence of two different taxa. One of these could be regarded as Steinmann's species. Since Chaloner's (1968) revision of *Cyclostigma kiltorkense,* it is apparent that the Peruvian plant cannot be assigned to *Cyclostigma* in view of the absence of parichnos markings. It may well belong to a new genus. The other taxon is comparable to *Bumbudendron*. One of the specimens in the British Museum shows lepidodendroid leaf cushions without a proper leaf scar (probably as a result of partial decortication) but displaying a depression within the raised apical part of the leaf cushion which, most likely, corresponds to the point of insertion of the leaf. Jongmans' (1954) illustrations of his various species of *Lepidodendropsis* show fairly substantial branches with leaves and sporophylls. This plant is certainly bigger than the small species of *Bumbudendron* described in the present paper. The phyllotaxis of Jongmans' material and certain characteristics of the leaf cushions tend to suggest that it may not be assigned to *Lepidodendropsis* in the strict sense. Whether or not his species of '*Lepidodendropsis*' may be assigned to *Bumbudendron,* can only be determined by a full revision of his collection, including the material in the Geologisch Bureau at Heerlen which the present writers have not been able to re-examine.

Conclusions

A review of the middle Carboniferous lycophytes recorded from Argentina shows a high proportion of unidentifiable specimens, including some that are not even fossil plants. Some specimens can be identified with taxa described in the present paper, and it is likely that four different species can be distinguished altogether. These are *Bumbudendron paganzianum* gen. et sp. nov., *Bumbudendron nitidum* sp. nov., *Bumbudendron* sp. (cf. *'Lepidodendropsis' peruviana* (Gothan) Jongmans), and *Malanzania nana* gen. et sp. nov. The three taxa described here all represent very small trees or shrubs, the compressed width of the stems being at most 3.5 cm. This includes the width of the basal stump of a standing *Bumbudendron.* Although it may be impossible to deduce the correct height of the stem from its width, particularly if the stem is bluntly terminated, it seems likely that they were only a few metres tall. Only the locality of Retamito, in the Precordillera of San Juan, shows larger stems. This locality is in an area where the Paganzo Basin shows marine influences, whereas the Sierra de Paganzo and the Sierra de los Llanos represent the purely continental, eastern part of this basin. It is possible that the proximity of the sea may have produced a slightly milder climate. The presence of dwarf lycophytes in the Tupe and Malanzán formations in the eastern, continental part of the basin, provides support for Retallack's suggestion (unpubl. Ph.D. thesis, 1977; summarized in 1980) that the Pennsylvanian flora of Gondwanaland may be compared to a tundra vegetation. In this respect it is worth mentioning that the fluviatile sandstones of the Tupe Formation show a notable absence of floated logs of any size. This is in marked contrast to the large trees in the lycophyte forests of the equatorial belt. The lycophytes of the (middle?) Carboniferous of Perú are larger than those found in Argentina, and one wonders if this reflects a more temperate climate in keeping with the lower palaeolatitude of Perú.

The presence of an infrafoliar bladder in the two species of *Bumbudendron* has invited comparison with lycophytes from Angaraland as described by Meyen (1976). Although the physiological significance of the infrafoliar bladder is unknown and anatomical details are lacking, the positioning of the infrafoliar bladder coincides with that of the two pairs of parichnos strands in equatorial belt lycophytes such as *Lepidodendron.* The fact that infrafoliar bladders occur in Gondwana as well as Angara lycophytes may have climatic significance since both the southern and northern high latitude areas are involved.

Bumbudendron paganzianum, which shows a fertile branch structure, ranges itself among the relatively primitive lycophytes without strobili. Fertile branch structures seem to have been common in the early Carboniferous worldwide, and this organisation seems to have persisted generally in the later Carboniferous (Pennsylvanian) of the Gondwana Realm, whereas it appears less commonly in the equatorial belt floras. The most likely explanation is that the latter area, with its warmer climate, provided the proper environment for the development of more specialised lycophyte trees which failed to penetrate into the higher latitudes. This is a general characteristic of the Gondwana floras of Pennsylvanian times which are both less diversified and more primitive looking than the contemporaneous floras of the equatorial belt.

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