

# The life and times of a Triassic lycopod

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The fossil lycopod *Pleuromeia longicaulis* (Burges) comb. nov. and its supposed cone *Cyclostrobus sydneyensis* (Walkom) Helby & Martin 1965 are common in the Scythian to Anisian Gari and Newport Formations north of Sydney, N.S.W. *P. longicaulis* probably lived in extensive monodominant stands in the inter-distributary bays of the 'Gosford delta' system, bordering a large coastal lagoon or lake. *C. sydneyensis* was borne as a single erect terminal cone. It was shed intact and may have floated some distance before breaking up and releasing its heterospores.

*Austrostrobus ornatum* Morbelli and Petriella 1973 from southern Patagonia is now included as a further species of *Cyclostrobus*.

The Pleuromeiaceae appear to have been facultative coastal halophytes. They probably originated in Eurasia and migrated along early Triassic shorelines, reaching eastern Australia by the mid-Scythian. The coastal habitat of the Pleuromeiaceae and other Triassic lycopods explains the biostratigraphic usefulness of the spores *Aratrisporites* spp., *Nathorstisporites hopliticus* Jung 1958, and *Banksisporites pinguis* (Harris) Dettmann 1961 compared with coexisting fully terrestrial fossil floras. These opportunistic lycopods appear to have expanded in times of recovery from global life crises.

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ALTHOUGH uncommon compared with those of the Carboniferous, the number of lycopods known from the Triassic has been steadily growing. Of these the Pleuromeiaceae are the most cohesive group. There are also several remains of uncertain supra-generic status.

The specimens on which *Pleuromeia longicaulis* (Burges) comb. nov. is based have been known from the Triassic of the Sydney Basin since 1935. The emendation was foreshadowed by Helby & Martin (1965). Full descriptions of the emended species are given in the last section of this article. What follows here is an interpretive resumé of the reconstructed plant as a prelude to a discussion of the wider significance of the Pleuromeiaceae in the Triassic world.

## The Sydney species of *Pleuromeia*

I have reconstructed the sporophyte of *Pleuromeia longicaulis* in Fig. 1. The reconstructed stem length is close to the maximum observed in a fragment without rhizophore or leafy apex. So the plant may have been considerably taller. The reconstruction is

generally similar to those of Hirmer (1933) and Mägdefrau (1956), but not those of Gothan (1924) or Walther (1912).

The sporophyte had a single unbranched stem, very slightly tapered upwards, with an average diameter of 24 mm. The rounded apex bore a crown of leaves. However, most of the stem was naked and showed spirally arranged lenticular leaf scars. The rhizophore was rounded, unlobed, and bore fine rootlets. Older rootlets abscised leaving round stigmatic scars.

The growth to a mature stem diameter in *Lepidodendron*, *Pleuromeia*, and *Isoetes* entails the continued expansion of the inner cortex of the lower portion of the plant after the outer cortex with leaves and cuticle is fully formed (Eggert, 1961; Chaloner & Boureau, 1967). The apex of *Pleuromeia longicaulis* bears long linear ligulate leaves which have grown on an outer cortex accommodated to the present diameter of the plant. Below the leafy apex is a zone where the growth of the inner cortex has disrupted the vascular bundles supplying the leaf, compelling the shaft to wither. Thus there is a zone of retained leaf bases similar to that

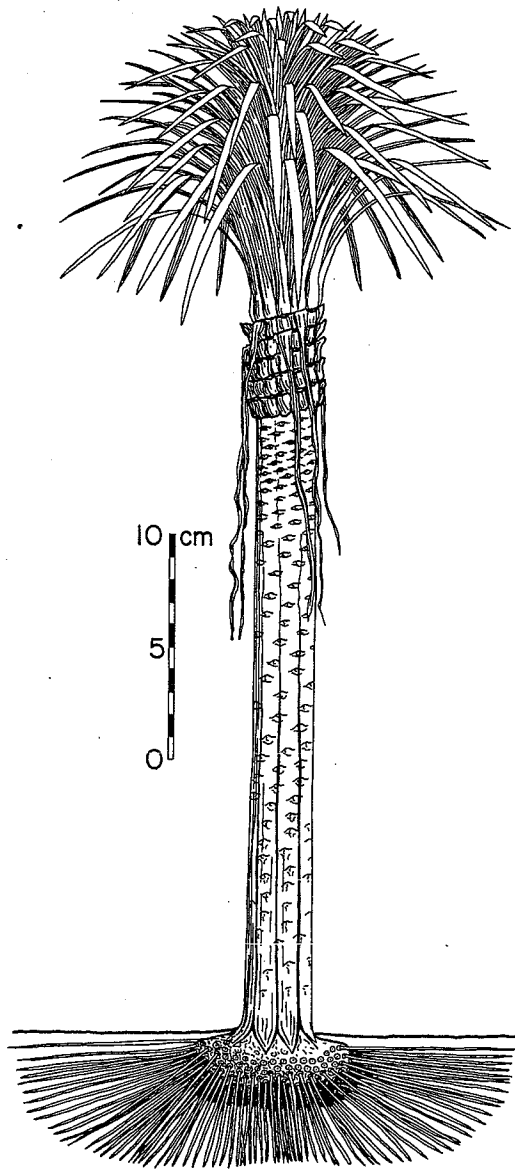


Fig. 1. A reconstruction of *Pleuromeia longicaulis*.

in *Isoetes hystrix* (Seward, 1910, p. 65). Below this the epidermis and leaf scars are exposed on a leafless stem. Further expansion towards the base of the stem is taken up by about eight major and many minor longitudinal cracks. Towards the base much of the outer cortex has been sloughed off and the stem displays a quite different subsurface expression of the leaf traces.

### The life environment of *Pleuromeia longicaulis*

It is likely that *Pleuromeia longicaulis* grew in extensive monodominant thickets perhaps partly submerged in the quiet interdistributary bays and lakes of a delta system debouching into a coastal lake or lagoon (Fig. 2). The arguments for this hypothesis are detailed below.

Stem remains of *P. longicaulis* occur in great abundance in a single 10 cm thick coaly layer in the sea cliff north of Avalon beach (Figs 3, 4D). This layer may be traced for about a kilometre along strike from near Avalon beach to near St Michael's Cave. To the south near the beach (University of New England locality number UNEL1384) the coaly layer contains flattened stems, rhizophores with shrivelled rootlets, leafy apices, strata-transgressive stems, isolated leaves, and leaf bases of *P. longicaulis*. South of St Michael's Cave (UNEL1388) the coaly layer contains stem fragments, elongate leaves, and leaf bases. Some fragments of gymnospermous cuticle, probably *Dicroidium*, were also macerated from the layer here (Slide number UNEF 14600). Just north of St Michael's Cave (UNEL1565) the coaly layer contains compressions and cross-sections of *P. longicaulis* stems scattered over the rock platform surface. These can only be inspected at low tide as the coaly layer dips below sea level just north of here.

Immediately below this coaly layer over its entire length is a palaeosol which becomes progressively more differentiated northward. Near the beach (UNEL1384) the palaeosol consists of a small thickness (5 cm) of ganister (*sensu* Williamson, 1967; McDonnell, 1974) with thin carbonaceous strata-transgressive rootlets. Around St Michael's Cave (UNEL1388, UNEL1392) the whole palaeosol is 36 cm thick. The well developed ganister and underlying leached claystone contain *in situ* carbonaceous rootlets, rare ganister metagranotubules (*sensu* Brewer, 1964; McDonnell, 1974), and narrow ganister dykes.

Above the coaly layer is an upward-coarsening unit of shale and sandstone 1.5 m thick. This unit is capped by the ganister of a palaeosol with siderite nodules in the old illuvial horizon. The shales and siltstones of this unit and the thin coaly layer im-

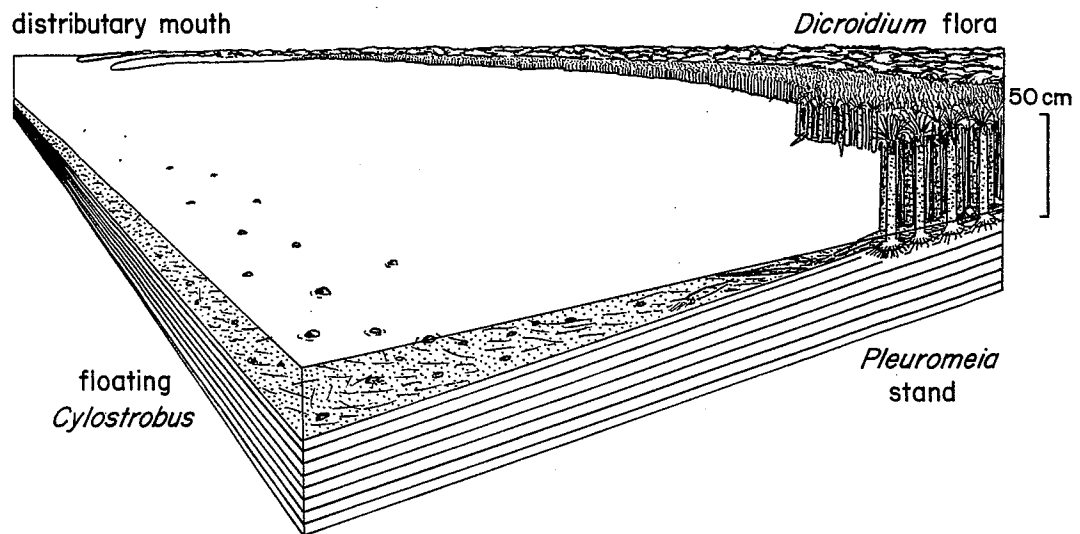


Fig. 2. Reconstructed life environment of *Pleuromeia* and *Cylostrobos* in the 'Gosford delta'.

mediately above it (UNEL1386) contain a diverse fossil flora; *Neocalamites*, *Cladophlebis*, *Gleichenites*, *Chiropteris*, *Taeniopteris*, *Dicroidium* leaves and reproductive structures, and indeterminate fragments. Some of the leaf horizons appear to be remains of leaf litter. The leaves are torn, clumped together, and show shallow scribing trails through them. Where the bedding has not been obscured by the palaeosol, the sandier upper portion of the unit shows scour and fill structures and medium scale cross bedding.

On a regional scale these deposits are interpreted as the base of a southerly prograding 'Gosford delta' (of Conolly, 1969) system with marine environments to the south and east (Bunny & Herbert, 1971; Retallack, 1973). Some authors (Bunny & Herbert, 1971; followed by Bowman, 1972; Bunny, 1972; Mayne, Nicholas, Bigg-wither, Rasidi & Raine, 1974) interpret the interbedded siltstone and shale of the lower Newport Formation as tidal flat deposits. However, there are no unequivocal marine fossils at this level while labyrinthodont bones and trackways have been found (Retallack, 1973; A. Ritchie, pers. comm.). The carbonate 'nodule' with 18.9% phosphate described by Lassak & Golding (1966) from this stratigraphic level, is possibly a bone or is recycled from the erosion of Permian sediments. Also Morgan & Swaine (1973) have analysed the boron content of some

coal samples from this level, including the *Pleuromeia* horizon at Avalon. They found that the boron content indicated only fresh-water conditions during growth and deposition of the plants (see also Swaine, 1966, 1971; Harder, 1970; Retallack, 1973; on this technique and its local application). Perhaps the delta debouched into a coastal lake or lagoon, like the Gippsland deltas (Bird, 1962).

On a local scale, the sequence at Avalon (Fig. 4D) shows a preponderance of palaeosols and evenly bedded sediments compared with the common sandstone channels of other localities (Fig. 4B). This suggests that it was a sedimentologically inactive part of the delta system, such as an inter-distributary area.

The fossil remains throughout the coaly layer suggests that they are close to where the plants lived. The locality nearest Avalon beach (UNEL1384) overlies the least differentiated palaeosol. The poor differentiation may be due to a high water table or to a relatively short period of formation. A high water table or swampy habitat seems more likely considering the palaeosol is better developed along strike.

The almost monospecific composition of the plant fossils in the coaly layer suggests monodominant stands for the living plants. Perhaps *Pleuromeia longicaulis* had exceptional tolerance to waterlogging compared with the coexisting *Dicroidium* flora.

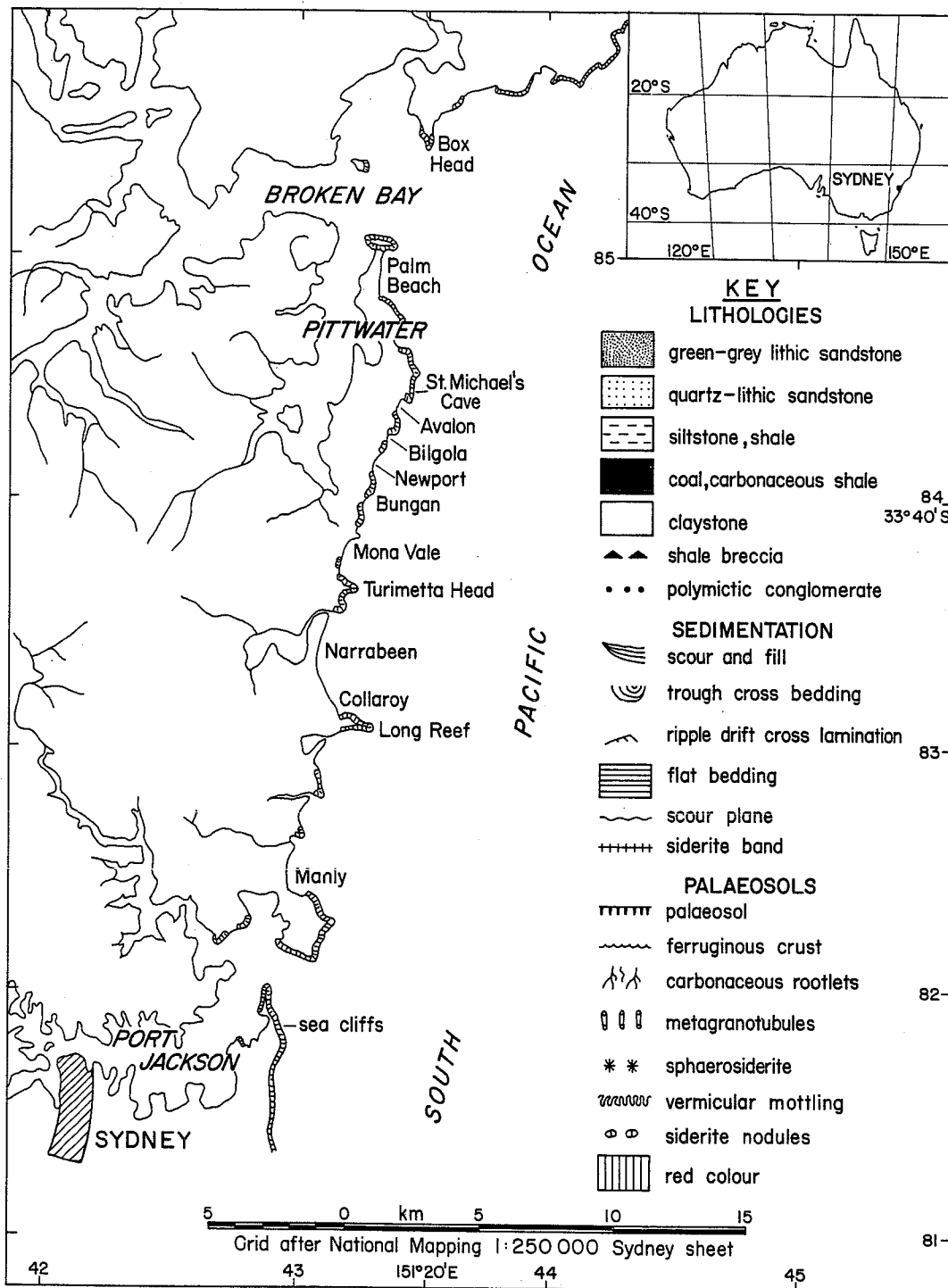


Fig. 3. Locality map and key for Fig. 4.

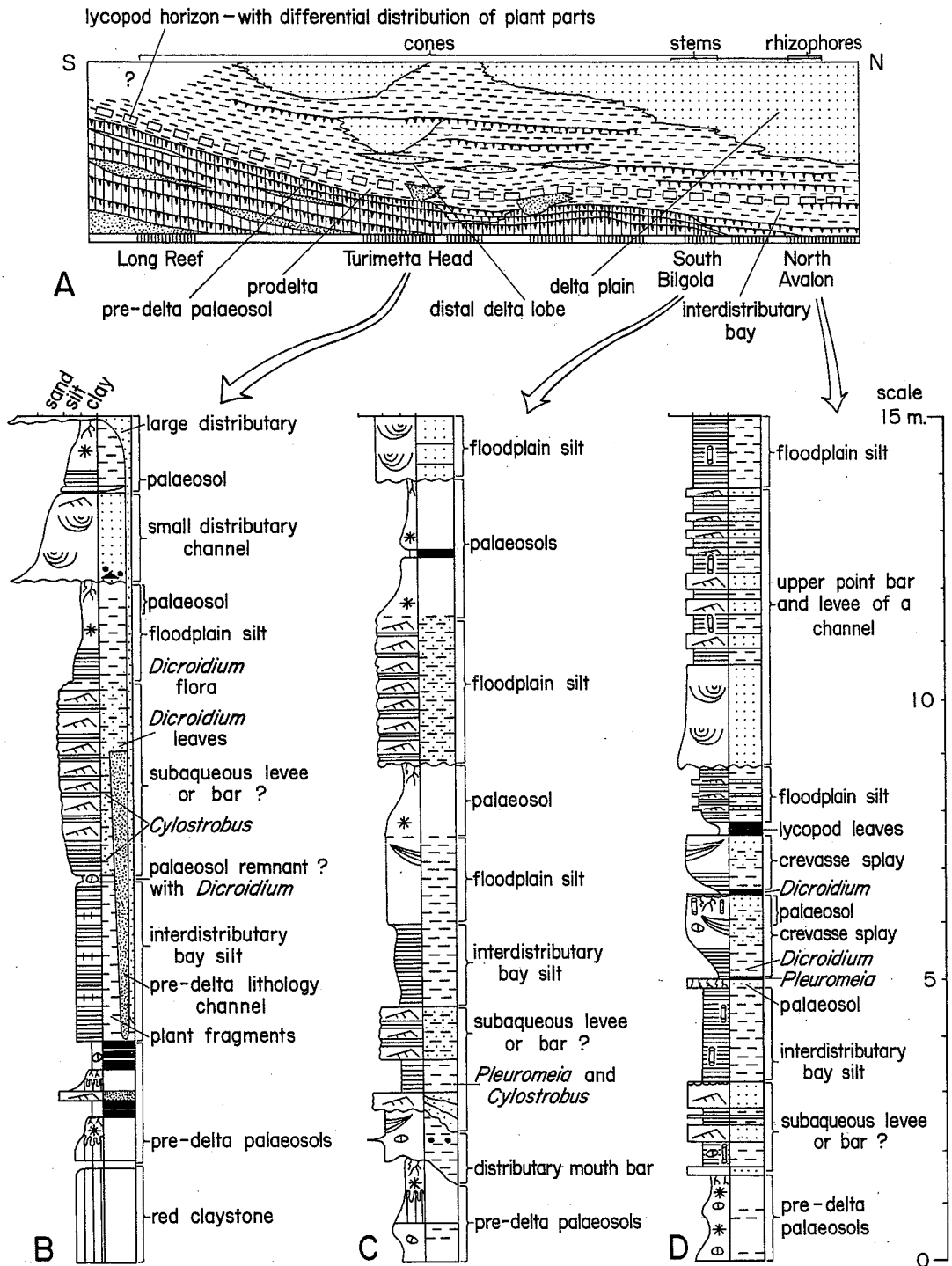


Fig. 4. Selected *Pleuromeia* and *Cylostrobus* localities in the Pittwater area. A, diagrammatic north-south cross section of the main rock types from Avalon to Long Reef. B-D, columnar sections: B, Turimetta Head; C, south of Bilgola; D, north of Avalon beach.

The upward-coarsening unit above the *Pleuromeia* layer north of Avalon beach (Fig. 4D) is probably a distal crevasse splay deposit. A crevasse splay is a lobe of sediment building out into the floodplain through a breach in the levee bank during flood stage (Coleman, 1969; Allen, 1970). Stratigraphic sections generated by crevasse splays are variable (McKee, Crosby & Berryhill, 1967; Coleman, 1969). Within or near the levee the deposits are mainly sandy with an erosional base. Further out on the floodplain the sandy sediments may over-ride peat, clay and silt deposited distally with the splay, or earlier in the flood cycle, or prior to the flood. The crevasse splay sediments are soon revegetated. Soils develop once again at a somewhat higher level.

Flood waters may easily uproot herbaceous or shallow-rooted plants, such as *Pleuromeia*, and scatter these and their leaf litter into current-sorted assemblages. At North Avalon the lighter leaves have been transported farther than the heavier tangled stems. The buoyant cones are not found at all. The *Pleuromeia* stands were knocked down into their leaf litter or carried off by the first impact of flood waters. The overlying sediments contain leaf litter and other remains of the *Dicroidium* flora carried in from more elevated areas upstream as the flood gained in intensity.

### *Cylostrobos* as the cone of *Pleuromeia longicaulis*

Several hundred small heterosporous lycopod cones from the same stratigraphic level as *Pleuromeia longicaulis* were described by Helby & Martin (1965) under a new genus, *Cylostrobos* (Fig. 5). Even at that time it was suspected that both fossils belonged to the same plant. *Cylostrobos* and *Pleuromeia* both commonly occur in almost monospecific assemblages and are the most prominent lycopods in the fossil flora of the upper Narrabeen Group. However, in 1965 no locality was known where *Cylostrobos* and *Pleuromeia* were associated. Such a locality has now been found. This and a further locality are now described before proceeding with the argument for association.

*South Bilgola.* In May 1972 a large rock-fall from the sea cliff south of Bilgola beach (Fig. 4C) exposed some well preserved

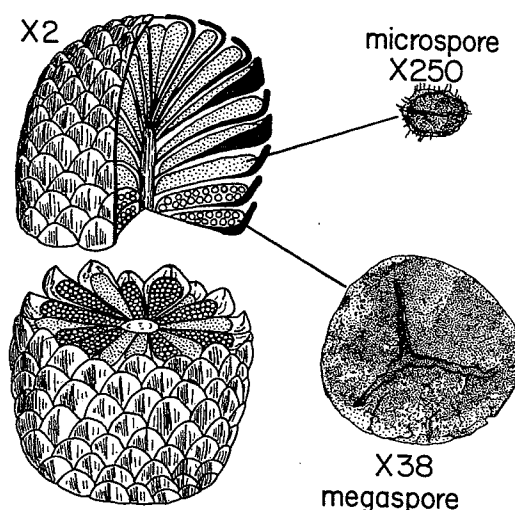


Fig. 5. Diagrammatic reconstruction of *Cylostrobos sydneyensis* (modified after Helby & Martin, 1965).

*Pleuromeia* and *Cylostrobos* remains. Judging by the fresh surfaces exposed and the lithologies, these remains appeared to have fallen from a shale layer in the cliff about 3 m above the level of the rock platform. The rock-fall (UNEL1408) consisted of large blocks of interbedded silt, shale and claystone. The grey claystone layers contained several types of lycopod leaves, small isolated fragments of *Pleuromeia* outer cortex, leafy apices of *P. longicaulis*, *Cylostrobos* cones, equisetalean pith casts referable to *Paracalamites*, and some poorly preserved *Dicroidium* leaf fragments.

Unconformably overlying the pre-delta palaeosols here is a grey silty sandstone with low-angle scour and fill structures. More quartz-rich sandstone lenses and stringers of siderite nodules are laid out along some scour planes. This style of deposition is also seen north of Mona Vale and at the southern end of Turrimetta Head (Fig. 4) in the lower and southern parts of the Gosford delta system. Some of this is resorted palaeosol material, containing leached *Dicroidium* leaves and reproductive structures. There are also some scattered *in situ* carbonaceous roots. I interpret it as an irregularly exposed distributary mouth bar sand (*sensu* Gould, 1970).

Unconformably overlying this again is a sequence of interbedded quartzose sandstone and grey shale containing *Pleuromeia* and *Cylostrobos*. By their stratigraphic position and appearance I interpret them as the distal

portion of the subaqueous distributary levee and interdistributary bay deposits.

The upper levels at this locality are a succession of leached silts and palaeosols indicating a floodplain environment. These rocks contain a diverse *Dicroidium* flora.

*Turimetta Head.* Localities in which *Cylostrobos* is abundant are widespread south of Bilgola. *Cylostrobos* occurs in siltstones above the Bald Hill Claystone redbeds south of Newport, north of Bungan, north of Mona Vale, and at Long Reef. Most of the previously described specimens of *Cylostrobos* were found at Turimetta Head. Figure 4B is a composite stratigraphic column of the south-east facing sea cliff for 200 m south of the point at Turimetta Head.

Near the base of the cliff at Turimetta Head there are at least two palaeosols, separated by a thin green lithic sandstone. Overlying the palaeosols is a grey shale containing plant debris and several horizons of 5 cm thick, hard siderite bands.

The shale is overlain by a thin layer of siderite nodules in a khaki to olive claystone with some poorly preserved *Dicroidium* leaves and large seeds (UNEL1442). This may be a transported or eroded palaeosol.

The overlying unit of shales and siltstones contains *Cylostrobos* cones, isolated sporophylls, and isolated lycopod leaves in abundance, as well as rare fragments of *Asterotheca* and *Paracalamites* (UNEL1443, UNEL1444). This unit is sandier up-section and to the southwest end of the outcrop. In the sandier portions of the unit there are alternating laminae of ripple-marked sandstone and draped claystone. Some of these clay horizons contain abundant *Cylostrobos* cones (UNEL1447). Other horizons show various types of burrows, tracks and trails, syneresis cracks (*sensu* Glaessner, 1969; Coneybeare & Crook, 1968), and comminuted plant debris. These shales are interpreted as prodelta deposits.

All these shales, siltstones and sandstones are scoured out locally down to the level of the palaeosols by a lenticular body of lithic sandstone. This sandstone is composed largely of devitrified volcanic rock fragments (58%) and iron-stained sideritic claystone (36%), with minor quartz (4%) and matrix (2%). Petrographically the sandstone is more closely related to the underlying Bald Hill Claystone and the Bulgo

Sandstone than the more quartz-rich sandstones of the Newport Formation (Ward, 1972). It is possible that this is a channel deposit of an independent creek system derived from the east, on the flats adjacent to the southerly prograding quartz-rich Gosford delta. In the Pittwater area I have used this lithic sandstone as the distinctive lithology of the Garie Formation, in line with nomenclature in the southern Sydney Basin (Loughnan, 1969; Bunny & Herbert, 1971; Retallack, 1973).

The remainder of this section is composed of quartz-lithic channel sandstones. They have uneven erosional bases lined with poly-mictic conglomerate and shale breccia, and are cross-bedded. The two channels at Turimetta Head increase in size up-section (Fig. 4B). This size increase proceeds upwards through the Newport Formation into the Hawkesbury Sandstone. The siltstone units below these two channel sandstones have yielded the diverse *Dicroidium* flora described by Walkom (1925), Burges (1935), and Retallack (1973).

*The Association.* Generally speaking, from Avalon to Long Reef there is an horizon containing lycopod remains lying between the Bald Hill Claystone and the quartz-lithic sandstone channels of the Newport Formation or 'Gosford delta' (Fig. 4). *Pleuromeia* rhizophores and stems are found in the northern part of the horizon near where the plants grew in quiet interdistributary bays. *Pleuromeia* stems, leaves, and *Cylostrobos* cones are found together in the central part of the horizon at the bottom of the interdistributary bay or lake some distance from where the plants lived. Further south near the more active channels of the delta, only *Cylostrobos* and leaves are found. This may be attributed to the differential reaction of leaves, stems, and cones of the same plant to hydraulic transport. Buoyant cones are transported further and more readily than waterlogged stems. Thus association and environmental analysis support the contention that *Pleuromeia longicaulis* and *Cylostrobos sydneyensis* belong to the same plant.

Morphological arguments for the connection of *P. longicaulis* and *C. sydneyensis* are weak. No clear cuticle has been obtained from either fossil. Together they compare only in a general way with other species of *Pleuromeia*. Unlike the cone of *P. rossica* (Neuburg, 1961), *Cylostrobos* is more com-

pact, apparently without peduncle, and has keeled sporophylls and monolete microspores. Monolete microspores cannot be regarded as an important difference as many modern pteridophyte genera have both trilete and monolete spores (Kuprianova, 1969). *P. rossica* and *C. sydneyensis* agree in the absence of trabeculae, in possessing trilete megaspores, in the ovate shape of the cone, and in the distribution of the heterospores within the cone.

The presence of other lycopods in the flora of the upper Narrabeen Group adds caution to the suggested connection of *P. longicaulis* and *C. sydneyensis*. Apart from remains of Isoetaceae, I have found stem fragments of further arborescent lycopods with leaf scars quite unlike those of *Pleuromeia*. These are rare and are generally found stratigraphically above the *Pleuromeia-Cylostrobos* horizon (Retallack, 1973). On the evidence of association, environmental analysis, and general morphology I consider *Cylostrobos sydneyensis* to be the cone of *Pleuromeia longicalis*.

### The Sydney species of *Cylostrobos*

Helby & Martin (1965) established three species of *Cylostrobos* on material largely from Turimetta Head. However, the existence of three species is a possible but by no means necessary interpretation of their information. These species were based largely on a size frequency distribution and 'somewhat different spore types'.

The size differences in themselves could all be attributed to simple growth of a single species. The three species of Helby & Martin (1965) as a group show allometric increase in sporangial length to width and isometric increases in cone length to diameter and cone axis diameter to cone diameter. The following measurements show a regular increase through the three species; cone length, cone diameter, sporangium length, number of sporophylls, and number of megaspores per sporangium.

The principal evidence for three species was a trimodal size frequency distribution of the diameter of 232 cones (Helby & Martin, 1965, fig. 1). Helby & Martin (1965) assumed that, apart from the two rare large cones, two normally distributed populations are present. However, although size frequency distributions of fossil species are commonly normal, they may also be

polymodal or irregular. Olson (1957) shows that, apart from changes due to transport, preservation and sampling, polymodal or irregular distributions may be produced in populations of dead organisms by the variable interaction of mortality and growth rate. Moreover, for fossils, the nature of the original dead population cannot be determined without making gross assumptions about the mode of growth, ecology, natural variability, transport and fossilisation of the organism.

A further objection to Helby & Martin's (1965) species is the method of sampling. Their size frequency distribution includes material subjectively selected from several localities and horizons.

The two features of the spores used for discrimination of the three species are within the range of natural variation in spores of a single modern species. These features are the increasingly wide separation of the intexine from the exoexine in the spores of larger cones and the slightly larger size range of megaspores in the cones of intermediate diameter (13-32 mm). The size range of megaspores is a variable feature in *Selaginella* (Bower, 1959; Sporne, 1966) and *Bothrodendrostrobos watsonii* (Holden, 1932; emendation of Chaloner & Boureau, 1967). In general, the more numerous the megaspores the smaller they are. In extant *Isoetes*, *Selaginella*, and fossil *Banksisporites* spores, the intexine is of smaller radius and distinct from the exoexine in immature spores, whereas in mature spores it is thin and hardly visible, pressed up against the exoexine (Dettmann, 1961; Parihar, 1955, fig. 31). This may be independent of the maturity of the surface ornament. As Wodehouse (1935) notes, pollen walls develop to completion once they have been initiated even when the cell within is dead.

If all the cones belong to one species, how can the trimodal size distribution be explained? My sedimentary interpretation of the *Cylostrobos* localities suggests that all the fossil assemblages are transport distance and current sorted. Also, there may be many years of populations or different local populations in the curve of Helby & Martin (1965). Any of these features could produce a polymodal size frequency distribution. However, the polymodal curve could also have been the original distribution of the dead population of a single species. To see



clearly that this is a possibility, consider the following tentative model. A stand of *Pleuromeia longicaulis* developed a very heterogeneous sized crop of *Cylostrobos* due to environmental factors. As the plant formed monodominant stands, this could be related to the environmental differences between the centre and margins of the stand, as in modern bracken fern (Watt, 1971). The chance of cone fall increased with age, but the actual fall was dependent on agitation by wind and water. Thus the larger cones were more easily dislodged when their spores were more immature. The peaks of the size frequency distribution represent discrete phases of stormy activity whose energy was above the critical level for cone fall. The lowest size peak presumably also has a considerable component of still weather fall at the end of reproductive activity.

Although the detailed interpretation of the peaks is uncertain, there is no necessary evidence for the existence of three species. Accordingly, all three are placed within *Cylostrobos sydneyensis* (Walkom) Helby & Martin 1965.

### The reproductive biology of the *Pleuromeia longicaulis* plant

As in *Pleuromeia sternbergii* (Münster) Corda in Gernar 1852 and *P. rossica* Neuburg 1960, the *Cylostrobos sydneyensis* cones were probably single, terminal and erect on the *P. longicaulis* axes. This is also indicated by the lack of peduncle scars and single unbranched stem of *P. longicaulis*, and the distribution of the heterospores and absence of asymmetric cones in *C. sydneyensis*.

With regard to this last argument, Schoute (1938) has pointed out that in any growth orientation of heterosporous strobili, the megasporangia are distributed closer to the ground. In *Selaginella* the megasporangia are apical in pendulous cones, ventral in horizontal cones, and basal in erect cones. Of the monoecious heterosporous cones discussed by Chaloner & Boureau (1967), *Bothrodendrostrobos*, *Lepidostrobos*, and *Cylostrobos* probably all had erect cones by this argument. Similarly, among the Calamitaceae discussed by Boureau (1964), the cones were probably erect in *Paracalamostachys* and *Calamostachys* (excepting *C. solmsi* which had apical megasporangia).

*Cylostrobos* was neatly ellipsoidal, apparently apendunculate, and had closely imbricate sporophylls lacking a distal limb. All these features presumably made it buoyant and easily moved by wind or in water. The cones of *Pleuromeia sternbergii*, *P. rossica*, and *P. hataii* Kon'no 1973 were less compact, more elongate, and larger. They similarly lack the spinous or elaborate distal limb on the sporophylls of Carboniferous *Lepidodendrales*.

Helby & Martin (1965) suggest that *Cylostrobos* was shed entire and broke up on the ground. Most commonly the megasporangia opened before microsporangia (e.g. Helby & Martin, 1965, pl. 1, fig. 4). Thus the cone tended towards protogyny. Helby & Martin also note that isolated sporophylls seldom have attached sporangia. They suggest this may be due to the abscission of the sporangium from the sporophyll, possibly while the cone was still intact.

Abscission of the sporangium in the cone may explain the seam of sediment between the sporangium and the underlying sporophyll in *Pleuromeia sternbergii*. This feature led several European workers to suppose that the sporangia were abaxial (Mägdefrau, 1931a). This view is commonly held as a mistake (Sporne, 1966; Dobruskina, 1974).

In conclusion it is likely that the single erect sessile cone of *Pleuromeia longicaulis* was shed intact. It was capable of being transported great distances. The cones broke up on the ground, generally under water. Megaspores were usually released before microspores.

### *Cylostrobos* from South America

Morbelli & Petriella (1973) recently described a single large petrified lycopod cone under the name *Austrostrobos ornatum*. According to these authors, the cone is identical to *Cylostrobos* in all respects except the exoexine structure of the megaspores. Different genera of dispersed spore from a single palaeobotanical genus of cone is not unusual (e.g. Harris, 1973). Also Dijkstra (1958) points out that the spores of living *Isoetes* fall into three genera of dispersed spores. Moreover, in the case of *Austrostrobos*, the differences between the megaspores of the petrification and of *Cylostrobos* compressions may be considered due to a combination of preservation and maturity.

In the petrified megaspores of *Austrostrobos* (Morbelli & Petriella, 1973) 420 to 452  $\mu\text{m}$  in equatorial diameter, the exoexine is thick (22-40  $\mu\text{m}$ ) and spongy, while the intexine is thin (2-10  $\mu\text{m}$ ), laminated, and closely adpressed to the exoexine. In section the spongy exoexine shows a polygonal network. The polygons are elongated within the laesura lips and the equatorial zone. They are also progressively smaller towards the inner surface of the exoexine. The surface ornament of the exoexine is granular.

In compressed megaspores of *Cylostrobos* (Helby & Martin, 1965) 400 to 631  $\mu\text{m}$  in equatorial diameter, there is a thick (12-18  $\mu\text{m}$ ) layered exoexine and a thin (3-4  $\mu\text{m}$ ) layered intexine. The intexine may be detached from the exoexine away from the laesura. The exoexine ornament is granular on well-preserved specimens but with overmaceration the exoexine readily blisters to give a ragged pseudo-ornament.

The separation of the intexine from the exoexine in the compressed megaspores of *Cylostrobos* indicates that they are more immature than those of *Austrostrobos* (Dettmann, 1961; Parihar, 1955, fig. 31). The exoexine of the compressed spores is only half as thick as that of the petrified spores of comparable diameter. The layered exoexine could be compressed spongy tissue which is only liberated to a limited extent during over-maceration. So, besides the doubtful validity of generic separation of macrofossils on the basis of detailed spore structure, the petrified megaspores may appear different because they are more mature and less compressed. Accordingly, the South American species is generically reallocated to *Cylostrobos ornatus* (Morbelli & Petriella) comb. nov.

### The Pleuromeiaceae— Triassic mangroves

Several authors (Mägdefrau, 1931a, 1931b; Neuburg, 1961; Kon'no, 1973) have suggested that *Pleuromeia* was a tidal flat plant, occupying a similar habitat to present-day salt marsh and mangrove plants. In some cases they are associated with marine fossils and in other cases are somewhat further inland in coastal plain and deltaic sedimentary complexes. The inland occurrences may be

relicts around salty areas (Beard, 1967). However, it is more likely that the Pleuromeiaceae were facultative halophytes like many modern coastal plants adapted to the highly variable salinities of tidal flat seashores (Chapman, 1960; 1964; Clarke & Hannon, 1969, 1970). As with modern plants of this type their landward spread was probably checked by factors other than salinity, such as interspecific competition, spore dispersal mechanisms, and germination requirements (Clarke & Hannon, 1971).

The evidence for this view of the ecology of *Pleuromeia* is developed below under functional morphology, interpretation of selected overseas localities, and the environmental history of lycopods.

*Functional morphology.* Deductions from functional morphology are particularly weak for fossil arborescent lycopods. The relative inadequacy of their photosynthetic system compared to modern plants may indicate an atmosphere and physiology quite different from that of modern plants (Chaloner & Boureau, 1967, p. 502).

Mägdefrau (1931a) details several arguments suggesting that *Pleuromeia sternbergii* was a succulent plant. The deep leaf scars and transverse wrinkles on compressed leaves suggest a thick fleshy leaf. The coalified vascular bundles and sclerenchyma plates in the matrix of the stem steinkern indicates that the surrounding tissue was more easily degraded. Perhaps it was water-bearing parenchyma. The thick columnar trunk has a general resemblance to some living Cactaceae. Succulence may be a response to high salinity or aridity. The usual occurrence of *P. sternbergii* in monospecific taphofloras also suggests that it possessed exceptional physiological tolerances.

The shallow and feeble root system of *Pleuromeia* compared to modern plants and Carboniferous stigmarians could be due to dry, saline, or waterlogged soil (Maximov, 1929; Walter, 1963; Weaver & Clements, 1938). However, it is doubtful whether *Pleuromeia* could have withstood the highly variable water stress of coastal or desert dunes (Willis & Jefferies, 1963).

*A German coastal plain.* Unfortunately the interpretation of *Pleuromeia sternbergii* as an oasis plant in a 'sandy Buntsandstein desert' has been widely accepted (Seward, 1910; Mägdefrau, 1931a, 1956; Kon'no, 1973).

There is some evidence for regional aridity and/or sparse vegetation (Burek, 1970; Gignoux, 1955; Mägdefrau, 1931a; for vegetation-sedimentation-aridity relations see Schumm, 1968). However, more recent work shows that the Buntsandstein was deposited in a variety of coastal plain river, delta, and shoreline environments (Brinkmann, 1960; Kramer & Kunz, 1969; Burek, 1970; Gall, 1972; Gignoux, 1955).

When the Middle Buntsandstein was deposited, streams derived from the Gallic uplands flowed northeast into a lagoonal coast in northern and eastern Germany (Burek, 1970). At Bernburg, *P. sternbergii* forms a monospecific autochthonous assemblage and is associated with amphibian remains which indicate fresh water conditions (Mägdefrau, 1931a). However, other *Pleuromeia* assemblages occur with dolomites (possibly caliche, Burek, 1970), 'Strandkegel' (beach wedges) and rock salt pseudomorphs (probably diagenetic, Haude, 1970). *Pleuromeia* was most abundant seaward of a mixed equisetale, fern, and conifer flora. As the transgression of the Röt gypsum and dolomite lagoonal deposits proceeded over Germany, these floral associations were driven southwest (Mägdefrau, 1931b). The peak transgression of the shallow Muschelkalk set is marked by limestones over most of Germany and beach and deltaic shorelines, forested by conifers, in northern France (Gall, 1972).

*A Vladivostok lagoon. Pleuromeia* sp. nov. of Srebrodol'skaya 1966 from Russki Island in the bay off Vladivostok occurs with ammonites, *Lingula*, and marine bivalves. The only other associate of *Pleuromeia* is an equisetalean pith cast referable to *Schizoneura* or *Neocalamites* (Kryschtofovich, 1923; Srebrodol'skaya, 1966).

At two localities on the mainland around Vladivostok, the associated marine fauna is poorer. There are ammonites and two species of *Velopecten*, but no elements in common with the Russkiy Island fauna. *Pleuromeia* is also associated with other plant fossils at these localities; *Equisetites*, 'possibly' *Lepidopteris*, and a 'different type of seed' at 'Vtoroya rechka', and *Cladophlebis* sp. on the Sibichuan River (Srebrodol'skaya, 1966). The restricted fauna and extra floral elements suggest that the mainland localities were deposited in a coastal lagoon.

*A Japanese seashore.* Remains of *Pleuromeia hataii* Kon'no 1973 are found near Motoyishi as an almost monospecific taphoflora with *Neocalamites muratae* Kon'no 1973 and 'very few plants of uncertain affinity' (Kon'no, 1973). The fine preservation and abundance of *Pleuromeia* and the association of stems, rhizopores, leaves, and cones suggest the remains are subautochthonous. The remains are associated with ammonites and other marine molluscs.

*Ecology of related plants.* Modern lycopods show a preference for moisture, low sunlight, and sparse vegetation (Seward, 1910; Sporne, 1966). *Lycopodium*, *Phylloglossum*, and *Selaginella* can withstand relatively dry conditions, at least seasonally (Osborn, 1918, 1919; Cheeseman, 1906; Wakefield, 1955). However, these genera diverged very early from the mainstream of lycopod evolution (Banks, 1968; Chaloner & Boureau, 1967).

The living *Isoetes* and *Stylites* are generally seen as products of the lineage which also produced *Pleuromeia* (Mägdefrau, 1931a; Chaloner & Boureau, 1967). Schoute's (1938) objections to this have been countered by Stewart (1947). Greguss (1968) uses the polyciliate spermatozoid, suspensorless embryo, and stippled parenchyma in the outer cortex of *Isoetes* to ally it with Filicales and Cycadales rather than *Lycopodium* and *Selaginella*. The comparison is unfair as none of these features is preserved in Lepidodendrales, *Pleuromeia*, or *Nathorstiana*, which resemble *Isoetes* in all the other features treated by Greguss. *Isoetes* is commonly found submerged in lakes or tarns, but some species grow in damp soil. *Stylites* is only known from lake-side tussocks at 4750 m elevation in the Peruvian Andes (Rauh & Falk, 1959).

The Carboniferous Lepidodendrales were the probable ancestors of *Pleuromeia*. These commonly grew in coal-forming swamps associated with marine or brackish sediments containing pelecypods, brachiopods and goniatites (Ferm, 1970; Cavaroc & Ferm, 1968; Wanless, Baroffio & Trescott, 1969). The common occurrence of *Spirorbis* around parichnos scars of *Lepidodendron* may indicate that the base of the stem was submerged in salt water (Seward, 1910, p. 103). The Carboniferous Lepidodendrales were probably facultative halophytes as some coals formed in alluvial plains and lakes (Hacquebard & Donaldson, 1969).

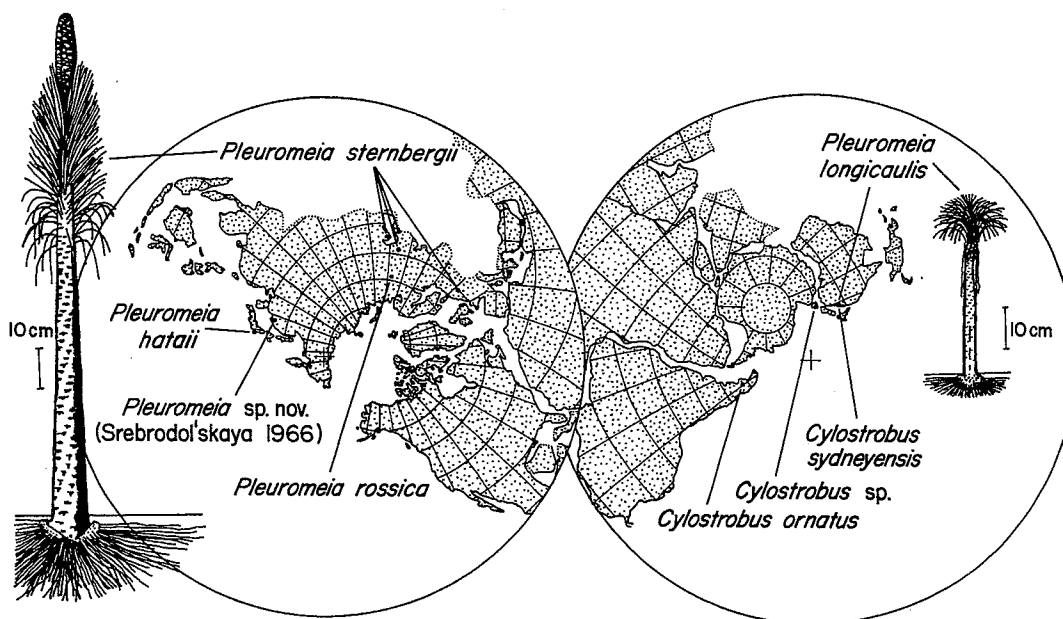


Fig. 6. The geographic distribution of Pleuromeiaceae (reconstruction simplified after Hirmer, 1933; Chaloner & Boureau, 1967).

### Pleuromeiacean shorelines and provinces

The world-wide occurrences of Pleuromeiaceae are listed in Appendix 1 and shown on the Triassic map of Smith, Briden & Drewry (1973) (Fig. 6). As a realistic Triassic map this has many shortcomings. It was used here because it shows general continental relations and accurate locations with respect to the modern geographic grid and coastlines.

In the northern hemisphere the occurrences follow a line along the northern shore of the Triassic Tethys Ocean from Germany to the Caspian Sea, thence through Vladivostok to Japan. A Triassic seaway in this position has been postulated by Burrett (1974).

In the southern hemisphere the occurrences are not associated with marine fossils. They were probably near coastal deposits on the Eopacific rim of Gondwanaland.

This bipolar distribution is in some ways comparable to the Indo-Pacific and Atlantic provinces of modern mangroves (van Steenis, 1962). The northern Pleuromeiacean province is apparently more diverse than the southern province. *Pleuromeia* probably originated here, as the morphological features of these northern species are closer to

the Carboniferous *Lepidodendrales* than to *P. longicaulis* and the living *Isoetales*. These features of the northern Pleuromeiaceae are the larger, elongate, pedunculate cone, trilete microspores (at least in *P. rossica*), and more elongate rhizophores. Less variation is known from the southern province species which have ovate, apparently apedunculate cones with monolete microspores, unlobed rhizophores, and are generally smaller in size.

An indigenous origin of the southern Pleuromeiaceae is unlikely. Gondwanaland Carboniferous '*Lepidodendron*' is probably eligulate *Lepidodendropsis* (Rigby, 1969) or *Sublepidodendron* (Rigby, 1973). The Gondwanaland Permian Lycopodiopsidae are also eligulate and bear sporophylls on unspecialised axes (Chaloner & Boureau, 1967). A shoreline migration of the southern Pleuromeiaceae from Eurasia seems more likely.

A southern Tethys shoreline route through north Africa and peninsular India would be most direct. In this respect some possible Western Australian *Pleuromeia* remains are worthy of further attention (Appendix). Some '*Araucarites*' cone scales from the Scythian Parsora Beds of India described by Lele (1961) are similar to isolated *Cylo-*

*strobis* sporophylls in their lack of sporangium, weak cutinisation and strong wedge-shaped keel. The possibility of Indian *Cylostrobis* is also worthy of further attention (Appendix).

A northern route through Japan is also possible. The wedge-shaped sporophylls and weakly lobed rhizophore of *Pleuromeia hataii* are intermediate between the characters of the northern and southern provinces. However, not enough essential details of *P. hataii* are known.

### The heyday of *Pleuromeia*

In Fig. 7 the ages of the various occurrences of *Pleuromeia*, *Cylostrobis*, and selected spores are shown against the Triassic time scale of Tozer (1965, 1971).

The time evidence alone cannot be regarded as reliable or complete enough to deduce the centres and migration paths of the Pleuromeiaceae. The occurrences are mainly Scythian with some Anisian lingerers. The use of the Pleuromeiaceae as indicators of Early Triassic age is reasonable. However, as they are known to be facies controlled, their absence cannot be used to determine age.

The idea that many extinct lycopods formed specialised coastal associations, developed here, has also been suspected by palynologists (Balme, 1969; Helby, 1973). This habitat explains the biostratigraphic usefulness of *Aratrisporites* (in part of *Cylostrobis* Helby & Martin 1965), *Nathorstisporites hopliticus* Jung 1958 (of *Lycostrobis scottii* Nathorst 1908), and *Banksisporites pinguis* (Harris) Dettmann 1961 (of *Selaginella hallei* Lundblad 1950) (Townrow, 1962; Jung, 1961; Balme, 1970; Helby, 1967, 1969; Playford & Dettmann, 1965; Dettmann, 1961). These spores have been used to correlate Australian terrestrial sequences with European sequences. They cut across Triassic provincial boundaries based on the rest of the terrestrial micro- and megafloora.

The expansion of the Pleuromeiaceae coincides with the recovery of the world biota from a long drawn out ecological and environmental crisis (see Logan & Hills, 1973). Similarly, the Rhaeto-Liassic spores and cones (Fig. 7) also coincide with a global life crisis. The recovery of the world flora from these life crises is in some ways similar to the process of ecological succession

(Balme & Helby, 1973; Tappan & Loeblich, 1973). However, its duration is much longer than that involved in succession as understood by ecologists (Whittaker, 1953; Richards, 1955; Crocker & Dickson, 1957). Opportunistic species, such as *Pleuromeia*, appear to have flourished as conditions slowly improved. With further improvement the opportunists were displaced by more aggressive but less tolerant upland species, such as the *Voltzia* flora of Germany and the Middle Triassic *Dicroidium* floras of eastern Australia.

### Systematic palaeobotany

In this section the following abbreviations are used for institutions: UNE, Department of Geology, University of New England (Australia); SUGD, Department of Geology and Geophysics, Sydney University. Locality grid references are prefixed by BB and were taken from the National Mapping Broken Bay 1:63 360 sheet. The informal system of Matthews (1973) has been used in synonymy lists.

Class Lycopsidea

Order Lepidodendrales

Family Pleuromeiaceae

PLEUROMEIA Corda in Gernar 1852

*Type species. Pleuromeia sternbergii* (Münster) Corda in Gernar 1852.

*Remarks.* The reconstructions (Figs 1, 6) give a quick visualisation of this genus. The type species remains incompletely known. *P. rossica* gives perhaps the best morphological information of the western Eurasian species (Neuburg, 1961; Dobruskina, 1974). *Nathorstiana* (Mägdefrau, 1932), *Nathorstianella* (Glaessner & Rao, 1955), *Isoetites* (Chaloner & Boureau, 1967) and the extant *Stylites* (Rauh & Falk, 1959) and *Isoetes* are all shorter stemmed or herbaceous plants. *Paurodendron* is now a junior synonym of *Selaginella* (Schlanker & Leisman, 1969). According to Dobruskina (1974) *Pleuromeiopsis* only includes the poorly preserved fragmentary holotype of the type species. The remaining material from the same type locality has been removed to *Ferganodendron* Dobruskina 1974, which is a larger plant with more dense smaller leaf cushions and narrower leaves, lacking a basal expansion, unlike *Pleuromeia*.

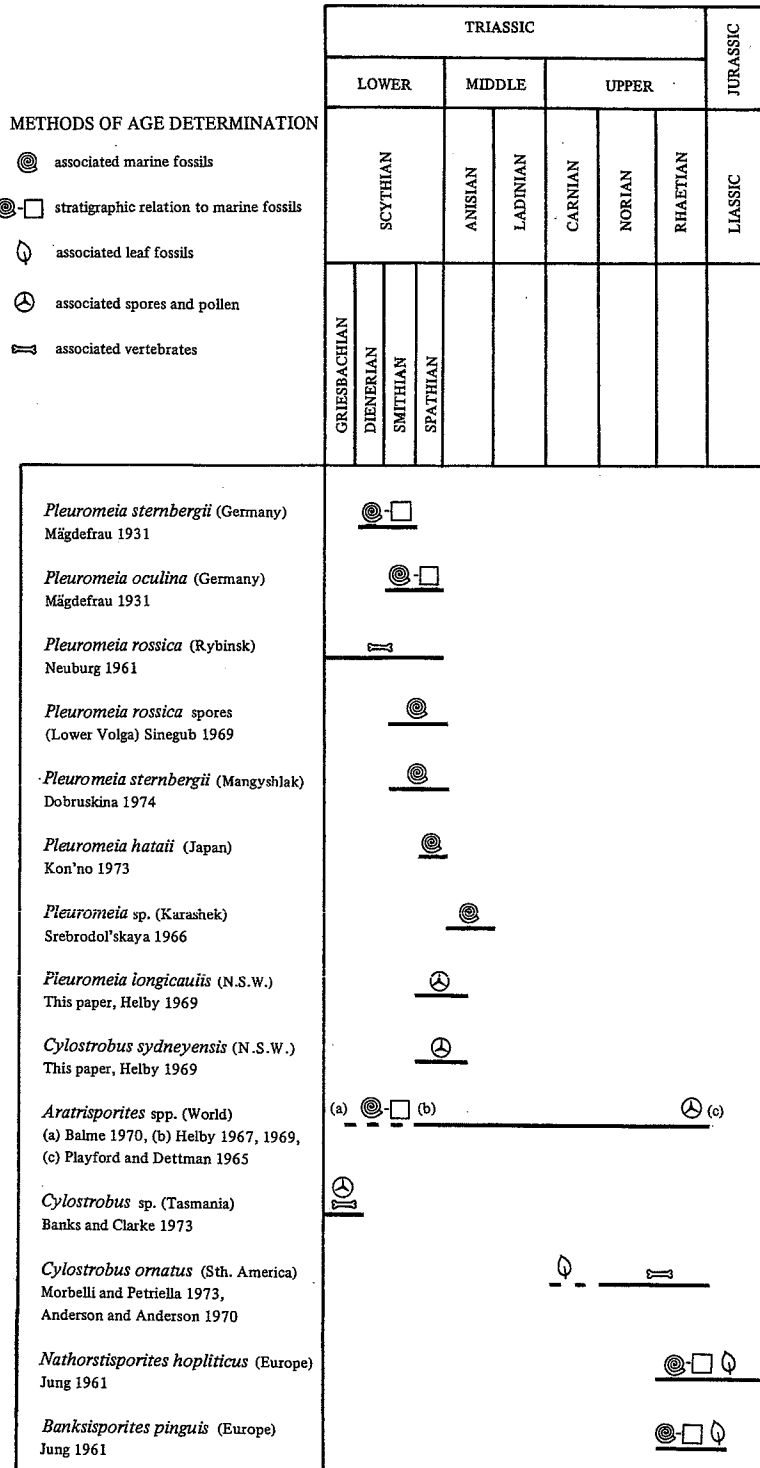


Fig. 7. The temporal distribution of selected Mesozoic lycopod megafossils and microfossils.

*Pleuromeia longicaulis* (Burges) comb. nov. (Figs 1, 8, 9, 10)

- v\*1935 *Lycostrobus longicaulis* Burges, p. 259, text-fig. 1.  
 v. 1935 *Caulopteris* sp.; Burges, p. 260, text-figs 3, 4, 5.  
 . 1965 '*Caulopteris*' sp.; Helby & Martin, fig. 5.  
 1967 *Lycostrobus longicaulis*; Chaloner & Boureau, p. 751.

*Holotype*. SUGD2003 Burges 1935 text-fig. 1 (figured here in Figs 8A, 9A).

*Type locality*. 'Avalon' in 'extensive beds with *Williamsonia* stems' (Burges, 1935). This is the *Pleuromeia* horizon in the sea cliffs at North Avalon (Fig. 4D, UNEL 1384), lower part of the Newport Formation, Narrabeen Group, Sydney Basin (Herbert, 1970), late Scythian to early Anisian age (Helby, 1969).

*Additional material*. SUGD2006 (Burges, 1935, text-figs 3, 4, 5); UNEF13804 to UNEF13816 and UNEF14603 to UNEF14606 inclusive; collodion peels UNEF13806, UNEF13812, UNEF13809; thin sections and specimens UNEF14601, UNEF14602.

*Additional localities*. UNEL1388, along strike from the type locality, south of St Michael's Cave, at BB345445; UNEL1565, along strike from the type locality, on rock platform, just north of St Michael's Cave, at BB345446; UNEL1408, rock-fall south of Bilgola at BB333423 (Fig. 4C).

*Distinguishing features*. Small *Pleuromeia* with unlobed rhizophores and a compressed stem diameter of 30-43 mm.

*Diagnosis*. Leaves long, parallel sided, 5-9 mm wide, ?univeined with two parallel stomatal furrows and elongate rectangular cells 30  $\mu$ m wide. Leaf bases retained in a zone below the elongate leaves, with a distinct ligule 4.8 mm by 0.9 mm, lacking distinct stomatal furrows. Epidermis of stem not extending over leaf scars, with elongate cells 30  $\mu$ m wide forming a striation transverse to the axis of the stem. Compressed stems 30-43 mm wide with spirally arranged leaf bases. Fresh leaf scars transversely lens shaped 6 mm by 1.7 mm with two lateral depressed triangular fields and a central round pit containing a single slightly projecting leaf trace. Leaf scars towards the base of the stem with more prominent and elongate leaf trace. Stem with numerous major and minor longitudinal creases, especially towards the base. Rhizophore rounded,

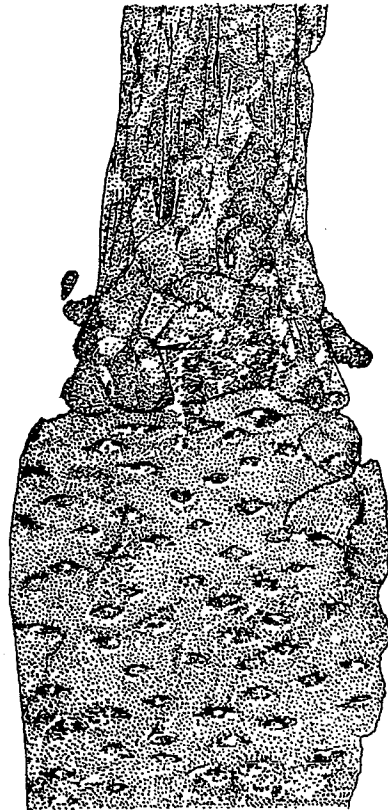
unlobed, bearing numerous rounded appendage scars 2-5 mm in diameter, with a central pit and indistinct radial ridges.

*Description*. The stems are preserved as steinkerns with a thin coating of cuticle and carbonised outer cortex. They have a compressed width of 30-43 mm and a maximum observed length of 217 mm. An estimate of life diameter by averaging the ellipse axes of four specimens preserved in cross section (e.g. Fig. 9C) was 23-24 mm. This agrees with a life diameter of 19-27 mm calculated on the assumptions that the compressed width is half the life circumference and that the stem could spread laterally when flattened. Thus Walton's (1936) compression theory does not necessarily hold for peat 'compactions' (*sensu* Walton, 1936). In this case lateral spreading is allowed by the paucity of confining sediment, rotting of the stem interior and some flattening prior to the deposition of overburden on the original 'leaf litter' of the coaly layer. Lateral spreading appears to be slightly greater in the less lignified sterile apex than lower on the stem (Figs 8A, 9A).

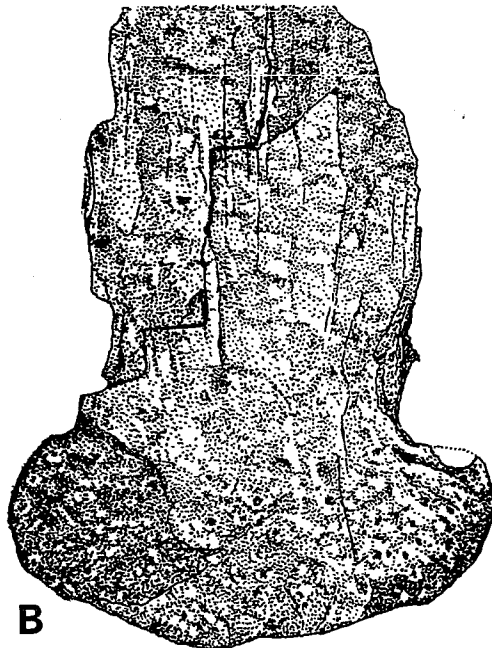
The leaf scars are lenticular and arranged in a spiral of variable pitch. They are 5-7 mm wide and 1.5-2 mm high when well preserved. The fresh leaf scar on stems with epidermis (Figs 8E, 10D) is recessed from the surface of the stem. The recessed area is outlined by low lips both above and below. The leaf trace protrudes slightly from the centre of a round pit within the lensoidal recessed area. Less well preserved leaf scars towards the base of the stem are decorticated to subepidermal levels (Fig. 8F). These show a vertically elongated leaf trace, indicating that the leaf trace curves sharply downwards within the outer cortex.

Towards the base of the compressed stem there are several minor and three or four deep creases which die out gradually towards the apex and rapidly into the rhizophore.

There is no evidence of lobing of the rhizophore as in other species of *Pleuromeia* (Figs 9D, 9E). The appendage scars consist of a slightly elevated ring of tissue 2-5 mm in diameter surrounding a central pit which represents the appendage trace (Fig. 10H). Better preserved appendage scars may show low radial ridges (Fig. 8G). A similar feature is seen in *Stigmara stellata*. As in that species it is probably due to wedges of thick walled cells in the outer cortex (Jennings,



A



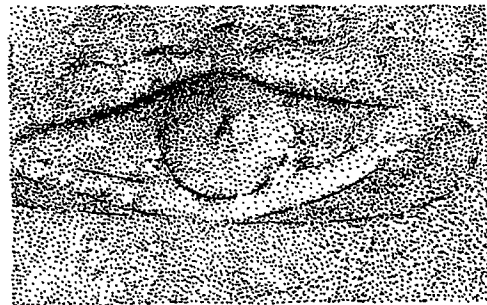
B



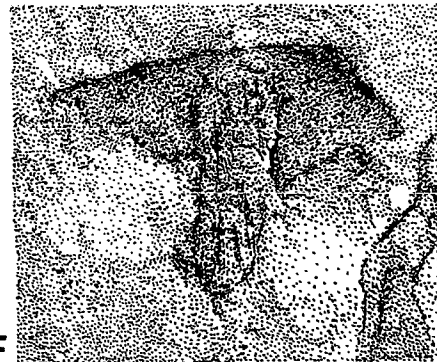
C



D



E



F



G



1973). Some carbonised rhizophore surfaces show traces of shrivelled appendages (Fig. 10G). The appendages function as roots (Stewart, 1947).

The upper part of the axis is clothed in leaves and terminates in an abrupt rounded apex (Figs 8A, 9A). Both leaf bases and elongate leaves are found attached to axes and in isolation. The leaf bases are 5-7 mm wide, often with a ragged apex broken off short and a neatly rounded abscission base (Figs 8D, 9C, 10A). The external mould of the adaxial face of a leaf base shows a clear finger-shaped ligule about 4.8 mm by 0.9 mm in size.

Above the zone of retained leaf bases the apex bears elongate leaves (Fig. 9A). The leaves show two distinct well-spaced parallel carbonised grooves (Figs 8C, 10B, 10C). I interpret these as a triple thickness of cuticle in two stomatal furrows rather than a twin midrib. No cuticle could be obtained to confirm this, nor did collodion peels of leaf surface or thin sections of leaves give firm evidence. This interpretation is based on the single leaf trace in leaf scars, the more convex central area between the furrows on leaves attached to axes than in isolated leaves, and the broad single midrib of other species of *Pleuromeia* (Mägdefrau, 1931a; Kon'no, 1973). Attached to the apex the leaves are up to 5 mm wide and the furrows 1.9 mm apart (Figs 8C, 10B). Isolated leaves have been found up to 8.7 mm wide with furrows 2.9 mm apart. In thin section isolated leaves have the appearance of a flattened 'W' (Fig. 10E) or may be rolled along their length.

I could not isolate any cuticle. Cuticle on carbonised cortex and leaves, chipped away or floated off in HF, did not withstand treatment with dilutions of nitric acid. Collodion peels (Andrews, 1961, p. 466) of epidermal surfaces showed very indistinct outlines of rectangular cells (Fig. 10F). These were arranged parallel to the margin on leaves and transversely on stems. On both stems and leaves the cell width is about 30 µm. There are no clearly recognisable cell outlines within the leaf scar. The relationship between

stem, ligule, and leaf cuticle on the living plant and selected fossils is shown diagrammatically in Fig. 11.

*Comparison.* Only *Pleuromeia sternbergii* (Mägdefrau, 1931a), *P. rossica* (Neuburg, 1961), and *P. hataii* (Kon'no, 1973) are sufficiently well characterised for comparison. All three species have a distinctly lobed rhizophore unlike *P. longicaulis*. *P. sternbergii* attained a much larger size, probably up to 2 m high, and its leaves are distinctly lanceolate. *P. rossica* is also much larger (up to 1 m high). *P. hataii* is smaller and its leaf scars are quadrangular in outline.

#### CYLOSTROBUS Helby & Martin 1965

*Type species.* *Cylostrobos sydneyensis* (Walikom) Helby & Martin 1965.

*Remarks.* The essential features of this genus are summarised in Fig. 5 and in the diagnosis of Helby & Martin (1965, p. 391).

Comparable Mesozoic lycopod cones may be arranged in the following way (Table 1): poorly known, *Poecilostachys haugi* (Chaloner & Boureau, 1967), *Lycostrobos chinleana* (Daugherty, 1941; Miller, 1968); unrelated to *Cylostrobos*, *Selaginella hallei* (Lundblad, 1950); possibly related to *Cylostrobos*, *Lycostrobos scottii* (Nathorst, 1908; Seward, 1910), *Selaginellites polaris* (Lundblad, 1948); related to *Cylostrobos*, *Pleuromeia sternbergii* (Mägdefrau, 1931a), *P. rossica* (Neuburg, 1961; Dobruskina, 1974), *P. hataii* (Kon'no, 1973), and *P. sp. nov.* (Kryshchtofovich, 1923; Srebodol'skaya, 1966). *Poecilostachys haugi* is possibly a leafy twig fortuitously associated with sporangia. *Lycostrobos chinleana* is larger than *Cylostrobos*, pedunculate, and has acuminate sporophyll tips. *Selaginella hallei* has trilete microspores and is borne on narrow dichotomising axes with dimorphic leaves. *Lycostrobos scottii* is pedunculate, more elongate (length to diameter is 4:1), and has acuminate sporophyll tips. Its microspores are monolet with obscure exoexine ornament and its megaspores are trilete with long ectexinous spines, especially on the laesura. The sporophylls of *Selaginellites polaris* have shortly acuminate sporophyll tips and are

Fig. 8. *Pleuromeia longicaulis* (Burgess) comb. nov. A, stem apex bearing leaf bases and elongate leaves, holotype, SUGD2003, x1. B, rhizophore with appendage scars (right) and shrivelled appendages (left), UNEF13806, x1. C, elongate leaf showing stomatal furrows, UNEF13809, x2. D, leaf base adaxial external mould showing ligule, UNEF13812, x2. E, fresh leaf scar on an epidermal surface, UNEF13809, x10. F, subepidermal expression of a leaf scar, UNEF13806, x10. G, appendage scar showing indistinct radial ridges, UNEF13811, x10.

not as closely imbricate as *Cylostrobos*. Its megaspores and microspores are both trilete. Its size and fleshy axis (for a 'Selaginellites') are similar to *Cylostrobos*. *Pleuromeia rossica* differs from *Cylostrobos* in its rounded sporophylls and trilete microspores. *P. sternbergii* has a larger elongate cone (up to 20 cm long) with well rounded sporophylls. The microspores are possibly monolete but it appears that only intexines were examined. *Pleuromeia* sp. nov. (of Srebrodol'skaya, 1966) has a large elongate cone with rounded sporophylls. *Pleuromeia hataii* is imperfectly known. Its cone is larger (4.1 cm in diameter) and only trilete megaspores are known.

*Cylostrobos sydneyensis* (Walkom) Helby & Martin 1965 (Fig. 5)

- 1925 *Araucarites sydneyensis*; Walkom, p. 221, pl. XXXI, figs 2, 7.  
 v. 1935 *Araucarites sydneyensis*; Burges, p. 262, text-figs 10, 11.  
 v\*1965 *Cylostrobos sydneyensis*; Helby & Martin, p. 395, fig. 3; pl. 1, figs 3, 5-7; pl. 2, figs 10, 11, 18; pl. 3, figs 22-27.  
 v. 1965 *Cylostrobos major*; Helby & Martin, p. 396, pl. 1, figs 2, 4, 8, 9; pl. 2, figs 12, 13, 19.  
 v. 1965 *Cylostrobos grandis*; Helby & Martin, p. 397, pl. 1, fig. 1; pl. 2, figs 14, 15, 17, 20, 21.  
 1967 *Cylostrobos sydneyensis*; Chaloner & Boureau, p. 658, fig. 453B-D.  
 1967 *Cylostrobos major*; Chaloner & Boureau, p. 658.  
 1967 *Cylostrobos grandis*; Chaloner & Boureau, p. 659.

*Neotype*. As they could not locate Walkom's (1925) holotype, Helby & Martin (1965) nominated a neotype (SUGD16016, Helby & Martin, pl. 1, fig. 3).

*Type locality*. Walkom's (1925) specimen came from 'about 6-8 feet above high water mark at Turimetta Head'. The neotype is from the 'upper part of the Collaroy Claystone, Turimetta Head, N.S.W.' (Helby & Martin, 1965). Both probably refer to the siltstone associated with the green lithic sandstone channel at Turimetta Head (Fig. 4B, UNEL1443). The drab upper portion of the red Bald Hill (formerly Collaroy) Claystone is now called the Garie Formation (Loughnan, 1969; Herbert, 1970; Retallack, 1973), Narrabeen Group, Sydney Basin, of late Scythian to early Anisian age (Helby, 1969).

*Additional material*. All described and figured specimens of Helby & Martin (1965) and Burges (1935) are in SUGD. I have lodged a smaller collection at UNE; UNEF 13800-UNEF13803, UNEF13828, and cone and spore preparation UNEF14598. There are also representative specimens catalogued by locality number for all localities from which I have collected this species.

*Additional localities*. All in the sea cliffs between Avalon and Long Reef; UNEL1393, north of St Michael's Cave BB345448, siltstone 3 m above rock platform; UNEL1403, Newport BB324423 rock-fall at north end of beach; UNEL1408, south of Bilgola BB333423 rock-fall from 3 m above rock platform; UNEL1413, north of Bungan BB328404, large fallen boulder; UNEL 1417, north of Bungan BB329405 carbonaceous shale, directly above talus slope; UNEL1420, Mona Vale BB324391 rock-fall, grey siltstone; UNEL1433, Turimetta Head BB318366, shale under roof sandstone; UNEL1434, Turimetta Head BB317367, shale under roof sandstone; UNEL1435, Turimetta Head BB320365, rock-fall at point; UNEL1436, Turimetta Head BB320365, rock-fall 15 m south of point; UNEL1437, Turimetta Head BB319365, rock-fall ripple-marked sandstone and shale; UNEL1444, Turimetta Head BB320365, shale directly above lithic sandstone channel 8 m above rock platform; UNEL1560, Long Reef BB323310, shales at top of point.

*Distinguishing features*. Compressions of *Cylostrobos* 4-42 mm in diameter.

*Remarks*. See Helby & Martin (1965) for full descriptions.

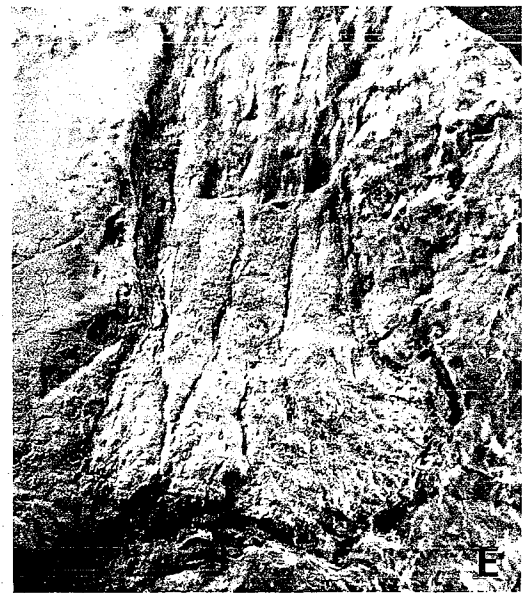
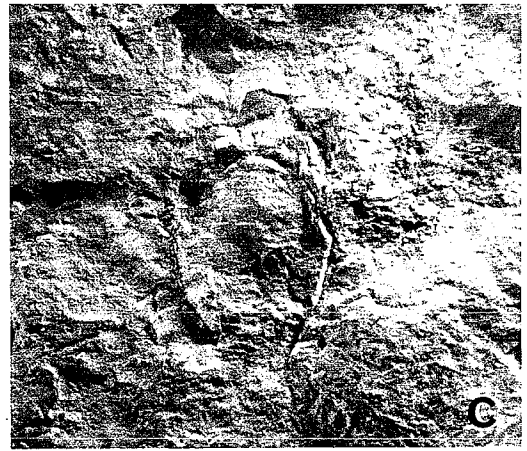
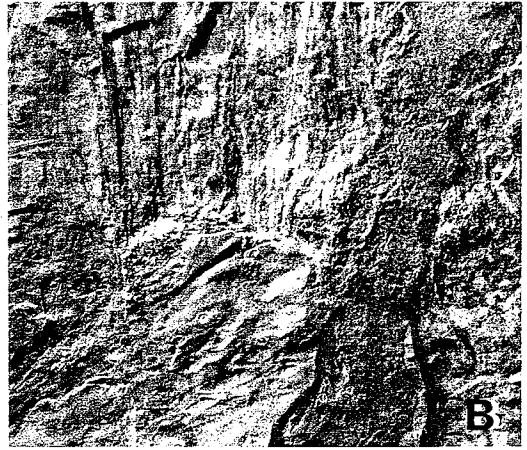
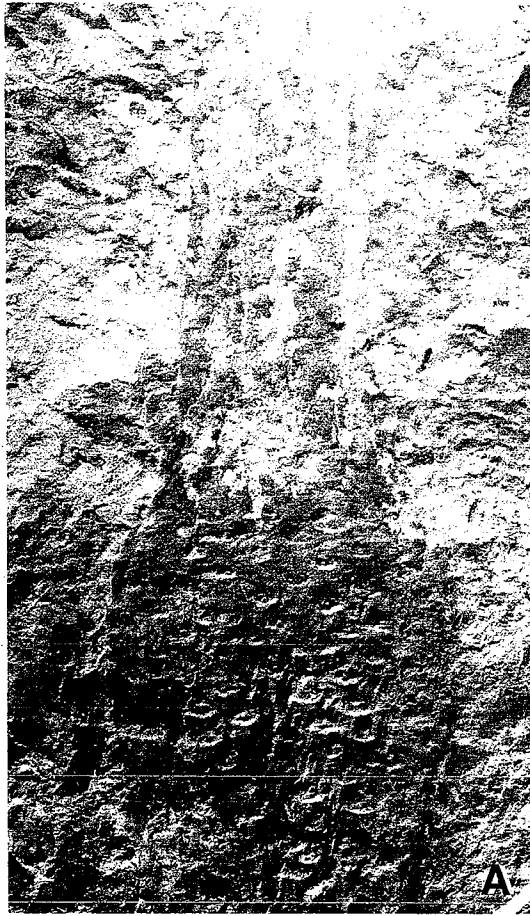
*Cylostrobos ornatus* (Morbelli & Petriella) comb. nov.

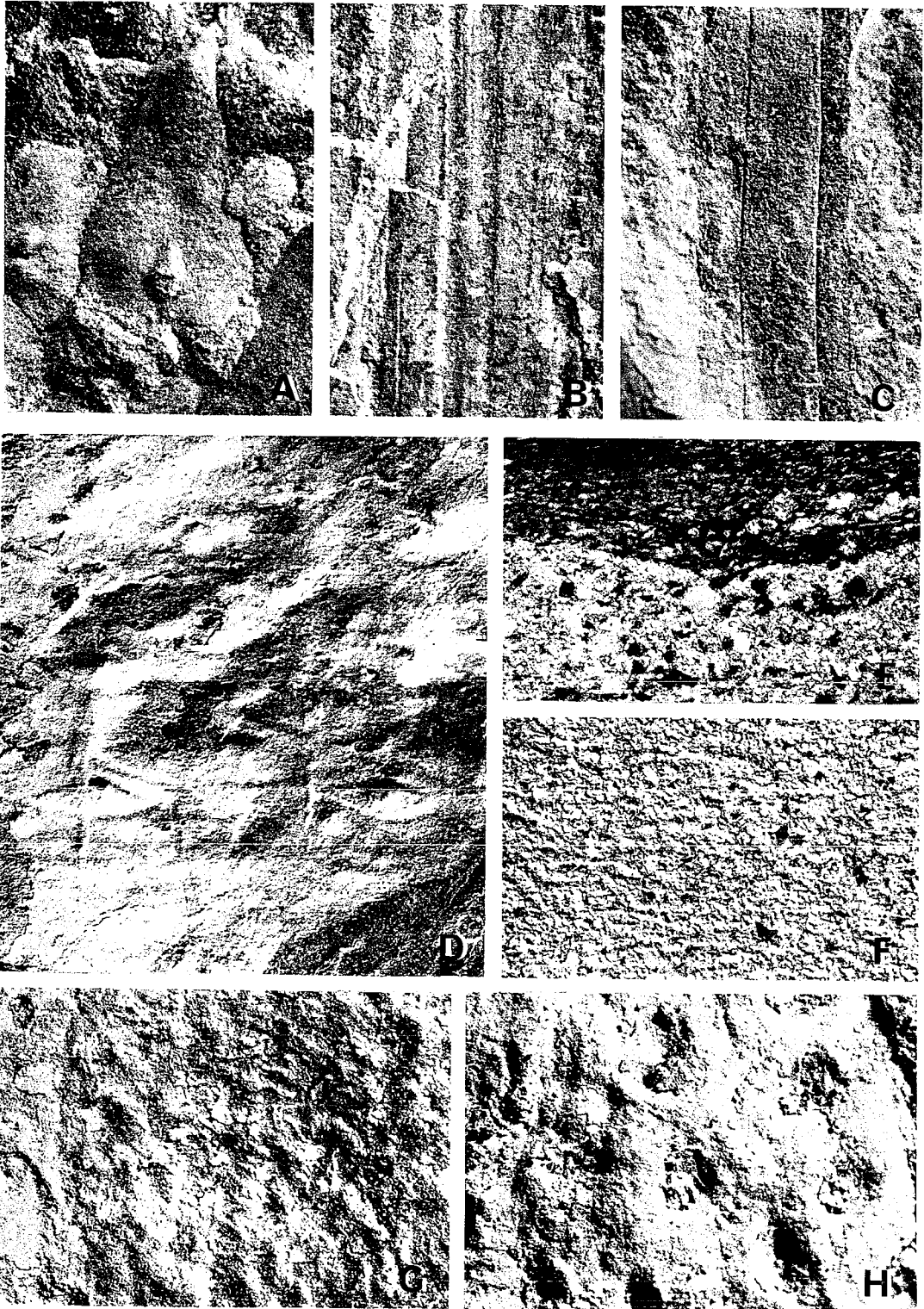
- 1973 *Austrostrobos ornatum*; Morbelli & Petriella, p. 280, fig. 1, lam. I, II.

*Holotype*. LP-PB9201 and slides 831, 832, 833 in the 'División Paleobotánica, Facultad de Ciencias Naturales y Museo de la Plata' (Morbelli & Petriella, 1973).

*Type locality*. 'Estancia Canadón Largo, Prov. de Santa Cruz', Patagonia, El Tranquilo Formation (Morbelli & Petriella, 1973), El Tranquilo Basin, of Norian to

Fig. 9. *Pleuromeia longicaulis* (Burges) comb. nov. All figures natural size. A, leafy stem apex, holotype, SUGD2003. B, leafy stem apex, UNEF13809. C, leaf bases attached to a strata transgressive stem, UNEF13813. D, rhizophore, UNEF13806. E, rhizophore, UNEF13805.





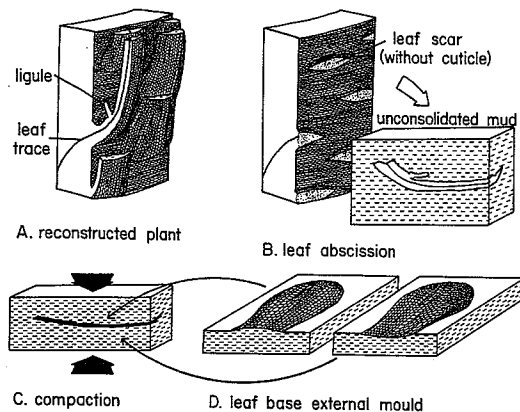


Fig. 11. A diagrammatic representation of the relationship between stem, ligule, and leaf cuticles in living and fossilised *Pleuromeia longicaulis* plants.

Carnian (or older?) age (Anderson & Anderson, 1970).

**Distinguishing features.** Petrified *Cylostrobus* 6 cm in diameter; megaspores with spongy exoexine and narrow zona, microspores with ornate intexine.

**Remarks.** Only a single petrified cone is known. Morbelli & Petriella (1973) give a full description.

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Fig. 10. *Pleuromeia longicaulis* (Burgess) comb. nov. All figures enlarged as indicated. A, leaf base adaxial external mould showing ligule, UNEF13812, x4. B, elongate leaf, UNEF13809, x4. C, isolated elongate leaf, UNEF14601, x4. D, stem epidermal surface with leaf scars and longitudinal cracks, UNEF13809, x4. E, thin section through a ?stomatal furrow of an isolated leaf lying on the boundary between sandstone and shale, UNEF14601, x70. F, collodion peel of the epidermal surface of a leaf, UNEF13809, x70. G, shrivelled appendages on a rhizophore, UNEF13806, x4. H, well preserved appendage scars showing indistinct radial ridges, UNEF13811, x4.

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## APPENDIX

World distribution of *Pleuromeiacean* remains. Geological ages adjusted to the time scale of Tozer (1965, 1970).

## 1. Well documented records with illustrations

A. *South America*, Santa Cruz, Patagonia; El Tranquilo Fm., El Tranquilo Basin, Norian-Carnian (or older?) (Morbelli & Petriella, 1973, this paper); *Cylostrobos ornatus* (Morbelli & Petriella) comb. nov.

B. *New South Wales*, sea cliffs from Long Reef to North Avalon, north of Sydney; Newport and Garie Fms., upper Narrabeen Group, Sydney Basin, late Scythian to early Anisian (Helby & Martin, 1965, this paper); *Cylostrobos sydneyensis* (Walkom) Helby & Martin 1965, *Pleuromeia longicaulis* (Burges) comb. nov.

C. *Germany*, 13 localities in the Middle to lower part of the Upper Buntsandstein, middle to late Werfenian (Dienerian-Spathian) (Mägdefrau, 1931a, 1931b; Chaloner & Boureau, 1967; Dobruskina, 1974, fig. 2); *Pleuromeia sternbergii* (Münster) Corda in Germar 1852.

D. *Western U.S.S.R.*, near the confluence of the upper Volga and Sheksna Rivers, near Rybinsk Reservoir (Neuburg, 1961) and several other unspecified localities in the same region (Dobruskina, 1974); Rybinsk Suite, Veltugian Stage, Scythian (Neuburg, 1961; Dobruskina, 1974; Chaloner & Boureau, 1967; Radcenko *et al.*, 1973); *Pleuromeia rossica* Neuburg 1960.

E. *East of the Caspian Sea*, several localities in the Mangyshlak Peninsula (Dobruskina, 1974; Srebrodol'skaya, 1966); the geological succession begins with the Dolnapinskoy Suite containing *Pleuromeia* sp. (poorly preserved). The overlying units, detailed below, contain good remains of *Pleuromeia sternbergii* (Münster) Corda in Germar 1852 throughout; beginning with the Tartalinskoy Suite also containing *Columbites* zone, Olenekian (Spathian) ammonites, then the Karadzhatskoy Suite with *Prohunganites* zone, Olenekian (Spathian) ammonites, the Karaduanskoy Suite and finally the Khozbulakskoy Suite with a pelecypod fauna which has been regarded as Carnian but is more likely Anisian (Dobruskina, 1974).

F. *Southeast Siberia*, near Vladivostok, 3 localities on Russkiy Island and 2 mainland localities; associated with an Olenekian fauna (Smithian-Spathian) (Kryshchtofovich, 1923; Srebrodol'skaya, 1966; Dobruskina, 1974); *Pleuromeia* sp. nov. Srebrodol'skaya 1966.

G. *Japan*, Motoyishi, northeast coast of Honshu; Osawa Fm., Inai Series, Kitakami Massif, associated with a *Columbites* fauna (Spathian) (Kon'no, 1973); *Pleuromeia hataii* Kon'no 1973.

## 2. Reliable records without illustrations

H. *Tasmania*, Knocklofty Quarry, west Hobart; Knocklofty Sandstone and Shale, ?Octoceratan (?Griesbachian) (identification of Townrow in Banks, Cosgriff & Townrow, 1967; and Banks & Clarke, 1973); *Cylostrobos* sp.

I. *Northwest of the Caspian Sea*, lower Volga, Bol'shoye Bogdo (Mtn. 48.1°N, 46.8°E); Bogdinskoy Suite, with middle Olenekian ammonites (Smithian-Spathian) (Dobruskina, 1974); *Pleuromeia sternbergii* (Münster) Corda in Germar 1852. J. *West of the Caspian Sea*, drillhole core from the Caspian Plain, northeastern foothills and northern slopes of the Caucasus Mountains; geological setting not specified (Dobruskina, 1974); *Pleuromeia sternbergii* (Münster) Corda in Germar 1852.

## 3. Records doubted or redetermined by later workers

K. *Pleuromeia oculina* (Blankenhorn) Potonie 1902 from near Commern, north Rhineland, Germany (Seward, 1910; Kryshchtofovich, 1923; Mägdefrau, 1931; Chaloner & Boureau, 1967) is based on a single specimen and an apparently unreliable figure (Dobruskina, 1974).

L. *Pleuromeia* from the Triassic of Spain is doubted by Srebrodol'skaya (1966).

M. *Pleuromeia sternbergii* from Chauffontaine, near Luneville, France, is doubted by Srebrodol'skaya (1966) and Chaloner & Boureau (1967).

N. *Pleuromeia sternbergii* from the Lower Keuper of Ballstedt, near Gotha, is regarded as a *Caulopteris* by Mägdefrau (1931a).

O. The isolated bark fragments of *Pleuromeia semejtavica* Salmenova (MS) in Srebrodol'skaya (1966), from the Semeytau Mountains of northeast Kazakhstan were examined by Dobruskina (1974), who concluded that they did not belong to either *Pleuromeia*, *Pleuromeiopsis*, or *Ferganodendron* and may not even be lycopodiaceous.

P. *Pleuromeiopsis kryshchtofovichii* Sixtel 1962 was based on abundant material from the Madygen Suite of Southern Fergana, Uzbekistan. However, Dobruskina (1974) has removed most of this material to *Ferganodendron sauktangensis* (Sixtel) Dobruskina 1974, leaving *Pleuromeiopsis kryshchtofovichii* to include only Sixtel's holotype, which Dobruskina regards as too poorly preserved to be of any value. Dobruskina maintains the remains are of lower to middle Keuper age, contrary to previous workers (Srebrodol'skaya, 1966; Radcenko *et al.*, 1973). However, his new name removes any inference of relationship to the *Pleuromeiaceae*, which remains to be elucidated.

Q. *Pleuromeia* sp. was reported from Mongolia by Meyen (1973) as the 'latest data of I. A. Dobruskina pers. comm.'; however, it is not mentioned in Dobruskina's (1974) extensive review.

R. *Pleuromeiopsis* sp. from the lower Triassic Malaysarin Suite of Dzungara (Radcenko *et al.*, 1973) probably refers to the isolated bark fragments from southern Kazakhstan which Dobruskina (1974) believes are unidentifiable.

S. *Pleuromeia* sp. 'in the basin of the Amga River' of Siberia (Srebrodol'skaya, 1966) probably refers to the unidentifiable isolated bark fragments seen by Dobruskina (1974) from Tunguska and western Verkhoyan'ya.

	cone length	cone attachment	sporophyll tips	megaspores	microspores	age
FAMILY SELAGINELLACEAE						
<i>Selaginella halleti</i> (Lundblad) Lundblad 1950	5mm	on dichotomising slender axes with dimorphic leaves	acutely pointed	<i>Banksisporites pinguis</i> (Harris) Dettman 1961; trilete, granulate	cf. <i>Densosporites</i> (Berry) Butterworth, Jansonius, Smith and Staplin in Butterworth 1964; trilete, thick cingulum, reticulate to pitted.	Rhaetian (cone and megaspore)
ARBORESCENT LYCOPODS POSSIBLY RELATED TO PLEUROMEIACEAE						
<i>Selaginellites polaris</i> Lundblad 1948	about 1.8cm	? trace of peduncle, axis fleshy for a <i>Selaginella</i>	acuminate	<i>Banksisporites</i> Dettmann 1961; trilete, smooth to granulate	<i>Lundbladispora</i> Balme 1963; trilete, spinose	Scythian
<i>Lycostrobus scottii</i> Nathorst 1908	11 to 12 cm	peduncle present	acuminate	<i>Nathorstisporites hopliticus</i> Jung 1958; trilete, spinose especially about laesurae	<i>Aratrisporites</i> Leschik mut. char. Playford and Dettman 1965; monolete, ornament obscure	Rhaetian (cone), Rhaeto- Liassic (megaspores)
FAMILY PLEUROMEIACEAE						
<i>Pleuromeia sternbergii</i> (Münster) Corda in Germar 1852 (spores in Mägdefrau 1931)	15 to 20 cm	sessile on <i>Pleuromeia</i> axes	rounded	cf. <i>Trileites</i> (Erdtman) Potonié 1956; trilete, smooth	"cf. <i>Laevigatosporites</i> " (Ibrahim) Schopf, Wilson and Bental 1944; however only intexines were examined (Neuburg 1961)	Scythian (Dienerian to Spathian)
<i>Pleuromeia rossica</i> Neuburg 1961	more than 4 cm	pedunculate, associated with <i>Pleuromeia</i> axes	rounded	cf. <i>Trileites</i> (Erdtman) Potonié 1956; trilete, smooth	cf. <i>Punctatosporites</i> (Ibrahim) Potonié and Kremp 1954; trilete, smooth	Scythian
<i>Pleuromeia hataii</i> Kon'no 1973	more than 14 cm	not known, associated with <i>Pleuromeia</i> axes	rounded, keeled	cf. <i>Trileites</i> (Erdtman) Potonié 1956; only tetrads described	not found	Scythian (Spathian)
<i>Cylostrobus sydneyensis</i> (Walkom) Helby and Martin 1965	0.8 to 5.8 cm	apedunculate, associated with <i>Pleuromeia</i> axes	obtusely pointed, keeled	<i>Banksisporites</i> Dettmann 1961; granulate, laminated exoexine (compression)	<i>Aratrisporites</i> Leschik mut. char. Playford and Dettman 1965; monolete, spinose.	late Scythian to early Anisian
<i>Cylostrobus ornatus</i> (Morbelli and Petricella) comb. nov.	12 cm (calculated)	not found	obtusely pointed, keeled	cf. <i>Banksisporites</i> Dettmann 1961; trilete, granulate, spongy exoexine (petrification).	<i>Aratrisporites</i> Leschik mut. char. Playford and Dettmann 1965; monolete, spinose, reticulate intexine	Norian to Carnian (or older?)

Table 1. Comparison of well-known Triassic lycopod cones (palynology after Chaloner, 1969; Chaloner & Boureau, 1969; Dettmann, 1961; Jung, 1961).

4. Brief or uncertain records deserving further attention

T. Y. D. Krasilov has identified a new species of *Pleuromeia* from the stratotype Olenekian of the lower Olenek River, Siberia (Dobruskina, 1974). This was also referred to the mistaken specific epithet '*Pleuromeia sporangium*' by Zakharov (1974).

U. A new species of *Pleuromeia* from the Alikagarskoy Suite, containing Olenekian ammonites, and also from the overlying Yokun'zhskoy Suite of Darvaza, southern Kazakhstan (Dobruskina, 1974).

V. cf. *Pleuromeia* sp. from the Somabula Beds (?) of Southern Rhodesia (Seward & Holtum, 1921; du Toit, 1927) is a very indistinct rhizophore

which could belong to any sort of arborescent lycopod.

W. Records of *Pleuromeia* from the Erskine Sandstone at Yarralla (or Yarrada) Hill, Western Australia (Brunnschweiler, 1954) are based on the figures of Foord (1890, pl. IV, figs 4, 5, 7, 8). These are indeterminate small fragments of lycopods, suggesting *Pleuromeia* and *Cylostrobos*, but further material is required for confident identification.

X. Some isolated '*Araucarites*' cone scales from the early Triassic Parsora Beds of India (Lele, 1961) are in some ways more like those of *Cylostrobos* (this paper).

Y. Stipanovic (1967) mentions possible *Pleuromeia* remains from the Puesto Viejo Fm. (Scythian), west of San Rafael, Mendoza, Argentina.

