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PLEUROMEIA FROM THE LOWER TRIASSIC OF THE FAR EAST OF THE U.S.S.R.

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ABSTRACT

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Pleuromeia obrutschewii Elias from Russian Island (Russkiy Ostrov, near Vladivostok) is hardly distinguishable from the European P. sternbergii (Muenster) Corda. The sporangia are adaxial, filling spoon-like depressions of the megasporophylls which have sterile tips. P. olenekensis sp. nov. from the Olenek River (northeastern Siberia) has larger sporangia and much larger megaspores with three-layered walls. The outer layer (ectexosporium) is reticulate. It is assumed that in other species this layer is lacking due to imperfect preservation. Mature megasporophylls, when shed, have a buoy-like shape and are often deposited together with cephalopod shells. This suggests a special mechanism of propagation by means of megasporophylls dispersed by water currents. The cosmopolitan distribution of Pleuromeia points to weakened climatic zonation in the Early Triassic.

INTRODUCTION

Pleuromeia is famous for its spectacular habitus, its alleged phylogenic role as a link between the arborescent lycopods and the reduced *Isoetes*, and its geological history which is unusually short for a plant genus (Early— Middle Triassic). Discovered over 100 years ago in a stone of the Magdeburg cathedral, it had been for a long time known only from Western Europe. New localities have been found in the Russian platform, Kazakhstan, Uzbekistan, East Siberia, the Far East (Kryshtofovich, 1923; Neuburg, 1960; Srebrodolskaja, 1966; Dobruskina, 1970; Tuchkow, 1973) and recently near the mouth of the Olenek River in northeastern Siberia.

The information on *Pleuromeia* morphology provided by the type-species *P. sternbergii* (Muenster) Corda has been augmented and corrected by Neuburg (1960) in her detailed description of *P. rossica* Neuburg. Other species are insufficiently known or only mentioned as *nomina nuda*. Two of them are described below.

DESCRIPTION OF THE SPECIES

Pleuromeia obrutschewii Elias (Plate I, 1-5; Plate II, 1-5; Plate IV, 1, 2)

This species came from the Early Triassic of Russian Island (near Vladivostok) and is represented by stem impressions, cones and isolated megasporophylls. *Pleuromeia* associates with marine invertebrate fossils assigned to the *Neocolumbites insignis* zone of the Russian Stage (Zakharov, 1973). A number of hand specimens with megasporophyll remains also contain cephalopod and bivalve shells.

The original description by Kryshtofovich (1923) was based on stem fragments with characteristic leaf scars which are lens-shaped, about 13-14 mm long, 4.5 mm wide, with two parichnos. Kryshtofovich assigned them to *Pleuromeia* cf. *sternbergii* (Muenster) Corda although he pointed to the dense arrangement of leaf scars as a distinction from the European species.

The name *Pleuromeia obrutschewii* appeared in "Geologie von Sibirien" by Obrutschew (1926, p. 482). It was explained in a footnote that Eliashewitch (who later spelled his name as Elias) coined this binominal for *Pleuromeia* cf. *sternbergii* from Russian Island which, in his opinion, differed from the European species by the more regular arrangement of sporophylls provided with sterile apices. Mägdefrau (1931) and Neuburg (1960) doubted the assignment of the Far-Eastern fossil to *Pleuromeia sternbergii*. Neither of them was acquainted with Elias' proposal. According to Mägdefrau, the major distinctive characters of the Far-Eastern *Pleuromeia* were crowded leaf scars and the absence of vascular scars. The latter feature surely resulted from poor preservation. In *Pleuromeia sternbergii*, the spacing of leaf scars is known to be extremely variable: there are zones of fairly crowded leaf scars ("Wechselzonen") corresponding to periods of retarded growth. Thus, such vegetative characteristics are hardly reliable in delimiting the Far-Eastern species.

The strobili of *P. obrutschewii* are elongated, more than 200 mm long, with the transverse section elliptical, about 20×12 mm; they agree with those of *P. sternbergii* in both dimensions and general outline, whereas *P. rossica* has much smaller strobili. Only megaspores have been observed in the available strobili of *P. obrutschewii* which are thus unisexual, again in agreement with *P. sternbergii* and in contrast to the bisexual strobili of *P. rossica*. The strobili of the latter are described as supported by a stalk. Similar "stalks" have been observed in *P. obrutschewii*. However, there are occasional sterile

PLATE I

Pleuromeia obrutschewii Elias (Russian Island)

1. Strobilus, 99-1, \times 1.

- 3. Part of 2 showing megaspore casts, \times 12.
- 4. Megasporangium, oblique section showing sterile apex, 99-4, \times 5.
- 5. Part of 1, \times 3.

^{2.} Megasporophyll with megasporangium, 99-5, \times 3.

PLATE I



PLATE II



leaves arising from them. These leaves are thin, awl-shaped, and sharply delimited from the proximal sporophylls. The "stalks" are, thus, partially macerated distal portions of main stems.

The sporophyll arrangement in *P. obrutschewii* is essentially the same as in *P. sternbergii*. Elias evidently got the impression of an irregular sporophyll arrangement in the latter from strobili with partially shed sporophylls depicted by Potonié and other authors. Isolated megasporophylls are reniform, about 18×15 mm. The central part is occupied by a sporangium flanged by 2–3 mm wide sterile tissue forming an apical beak. Sterile tips have also been observed in the sporophylls of *P. rossica*, but have not been mentioned in numerous descriptions of *P. sternbergii*. However, a lack of this feature can be attributed to unfortunate preservation. Sporophylls are abaxially ribbed (Plate II, 5) and proximally plicated, as can be seen in transverse section (Plate II, 1, 3).

Neuburg (1960) stated that the sporangia of P. rossica were adaxial as in other lycopods and not abaxial as they were thought to be in P. sternbergii. She cast doubts on the validity of the interpretation of the sporangium position in P. sternbergii. In our material from Russian Island the sporangia fill a spoon-like depression of the adaxial face of the megasporophyll. The sporangia are hemispherical, about 11 mm in diameter, and the outer surface is flat, fully exposed. There are no protective structures comparable to the velum of *Isoetes*. In transverse section, the sporangium wall is clearly demarcated from that of the megasporophyll (Plate II, 4). Thus, sporangia were not immersed in sporophyll tissue. Mägdefrau (1931) and other authors who advocated an abaxial position of the sporangia pointed to a suture between sporophyll and sporangium. Such "suturae" are clearly seen in both Neuburg's and in our material, which, however, allows a different interpretation: the "suture" is formed at the junction of the sporangium cast with a flange bordering the spoon-like depression. It appears that difference in sporophyll organization between P. obrutschewii and P. sternbergii is a matter of interpretation only. Megaspores are liberated through a thin wall of the megasporangium. The complete megaspores are nearly spherical, about $370-390 \mu$ in diameter, the triradiate mark is conspicuous, the contact area elevated, and the surface smooth. They are similar to the megaspores of the European *P. sternbergii* which are about 500 μ in diameter, with smooth or granular surface. The megaspores of P. rossica are somewhat smaller $(300-340 \mu).$

PLATE II

Pleuromeia obrutschewii Elias (Russian Island)

- 1. Megastrobilus, transverse section, 99-2, \times 5.
- 2. Part of 1, megasporangium, \times 12.
- 3. Part of 1, plicated wall of megasporangium, \times 12.
- 4. Part of 1, illustrating separation of sporangium wall from megasporophyll (double line), \times 12.
- 5. Megasporophyll, ribbed abaxial surface, 92-3, \times 7.

We may conclude that *P. obrutschewii* has no significant distinctions from *P. sternbergii* and may even be conspecific to it, despite the great spatial separation.

Pleuromeia olenekensis Krassilov, sp. nov. (Plate III, 1–6; Plate IV, 3–5; Plate V, 1, 2)

Holotype: 221-1, Institute of Biology and Pedology collection, Vladivostok.

This species came from outcrops of black shales with a rich marine fauna situated near the mouth of the Olenek River and referred to as the Olenekian beds (Mojsisovics, 1886). These beds are assigned to the *Olenekites spiniplicatus* zone of the Lower Triassic. According to Zakharov (1973) they correspond to the Russian Stage of Russian Island.

The invertebrate fauna comprises abundant cephalopods and less numerous bivalves, gastropods, scaphopods, and conodonts. They occur mostly in carbonate concretions. About one thousand concretions have been split in search of cephalopods and three of them occasionally yielded megaspores and megasporophylls of *Pleuromeia* in association with *Nordophiceras schmidti* (Mojsisovics), *Xenoceltites glacialis* (Mojsisovics), *Olenekites spiniplicatus* (Mojsisovics), and *Keyserlingites middendorfii* (Keyserling).

In the holotype the megasporangium is elliptical, 26 mm long, 10 mm wide, and contains no less than 500 calcite casts of megaspores. The megaspores are opaque or semitranslucent. Their surface features have been studied in reflected light and by a JEOL scanning electron microscope.

All megaspores are approximately equal in size (about 1 mm). They are nearly spherical, the equatorial outline is roundly triangular, and the diameter 990–1120 μ . The axial plane is roundly diamond-shaped, the proximal face more convex than the distal, and the polar axis is about 900 μ long. The triradiate ridges are conspicuous, straight, reaching up to the equator. The arcuate ridges attain maximum width of 16 μ , but often much reduced and indistinct. The outer layer of the spore coat is ornamented with a reticulum formed by thick anastomosing muri. The lumina are polygonal or roundly rhomboidal, about 50–60 μ wide on distal face and about 30 μ wide on proximal face. Both muri and lumina are infragranulate (Plate V, 1, 2).

In some megaspores, the reticulate layer of which was presumably lost, the next layer of spore coat which is smooth or indistinctly granular (Plate IV, 4) is exposed. Although megaspore casts are incompletely translucent, the inner sac formed by the mesosporium is clearly seen in most of them due

PLATE III

Pleuromeia olenekensis sp. nov. Holotype, 221-1 (Olenek River)

- 1. Megasporophyll with megasporangium, \times 1.
- 2, 3. Parts of 1 showing megaspore casts, \times 7.
- 4, 5. Megaspores, polar and distal aspects, SEM micrographs, \times 70.
- 6. Megaspore, reticulum of proximal face, SEM micrograph, \times 1,000.

PLATE III







to the dark colour of its calcite filling (Plate IV, 5). The inner sac is about $600-670 \mu$ in size.

Pleuromeia olenekensis differs from other species chiefly in the dimensions of available organs. Its megasporangia are much larger than those of P. rossica and exceed the upper size limit of those of P. sternbergii. The megaspores are 1.5-2 times larger than those of P. sternbergii and three times as large as those of P. rossica. They differ also in reticulate ornamentation, but megaspores lacking a reticulum look much like those of other species. This problem is further considered below.

MORPHOLOGICAL IMPLICATIONS

Héeg et al. (1955) have called attention to the inner cutinized membrane, or mesosporium, forming inner sacs in a number of fossil megaspores and variously termed internal body, endospore, etc. They suggested that some microfossils described as megaspores are actually inner sacs (mesosporia) which have escaped from their enveloping exosporia. In some modern megaspores, as well as in fossil *Talchirella*, *Zeillerisporites* and others (Pant and Srivastava, 1961, 1964), the outer sac, or exosporium, is composed of two layers closely appressed to each other and separated from the inner sac (sometimes also two-layered) by a considerable gap. The two exosporium layers are presumably homologous to the ectexosporium and endexosporium of isosporous ferns distinguishable by electron microscopy (Kedves and Párdutz, 1973).

In megaspores, the ectexosporium is usually thinner and more conspicuously ornamented than the endexosporium. When stripped of their ectexosporia, the megaspores often lose their diagnostic features, e.g., *Talchirella* lacking its papillate outer layer, becomes smooth or granular and can be mistaken for the spore-genus *Duosporites*.

Megaspores of *Pleuromeia olenekensis* exhibit a mesosporium separated from the exosporium, which is presumably two-layered. The outer layer is reticulate, whereas the inner layer is smooth or indistinctly granular. Megaspores exposing the endexosporium are similar to those of *P. sternbergii* and *P. rossica*. This leads to the suggestion that in the latter species the ectexosporium has been lost by natural maceration or chemical treatment.

PLATE IV

- 1, 2. Pleuromeia obrutschewii Elias. Megaspores, 99-5, SEM micrographs, \times 150.
- 3. Pleuromeia olenekensis sp. nov. Megaspore, 221–1, proximal aspect, SEM micrograph, \times 70.
- 4. Pleuromeia olenekensis sp. nov. Megaspore, 221-1, proximal aspect, reticulate ectexosporium lacking, SEM micrograph, \times 70.
- 5. Pleuromeia olenekensis sp. nov. Megaspore, showing endosporium, 221-1, \times 40.





ECOLOGICAL AND PALAEOGEOGRAPHICAL IMPLICATIONS

Pleuromeia has been regarded as a xerophyte living in semi-desert environments. However, this widely accepted reconstruction seems doubtful in the light of the following observations:

(1) *Pleuromeia* occurs mainly in marine or deltaic deposits (including the red beds, which are no longer considered as desert or semi-desert sediments).

(2) Different organs of *Pleuromeia* (stems, rhizophores, strobili, sporophylls) are in most cases deposited together, indicating a near-shore habitat.

(3) In a number of localities *Pleuromeia* associates with *Neocalamites* and *Equisetites* which dominated Mesozoic coastal marshes.

(4) Rhizophores of *Pleuromeia* are similar to those of aquatic *Isoetes* and Paleozoic arboreal lycopods inhabiting mangrove swamps.

The fact that *Pleuromeia* thrived along the coasts, together with its xerophytic habitus and rhizophores, may point to mangrove adaptations.

A peculiar feature of *Pleuromeia* palaeoecology is the rather frequent occurrence of isolated megasporophylls which usually outnumber other organs. In both the Olenek and Russian Island localities sporophylls are mixed with small to middle-sized cephalopod shells which are irregular orientated in the rock matrix and have probably been transported by currents. To produce such localities there may have been numberless sporophylls floating in shallow waters, their buoyancy comparable with that of cephalopod shells. These taphonomical considerations, as well as the mature sporophyll shedding and their buoy-like shape, suggest a special mechanism of dispersion: *Pleuromeia* propagated by means of whole megasporophylls which were adapted to transportation by water currents just as the buoyant fruits of some modern angiosperms.

Pleuromeia has been interpreted as a termophilous plant, and this aspect of its palaeoecology is not disputed here. However, the assumption that Pleuromeia has been confined to southern regions of Eurasia and may even be used for defining the boundary between the southern and northern (Angarian) floristic provinces, has now been proved wrong. The cosmopolitan distribution of Pleuromeia may evidence weakened climatic zonation. The active spreading of the proto-Pacific Ocean in the Early Triassic (Force, 1973) might have altered a system of oceanic currents imposing climatic anomalies. In contrast with the situation on land, there were considerable differences between the Tethyan and Boreal cephalopod faunas of middle and high latitudes. A possible explanation is that marine provincial boundaries have been sharpened by the abnormal salinity of Arctic seas.

PLATE V

1, 2. Pleuromeia olenekensis sp. nov. Megaspore, 221–1, distal face, infragranulate reticulum of ectexosporium, SEM micrographs, \times 300 and \times 3,000.

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