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THE HISTORY OF LAND PLANTS IN THE NORTHERN HEMISPHERE DURING THE TRIASSIC WITH SPECIAL REFERENCE TO THE FLORAS OF EURASIA

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With 2 charts and 7 figures

Abstract: Triassic period is a period of reconstruction ("perestroyka") in the plant kingdom. During the Triassic Paleophytic plant assemblages gradually changed to Mesophytic ones. The greatest break in the plant life took place in the middle of the Triassic and "perestroyka" itself occurred during the late Permian and the first half of the Triassic, i.e. during about 60 millions of years.
Late Permian and Lower Triassic stage of development of plants may be characterized as the last stage of the Paleophytic. Reconstruction continued during Ladinian-Karnian stage which may be considered as the first stage of Mesophytic. "Normal" Mesophytic begins from Norian (middle Mesophytic) and continues during the Jurassic and Lower Cretaceous (late Mesophytic).
The reconstruction in floral composition was accompanied by the reconstruction of the paleogeographical zonation. The great isolation and fractionality of the Paleozoic Phytochoria were replaced by more simple zonation, similar to the recent one.
Zusammenfassung: Während der Trias erfuhr die Pflanzenwelt eine grundlegende Änderung. Die paläophytische Florenvergesellschaftung wurde von der mesophytischen abgelöst. Der stärkste Florenschnitt erfolgte in der Mitteltrias, wobei sich die Änderung in der Pflanzenwelt bereits während des Oberperms und der Untertrias vollzog, d.h. während eines Zeitraums von ca. 60 Mill.J.
Die oberpermische und untertriadische Entwicklungsstufe der Pflanzen kann als spätes Stadium des Paläophytikums charakterisiert werden. Der Umbau erfolgte während des Ladins und Karns, was als erstes Stadium des Mesophytikums aufgefaßt werden kann. Das eigentliche ("normale") Mesophytikum beginnt mit dem Nor (mittleres Mesophytikum) und setzt sich bis in den Jura und die Unterkreide (spätes Mesophytikum) fort.
Die Änderung der Florenvergesellschaftung war begleitet von einer Änderung der paläogeographischen Zonierung. Die starke Isolation und Zonierung der paläozoischen Phytochoria wird von einer einfacheren Zonierung, ähnlich der heutigen, abgelöst.

1. Introduction

The Triassic period is in many respects a time of great changes. In fact some researchers even consider it to be unique because of the significance of these events (TRÜMPY, 1982). It is with the Triassic that the Mesozoic era began, a time when great changes took place in both the plant and animal kingdoms. During the Triassic the Paleophytic flora which had been in existence since the origin of land plants in the early Paleozic disappeared and was replaced by a different flora, the so-called Mesophytic flora (KRYSHTOVICH, 1957). In addition the phytogeographic zonation which developed during the Mesophytic is very close to that of the present day. The Triassic is thought to have been one of the warmest periods in earth history when the average temperature is estimated by paleoclimatologists to have been 20° higher than at present (FRAKES, 1975). Triassic deposits contain conspicuous quantities of redbeds and the quantities of clastic rocks reach 70% (RONOV & KHAIN, 1961). Many tectonic events occurred in the Triassic, although they are explained in various ways by different geologists. A number of them believe that riftzones began to form in the early Triassic or in the late part of the Permian in Laurasia, and that one of these riftzones was responsible for the origin of the Atlantic Ocean during the Triassic. In other words Pangea had begun to break up during the Triassic. Other geologists think that Pangea did not form until the Triassic (see TRÜMPY, 1982). A third point of view is that Eurasia was formed during the Triassic (BELOV et al., 1982).

Significant floral changes occurred during the Triassic and here I briefly summarize them and attempt to relate them to tectonic events of the period. Detailed discussions of this material has been presented elsewhere in Russian (DOBRUSKINA, 1978, 1980, 1982).

2. Flora stages of the Triassic

Three floral stages have been recognized in the Triassic (DOBRUSKINA, 1978, 1982, chart 1 in present paper). The first is in the lower part of the Triassic (the Scythian and Anisian) and is so closely related to the Paleophytic that it is generally referred to as the late Paleophytic (Post-paleophytic of MEYEN, 1970). As shown in chart 1 the very provincial Permian floras were replaced during this time by most widespread floras which contained many forms that were close or identical to Permian genera. It was also characterized by the origin and expansion of a new family of lycopsids, the Pleuromeiaceae. The second floral stage, the early Mesophytic, occurs in the Ladinian and Carnian and was a transitional stage from the Paleophytic to the Mesophytic. The *Scytophyllum* flora with its pronounced meridional zonation is characteristic of this stage (DOBRUSKINA, 1982). The third floral stage or the middle Mesophytic occurs in the Norian and Rhaetian stages of the Triassic, together with the Early and Middle Jurassic. The Triassic portion of the stage is characterized by the *Lepidopteris* flora with its more modern type of biogeographical zonation. The beginning of the Middle Mesophytic is actually the real beginning of the Mesophytic with the domination of Cycadophyta, Ginkgophyta and Dipteridaceae (KRYSHTOFOVICH, 1957). (The late Mesophytic includes late Jurassic and early Cretaceous floras and is not discussed here).

First floral stage

The late Paleophytic began during late Permian time and was marked by (1) the extinction of many of the plants which had dominated the late Paleozoic plant assemblages, and (2) the beginning of the expansion of those plant groups that had been in the background. These changes probably were caused by the increased aridity which occurred following the great regressions of the sea during this time. In western Europe the late Paleophytic lasted from the Zechstein to the middle of the Triassic during the time of the *Voltzia* flora, a flora which was closely related to the Zechstein flora and contained practically no new plant groups. In eastern Europe, Siberia and northern China the late Paleophytic lasted from the Upper Tatarian (DURANTE, 1980) to the middle of the Triassic during the time of the analogues of the *Voltzia* flora and during the time of the Korvuntchana flora of Siberia.

New data confirm the traditional point of view (Resolutions, 1981), that the Korvuntchana flora of Siberia arose at the very beginning of the Triassic and lasted until Middle Triassic time. This conclusion is based on a study of Korvuntchana flora which consists principally of conifers (DOBRUSKINA, 1984, MOGUTCHEVA, 1984), the correlation of this flora with *Voltzia* flora of western Europe and China (DOBRUSKINA, 1985 - chart 2) and the correlation of volcanics of the Tunguska basin with the volcanics of the Kuznesk basin, Verkhojanie and Taymyr (MOGUTCHEVA, 1982).

During the first floral stage only one new family of land plants appeared, the Pleuromeiaceae (DOBRUSKINA, 1982, 1985 b). After its sudden appearance the family rapidly spread throughout most of the world.

The presence of the *Voltzia* flora in China, the existence of common forms of conifers and lycopsids in the floras of western Europe, China and Siberia and the uniform development of the early Triassic floras of Siberia and China indicates that the fragmented floras of the late Paleozoic had been replaced by a single flora which allowed the exchange of plants between them. At the very beginning of the Triassic there was no barrier between the Atlantic and Cathaysian plant kingdoms, and as a result a united European-Sinian floristic area developed. The barrier between this area and the Siberian area had now become much less significant than it was in the Permian. There is some question about what geologic events are connected with it.

As shown in figure 1 the southern boundary of the Angarian floristic area of the Permian (MEYEN, 1970, fig. g) coincides with the zone of the Variscean uplifts which extended from the Far East to the Donetz basin. The northern part of Urals separated the East-European area from the Angara area. From this point of view it is not important, if the isolation of the three phytogeographical kingdoms was caused by high mountains, marine basins, or by the separation of plates. But it is significant that by late Tatarian time this barrier did not exist and the *Tatarina* flora extended in a wide belt between the Angara area in the north and the Atlantic and Cathaysian areas in the south (DURANTE, 1983). It occupied the eastern European part of the Angarian kingdom and the northern part of Cathaysia where its traces are known in northern China at Nanshan and adjacent areas. But at the same time the isolation of the Atlantic and Cathaysian kingdoms continued. In the early Triassic (figs 1 and 2) this barrier disappeared and the floras of the west and of the east of European-Sinian areas became similar.

So, the role of Variscids as a barrier disappeared by the end of the Permian, or when the joining of the Cathaysian plate to the rest of Eurasia had been completed by this time, and the barriers between the west and east ceased to exist either at the beginning of the Triassic or possibly in

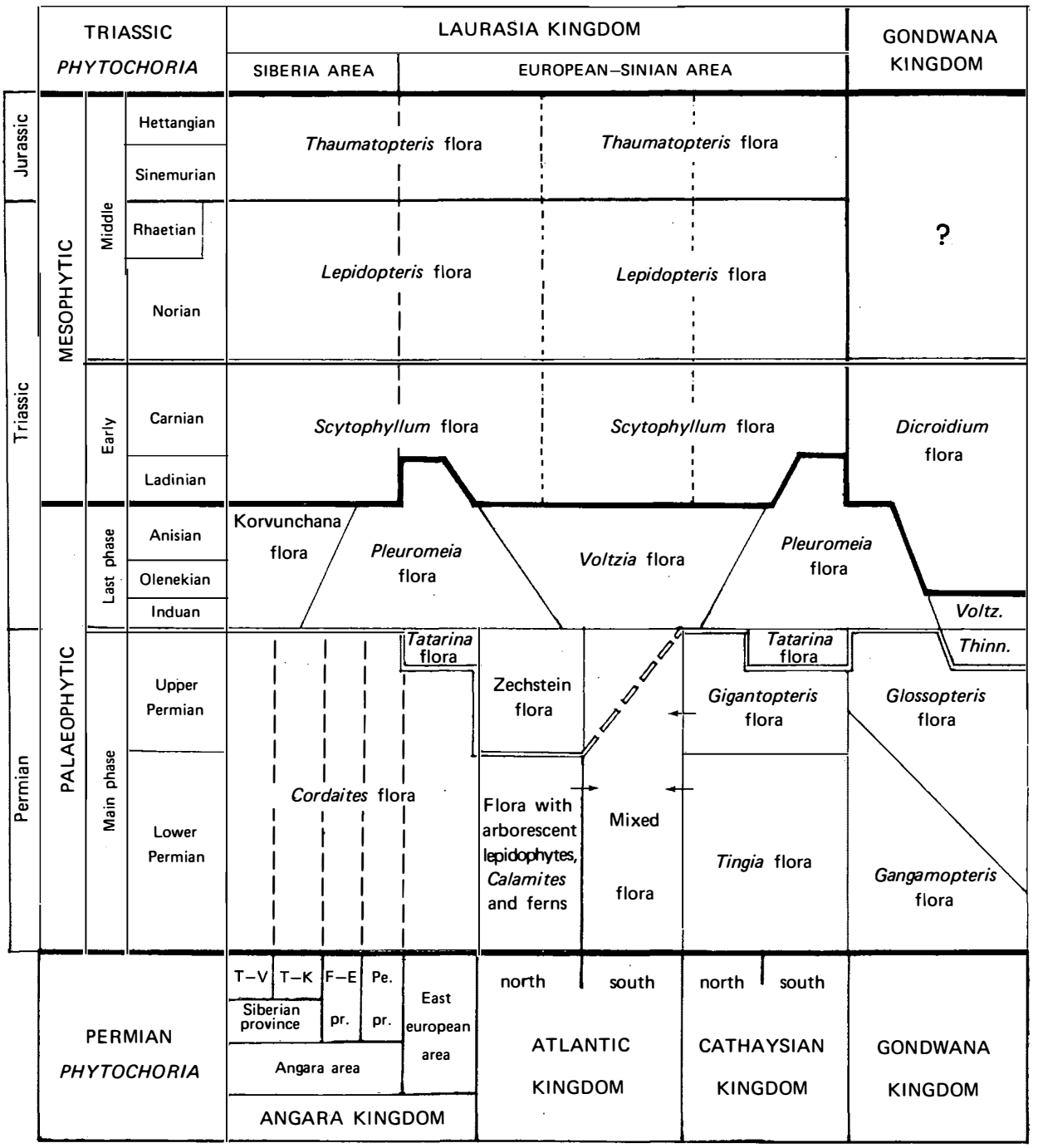

Chart 1:

The stages of development of the floras at the Paleophytic-Mesophytic transition

Phytochoria in the Permian, after MEYEN (1970); Gondwana kingdom, after RETALLACK (1977)

Abbreviations: T–V: Taymyr-Verkhoyansk count; T–K: Taymyr-Kuznetsk count; F–E: Far East province; Pe.: Pechora province; *Voltz.*: *Voltziopsis* flora; *Thinn.*: "*Thinnfeldia*" *callipteroides* flora

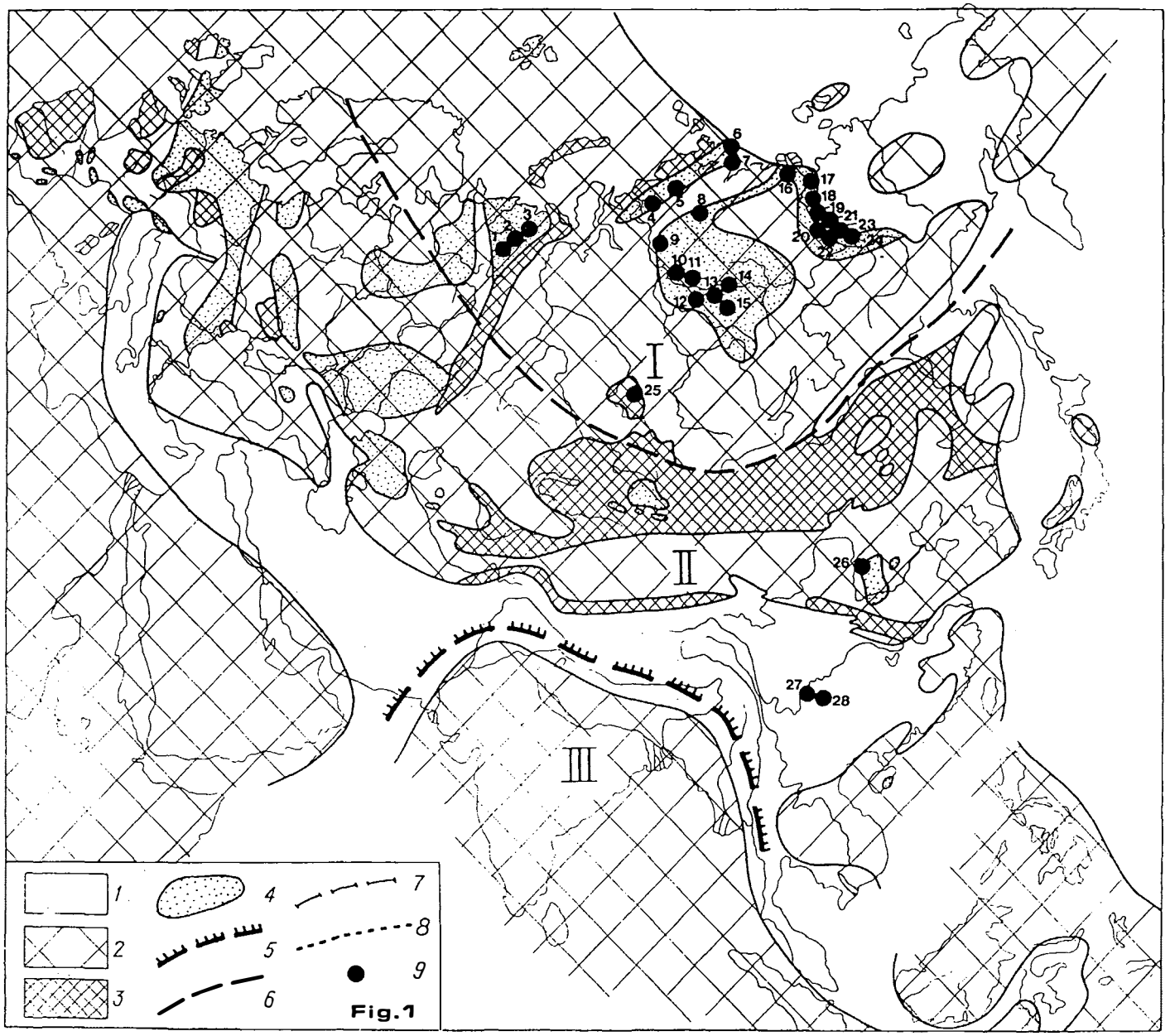

Fig. 1:

Distribution of floras and phytogeography in the lower part of the Lower Triassic (Induan stage):

1 - Novaya Zemlya, 2–4 - Petchora basin, 5 - Kuznetsk basin, 6–15 - Tunguska basin, 16–19 - Taymyr peninsula, 20–21 - Olenekian coast, 22–29 Verkhoyansk range, western slope, 30 - Vilyuy syneclise, 31 - Northern China, 32–33 - Southern China

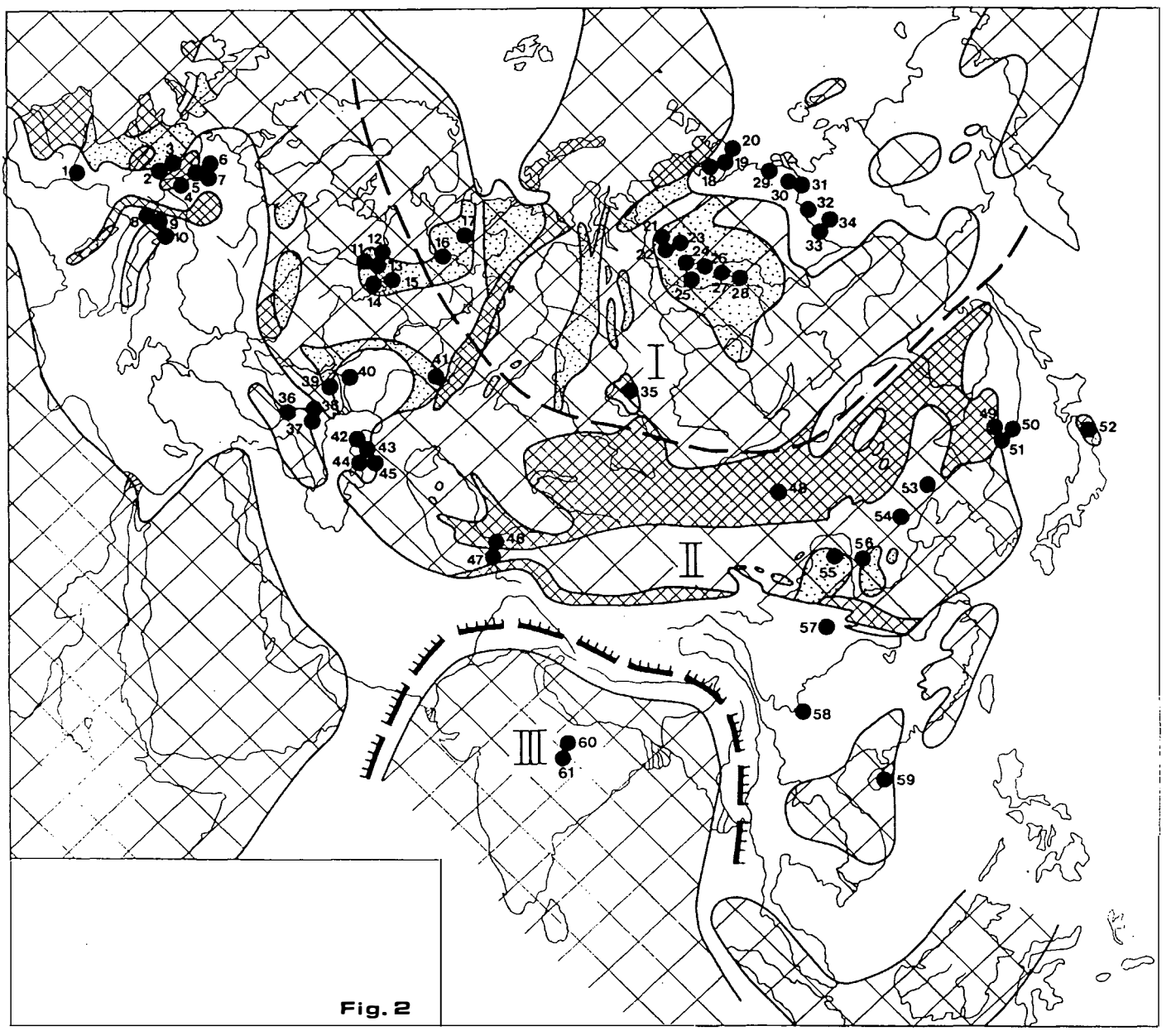

Fig. 2:

Distribution of floras and phytogeography in the Olenekian and Anisian: 1–6 - central part of the German basin, 7–11 - marginal parts of the German basin, 12–15 - the Alps and Balkans, 16–21 - southern part of Moscow syneclise, 22–23 - northern part of Moscow syneclise, 24 - southern Priuralye (Fore-Urals), 25–26 eastern Predkavkazye (Fore-Caucasus), 27 - northern Caucasus, 28–29 - Pricaspian depression, 30–33 - southern Mangyshlak, 34 - Darvaz, 35 - southern Fergana, 36 - Kuznetsk basin, 37–47 - Tunguska basin, 48–50 - Taymyr peninsula, 51–53 - Olenekian coast, 54 - Verkhoyansk range, western slope, 55 - Southern Mongolia, 56–59 - Northern China, 60–62 - Southern China, 63 - Japan, 64–66 - Soviet Primorye, 67–68 Central India, 69 - Salt Range

	Western Europe	Russian platform and adjacent areas	Siberia		Northern China	Southern China	
Anisian	Marls with Voltzia in Recoaro; Voltzien-sandstone / Röt	Upper formations with Pleuromeia in Mangyschlak	Korvunchana formation	Putorana horizon	Ermaying	Yunningzheng	Lingwen
Olenekian	Solling; Hardegsen	Formations with Pleuromeia and single conifers		Dvurogiy horizon	Heshankou	Upper Dongchuan	
Induan	Lower part of Buntsandstein without plants	Ust-Berezovka formation of Pechora basin		Tutonchana horizon	Liujiakou	Lower Dongchuan	
Upper Permian	Zechstein	Tatarian stage	Coalbearing formations		Sunjiakou	Changhsing	

Shischienfeng

Chart 2:

Correlation of plant-bearing deposits of Western Europe, USSR and China at the Permian-Triassic transition

the upper part of the Lower Triassic. Any continental reconstructions showing ocean basins between Angara and Cathaysia at the end of the Permian and in the Triassic are doubtful. In fact the basins could be present only in prelate Tatarian time.

Second floral stage

The beginning of the second stage is marked by the abrupt disappearance of the *Pleuromeia* flora and the appearance of the *Scytophyllum* flora. The *Scythophyllum* flora is the next stage of the development of the *Voltzia* flora and Korvuntchana floras The geological and botanical changes at the boundary between the first and second stages are different from those that occurred at the boundary between the Permian and the Triassic. The second stage is characterized by the appearance of several new groups of plants including the Dipteridaceae, Bennettitales, Czekanowskiales and Cycadocarpidiaceae, by the expansion of the Cycadophyta, by the wide distribution of the Peltaspermaceae and Glossophyllaceae. During the Ladinian and Carnian the last two families were present only in the Middle Asian sector (fig. 3) i.e., at the position of the Middle Eurasian zone of the later Permian with its *Tatarina* flora. This distribution suggests several questions: What prevented the Peltaspermaceae and Glossophyllacea from migration to the west and to the east in the middle of the Triassic? What prevented the Dipteridaceae and Cycadocarpidiaceae from migrating from Japan to China, the Bennettitales to Japan, the Czekanowskiales to the Far East? In other words, it seems that the new groups were fixed to the places of their origin during this stage and only the Sphenopsida (*Neocalamites*, *Equisetites*) seem to have had no barriers and became widely distributed all over Eurasia.

The disappearance of the Pleuromeiaceae at the beginning of the second stage may be easily explained by the appearance of the new groups of plants. But what caused such a sudden appearance of the new groups?

Tectonic activity at the boundary between the first and second floral stages is more significant in the Far East (Akiesi tectonic phase) and it is here where florogenesis was most active in the middle of the Triassic. In northern China less different formations occur in the first half of the Triassic than in its second half; the boundary between the two halves corresponds to the Middle Triassic. There is an important unconformity in western Eurasia at the end of the Anisian (MOVSCHOVICH, 1981). Could the tectonic activity have been responsible for the unconformity of the

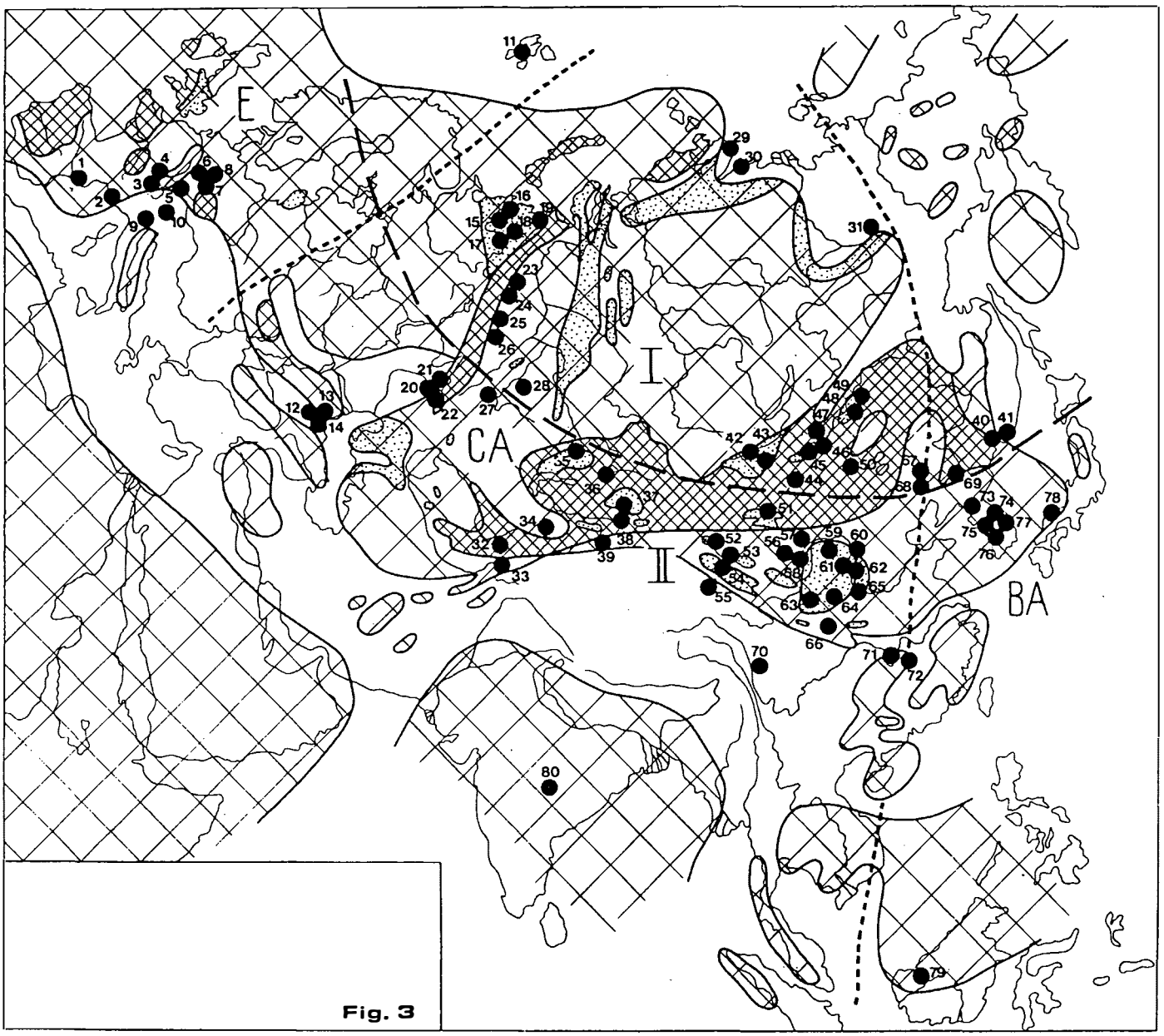

Fig. 3:

Distribution of floras and phytogeography in the Ladinian and Carnian:

1–4 - central part of the German basin, 5–6 - marginal parts of the German basin, 7–9 - the Alps, Carpathians, Balkans, 10–12 - Svalbard, 13 - Donets basin, 14–15 - Novaya Zemlya, 16–20 - Pechora basin, 21–23 - southern Priuralye (Fore-Urals), 24–26 - eastern Predkavkazye (Fore-Caucasus), 27–30 - depression of the eastern Urals, 31–33, Middle Asia, 34 - Taymyr peninsula, 35 - Olenekian coast, 36 - Verkhoyansk range, 37 - Semeytau mountains, 38–48 - Mongolia, 49–71 - Northern China, 72–76 - Southern China, 77 - Japan, 78 - Southern Primorye, 79 - Sarawak, 80 - India

florogenesis? Perhaps florogenesis occurred gradually during the first half of the Triassic and the tectonic activity in the middle of the Triassic only accentuated the differences between the floras of the two parts of the Triassic. At that time some new meridional barriers appeared and those that had existed in the Paleozoic and the firsthalf of the Triassic disappeared. To judge by paleogeographical maps these new barriers (the boundaries of the sectors) appear to be connected with marine basins. If this is thecase it is clear why they did not obstruct the migration of the Sphenopsida which lived along shorelines. In connection with the paleogeographical changes at the end of the Triassic the boundary between the Eastern Asian and Middle Asian sectors moved toward the west. The floras of China, Korea and Japan now became more similar. The clearness of the sectorial boundaries became less and the differences in the floras of the various sectors at the end of the Triassic and in the Jurassic as well as nowadays can be explained by their distance from the sea (although the history of the distribution of plants must not be forgotten).

Third floral stage

The third stage is marked by the disappearance of the *Scytophyllum* flora (i.e. *Danaeopsis-Bernoullia* flora) and appearance of the *Lepidopteris* flora (*Dictyophyllum-Clathropteris* flora). However, there is some question about the position of the boundary as the Chinese geologists think that these two floras are partly coeval with the *Scytophyllum* flora being distributed in the north and the *Lepidopteris* flora in the south of that country (KIMURA, 1984). At present there is no sufficient evidence to clarify this situation. Therefore the stratigraphical position of every locality in China must be carefully evaluated. In fig. 3, I show all localities with *Scytophyllum* flora of the Ladinian-Carnian and all localities with *Lepidopteris* flora of the Norian-Rhaetian (fig. 4). It was done because most of the *Scytophyllum* flora is Ladinian-Carnian and most of the *Lepidopteris* flora is Norian-Rhaetian. *Scytophyllum* floras east of Asia occur in terrestrial grey beds and *Lepidopteris* floras in coal bearing deposits of sea shores, shallow water and islands. Does it really correspond to the situation that the origin of the coal bearing formations began in the Norian or in some places it began earlier - now it is not clear. But the outlines on the paleogeographical and climatological maps depend on the answer to this problem.

Thus the position of the boundary between the second and third stages is still not clear. If the *Lepidopteris* flora changed to *Scytophyllum* flora everywhere at the same time (and that moment corresponded to the boundary of the Carnian and Norian or to the boundary of the lower and middle Norian as it is in the west of Eurasia) this moment was characterized by the extinction of those plant groups which came from *Tatarina* flora and Zechstein flora and by the distribution of the new Mesophytic groups which originated in the middle of the Triassic.

But if the *Scytophyllum* flora and the *Lepidopteris* flora are partly coeval (especially in the east) then a distinct boundary between the second and the third stages does not exist. In this case the transition between the *Scytophyllum* and *Lepidopteris* floras was gradual and that change did not take place simultaneously in different parts of Eurasia.

3. Conclusion

If we consider the history of the Triassic flora when we analyze the paleomagnetic reconstructions of continents for the second half of the Triassic (fig. 7), we see that (1) an ocean between Cathaysia and Angarida (KHRAMOV, 1982, BELOV et al., 1982) seems to be doubtful, (2) an ocean between Indochina and the rest of Eurasia (GORODNITSKI et al., 1978) also seems doubtful because the Norian-Rhaetian floras of Indochina as well as tetrapods are similar to the European ones, and the Ladinian-Carnian floras of Sarawack are similar to the coeval floras of the rest of South-Eastern Asia, (3) the position of New Zealand in the northern hemisphere (TOZER, 1982) is strange because it has a typical Middle Triassic Gondwana flora. The distribution of the floras of the first half of the Triassic is better in modern paleogeographic reconstruction (fig. 5) than in paleomagnetic reconstruction (fig. 6).

By the beginning of the Triassic the extinction of the dominants of the Paleophytic kingdom was completed (MEYEN, 1970). It took place in the four Paleozoic plant kingdoms and was probably initiated by the increasing aridity during the great regression. At the beginning of the Triassic the barriers between the three northern kingdoms disappeared - the mountains were leveled and/or the isolated plants were combined in the united Eurasia. We can judge about it because a single great community of plant assemblages developed in all Eurasia, especially in the European-Sinian area.

Some paleophytic plants survived in hot and arid conditions during the firsthalf of the Triassic together with the new plant groups formed the Mesophytic plant kingdom in the middle of the Triassic. During the first half of the Triassic when conditions were unfavourable for the "normal" plants we see the explosion and world-wide expansion of the peculiar Lycopsids, the Pleuromeiaceae.

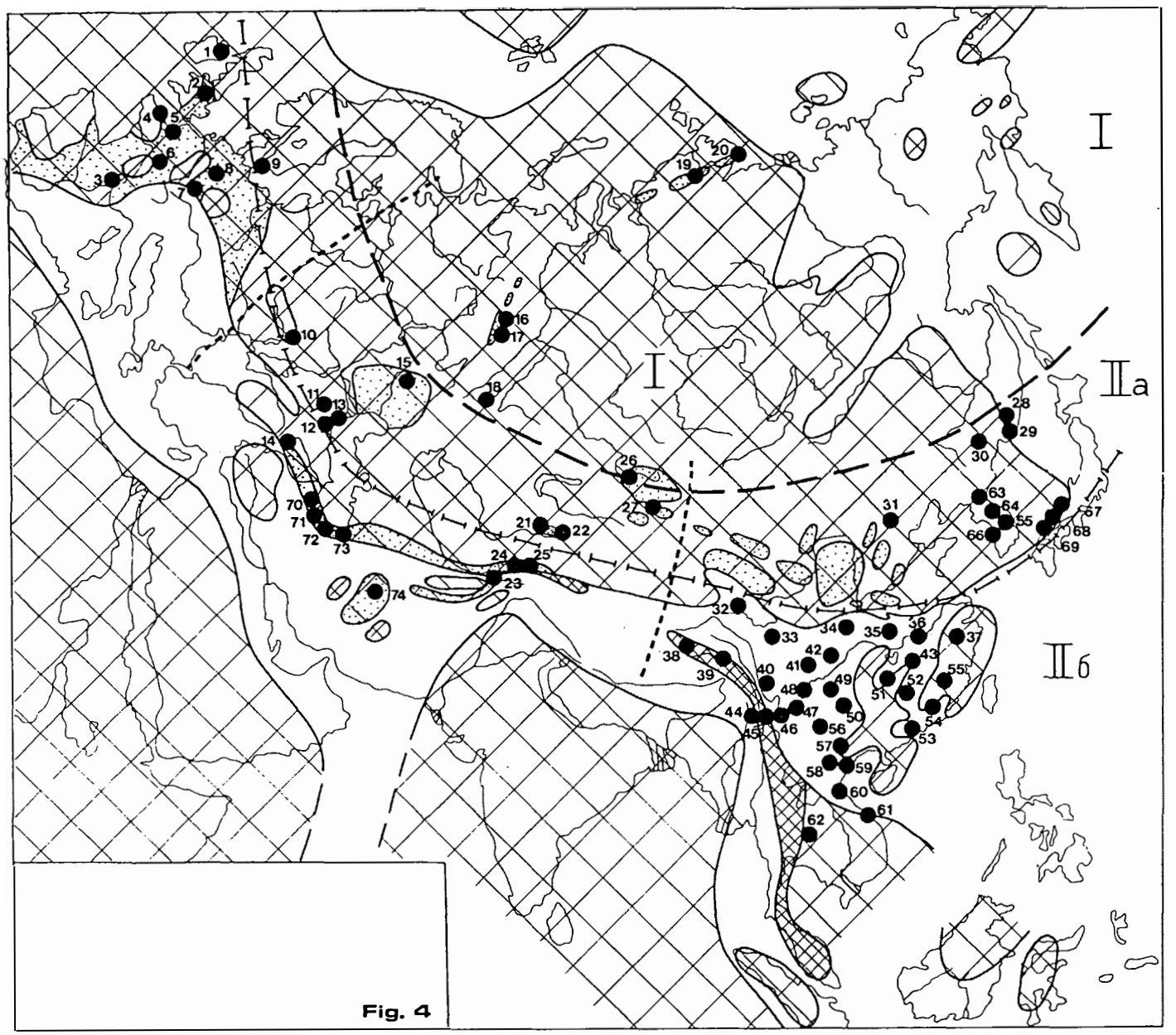

Fig. 4:

Distribution of floras and phytogeography in the Norian-Rhaetian:

1–3 - central part of the German basin, 4–13 - marginal parts of the German basin, 14–15 - the Alps, Carpathians, Balkans, 16 - Donets basin, 17 - Pricaspian depression, 18–20 - eastern Predkavkazye (Fore-Caucasus), 21 - eastern Urals, 22 - Turgay basin, 23 - Zakavkazye (Transcaucasus), 24–28 - Iran, 29 - Afghanistan, 32–34 - Middle Asia, 35–36 - Taymyr peninsula, 37 - the northeast of the USSR, 38 - the mountainous Altay, 39–41 - Northern China, 42–66 - Southern China, 67–68 - Japan, 69–70 - Soviet Primorye, 71–74 - Korea, 75–76 - Viet Nam, 77 - Thailand, 78 - Cambodia

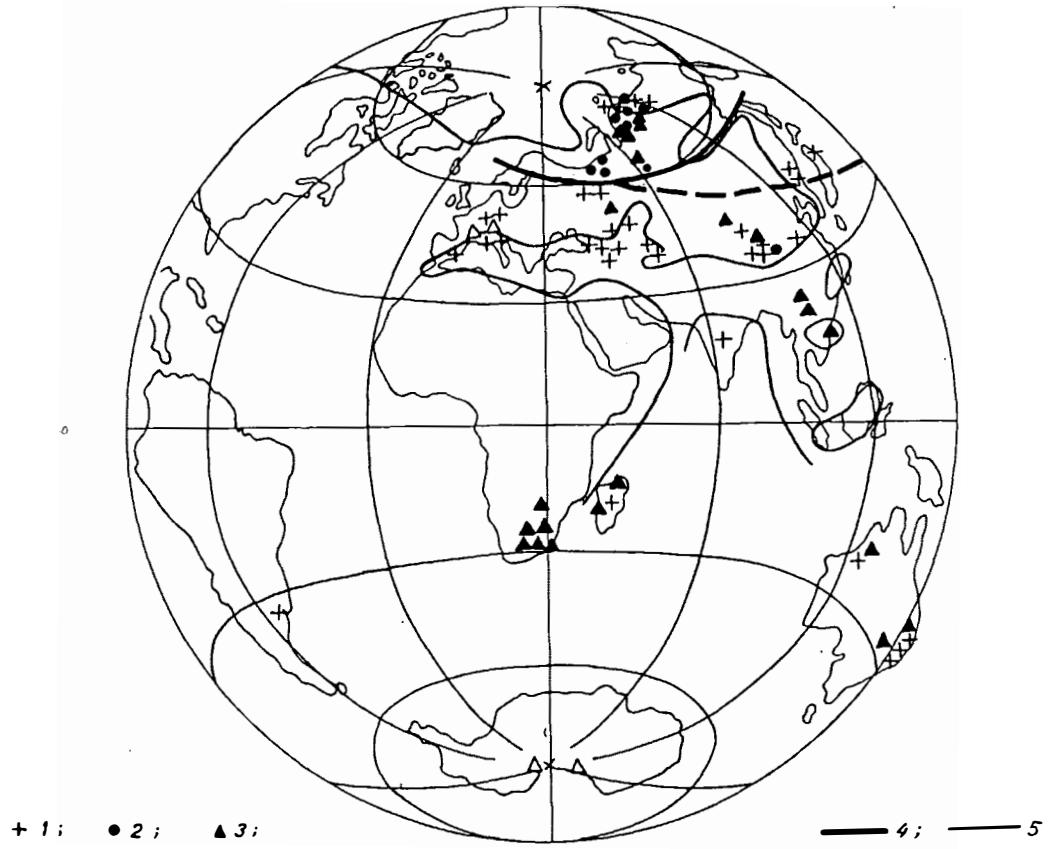

Fig. 5:

Distribution of floras of the first half of the Triassic in modern paleogeographic reconstruction:

1 - fam. Pleuromeiaceae, 2 - Korvuntchana flora, 3 - *Voltzia* and *Dicroidum* floras.

Fig. 6:

Distribution of floras of the first half of the Triassic on the paleomagnetic reconstruction map of KHRAMOV, 1982

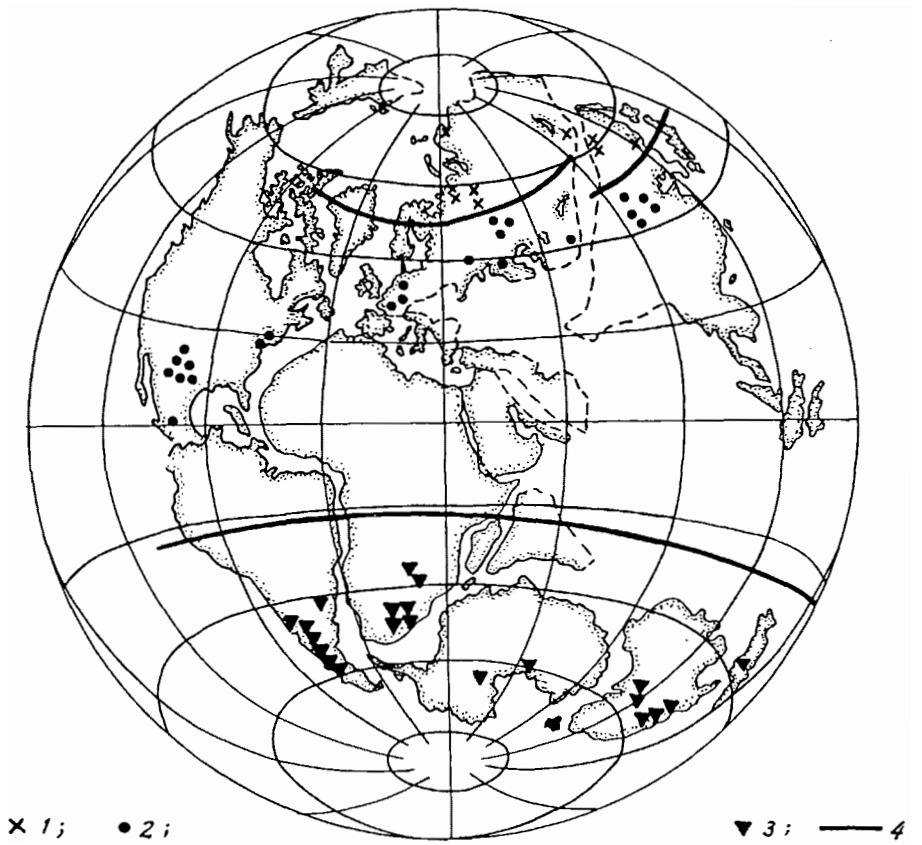

Fig. 7:

Distribution of floras of the Ladinian and Carnian on the paleomagnetic reconstruction map of KHRAMOV, 1982:
1 - northern non-tropical floras, 2 - tropical floras, 3 - southern non-tropical floras

Relatively high humidity was present at that time only in the Siberian area as indicated by the abundance of ferns and Sphenopsidae in the Korvuntchana flora (MOGUTCHEVA, 1973). But at the end of this stage when great quantities of conifers migrated into the Siberian area I can suggest that climatic conditions in all Eurasia had become more arid. However, abundant ferns and Sphenopsidae were still present only in the Siberian area (ibid.).

The absence of barriers, the similarity in climatic conditions, and the great new transgression resulted in conditions that were again favourable for the distribution and evolution of "normal" plants. We can judge about this because of the extinction of Pleuromeiaceae and of the good development of "normal" plant assemblages as the *Scytophyllum* flora throughout Eurasia. After the tectonic movements indicated by the unconformities of the end of the Anisian or between the Anisian and Ladinian and also after the change of the formations in the middle of the Triassic came the culmination of the Mesophytic flora. Together with the appearance of the new groups (Dipteridaceae, Cycadales, Bennettitales, Cycadocarpidiaceae, etc.) came the gradual extinction of the last representatives of the Paleophytic flora - most of the Peltaspermaceae, the Glossophyllaceae, the Equisetaceae, and the Pleuromeiaceae. Coexistence of the dying and flourishing groups is the most important feature of the *Scytophyllum* flora, the first stage of Mesophytic. The absence of the former and the abundance of the latter is the characteristic feature of the next stage of Mesophytae, which continued from the end of the Triassic into the middle part of the Jurassic.

During the second half of the Triassic the climate became colder and more differentiated: in the lower Ladinian in the very north of Siberia there lived such southern forms as *Anomozamites*, *Vittaephyllum*, and *Macrotaeniopteris* (MOGUTCHEVA, 1981); in the Carnian and later they are absent at such higher latitude. The southern boundary of the Siberian area in the Ladinian-Carnian corresponded with the boundary of the Greenland-Japan and Iran-Vietnam belts in the Norian-Rhaetian. It means that the more cold-resistant floras extended to the south, a tendency which continued into the Jurassic. At the same time the differences between the Boreal and Tethys fauna grew. It is important to note that this cooling was not very significant; during all Mesozoic it was actually very warm. There was an abundance of tropical Cycadales and Bennettitales present at this time in the European-Sinian area. The warmth

of the first half of the Triassic may be compared only with the warmth in the Eocene on the eve of the next glacial epoch.

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