

CHACASSOPTERIS — A FOSSIL INTERMEDIATE FORM

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ABSTRACT

A reconstruction of *Chacassopteris mongolica* from the Lower Carboniferous period is given.

The *Chacassopteris* leaf is discussed in its morphological relations to *Archaeopteris*, Coenopteridales, *Ginkgo* and *Polygala*.

Chacassopteris is regarded as a Lower Carboniferous intermediate form (missing link) which connects *Archaeopteris* with the Ferns and Ginkgophytes and perhaps also with the Pteridosperms and Angiosperms.

INTRODUCTION

NOBODY will suppose that species once existed in nature which correspond to our abstract conception of "the Fern", "the Pteridosperm" or "the Angiosperm". Such a "Nullwertahne"¹ (zero value ancestor) would not have been viable and would be an illusion created by our way of thinking that is oriented to abstractions and types. In the beginning of a period which led to a new, unprecedented structure there were intermediate forms, established by fossil finds, which make it possible to compare the structure of the old species and classes with that of the later species and classes, i.e. to homologize. These intermediate forms in biological history show specializations of their period, their habitat and their origin. They are valuable for us because they exemplify the transition from one structure to another, confirm assumed homologies or make us look for homologies that agree with their structures. The intermediate forms found in the history of the earth and of life on earth were biological systems in which the new element had already materialized while the old element was still present.²

Perhaps the actual intermediate forms are difficult to determine because they were too specialized in their way. The new element is typical and thus convincing only when its

mosaic of characteristics has become simple enough. So the intermediate forms referred to by the scientists are probably always the descendants of the real missing links.

The finding of an intermediate form supplies essential facts for a determination in the history of the earth and of life on earth: The period of the transition from one morphology to the next, from one form being effective to another form being effective and becoming even more effective is recognized, and thereof the circumstances which may have been essential conditions, can be examined. It is important to know whether an intermediate form had a wide or a locally limited distribution and whether its habitat flourished in the periods following or the whole interesting development of a continent was irretrievably lost by a transgression. Such considerations are necessary in view of a synthetic theory of evolution and thus, keep us from overestimating developments as that of Euramerican Pteridosperms of the Carboniferous which were far ahead of the general evolution.

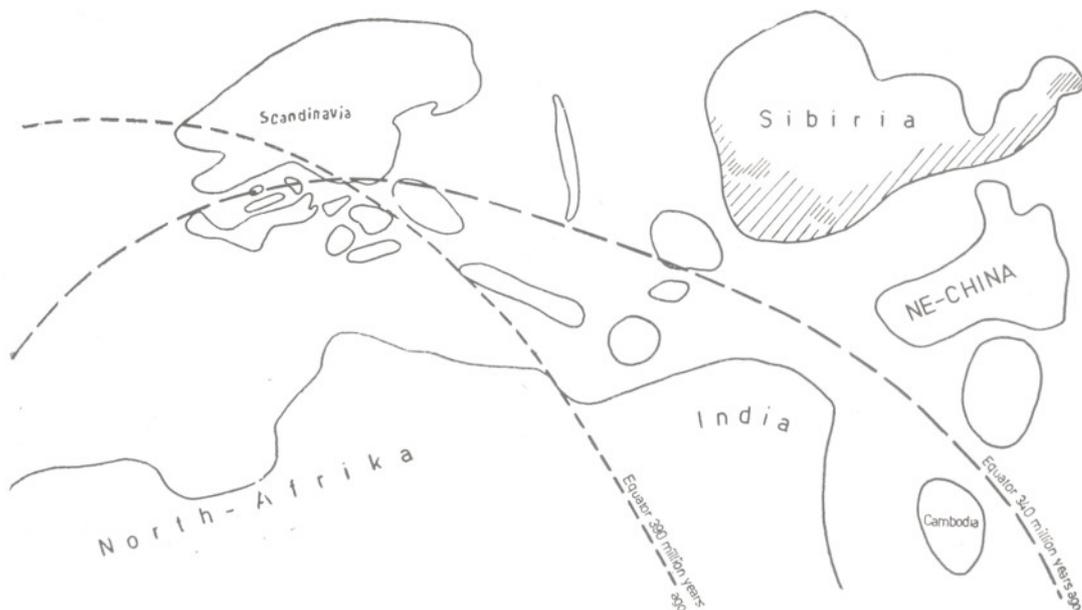
Figure 1 shows in outline the geography of a large part of the earth during the Carboniferous age. In the Devonian and Carboniferous periods Europe remained directly in the zone of the equator, while Siberia and Northeastern China lay in changing latitudes: Their climate, which had been cool to temperate in the Devonian age, grew warmer. These Asiatic regions served as the basis for the further development of the flora even in the Permian and Triassic periods when in Europe, the rich development of the flora in the Upper Carboniferous had been replaced by a poor, largely arid development of the flora.

Chacassopteris had a wide distribution on the continent of Siberia in the upper Lower

1. Remane (1956, p. 238) used the term "Nullwertahne" (zero value ancestor) to point out the limits of the assumption of a law of specialization and thus the limits of the assumption of an "adaptive radiation".

Engels (Dialectics of Nature, Notes and Fragments) already disagreed with Darwin on this assumption and referred to Hegel (§ 238, speculative method).

2. Mosaic nature of evolution, heterochrony in the development of the characteristics, heterobathism (various terms are used in the literature, cf. Takhtajan 1959, p. 13).



TEXT-FIG. 1 — Continents of the Lower Carboniferous age and their position in relation to the equator. Distribution of *Chacassopteris* in Sibiria (hatched).

Carboniferous (Visé). This permits the conclusion that the intermediate morphology of *Chacassopteris* is significant.

MORPHOLOGICAL COMPARISONS

There can be no doubt that in the Upper Devonian age *Archaeopteris* played a part in the biological history leading to the Ferns and Pteridosperms (Beck 1960, 1962, 1965). *Archaeopteris* was distributed over almost the whole of the earth, and only 40 million years after the first settlement of psilophytes on the continents it was the morphologically most advanced type of a land plant.

The morphology of both the sterile and the fertile leaf of *Chacassopteris* connects it with that of the *Archaeopteris* pinnule. With the *Archaeopteris* pinnule as well as with the *Chacassopteris* leaf the telomes grow fan-shaped, symmetrically "dachübergipfelnd" (roof overtopping). *Chacassopteris* has this "Dachübergipfelung" (roof overtopping) in a particularly primitive and clear form. Contrary to *Archaeopteris*, the sterile shoots of *Chacassopteris* still do not show any "Pendelübergipfelung" (oscillating overtopping) (fern-frond structure). The shoot of *Chacassopteris* appears to be

morphologically more primitive than the frond of *Archaeopteris* which is characterized by oscillating overtopping (Pendelübergipfelung) with intermediate pinnules. Dichotomously branching sterile shoots of *Chacassopteris*, bearing the forking leaves, thus resemble *Cladoxylon scoparium* KR. & W.

The fertile shoots of *Chacassopteris* show an apparently primitive overtopping: Main shoot and fertile lateral shoots along with the intervening pinnules on the main shoot.

The fertile pinnules of *Chacassopteris* greatly resemble the fertile pinnules of *Archaeopteris*. It is clearly discernible that the roof overtopped (dachübergipfelnden) and shortened lateral ends bear the sporangia, while the two median ends, which incline towards the symmetry plane, remain free and sterile. While earlier figures of the fertile *Archaeopteris* leaf Arnold (1939), Andrews (1961), Zimmermann (1959) and others showed it bordered with sporangia on one side and ending in one sterile telome, Beck (1962) (p. 374) was well advised to let in his reconstruction the pinnules terminate in two or more sterile telomes. The sporangia of *Archaeopteris* and *Chacassopteris* can be equally interpreted as fertile roof overtopping (dechübergipfelnde) telomes which may be formed on both halves (on

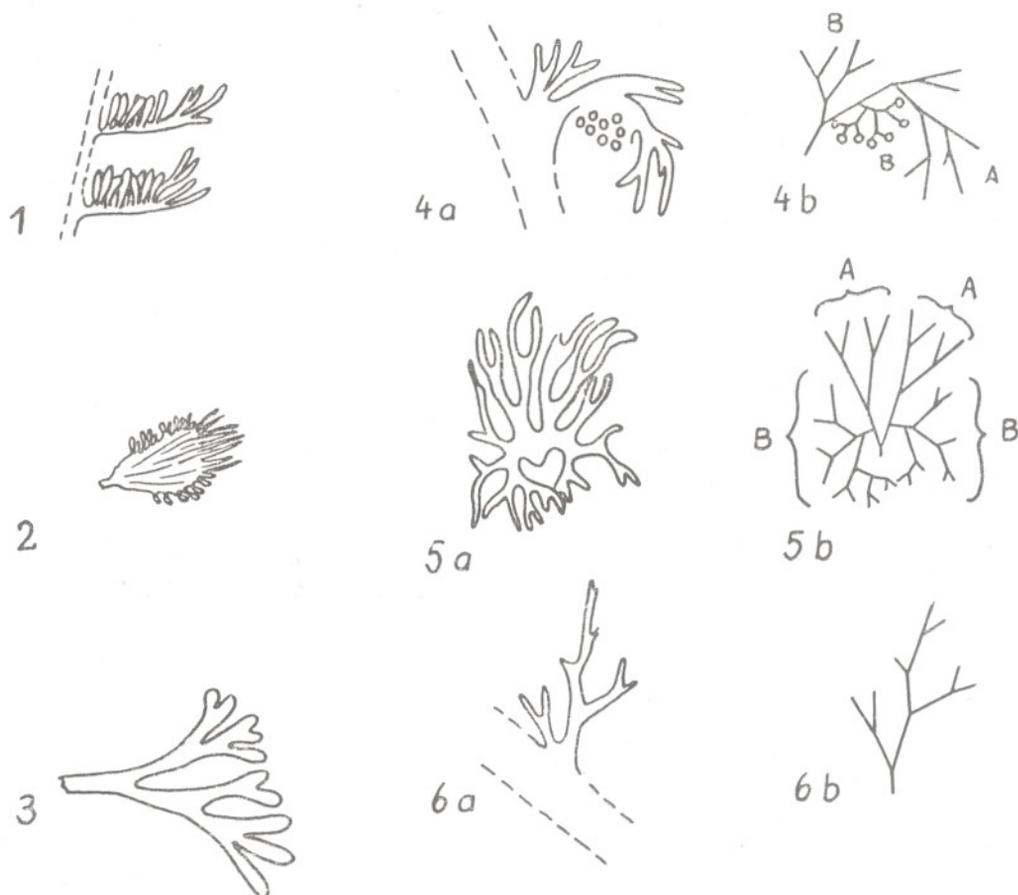


TEXT-FIG. 2 — Reconstruction of *Chacassoferis mongolica* from finds in the Lower Carboniferous (Tournai/Visé) layers of the People's Republic of Mongolia.

either half) of the pinnule. While in *Archaeopteris* they are directed towards the apex, in *Chacassoferis* they are curved inwards towards the base. A pinnule of *Archaeopteris* which was fertile on both sides as an exception was figured by Ananiev (1959) (table 18, fig. 3). The fertile pinnules of *Chacassoferis mongolica*, however, scarcely show the morphology of the sterile pinnules which is restricted to symmetrical roof overtopping, instead, they are combined with a small shoot, revealing a mixture of the *Chacassoferis* pinnule with the tendency of forming a small shoot.

The results of these comparisons of the leaf of *Chacassoferis* with those of *Archaeopteris* and *Cladoxylon scoparium* may be summed up in the conclusion that the principle of symmetrical roof overtopping as it is evident in the *Chacassoferis* leaf can be regarded as the basic pattern for the leaf forms of the Pterophytes.

Chacassoferis belongs to the "transition forms leading to 'typical' Cormophytes" as Zimmermann (1969, p. 75) called them in the sixth stage of plant life. But *Chacassoferis* is not a Middle Devonian plant as one might be tempted to conclude from its



TEXT-FIG. 3 — Comparisons between *Chacassopteris mongolica* (parts 4, 5) and *Archaeopteris* (parts 1, 2) or *Cladoxylon scoparium* (part 3) (according to Andrews, Phillips, Radforth 1965, Weyland 1964, Daber 1972).

Part 1 Fertile *Archaeopteris* pinnules with terminal, sterile forked tips.

Part 2 *Archaeopteris* pinnule fertile on both sides (according to Ananiev 1959).

Part 3 *Cladoxylon scoparium* pinnule with a tendency to roof-overlapping (Dachübergipfelung) (according to Weyland).

Part 4a Fertile leaf of *Chacassopteris mongolica*, schematized and explained in Part 4b.

Part 5a Sterile pinnule of *Chacassopteris mongolica*, schematized and explained in Part 5b.

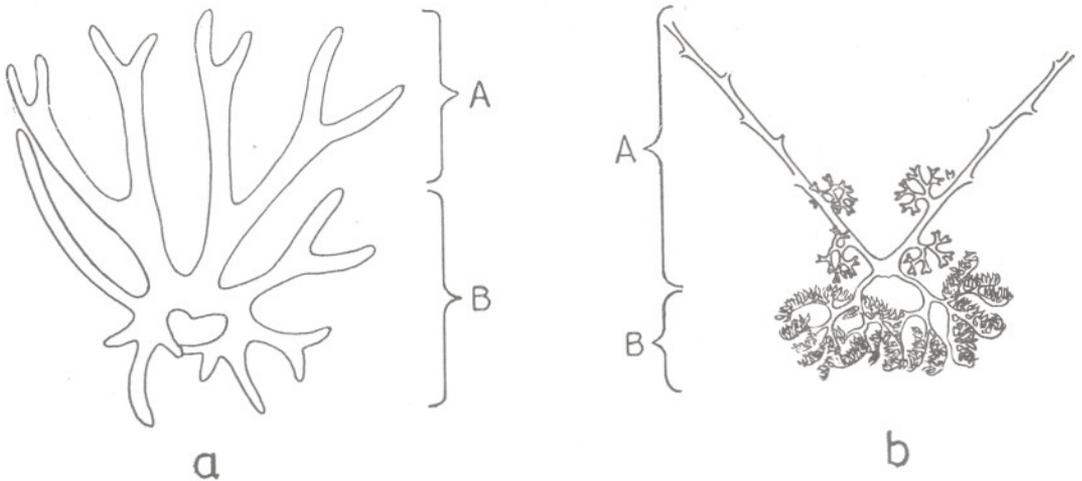
Part 6a Sterile pinnule of *Chacassopteris mongolica* which differs by oscillated overtopping (pendelnde Übergipfelung), schematized and explained in Part 6b.

The usual sterile leaf of *Chacassopteris mongolica* (Part 5b) differs in the behaviour of the forkings A from that of the forking B which are directed towards the base. With the fertile leaf the forkings A remain sterile while the roof overtopping forkings B become fertile. Strictly speaking, the whole fertile lateral shoot (the phyllophore and the fertile pinnules at it) is homologous to a sterile pinnule and originated by the addition of an oscillated overtopping to the symmetrical roof overtopping. Juxtaposed are the two forms of pinnules (Parts 5a and 6a), juxtaposed are sterile leaf and phyllophore, the fertile pinnule repeats the form of the sterile leaf, but modified.

morphological position between *Cladoxylon scoparium* and *Archaeopteris*. *Chacassopteris* lived for a long time—about 20 million years after the period of *Archaeopteris* (= Upper Devonian) and was a contemporary of the *Zygopterideae* and the *Pteridospermae*.

Chacassopteris mongolica had microsporangia and megasporangia, which suggests heterospory — a fact already proved for *Archaeopteris*.

Radczenko (1960, p. 45) already included *Chacassopteris* among the *Coenopteridales*



TEXT-FIG. 4 — Comparison between *Chacassopteris mongolica* (a) and *Rhacophyton zygopteroides* (b) (according to Leclercq). The "aphlebiae" arising at the phyllophore and the forked frond are compared with the sterile *Chacassopteris* leaf. The forkings B of the *Chacassopteris* leaf which are directed towards the base correspond to the sterile or fertile "aphlebiae" of *Rhacophyton*. The forkings A of *Chacassopteris*, which do not overtop, have been transformed into "fern fronds" by (pendelnde Übergipfelung) oscillated overtopping.

incertae sedis. The morphology of the *Chacassopteris* leaf offers a possibility to interpret the morphology of the Coenopteridales. If we take Leclercq's reconstruction (1950/51) as the basis for *Rhacophyton*, the shoot axes (T) of *Rhacophyton* may be compared to the creeping and also erect, irregularly branching and in the fertile region also overtopping shoots of *Chacassopteris mongolica*. The phyllophores of *Rhacophyton* would be comparable to the uniform, long shoots of *Chacassopteris* which bear the fertile pinnules. The complex of the V-shaped forked frond and its basal sterile or fertile aphlebiae would in its entirety correspond to the *Chacassopteris* pinnule. The morphology of the frond of *Rhacophyton*, developed by oscillating overtopping as with all the later Coenopteridales, would be equivalent to the two inner branched shoots (turned towards the symmetry plane) of the *Chacassopteris* leaf which do not show any tendency to overtopping. The aphlebiae of *Rhacophyton* would correspond to the leaf tips of *Chacassopteris* that are turned towards the base and originated by roof overtopping. These "aphlebiae" which are often fertile in *Rhacophyton* and other Coenopteridales of later periods would thus be interpreted not as independently developed organs but as belonging to the complex of the forked

frond. This interpretation would modify the exceptional position of those Coenopteridales that bear their sporangia not on the leaf fronds but on these "aphlebiae".

This comparison would result in the following conclusion: *Chacassopteris mongolica* may be regarded as a model for an intermediate form between Coenopteridales (*Lygopterideae*) and *Archaeopteris* and *Cladoxylon scoparium*. Consequently, *Chacassopteris mongolica* would be understood as a geographically very remote relative of *Saccoppteris* Stur (= *Alloiopteris* Potonié) which had morphologically remained particularly primitive. While in the more favourable climate of Europe the evolution had advanced to *Saccoppteris*, the morphological development in Siberia had remained in an undifferentiated state, related closer to the morphology of the psilophytes.

The publications of Andrews, Mamay and Phillips suggest the idea of the Coenopteridales as a Carboniferous group of Ferns which may have evolved into the modern leptosporangiate families of Ferns. Takhtajan published a scheme of such a phylogenetic tree in his manual "Foundations of Palaeontology" (1963, p. 539). In any case, the variety of the developments of the Coenopteridales in the Upper Carboniferous and Lower Permian periods is surprising. It seems that the original patterns



TEXT-FIG. 5 — A symmetrically roof overtopping "tag" at the petal of the flower of *Polygala* (here *P. oxyptera* RCHB.) as an example of a *Chacassopteris*-leaf-like rudiment in a highly differentiated dicotyledonous Angiosperm of the present (according to Pawlowski).

of the modern developments of the Ferns were at least experimented with already by the Upper Carboniferous species. Thus it is by no means incorrect to expect a recurrence of the morphology of the *Chacassopteris* leaf in much more highly developed plants of later periods.

The fact that the leaf of recent species of *Platycerium* corresponds in its outline and its bifurcation to the leaf of *Chacassopteris* illustrates the following problem: How can the pinnate frond of leptosporangiate Ferns be related to an originally branched, symmetrically roof overtopping basic form? The finds of *Chacassopteris* prove that the pattern of this recent *Platycerium* leaf does not result only from a prehistory on the level of seaweed or psilophytes but can be related to a morphology of Lower Carboniferous Ferns. In this connection also the Lower Cretaceous Fern *Weichselia* may be mentioned whose forked fronds have never been convincingly explained.

The *Ginkgo* leaf, too, is comparable to the *Chacassopteris* leaf, as Zimmermann (1959, p. 407) stated. It shows the asymmetrical roof overtopping in both halves of the leaf. *Ginkgo* apparently developed an insecticid instead of a reticulate venation, and thus

it was not at so great a disadvantage by its archaic venation as Potonié (1906, 1912) originally assumed. Consequently, the development of the Ginkgophytes also started from an actual Lower Carboniferous morphological state, and it hardly makes sense to seek the origin of the Ginkgophytes in earlier periods.

If the assumptions are correct that the pinnate leaf must have developed somehow from the forked leaf and that accordingly possibilities of a convincing homologization must yet be found, then this problem generally applies also to the morphology of the Angiosperm leaf. As the Carboniferous Pteridosperms had forked fronds, such a question is justified.

In the approximately 500 species of the recent genus *Polygala* we find in the region of the flowers a so-called "tag" which so far has been difficult to explain. This "tag" shows the forking and the roof overtopping which we know from *Chacassopteris*. Perhaps the "tag" of the *Polygala* species is a rudiment or atavism and indicates an ancient morphology of the leaf on which other chains of characteristics have been superimposed.

In this connection it seems reasonable to doubt the interpretation of *Polygala* as the last (youngest) branch of the phylogenetic tree of the Angiosperms. Considering that the species of the genus *Polygala* are distributed over Europe, North America and South America, Australia and Tasmania and also that the related genus *Securidaca* includes tropical trees and climbing lianas and was even identified with a fossil samara of the Eocene in the UAR (Egypt), these geographical and geological facts make it probable that the Polygaleae extend back to the Lower Cretaceous.

The forked venation of the Angiosperm herbs *Kingdonia* and *Circaeaster*, however, can not be as clearly related to the symmetrically roof overtopping leaf of *Chacassopteris*, even if some leaves of *Circaeaster* (e.g. Foster 1961, p. 972, fig. 2) resemble this basic pattern. The few specimens of leaves of primitive Angiosperms that are available for comparisons suggest that on the old morphology of the leaves which was due to symmetrical roof overtopping a dominant oscillated overtopping was superimposed, and that this produced the variety in the morphology of the leaves which is now so difficult to interpret.

REFERENCES

- ANANIEV, A. R. (1959). Die wichtigsten Fundstellen von Devonfloren im Ssajan-Altaj-Berggebiete. (in russischer Sprache mit deutscher Zusammenfassung). *Universität Tomsk*.
- ANDREWS, H. N. (1961). Studies in Palaeobotany. *New York*.
- ANDREWS, N., PHILLIPS, T. L. RADFORTH, N. W. (1965). Paleobotanical Studies in Arctic Canada, I. *Archaeopteris* from Ellesmere Island. *Can. J. Bot.* 43: 545.
- BECK, C. B. (1962). Reconstructions of *Archaeopteris*, and further Consideration of its Phylogenetic Position. *Am. J. Bot.* 49 (4): 373-382.
- DABER, R. (1971). Abbildungen und Beschreibungen unterkarbonischer Pflanzenreste aus der Mongolischen Volksrepublik. *Paläont. Abh. B. IV, 1, (im Druck)*.
- FOSTER, A. S. (1961a). The Phylogenetic Significance of dichotomous Venation in Angiosperms. *Rec. Adv. Bot.*, 10.
- Idem (1961b). The floral Morphology and Relationships of *Kingdonia uniflora*. *J. Arnold. Arbor.* 42.
- HEGEL, G. W. (1949) Encyclopädie der Philosophischen Wissenschaften, *Leipzig*.
- MAMAY, S. H. & ANDREWS, H. N. (1950). A Contribution to our Knowledge of the Anatomy of *Botryopteris*. *Bull. Torrey bot. Club.* 77 (6): 462-494.
- PAWLOWSKI, B. (1958) De *Polygalis polonicis* annotationes criticae *Frag. flor. geobot.* 3(2): 35-68.
- PHILLIPS, T. L. & ANDREWS, H. N. (1965). A Fructification of *Anachoropteris* from the Middle Pennsylvanian of Illinois. *Ann. Mo. bot. Gdn.* 52 (3): 251-261.
- Idem (1968). *Biscalitheca* (Coenopteridales) from the Upper Pennsylvania of Illinois. *Palaeontology* 11 (1): 104-115.
- POTONIE, H. (1912). Grundlinien der Pflanzen-Morphologie im Lichte der Palaeontologie. *Jena*.
- RADCZENKO, G. P. (1960). Coenopteridales *incertae sedis*. *Chacassopteris*. Neue Arten alter Pflanzen u. Invertebraten d. UdSSR. I. 45-49. (In russischer Sprache mit lateinischer Diagnosis). *Moskau*.
- REMANE, A. (1956). Die Grundlagen des Natürlichen Systems der vergleichenden Anatomie und der Phylogenetik. *Leipzig*.
- TAKHTAYAN, A. (1959) Die evolution der Angiospermen. *Jena*.
- ZIMMERMANN, W. (1959). Die Phylogenie der Pflanzen. *Stuttgart*.

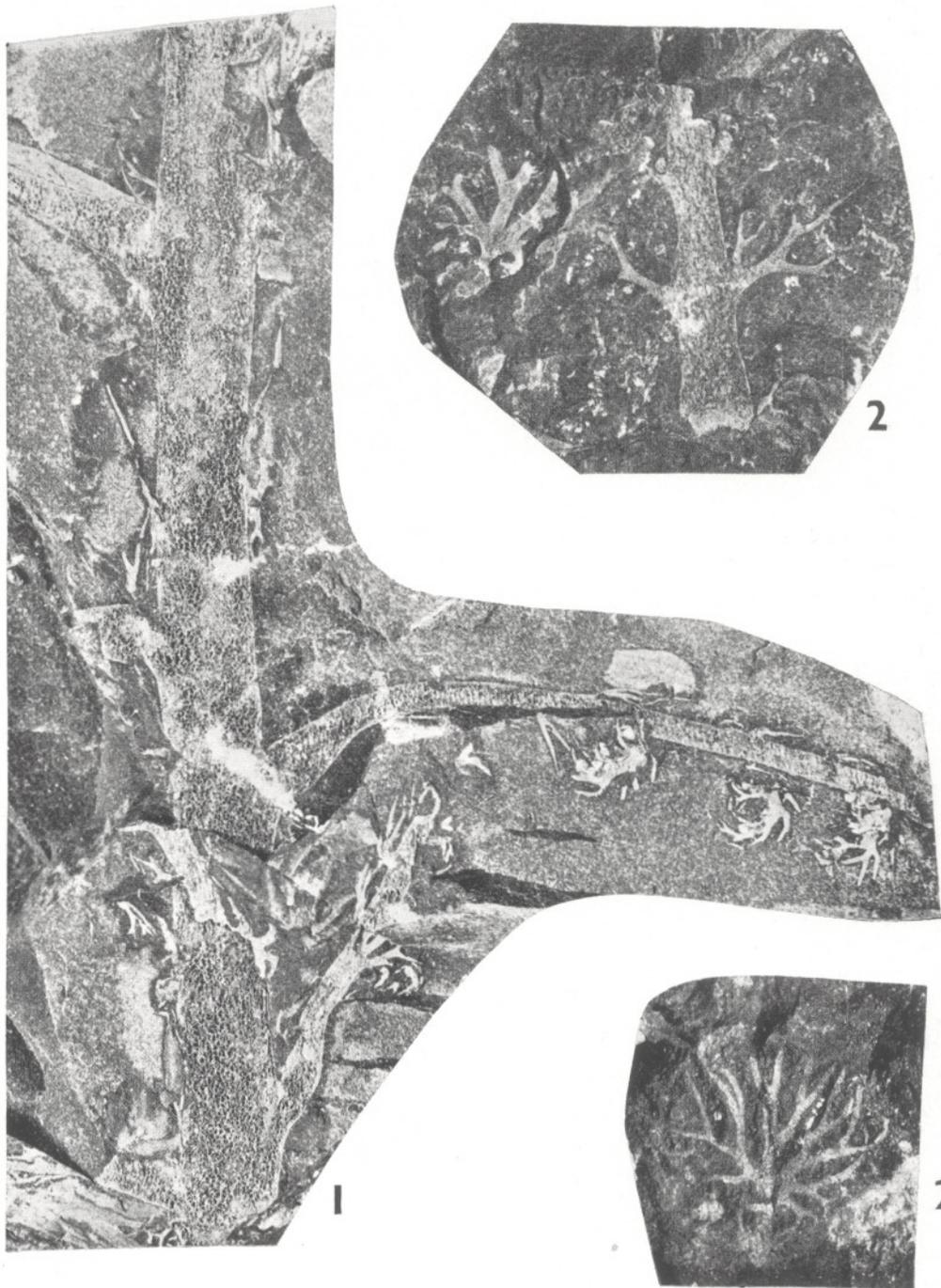
EXPLANATION OF PLATES

PLATE 1

1. *Chacassopteris mongolica* Daber, fertile, stem phyllophore, divided leaflets with Sporangia 2/1. (Peoples Republic of Mongolia, Aimak Bejanchongor, Zogt Chairman Uul; Tournai).
2. *Chacassopteris mongolica*, sterile leaflets 2/1.

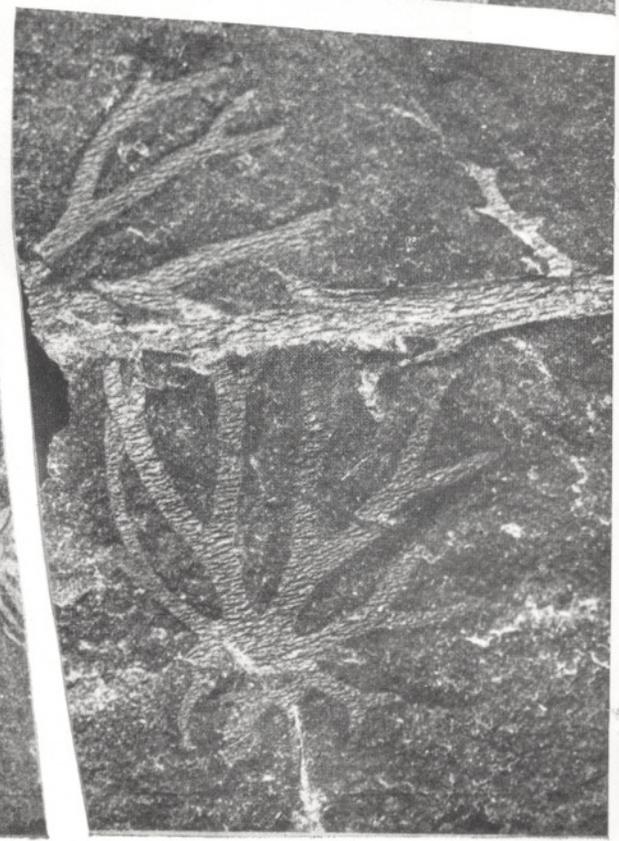
PLATE 2

3. *Chacassopteris mongolica*, Phyllophore with fertile leaflets, Sporangia single on apices curved towards the base 4/1.
4. *Chacassopteris mongolica*, sterile leaflets 4/1.





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