

# The genus *Nathorstia* (ferns)

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**ABSTRACT:** *Nathorstia* is a genus of Cretaceous fern with a broad distribution in the Northern Hemisphere. Previous authors have disagreed on the systematic position of *Nathorstia*, but investigation of the epidermis and sori of material from the lower Cretaceous of Primor'ye, Suyfun basin, has helped to clarify the problem. The genus was originally described by Heer, who assigned it to the family Marattiaceae, because of erroneous interpretation of the sori. However, the true affinity is apparently with the Matoniaceae, particularly with the genus *Phlebopteris* Brongniart. A diagnosis of *Nathorstia* is presented, and *N. pectinata* (Goeppert) Krasilov, n. comb. (formerly *Reussia pectinata* Goeppert) is designated the type species. --S.H. Mamay.

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Assigned to the genus *Nathorstia* Heer are fossil ferns widely distributed in the Cretaceous. The morphology of their leaves and the character of their spore formation are variously interpreted by different investigators, with the result that their systematic position is also a matter of opinion. It is now possible, mainly through study of the epidermis and fruiting structure in material from the Lower Cretaceous deposits of the Primor'ye, to add considerably to the description of *Nathorstia* and elucidate its systematic position and species composition. In studying the material we used Ashby's methods (transfer of the plant fossils to cellulose film by dissolving the rock in hydrofluoric acid) and also treatment in Schultze mixture and alkali.

The genus *Nathorstia* was erected by Heer (1880), who assigned to it two species of fossil ferns from the Cretaceous deposits of West Greenland — *N. angustifolia* Heer and *N. firma* (Heer) Heer. The latter had originally been described as *Danaeites firmus* (Heer, 1868). The genus *Danaeites* Goeppert had been erected by G. Goeppert for Paleozoic ferns with small pinnules and two rows of oval sori. Debey and Ettingshausen (1859) described a fern from the Cretaceous of Belgium, under the name *Danaeites schlotheimii*, with prolate synangia stretching from the median vein to the margin of the pinnule.

Heer had originally compared the impressions in his possession with *Danaeites schlotheimii*, but he later satisfied himself that the Greenland fern differed considerably from the Aachen specimen and suggested for it the generic name *Nathorstia*. The genus *Nathorstia* was described by its author as follows: leaves pinnate, pinnae long, narrow, coriaceous, free to the base;

median vein thick, lateral veins emerging at right angles, simple or dichotomous; sori round or oval, consisting of six sporangia in the case of *N. angustifolia*, seated in two rows on each side of the median vein and closely appressed to it. Heer did not succeed in studying the detailed structure of the sori, but suggested that they were similar to the synangia of the modern fern *Christensenia* Maxon and that *Nathorstia* was thus a new member of the family Marattiaceae. Heer mentioned also the close resemblance of *Nathorstia* to *Phlebopteris* (Laccopteris), an extinct fern of the family Matoniaceae.

In 1908 Nathorst described a third species, *N. latifolia* Nathorst, from the Atane formation of West Greenland, differing from *N. angustifolia* and *N. firma* in having larger pinnules (Nathorst, 1908). By treating the carbonized sori with Schultze's mixture Nathorst obtained a transparent separation which he was able to study under the microscope in transmitted light. The sorus turned out to contain 18 to 24 wedge-shaped sporangi arranged in a circle. No signs whatsoever of annuli could be seen on these preparations. Nathorst concluded that the *Nathorstia* sori were of similar structure to the synangia of *Christensenia*, as Heer had suggested.

While mentioning the general similarity of *Nathorstia* to *Phlebopteris*, Nathorst points out that the sporangia of the latter have an almost complete ring of thickened cells and that this constitutes its principal differences from *Nathorstia*. He refers also to the close similarity of *Nathorstia* to the fern described by Bayer from the Cenomanian of Bohemia as *Drynaria fascia* Bayer. On the impressions depicted in Bayer's work (1889), however, a reticulate venation can be clearly seen, whereas in the Greenland impressions only lateral veinlets diverging at right angles are visible, while the smaller details of the venation are indiscernible. Nathorst suggested that *Nathorstia latifolia* and *Drynaria fascia* might, on more detailed study, prove to be members of a single species, which would then have to be called *Nathorstia fascia* (Bayer).

Translated from *O rode Nathorstia* (paporotniki), Paleont. zhur., 1964, no. 2, p. 115-120. The author is with the Far Eastern Institute of Geology, U.S.S.R. Academy of Sciences.

Internat. Geology Rev. v.7, no.9

We may note that this plant had been known from the Lower Cretaceous deposits of the Russian Platform, under the name *Reussia pectinata* Geoppert (Murchison, Verneuil and Keiserling, 1845) before the appearance of Bayer's work.

In 1913 Halle described a fern which he called *N. alata*, from the Cretaceous deposits of South America. Although very similar to *N. latifolia*, *N. alata* was distinguished by the fact that the pinnules were joined basally, forming a fringe around the rachis. Halle commented also on the anastomoses of the lateral veins in *N. alata*. The reproductive apparatus was described as consisting of two rows of circular synangia on each side of the median vein of the pinnule, consisting of 12 to 15 loculi. The radial grooves in the impressions of the synangia were described as impressions of common walls between adjoining confluent sporangia. Halle thus confirmed Nathorst's conclusion that *Nathorstia* belonged to the Marattiaceae.

In 1919 Walkom described a species *N. willcoxii* from the Cretaceous of Queensland, on the basis of an impression of a sporiferous pinnule similar to those of *N. latifolia*. Walkom pointed to the similarity of *N. willcoxii* with certain members of the Polypodiaceae.

Hirmer and Hörhammer (1936), in a monograph on the family Matoniaceae, deleted from that family and assigned to the genus *Nathorstia* a series of ferns previously described under the generic names *Phlebopteris*, *Lacopteris*, *Microdictyon* and others, including the widespread species *Phlebopteris dunkeri* (Schenk) Schenk. In their opinion *Nathorstia* had nothing in common with *Phlebopteris*.

Prinada (1937) described the fern known as *Reussia pectinata* Geoppert from the Cretaceous of the Voronezh Province and assigned it to the genus *Lacopteris*, mentioning its close similarity to *Nathorstia latifolia*. "I adopted the generic name *Lacopteris* for the Latnayan form on the grounds that it covers a wider variety of forms, whereas the genus *Nathorstia* is based on the morphological characters of the sori and sporangia and can be used only if the structure of the latter is clear" (Prinada, 1937, p. 76).

A number of investigators, on the other hand, mainly English and American, cast doubt on the conclusions of Heer, Nathorst, Halle and other authors and have advocated combining *Nathorstia* with *Phlebopteris* (*Lacopteris*). Seward, who studied the Cretaceous flora of Greenland, wrote: "It is difficult to believe that leaves of identical form, venation and arrangement of the sori belong to ferns which are members of different families... I admit that the structure of the sori described by Nathorst and Halle in *Nathorstia* is in certain respects different from the typical *Lacopteris* structure, but in my opinion this difference is due to the state of preservation of

the impressions rather than to a real difference in their position among the Filices" (Seward, 1926, p. 80)(retranslated). In the light of these considerations, Seward included *Nathorstia angustifolia* Heer among the synonyms of *Lacopteris rigida* (Heer) Seward and described *Nathorstia latifolia* Nathorst as *Lacopteris latifolia* (Nathorst) Seward.

Miner, who described a fern which he called *Lacopteris galleyi* Miner (1935) from the Cretaceous of Kansas (U.S.A.), agreed with Seward. The material from the description of this species consisted of a fragment of sporiferous pinnule very similar to *N. latifolia* and *N. alata*. Sporangia ringed by thickened cells were clearly visible on the mounts.

Harris, in a work on the Jurassic flora of Yorkshire, also adduced arguments in favor of combining *Nathorstia* with *Phlebopteris*, but held back from expressing a definite opinion. A description of the genus *Nathorstia* is given below.

#### Genus *Nathorstia* Heer, 1880

Type species: *Reussia pectinata* Geoppert, 1845; Lower Cretaceous, Cenomanian; Moscow area; Voronezh Province; West Kazakhstan; Primor'ye; Czechoslovakia; West Germany.

**Diagnosis:** Leaves palmate and incised into oblate pinnae. Pinnules linear or linear-lanceolate. Venation reticulate; from the thick median vein secondary lateral veins run at right angles, dichotomizing at the margin of the pinnule. Thin veins of the third order run from the median and the lateral veins, dichotomizing and joining to form a fine network. Sori circular, numerous (up to several tens per pinnule), arranged in rows, two on each side of the median vein, in the spaces between the second-order veins. The number of wedge-shaped sporangia in the sorus varies from 8 to 24.

**Description:** The collection from the Lower Cretaceous deposits of the Primor'ye contains impressions of the basal parts of the leaves, in which the rachis is visible, dichotomously dividing at the apex into two branches, from which large, oblate pinnae arise, divided at the base. In general, the impression of a palmate-incised leaf is created. Such leaves in *Nathorstia* were described also by Seward (1926) from the Cretaceous deposits of Greenland, under the name *Lacopteris rigida* (Heer) Arnold. Usually, however, the *Nathorstia* leaves have been treated as simple. This can be explained by the fact that, because of the large size of the leaves, they have rarely been preserved entire and impressions of individual pinnae are more frequently encountered.

Pinnae oblate with a thick rachis (Plate I, illus. 1). Pinnules linear or linear-lanceolate,

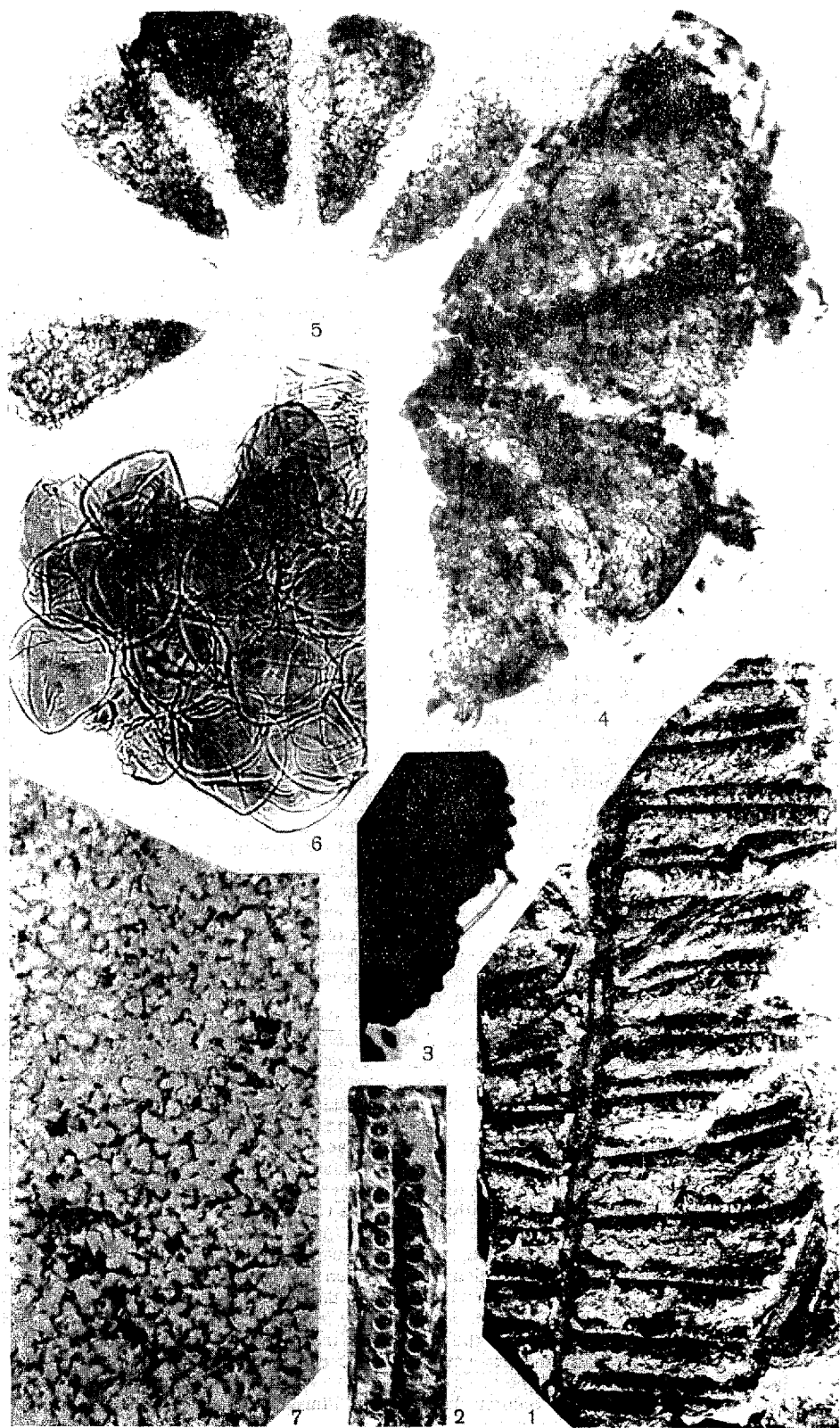


PLATE 1 (original Plate IX)

coriaceous, attached to the rachis at right angles, the base slightly dilated, the pinnules sometimes joined basally to form a narrow fringe along the rachis.

Heer, Halle and other authors mentioned that the terminal pinnules of *Nathorstia* were drawn out at the base. In reality the linear or linear-lanceolate pinnules of *Nathorstia* are attached by a slightly dilated base to the margins of the superior surface of the rachis. Owing to the considerable thickness of the rachis the margins of the pinnules were often broken off at the base when the ferns were buried, creating the impression of a drawn-out base. Usually a thick median vein, emerging as a ridge with longitudinal grooves, can be seen on the impressions of the pinnules. From this vein fairly thick lateral veins also run at right angles, dichotomizing outside the margin of the pinnule. Only in a few impressions is the fine network of third-order veins perceptible (fig. 1).

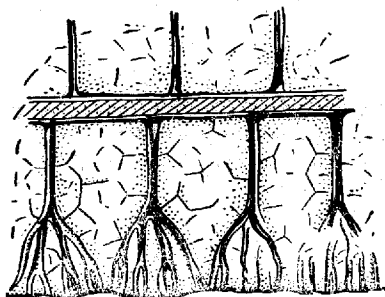


FIGURE 1. *Nathorstia pectinata* (Goeppert) comb. nov.; spec. No. 27/55, detail of venation (x4); Primor'ye, Suyfun basin, near the village of Lipovsty; Lower Cretaceous, coal-bearing strata

Sori up to 2 mm in diameter, numerous, arranged in two rows on each side of the median vein throughout its length up to the distal end of the pinnule (Plate I, illus. 2). Each sorus is seated between two neighboring second-order lateral veins and is equipped with numerous third-order veins forming a network above it. Sori circular, with a depression in the center, from which run radial grooves. Thin, concentric grooves are also visible, the origin of which Nathorst attributed to fracture of the sporangial

walls, and which are in reality thin cracks in the carbonaceous substance of the sorus.

The sporangia are wedge-shaped, arranged in a ring around the receptaculum, disclosed by an almost complete ring of thickened cells. Number of sporangia in sorus phytolite is transferred to cellulose film and treated with Schultze mixture the outlines of the sporangia, equipped with a ring of thickened cells, clearly emerge (Plate I, illus. 3). In *Nathorstia pectinata* the wedge-shaped sporangia are about  $800\ \mu$  long, sometimes crescentiform. The sporangial ring is about  $100\ \mu$  thick. On further treatment with alkali the sporangial walls rapidly disintegrate. If the reaction is interrupted at the very beginning, the outlines of the sporangial walls and thickened cells of the sporangial ring can be seen. An example is shown in Illus. 4 of Plate I. After a few minutes, however, the sporangial walls dissolve completely and only compact masses of spores remain, retaining the shape of sporangium (Plate I, illus. 5). Examples are shown in Nathorst's work (1908). The rapid dissolution in alkali of sporangia treated with Schultze's mixture has been the reason for erroneous interpretation of the *Nathorstia* sorus structure. The sori were described as synangia consisting of confluent sporangia without annuli. Spores circular-tetrahedral,  $23\text{--}30\ \mu$  in diameter. Exine thin and smooth. Scar triradiate with fringing along the rays. Rays about two thirds of the length of the spore radius (Plate I, illus. 6).

The cuticle of the *Nathorstia* leaf is also destroyed by various chemical reagents. It has been possible to obtain mounts of only small fragments of the cuticle (Plate I, illus. 6). Here the outlines of small, straight-walled cells of the epidermis can be seen but no stomata (Plate I, illus. 7).

**Species composition:** Several species, two of them well outlined. *N. dunkeri* (Schenk) Hirmer et Hoerhammer [= *N. angustifolia* Heer and *Lacopteris rigida* (Heer) Seq.], widely distributed in the Lower Cretaceous of Greenland, Western Europe, the Moscow basin, West Kazakhstan and the Primor'ye, occasionally found in the Middle and Upper Jurassic and Cenomanian (Peruc Beds) (Czechoslovakia). A similar species is *N. firma* (Heer) Heer from the Lower Cretaceous (Kome Beds) of

#### PLATE I (original Plate IX)

Illus. 1-7. *Nathorstia pectinata* (Goeppert) comb. nov.

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|--|---|
| 1 - spec. No. 27/55, part of Pinna (x 1);  | 5 - spec. No. 27/121, part of sorus, masses of spores filling sporangia visible (x 50)                                      |
| 2 - spec. No. 27/61, sporiferous pinnule (x 1.5)   | 6 - spec. No. 27/122, accumulation of spores (x 540)  |
| 3 - spec. No. 27/60, part of sorus transferred to cellulose film, outlines of thickened cells of sporangial rings visible (x 60) | 7 - spec. No. 27/123, cuticle (x 300); Primor'ye, Suyfun basin, vicinity of Lipovsty. Lower Cretaceous, coal-bearing strata |
| 4 - spec. No. 27/120, part of sorus, outlines of sporangia and sporangial rings visible (x 50)                                   |   |

Greenland. *N. pectinata* (Goeppert) Krassilov comb. nov. (= *N. alata* Halle, *N. urgatica* Pryn. and *Drynaria fascia* Bayer) is known from the Lower Cretaceous of the Russian Platform, West Kazakhstan, the Bureya basin, the Primor'ye and South America and also from the Cenomanian of Czechoslovakia (Peruc Beds) and Greenland (Atane formation). *N. oishii* Huzioka from the Lower Cretaceous of Japan and *N. willcoxii* Walcom from the Styx river series, Queensland (Australia) are presumably synonyms of *N. pectinata*.

**Comparison:** In the structure of the leaf, the manner in which the spores are carried and the structure of the sori and sporangia *Nathorstia* display great similarity to modern and fossil ferns of the family Matoniaceae. It was assigned to the Marattiaceae through erroneous interpretation of the sorus structure. Of the remaining Matoniaceae the closest to *Nathorstia* is *Phlebopteris* Brongniart, emend. Hirmer et Hoerhammer, which has talmate-incised leaves with linguiform or lanceolate terminal segments bearing two rows of sori without indusia. There are nevertheless important differences between the two, mainly in the venation. In *Phlebopteris* the lateral veins are joined by more or less frequent anastomoses. These usually form characteristic loops along the median vein. Third-order veins are missing. The sorus is usually situated on the acroscopic branch of a lateral vein. In *Nathorstia* venation is more complicated, with a network of third-order veins between the second-order lateral veins. Venation of this type is observed in ferns of the

families Dipteridaceae and Polypodiaceae. The sorus is situated between the second-order lateral veins and equipped with several third-order veins. Other differences too should be noted: the number of sori per pinnule of the sporiferous leaf in *Nathorstia* is much greater than in *Phlebopteris* (about 100 in *Nathorstia*) and the number of sporangia in a sorus is also usually greater (up to 24, against not more than 13 in *Phlebopteris*). The *Nathorstia* spores are smaller than those of *Phlebopteris*, with a thinner extine and less broad fringe along the rays of the scar. They resemble the spores of *Coniopteris* and, inevitably, are often described by palynologists under the name.

At the same time, the close similarity may indicate phylogenetic affinity between *Nathorstia* and *Phlebopteris*. Among the early Mesozoic members of the genus *Phlebopteris* two groups of species are distinguished. *P. braunii* (Goeppert) Hirmer et Hoerhammer and species similar to it are assigned to the first of these. Their leaves have comparatively short, linguiform pinnules. Anastomoses between the lateral veins are lacking or very rare. *P. polypodioides* Brong., *P. woodwardii* Leckenby and others which have leaves with long, lanceolate pinnules and frequent anastomoses between the lateral veins are assigned to the second group. It can be assumed that the evolution of the first group proceeded by reduction of the number of sori and formation of an indusium due to growth of the apex of the receptaculum (the series *Phlebopteris* - *Matonidium* - *Matonia*). The other group developed in the direction of more complicated

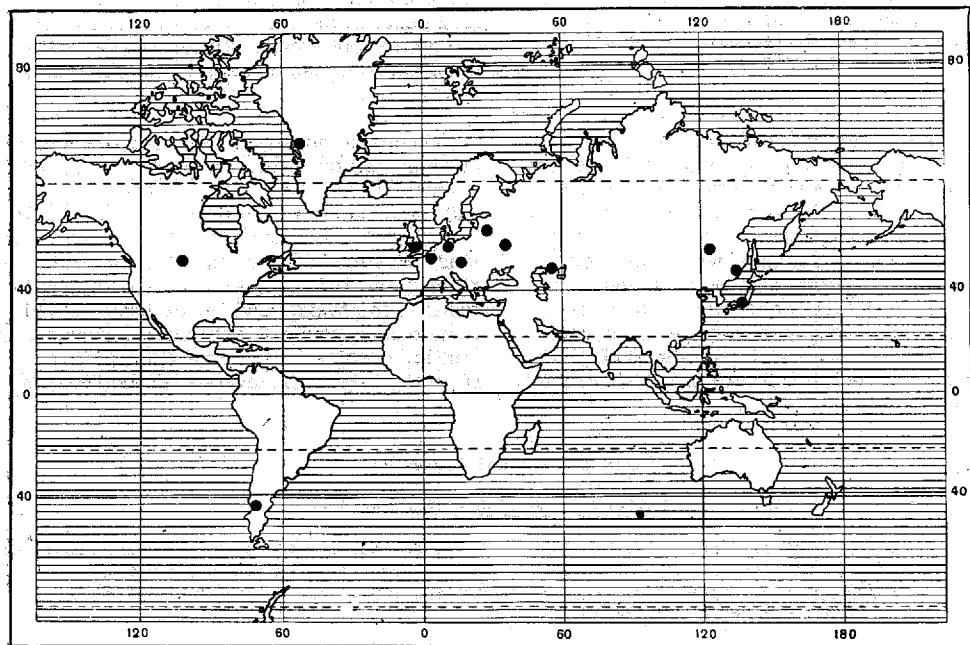


FIGURE 2. Locations of *Nathorstia* in the Lower Cretaceous and Cenomanian

venation and an increasing number of sori and of sporangia within the sori (the series *Phlebopteris* - *Nathorstia*).

**Comment:** *Nathorstia* reached its peak development in the Early Cretaceous and Cenomanian (fig. 2). It is found almost exclusively in flora of subtropical habit and is usually associated with *Gleichenia*, *Weichselia*, *Onychiopsis* and other thermophilic ferns. In the Siberian paleofloristic region *Nathorstia* occurs only in the southernmost, Early Cretaceous flora of Bureya (Vakhrameyev and Doludenko, 1961).

## REFERENCES

- Arnold, A.C., 1956, FOSSIL FERNS OF THE MATONIACEAE FROM NORTH AMERICA: J. Paleont. Soc. India, v. 1, no. 1, p. 118-121.
- Bayer, E., 1889, EINIGE NEUE PFLANZEN DER PERUCER KREIDESCHICHTEN IN BÖHMEN. SITZUNGSBER: Böh. Ges. Wiss. v. 26, p. 1-51.
- Debey, M.H. and C. Ettingshausen, 1859, DIE URWELTLICHEN ARCOBRYEN DES KREIDEGEBIRGES VON AACHEN UND MAASTRICHT: Denkschar. Akad. Wiss., v. 17, p. 1-68.
- Halle, T.G., 1913, SOME MESOZOIC PLANT-BEARING DEPOSITS IN PATAGONIA AND TIERRA DEL FUEGO AND THEIR FLORAS: Kgl. svenska vetenskapsakad. handl., v. 51, Nr. 3, p. 1-58.
- Harris, T.M., 1961, THE YORKSHIRE JURASSIC FLORA: Pt. 1, p. 1-212. London.
- Heer, O., 1868, DIE FOSSILE FLORA DER POLARLANDER: Flora Fossilis Arctica, v. 1, p. 1-192.
- \_\_\_\_\_, 1880, NACHTRÄGE ZUR FOSSILEN FLORA GRONLANDS: Flora Fossilis Arctica, v. 6, T. 1, H. 2, p. 1-17.
- Hirmer, M. and H. Hörhammer, 1936, MORPHOLOGIE, SYSTEMATIK UND GEOGRAPHISCHE VERBREITUNG DER FOSSILEN UND RECENTEN MATONIACEAE: Palaeontographica B, v. 81, p. 1-70.
- Miner, E.L. 1935, A NEW LACCOPTERIS FROM THE CRETACEOUS OF KANSAS: Contribs. Museum Geol. Michigan, v. 4, p. 287-290.
- Murchison, R., E. Verneuil and A. Keiserling, 1845, THE GEOLOGY OF RUSSIA IN EUROPE AND THE URAL MOUNTAINS: P. 1-505, London.
- Nathorst, A.G., 1908, PALÄOBOTANISCHE MITTEILUNGEN. 5. ÜBER NATHORSTIA HEER: Kgl. svenska vetenskapsakad. handl. v. 43, Nr. 6, p. 14-19.
- Prinada, V.D., 1937, K izucheniyu nizhnemelovoy flory Voronezhskoy oblasti [CONTRIBUTION TO STUDY OF THE LOWER CRETACEOUS FLORA OF THE VORONEZH PROVINCE]: VPO Ybk., v. 2, p. 71-89.
- Seward, A.C., 1926, THE CRETACEOUS PLANT-BEARING ROCKS OF WESTERN GREENLAND: Philos. Trans. Roy. Soc. London D, v. 215, p. 57-175.
- Vakhrameyev, V.A. and M.P. Doludenko, 1961, Verkhneyurskaya i nixhnemelovaya flora Bureinsko basseyne i yeye znachenie dlya stratigrafii [UPPER JURASSIC AND LOWER CRETACEOUS FLORA OF THE BUREYA BASIN AND ITS IMPORTANCE FOR STRATIGRAPHY]: Tr. GIN, no. 54, p. 1-132.
- Walkom, A.B., 1919, MESOZOIC FLORAS OF QUEENSLAND. PT. 3, 4. THE FLORAS OF BURRU AND STYX RIVER SERIES: Queens. Geol. Surv. publ., no. 263, p. 1-75.