FOSSIL IMPRINT • vol. 76 • 2020 • no. 2 • pp. 270–278
(formerly ACTA MUSEI NATIONALIS PRAGAE, Series B – Historia Naturalis)

NATIONAL MUSEUM

A NEW SPECIES OF THE GENUS *TUMIDOPTERIS* NAUGOLNYKH FROM THE PERMIAN OF THE PECHORA CIS-URALS, RUSSIA

SERGE V. NAUGOLNYKH[1,2]

[1] Geological Institute of Russian Academy of Sciences, Pyzhevsky per. 7, 119017 Moscow, Russia;
e-mail: naugolnykh@rambler.ru, naugolnykh@list.ru.
[2] Kazan Federal University, Kremlyovskaya str. 18, 420008 Kazan, Russia.

Naugolnykh, S. V. (2020): A new species of the genus *Tumidopteris* Naugolnykh from the Permian of the Pechora Cis-Urals, Russia. – Fossil Imprint, 76(2): 270–278, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (on-line).

Abstract: The paper considers a new species of gleicheniacean fern *Tumidopteris astra* Naugolnykh sp. nov. from the Lower Permian (Kungurian) and the Middle Permian (Roadian) deposits of the Pechora coal-basin, Russia. The new species is characterized both by macromorphology of the fertile and sterile pinnules and micromorphology of the sori and sporangia. Morphology of the most closely related leptosporangiate ferns is discussed.

Key words: ferns, Permian, new taxa, morphology, sori, Angaraland, evolution

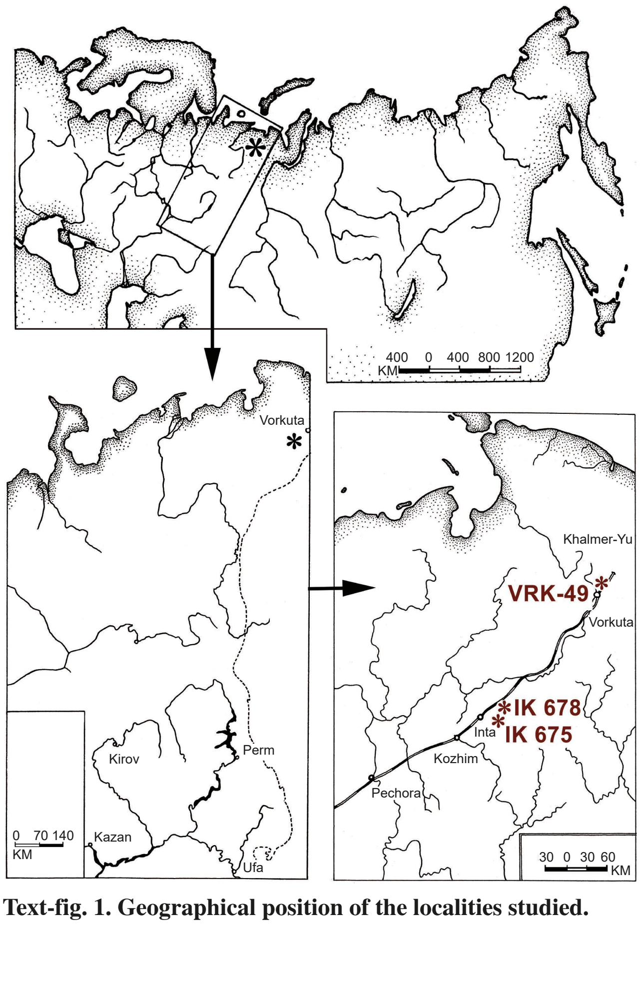
Received: July 14, 2020 | Accepted: August 20, 2020 | Issued: December 30, 2020

Introduction

Leptosporangiate ferns, in contrast to eusporangiate ferns, reached their highest diversity in Cenozoic times, but their phylogenetical roots descend deep into the Palaeozoic. The origin of many leptosporangiate fern families is still unclear, but for some of them we do have clear evidence that their first appearance was as early as the Late Palaeozoic. One of these ancient leptosporangiate fern families is the Gleicheniaceae.

Regarding the family Gleicheniaceae, we know for certain that these ferns appeared at least in the Late Carboniferous (Taylor et al. 2009) in tropical vegetation of the Euramerian palaeofloristic realm. There is some evidence of Permian Gleicheniaceae (Yao and Taylor 1988, Yao et al. 1997, Wang and Wu 1999, Wang et al. 1999), also mostly restricted to the low latitude floras of Cathaysia (see citations above) and Euramerica (Zodrow and McCandlish 1982). Nonetheless there is some evidence that Gleicheniaceae also existed in relatively high latitude floras in Gondwana (Cesari et al. 1998).

The present paper considers a new representative of the gleicheniacean ferns discovered in the uppermost Lower Permian and Middle Permian deposits of the Pechora coal-basin, i.e., the area which palaeogeographically belonged to the Angara palaeofloristic realm.



Text-fig. 1. Geographical position of the localities studied.

Material and methods

The collection studied originated from the uppermost Lower Permian (Kungurian) and Middle Permian (Ufimian

DOI 10.37520/fi.2020.022

or = Lower Roadian) deposits of the Pechora coal-basin, north-eastern part of the European part of Russia (Text-fig. 1). The plant fossils are represented by two main modes of preservation: (1) compressions and (2) impressions, sometimes with the partly preserved compressed coaly plant tissues present. The compressions (i.e., compressed sporangia) were studied by SEM (Vega Tescan MV 2300 scanning electron microscope at the Geological Institute of the Russian Academy of Sciences, Moscow). The collection studied is kept in the Geological Institute of Russian Academy of Sciences (GIN), and after detailed study will be officially transferred to the Monographic Department of the State Darwin Museum (Moscow).

Geological settings

The material studied came from the following localities (Text-fig. 1): (1) The city of Vorkuta, section 49 (VRK-49), layer 254 (spec. 4851/340, a sterile pinna); (2) the borehole IK-675, depth 961.7 m (holotype 4851/343, two fertile pinnae, the holotype is marked as "h"); (3) the borehole IK-677, depth 147.8 m (spec. 4851/344, a sterile pinna).

Section 49 (VRK-49) belongs to the uppermost part of the Kungurian – the Rudnitskaya Formation of the Lekvorkutskaya Series (after Pukhonto 1998: correlation chart in fig. 15). The IK-675 and IK-677 localities are somewhat younger and can be correlated with the local analogues of the Roadian on the International Stratigraphic Chart.

The rock matrix containing fern fossils is represented by dark-grey to black siltstones enriched by a substantial amount of organic matter. This kind of deposit corresponds to the coal-forming environments typical of the Early (partly), Middle and Late Permian time of the peat-forming processes in the Pechora Cis-Urals and Pechora Coal Basin.

Systematic palaeobotany

Division Pteridophyta Schimp., 1879
Class Gleicheniopsida Doweld, 2001
Order Gleicheniales A.B.Frank in Leunis 1877
Family Gleicheniaceae C.Presl, 1825

Genus *Tumidopteris* Naugolnykh, 2013

***Tumidopteris astra* Naugolnykh sp. nov.**
Text-figs 2a–e, 3a–e, 4a–f, 5a, b

Holotype. GIN 4851/343h; the holotype is figured here in Text-figs 2a, d, 3a–e, 4a–c, e, 5a–c.

Plant Fossil Names Registry Number. PFN001847.

Repository. Monographic Department of the State Darwin Museum (Moscow, Russian).

During study, the collection is kept in the Geological Institute of Russian Academy of Sciences (Moscow, Russia)

Derivatio nominis. From "astra" (Latin for "star"; as in: "Per aspera ad astra"); after the star-like shape of the sori in this new species.

Type locality. Borehole IK-675, depth 961.7 m, Pechora coal-basin; Middle Permian, Roadian.

Diagnosis. Fronds at least bipinnate. Fertile pinnules from pecopteroid to sphenopteroid, of subtriangular shape, with acute apices. Venation pinnate, with thin undulating midvein and three to five pairs of lateral veins. Lateral veins simple to dichotomizing up to three times. Terminations of lateral veins on fertile pinnules bear rosette-like sori. Each sorus consists of six to seven sporangia fused by their basal parts. Sporangia of short-clavate or prolonged ovoid shape, with small shallow sinus at apex, with wide indistinct annulus and vertical split for releasing spores. Sterile pinnules similar to fertile ones, but lacking sporangia. Associated spores round to ovoid, with small trilete mark.

Measurements of morphological structures are as followed: largest pinnule size: 7 mm long and 4 mm wide; average size of sporangia: 500 µm long, 300 µm wide; size of sporangial cells: 150 µm long, 60–70 µm wide; number of rows of cells in the annulus: presumably 1.

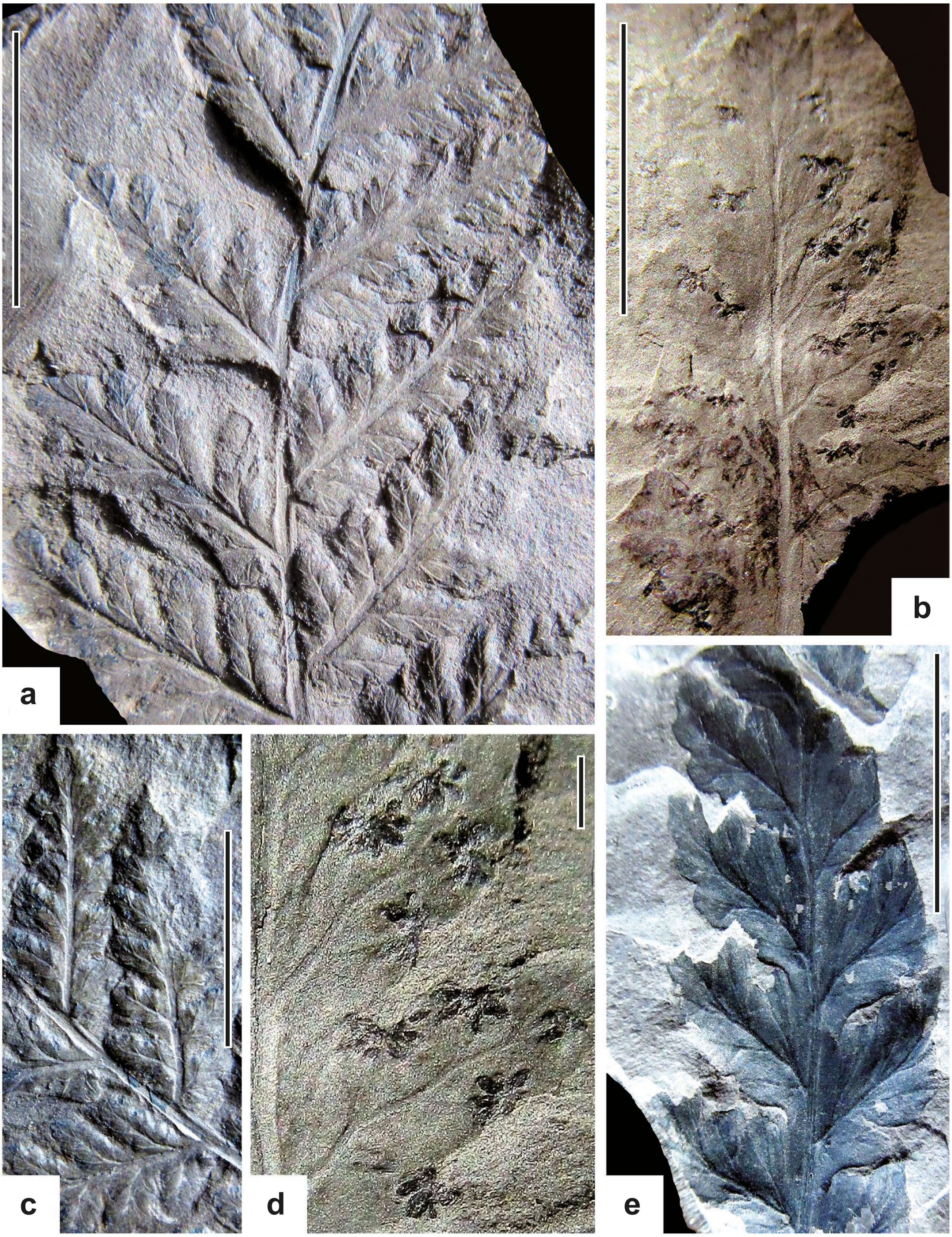
Description. Four specimens of well-preserved frond fragments are attributed to this new species. Two of them are fertile, and two are sterile.

The most complete frond fragment is a bipinnate sterile pinna of penultimate (last-but-one) order (Text-fig. 2a). Although this specimen is sterile, the details of venation are completely identical to venation on the fertile pinna selected as the holotype (Text-fig. 2b, d).

The pinna rachis of penultimate order is slightly curved presumably towards the frond apex. Maximal observed width of the pinna rachis does not exceed 1 mm. The rachis has a well-defined prolonged axial furrow located on its adaxial surface (Text-fig. 2c). Similar but smaller furrows are present on the rachises of the ultimate pinnae (= pinnae of the last order or segments of the last-but-one order). The ultimate pinnae (pinnae of the last order) is attached to the rachis of the penultimate order in regularly alternate order, at an angle of 45–50°. The most well-developed penultimate pinnae possess five to six pairs of pinnules (segments of the last order). The pinnules are attached to the pinna rachis at an angle of 55–65°. The largest pinnules are 7 mm long and 4 mm wide. The size of the pinnules gradually decreases towards the pinna apex. The shape of the pinnules varies from subtriangular (apical pinnules) to ovoid (proximal or basal pinnules). The pinnule apex is acute; pinnule margin is lobate. The lobes are of subtriangular shape, with acute to round apices. The pinnules are fused by their bases and form a wing (= limb) of the last-order pinna rachis (Text-fig. 2c, e). Venation is pinnate. The midvein is thin, undulating variably. The lateral veins are thin, dichotomizing only once. The anterior branch of the lateral vein usually dichotomizes once more.

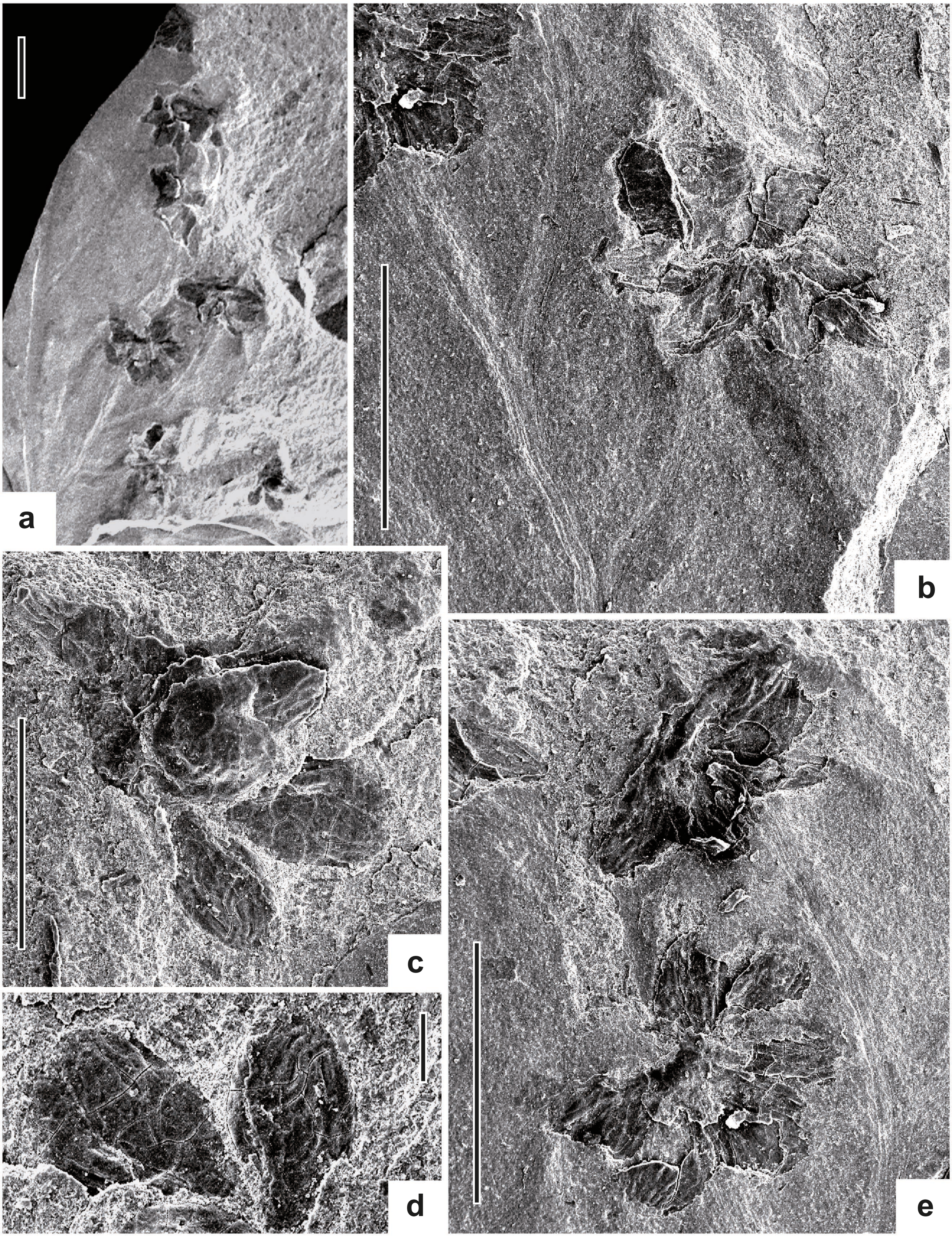
Gross morphology of the fertile pinnae in general is the same as that of sterile pinnae, but the venation of the fertile pinnules is somewhat simpler.

The best-preserved fertile pinna, which was selected as the holotype, shows a clear pattern of arrangement and structure of the sori and sporangia (Text-figs 2b, d, 3a–e, 4a, b, d). Each fertile pinnule has one to two sori (on apical pinnules) extending to seven or eight sori (on proximal or basal pinnules). Each sorus consists of six to seven short-ovoid



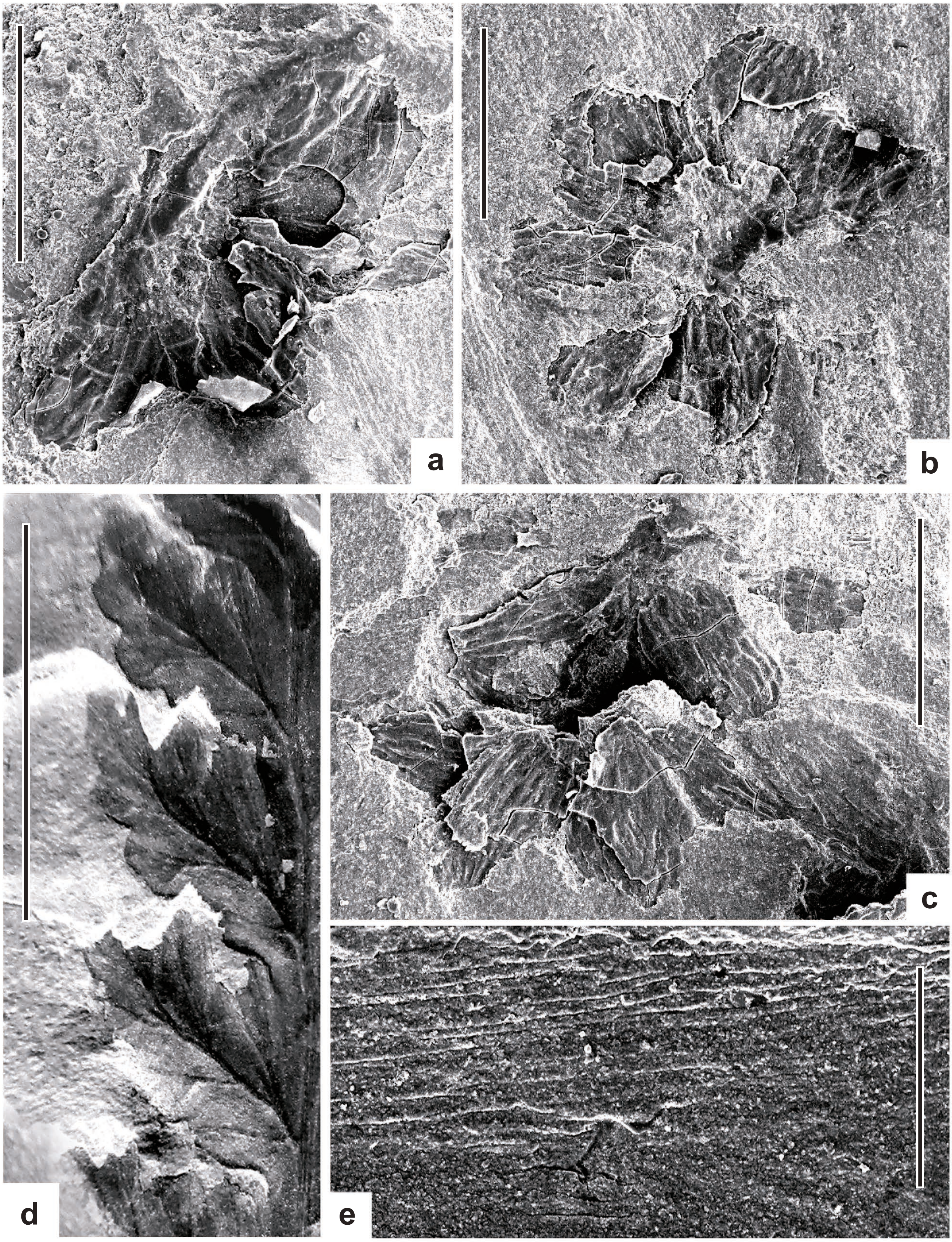
Text-fig. 2. ***Tumidopteris astra*** **sp. nov., macromorphology. a, c: sterile pinna, spec. GIN 4851/340; b, d: holotype GIN 4851/343h; e: sterile pinna, spec. GIN 4851/344. Localities: the city of Vorkuta, Section 49, layer 254 (a, c), the borehole IK-675, depth 961.7 m (b, d), the borehole IK-677, depth 147.8 m (e). Scale 1 cm (a, b, c, e), 1 mm (d).**

sporangia. The sporangia are free along almost the whole of their length, but are slightly fused by their bases where they attach to the common base (placenta or receptaculum). The average diameter of the sori is 1 mm. The average length of the sporangium is 500 μm, and width of the sporangium is 300 μm. The apex of the sporangia has a small apical sinus



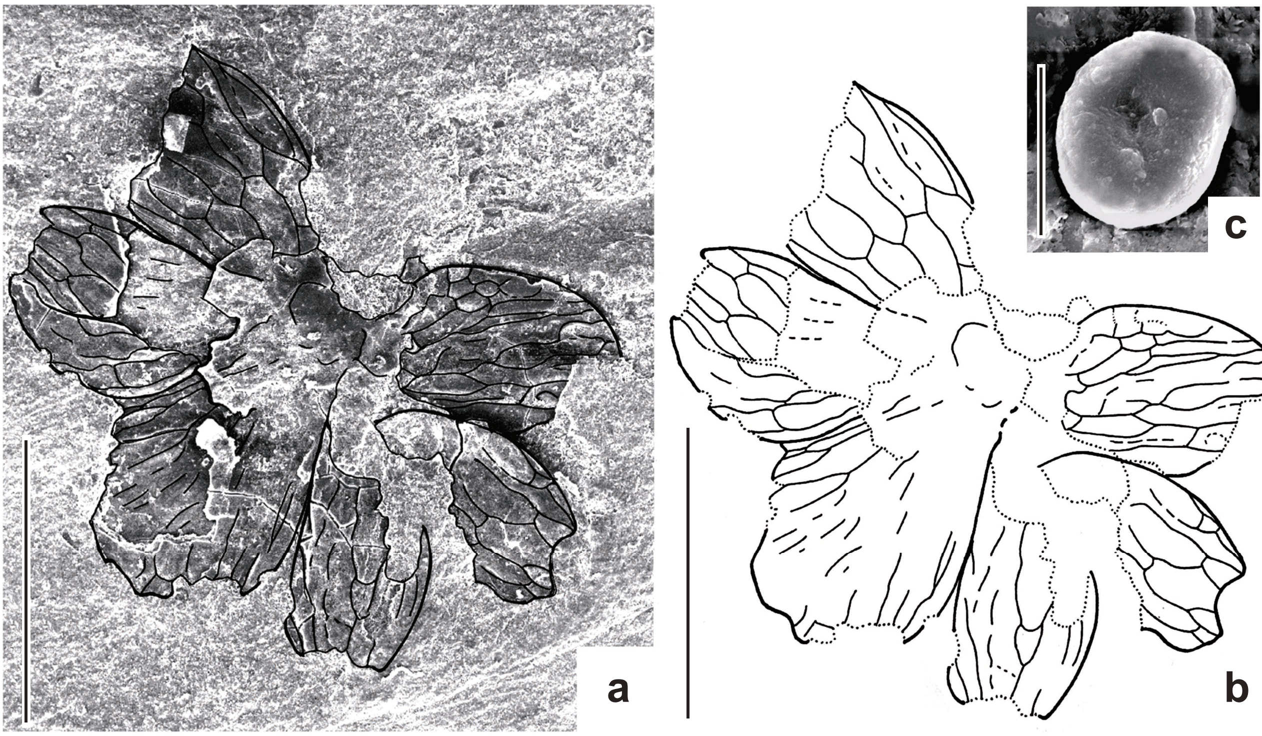
Text-fig. 3. ***Tumidopteris astra*** **sp. nov., holotype GIN 4851/343h, morphology of sori. a: part of fertile pinnule; b: one practically complete sorus located on the terminal part of a lateral vein; c: sorus with four visible sporangia; d: partly damaged sorus with three visible sporangia; e: two neighbouring sori. Locality: the borehole IK-675, depth 961.7 m. Scale 1 mm (a, b, e), 500 µm (c), 100 µm (d).**

or notch. The sporangial wall consists of elongated polygonal cells. The annulus is wide and indistinct having a subequatorial position on the sporangia, most probably consisting of a one cell wide row, situated along both sides of the sporangium



Text-fig. 4. ***Tumidopteris astra*** **sp. nov., holotype GIN 4851/343h, morphology of sori (a, b, c), epidermal structure (e) and the sterile pinna (d; spec. 4851/344). a: partly damaged sorus; b: partly damaged sorus with six sporangia; c: two neighboring sori; d: part of the sterile pinna; e: costal epiderma. Scale 500 µm (a, b, c), 1 cm (d), 200 µm (e).**

split. The vertical split is hardly visible on the sporangia. It can be traced by the small narrow elongated cells surrounding the split (Text-fig. 3e, uppermost sporangia of both sori). The average size of the cells is 150 µm long and 60–70 µm wide.



Text-fig. 5. *Tumidopteris astra* sp. nov., holotype GIN 4851/343h, morphology of sori. a, b: line tracing of the sorus; c: an isolated spore preserved on the sporangium. Scale 500 µm (a, b), 20 µm (c).

Several spores were found on the surface of the holotype fertile pinnules, on the wall of an open sporangium. The spores are round to ovoid (Text-fig. 5c), with finely granulate sporoderm and a small trilete scar.

C o m p a r i s o n   a n d   r e m a r k s . The new species is different from the type species *Tumidopteris clavata* NAUGOLNYKH in the smaller number of sporangia per sorus (six to seven sporangia per sorus in *T. astra* compared to nine to eleven in *T. clavata*), also in the shorter pinnules, and the weak development of the sporangia apical sinuses.

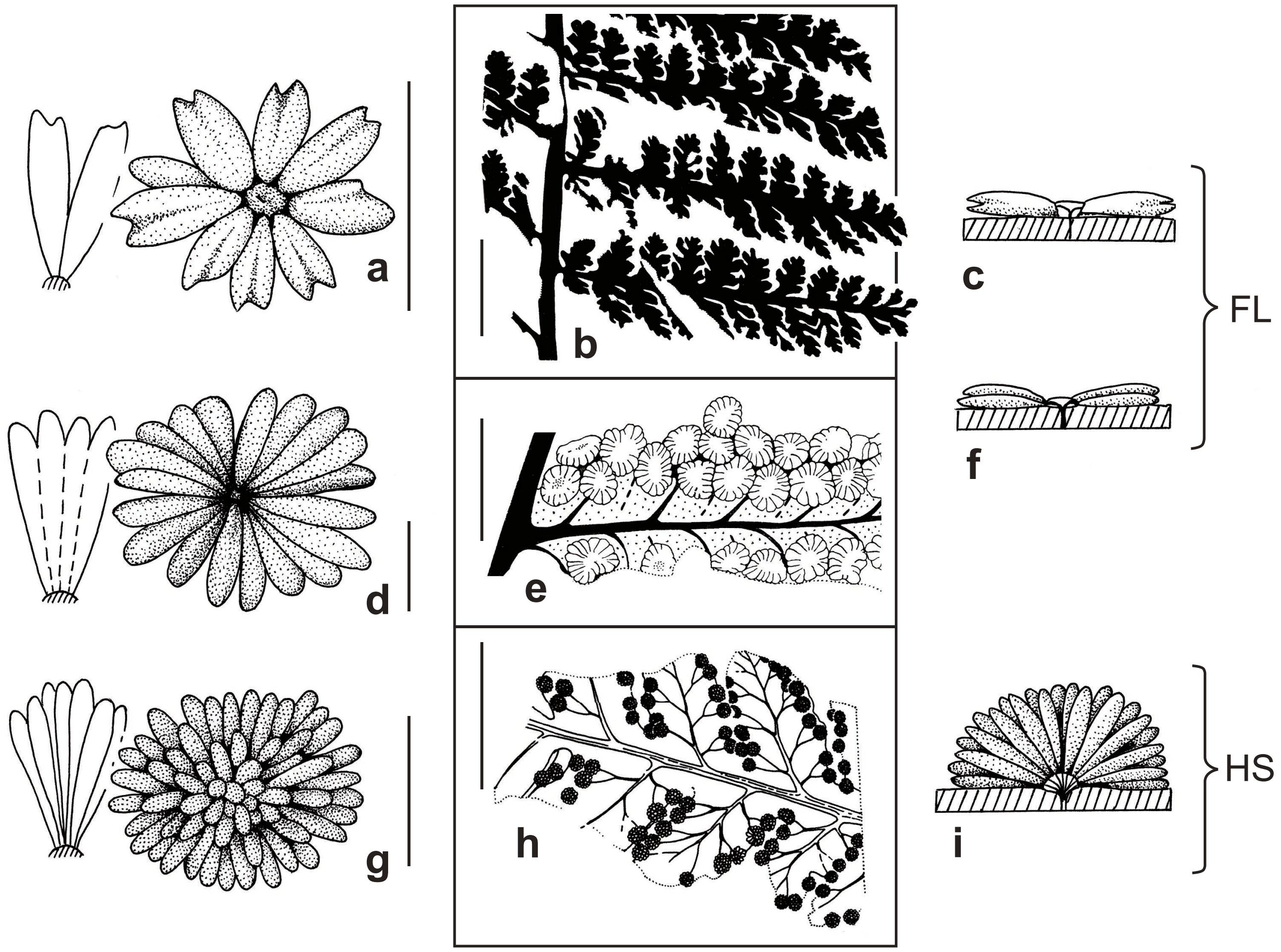
The spores of *T. astra* are similar to the spores extracted from sporangia of *Dichotomopteris lindleyii* (ROYLE) MAITHY, the fern from the Lower Gondwana (Lower Permian) deposits of India (Lele et al. 1981, see for example, text-fig. 8A–F, pl. 2, figs. 12–17), but the exact taxonomic position of the genus *Dichotomopteris* MAITHY is still unclear. The same or very similar type of in situ spores is known in the presumably gleicheniaceous fern *Wingatea plumosa* (DAUGHERTY) ASH from the Late Triassic age Chinle Formation, North America (Litwin 1985, see for example, pl. VI, figs 1–5, pl. VII, figs 1–7). Small round spores with trilete tetrad scar were extracted from the gleicheniaceous fern *Oligocarpia lindsaeoides* (ETTINGSH.) STUR from the Carboniferous (Westphalian) of the Czech Republic (Pšenička and Bek 2001: pl. 3) and Lower Permian fern *Oligocarpia kepingensis* Y.D.WANG et WU from China (Wang and Wu 1999: figs. 15, 17, Wang et al. 1999: fig. 1E, G).

Similar spores were reported in some other Late Palaeozoic sphenopterid ferns, for instance, *Discopteris opulenta* DANZÉ from Westfalian C and D (Upper Carboniferous) of Western Europe (Brousmiche 1979: pl. IX, figs 8–10). The in situ spores with relatively small trilete tetrad scar were obtained from the sporangia of the Upper Carboniferous ferns *Doneggia complura* G.W.ROTHWELL (Rothwell 1978: figs 21, 22) and *Grambastia goldenbergii* (ANDRAE) BOUSMICHE (Brousmiche 1978: pl. 4, figs 6, 7). Similar spores are characteristic of many geologically younger ferns. Thus, spores practically identical to the spores found on the sporangia and cuticles of *Tumidopteris astra*, were found in sporangia of leptosporangiate ferns (Aspidiacae and Polypodiaceae) from Paleogene deposits in the Russian Far-East (Fedotov 1970: pl. XV, figs 8, 16, 17).

Some remarks comparing *T. astra* and completely extinct Palaeozoic fern families Sermayaceae (*Sermaya* D.A.EGGERT et DELEV. and *Doneggia* G.W.ROTHWELL) and Tedeliaceae (e.g., *Tedelia glabra* D.A.EGGERT et T.N.TAYLOR) should also be made here.

All the sermayacean and tedeliacean ferns (for details see Eggert and Taylor 1966, Eggert and Delevoryas 1967, Rothwell 1978) are characterized by fronds generally similar to those of *T. astra*. Nonetheless, these taxa vary considerably in important characters such as type and presence of morphologically pronounced annulus and general shape of the sporangia, which are round to obovoid in contrast to the elongated sporangia of representatives of the genus *Tumidopteris* NAUGOLNYKH. The construction of the sori in sermayacean and tedeliacean ferns is also different. The sori of the two latter fern groups are represented by looser clusters in contrast to the compact sori of *Tumidopteris*. In addition, the leaf lamina could be strongly reduced in the fertile pinnae of *Tedelia glabra*, and thus the sori of this fern extend outwards from the fertile pinnule margin.

D i s t r i b u t i o n . Upper part of the Lower Permian (Kungurian) to Ufimian (lower Roadian) stages of the Pechora coal-basin and probably adjacent areas of the Cis-Urals and Russian platform.



Text-fig. 6. Comparative analysis of the three genera (*Prynadaeopteris* Radcz., *Geperapteris* S.V.Meyen, *Tumidopteris* Naugolnykh) with possible affinity to Gleicheniaceae from the Permian deposits of Angaraland. a–c: *Tumidopteris* Naugolnykh; d–f: *Prynadaeopteris* Radcz. (based on Radczenko 1955, 1956, Naugolnykh 2013); g–i: *Geperapteris* S.V.Meyen (based on Meyen 1982, Naugolnykh 2013). Left column – sori in plan (frontal view); central column – leaves; right column – sori in cross-section; FL – flattened sori; HS – hemispherical sori. Scale 1 cm (b, h), 5 mm (e), 1 mm (a, d), 0.5 mm (g); c, f, i – figures schematically drawn without scale.

Discussion

The most ancient gleicheniacean ferns, which are unequivocally botanically understood and convincingly interpreted, are known from the Upper Carboniferous and Lower Permian deposits around the world. They appeared in the geological record very suddenly and demonstrated almost all the characters typical of the family Gleicheniaceae.

Morphological archetype of the family Gleicheniaceae includes sori lacking indusium, relatively small number of sporangia per sorus, sporangia relatively large, round to fusiform, often stalked, but stalk very short and thick, with equatorial annulus, narrow vertical split for releasing spores (Takhtajan 1956).

The most well-studied Palaeozoic gleicheniaceous fern is *Oligocarpia leptophylla* (Bunbury) Grauvogel-Stamm et Doub., which is typical of the uppermost Carboniferous and Lower Permian (Rotliegend) deposits of Central and Western Europe (Wagner and Lemos de Sousa 1983, Barthel and Rössler 1995, Barthel 2005). *Oligocarpia leptophylla* had round sori with the sporangia possessing a distinct annulus. A similar arrangement of sporangia is known in *Damudosorus* D.D.Pant et L.Misra from the Lower Permian deposits of India (Pant and Misra 1983: pl. 6, fig. 25), but the latter genus has more isometric sporangia of more or less round shape.

The first Permian representative of the family Gleicheniaceae in Russia was described by L. A. Fefilova from the Kazanian (Wordian) deposits of the Pechora coal-basin (Fefilova 1973). This fern was attributed to Gleicheniaceae with a question mark and described as *Oligocarpia permiana* Fefil. In contrast to *Tumidopteris clavata* and *T. astra*, the species *Oligocarpia permiana* had more or less isometric sporangia with a distinct subequatorial annulus. The sterile pinnules of *Oligocarpia permiana* had round apices very different compared to the acute pinnule apices of *Tumidopteris astra*. The in situ spores of *Oligocarpia permiana* are also quite different in comparison with the in situ spores of *Tumidopteris astra*. The spores of *Oligocarpia permiana* are triangular, with a well-developed trilete mark.

One very uncommon leptosporangiate fern was described from the Upper Carboniferous deposits of Bulgaria (Pšenička and Bek 2004). This fern was attributed to a new genus and species *Tenchovia bulgariaensis* Pšenička et Bek. *T. bulgariaensis* shows some characters typical of the family Gleicheniaceae and can be considered as a close relative of this group. The spores found in situ in sporangia of *Tenchovia bulgariaensis* are somewhat similar to the spores of *Tumidopteris astra*. They are subtriangular to rounded, micrograngulate, and can be assigned to the genus *Granulatisporites* R.Potonié et Kremp (Pšenička and Bek 2004).

A comparative analysis of the three genera (*Prynadaeopteris* Radcz., emended by Naugolnykh (2013), *Geperapteris* S.V.Meyen, *Tumidopteris* Naugolnykh) having some possible affinity to Gleicheniaceae from the Permian deposits of Angaraland was previously published by the present author (Naugolnykh 2013). Briefly summarizing the main difference between these genera (Text-fig. 6) we should note that the genus *Tumidopteris* is different from the closely related genus *Prynadaeopteris* in having fusion of the basal parts of the sporangia, a smaller number of sporangia per sorus (8 to 10 sporangia per sorus in *Tumidopteris* and 14–20 sporangia per sorus in *Prynadaeopteris*), the presence of a small apical notch on the sporangia of *Tumidopteris*, and the distinctly sphenopteroid pinnules (both fertile and sterile; when they are adult and well-developed) of *Tumidopteris*. There is some similarity between *Tumidopteris* and the enigmatic fern genus *Hapalopteris* Stur, but in contrast to the latter genus the fronds of *Tumidopteris* bear well-developed wings on the pinna rachis, have an acute pinnule apex (not round as it is typical of *Hapalopteris*). Moreover, the fertile pinnules of *Tumidopteris* have a larger number of sporangia per sorus, i.e., not less than eight sporangia per sorus, in contrast to *Hapalopteris* which has four to five sporangia per sorus. The sterile pinnules of *Tumidopteris* are different from the sterile pinnules of another related fern, *Geperapteris*, in their sphenopteroid shape, which is atypical for *Geperapteris*. Sori of the latter genus are different from the sori of both *Tumidopteris* and *Prynadaeopteris* in their hemispheric shape, in contrast to the flattened sori of *Tumidopteris* and *Prynadaeopteris*.

The sterile leaves of *Tumidopteris astra* are similar to the sterile leaves of other Late Palaeozoic ferns of gleicheniacean affinity (for example, the species already cited above *Oligocarpia leptophylla* (Wagner and Lemos de Sousa 1985: fig. 1, pl. 1, figs 1, 2, Barthel and Rössler 1995: Abb. 3), and the Cathaysian gleicheniacean fern *Szea sinensis* Z.Q.Yao et T.N.Taylor (Yao and Taylor 1988: pl. I, figs. 3, 5).

Other similar ferns were reported from the Permian of Greenland (the Midtkap locality: Wagner et al. 2002: pl. 3, figs. 2, 5), where they were preliminarily identified as *Prynadaeopteris anthriscifolia* (Göpp.) Radcz. Of course, well-preserved large portions of the fronds are needed for adequate comparison of the sterile fronds, since the basic individual and onthogenetical diversity of the fern fronds could be quite high, and this assumption is especially true for sphenopterids (Danzé 1955, Pfefferkorn 1978, Brousmiche 1978, Langiaux 1982).

Acknowledgements

The author is grateful to S. K. Pukhonto (the State Geological Museum named after V. I. Vernadsky RAS, Moscow, Russia) for the collection of *Tumidopteris astra* sp. nov. provided for the present study. Dr. O. A. Cook is greatly acknowledged for linguistic improvement of the manuscript. This work was funded by the State Program No 0135-2019-0044 of the Geological Institute of the Russian Academy of Sciences "Phytostratigraphy, palaeofloristics, crises events in Cenozoic, Mesozoic, and Palaeozoic of the various regions of Eurasia; palaeoclimatic, palaeophytocoenotic and palaeophytogeographical reconstructions", and RFBR project No 18-04-00322. The author expresses his sincere gratitude to two anonymous reviewers, whose valuable comments and advice significantly improved the initial version of the manuscript.

References

Barthel, M. (2005): Die Rotliegendflora des Thüringer Waldes: Teil 3. Farne. – Veröffentlichungen, Naturhistorisches Museum Schleusingen, 20: 27–56.

Barthel, M., Rössler, R. (1995): Rotliegend-Farne in weisen Vulkan-Aschen „Tonsteine“ der Dohlen Formation als paläobotanische Fundschichten. – Veröffentlichungen des Museums für Naturkunde Chemnitz, 18: 5–24.

Brousmiche, C. (1978): *Grambastia* (*Sphenopteris*) *goldenbergii* (Andrae) nov. comb., espèce-type d'un nouveau genre de fougère leptosporangiée du Carbonifère. – Géobios, 11(2): 157–173. https://doi.org/10.1016/S0016-6995(78)80086-2

Brousmiche, C. (1979): Précisions sur *Discopteris opulenta* Danzé (Pteridophyta du Westphalen C et D inférieur d'Europe Occidentale). – Annales de la Société Géologique du Nord, 98: 105–112.

Cesari, S. N., Cuneo, N. R., Archangelsky, S. (1998): Una nueva probable Gleicheniaceae del Permico Inferior de Patagonia, Argentina [Probable new Gleicheniaceae from the early Permian of Patagonia, Argentina]. – Revista Espanola de Paleontologia, 13(1): 81–92. (in Spanish)

Danzé, J. (1955): Rôle du dévelopment ontogénique dans la diagnose paléobotanique. – Annales de la Société Géologique du Nord, 75: 83–93.

Eggert, D. A., Delevoryas, T. (1967): Studies of Paleozoic ferns: *Sermaya*, gen. nov. and its bearing on filicalean evolution in the Paleozoic. – Palaeontographica, Abt. B, 120: 169–180.

Eggert, D. A., Taylor, T. N. (1966): Studies of Paleozoic ferns: on the genus *Tedelia* gen. nov. – Palaeontographica, Abt. B, 118: 52–73.

Fedotov, V. V. (1970): New species of aspidean and polypodian ferns with the preserved sori from the Paleogene of the Zea-Burea Depression. – Paleontological Journal, 4: 92–99.

Fefilova, L. A. (1973): Paporotnikovidnye permi severa Pred-ural'skogo progiba [Fern-like plants from the Permian of northern part of the Cis-Urals depression]. – Nauka, Leningrad, 192 pp. (in Russian)

Langiaux, J. (1982): Frondes sphenopteridiennes dans le Stephanien terminal du basin de Blanzy-Montceau (Massif Central, France). – La Physiophile, 97: 81–100.

Lele, K. M., Maithy, P. K., Mandal, J. (1981): *In situ* spores from Lower Gondwana ferns – morphology and variation. – The Palaeobotanist, 28-29: 128–154.

Leunis, J. (1877): Synopsis der Pflanzenkunde. Bd. 3: Specielle Botanik, Kryptogamen (2nd ed.). – Hahn'sche Buchhandlung, Hannover, 675 pp.

Litwin, R. J. (1985): Fertile organs and *in situ* spores of ferns from the Late Triassic Chinle Formation of Arizona and New Mexico, with discussion of associated dispersed spores. – Review of Palaeobotany and Palynology, 44: 101–146. https://doi.org/10.1016/0034-6667(85)90030-2

Meyen, S. V. (1982): The Carboniferous and Permian floras of Angaraland (a synthesis). – Biological Memoirs, 7(1): 1–109.

Naugolnykh, S. V. (2013): Permian ferns of Western Angaraland. – Paleontological Journal, 47(12): 1379–1462. https://doi.org/10.1134/S0031030113120010

Pant, D. D., Misra, L. (1983): *Cuticulopteris* gen. nov. and some other pteridophylls from the Raniganj coalfield, India (Lower Gondwana). – Palaeontographica, Abt. B, 185(1-3): 27–37.

Pfefferkorn, H. W. (1978): Revision der sphenopteriden *Discopteris karwinensis* Stur, *Discopteris vuellersi* Stur und der Gattung *Discopteris* Stur. – Argumenta Palaeobotanica, 5: 167–193.

Pšenička, J., Bek, J. (2001): *Oligocarpia lindsaeoides* (Ettingshausen) Stur and its spores from the Westphalian of Central Bohemia (Czech Republic). – Acta Musei Nationalis Pragae, Series B – Historia Naturalis, 57(3-4): 57–68.

Pšenička, J., Bek, J. (2004): *Tenchovia bulgariaensis* gen. et sp. nov. from the Pennsylvanian of the Dobrudzha Coalfield, Bulgaria. – Geologica Balcanica, 34(1-2): 69–76.

Pukhonto, S. K. (1998): Stratigrafiya i floristicheskaya kharakteristika permskikh otlozheniy ugol'nykh mestorzhdeniy Pechorskogo basseyna [Stratigraphy and floristic characteristics of the Permian deposits of the coal mines of the Pechora basin]. – Nauchny mir, Moskva [Moscow], 312 p. (in Russian)

Radczenko, G. P. (1955): Rukovodyashchie formy verkhnepalezoyskoy flory Sayano-Altayskoy oblasti [Index forms of Upper Paleozoic floras of the Sayany-Altai region]. – In: Khalfin, L. L. (ed.), Atlas rukovodyashchikh form iskopaemykh fauny i flory Zapadnoy Sibiri [Atlas of Index Forms of the Fossil Fauna and Flora of Western Siberia], vol. 2. Gosudarstvennoe Nauchno-Tekhnicheskoe Izdatelstvo Literatury po geologii i okhrane nedr, Moskva [Moscow], 42–154. (in Russian)

Radczenko, G. P. (1956): Rukovodyashchie formy iskopaemykh rasteniy uglenosnykh otlozheniy Kuznetskogo basseyna [Index forms of fossil plants from coal-bearing deposits of the Kuznetsk Basin]. – In: Atlas rukovodyashchikh form iskopaemykh fauny i flory permskikh otlozheniy Kuznetskogo basseyna [Atlas of Index Forms of the Fossil Fauna and Flora of Permian Deposits of the Kuznetsk Basin]. Gosudarstvennoe Nauchno-Tekhnicheskoe Izdatelstvo Literatury po geologii i okhrane nedr, Moskva [Moscow], 110–202. (in Russian)

Rothwell, G. W. (1978): *Doneggia complura* gen. et sp. nov., a filicalean fern from the Upper Pennsylvanian of Ohio. – Canadian Journal of Botany, 56: 3096–3104. https://doi.org/10.1139/b78-372

Taylor, T. N., Taylor, E. L., Krings, M. (2009): Paleobotany. The Biology and Evolution of Fossil Plants. – Elsevier, Amsterdam, Boston, Heidelberg, 1230 pp.

Takhtajan, A. L. (1956): Vysshie rasteniya. T. 1: Ot psilofytovykh do khvoynykh [Telomophyta. Vol. 1: Psilophytales to Coniferales]. – Izdatel'stvo AN SSSR [USSR Academy of Sciences Press], Moskva [Moscow], Leningrad, 488 pp. (in Russian)

Wagner, R. H., Lausberg, S., Naugolnykh, S. (2002): The Permian Angara flora from North Greenland: A progress report. – In: Hills, L. V., Henderson, C. M., Bamber, E. W. (eds), Carboniferous of the World. Cananadian Society of Petroleum Geology, Memoirs, 19: 382–392.

Wagner, R. H., Lemos de Sousa, M. J. (1985): *Oligocarpia leptophylla* (Bunbury), nomenclatorial history and description of the lectotype. – In: Lemos de Sousa, M. J., Wagner, R. H. (eds), Papers on the Carboniferous of the Iberian Peninsula (Sedimentology, Stratigraphy, Palaeontology, Tectonics and Geochronology). Anais da Faculdade de Ciências, Universidade do Porto, Supplement to volume 64(1983): 481–490.

Wang, W., Guignard, G., Barale, G. (1999): Morphological and ultrastructural studies on *in situ* spores of *Oligocarpia* (Gleicheniaceae) from the Lower Permian of Xinjiang, China. – International Journal of Plant Sciences, 160(5): 1035–1045. https://doi.org/10.1086/314178

Wang, Y., Wu, X. (1999): *Oligocarpia kepingensis* sp. nov. from the Lower Permian of the northern Tarim Basin, Xinjiang and its *in situ* spores. – Chinese Science Bulletin, 44(2): 108–111. https://doi.org/10.1007/BF02884728

Yao, G., Sheng, A., Wang, H. (1997): A new species: *Szea* (*Cladophlebis*) *henanense* sp. nov. in Henan Province and its evolutional significance. – Chinese Science Bulletin, 42(12): 1023–1027. https://doi.org/10.1007/BF02882625

Yao, Z.-Q., Taylor, T. N. (1988): On a new gleicheniaceous fern from the Permian of South China. – Review of Palaeobotany and Palynology, 54: 121–134. https://doi.org/10.1016/0034-6667(88)90008-5

Zodrow, E. L., McCandlish, K. (1982): *Oligocarpia bellii* sp. nov. from the middle Upper Carboniferous of Cape Breton Island, Nova Scotia, Canada. – Palaeontographica, 181(4-6): 109–117.