Wulfenia **21** (2014): 1–20

Wulfenia
Mitteilungen des
Kärntner Botanikzentrums
Klagenfurt

Permocallipteris, a new genus from the Permian of Angaraland

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Summary: This paper deals with Permian peltasperm foliages attributed to a new genus *Permocallipteris* Naug., gen. nov., which is characteristic of Angaraland paleofloristic realm. The genus is proposed for two- or three-pinnate fronds with entire-margined last order segments (pinnules), normally with obtuse round to slightly acute apex, wide base, well-developed midvein and pinnately disposed lateral (secondary) veins. The fronds always possess clear additional (intercalated) pinnules attached directly to the frond rachis. The intercalated pinnules can be identical to common pinnules or be slightly modified and form wings on the frond rachis. The epidermal-cuticular structure of *Permocallipteris* fronds is characterized. The leaves are amphystomatic, the lower (adaxial) leaf cuticle is thinner and has numerous papillae. Stomata are monocyclic to incompletely dicyclic, with thick cutinization of the subsidiary cells.

Keywords: peltasperms, taxonomy, new taxon, gen. nov., callipterids, Permian, Angaraland, *Permocallipteris*

In Permian deposits of Angaraland or Angara floristic realm, from the Urals to Siberia and Russian Far-East, southwards to Mongolia and North China, there were many endemic Angaran taxa, making this area a separate distinct paleofloristic realm. The most typical endemic taxa of Permian of Angaraland are equisetophytes of Tchernoviaceae, several genera of both eusporangiate and leptosporangiate ferns (including *Prynadaeopteris* Radczenko, *Geperapteris* S. V. Meyen, *Acrogenotheca* Naugolnykh, *Convexocarpus* Naugolnykh and *Tumidopteris* Naugolnykh), gymnosperms of Vojnovskyales (*Vojnovskya* Neuburg, *Nephropsis* Zalessky, *Rufloria* S. V. Meyen) and some other morphologically specific and uncommon plant groups.

Peltasperms are widely spread in the Permian deposits of Angaraland, but their taxonomical attribution was disputable and unclear till the present time. This paper deals with the taxonomy of compound pinnate leaves of peltasperms attributed to the new genus *Permocallipteris* Naugolnykh, gen. nov.

Materials and methods

Some of the materials, which were used in the present paper, were collected from the Permian deposits of the Urals and adjacent regions by the author (Fig. 1). Most of the specimens are kept at the Geological Institute of Russian Academy of Sciences, Moscow [GIN collections 4851, 4856, 3773(11)]. A large and valuable collection of leaves and reproductive organs of peltasperms from the Permian deposits of Pechora Coal Basin was provided by S. K. Pukhonto (V. I. Vernadsky State Geological Museum, GGM, Russian Academy of Sciences, Moscow; detailed information about the regional stratigraphy and geographical position of the localities see in: Pukhonto 1998). Several specimens from collections of V. A. Tsymbal, A. G. Sharov (Moscow) and O. V. Abrosimova (Krasnoufimsk; now this collection is kept at the Urals Geological Museum of the Mine 'Gorny'

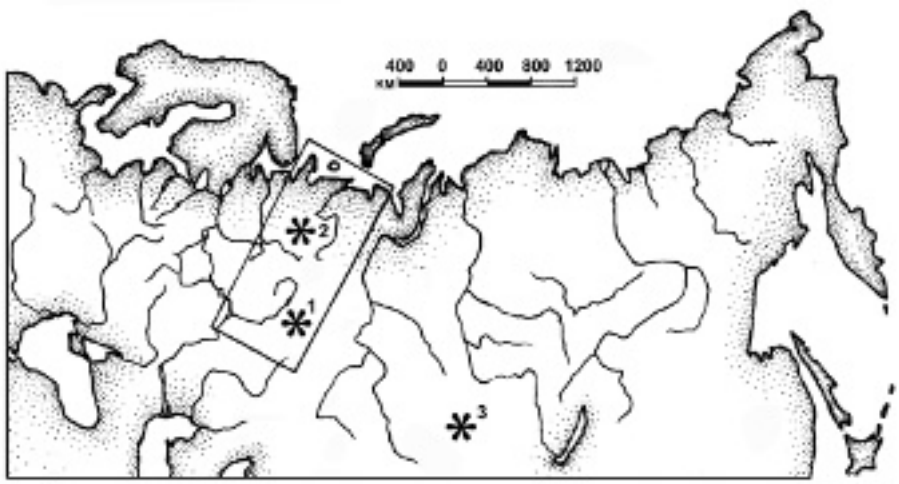

Figure 1. Geographical position of the main localities cited in the text. 1 – the Middle Cis-Urals (localities: Molebka, Krutaya Katushka-1, Krutaya Katushka-2, Krasnaya Glinka, Matveevo, Taezhnoe-1, Taezhnoe-2, Chekarda-1, Yulaevo, Mazuevka. Rakhmangulovo); 2 – Pechora Cis-Urals and Pechora Coal Basin; 3 – Kuznetsk basin.

University, the City of Ekaterinburg; UGM) were studied as well. An important collection of the callipterid leaves assigned to *Permocallipteris retensoria* (Zalessky) Naug., comb. nov., and *P. artipinnata* (Zalessky) Naug., comb. nov., from the Mazuevka locality was provided for the present study by L. A. Dolgikh from the Kungur Historical-Architecture and Art Museum (KKM), Perm region.

Brief historical overview

A detailed study of research history of callipterid leaves from Permian of Western Angaraland has recently been published (Naugolnykh & Pukhonto 2012).

The first image of the fossil leaf of callipterid morphology from the Permian deposits of the Urals, Russia, was published by Kutorga (1838: Taf. VII, Fig. 4) under the name *Pachypteris latinervia* Kutorga. Exact taxonomical assessment of this leaf remains unclear, because details of venation are not visible on this specimen.

Second publication focused on fossil plants from the Carboniferous and Permian deposits of Russia (Kutorga 1842) includes descriptions of three species, previously reported by G. I. Fischer von Waldheim without images (Fischer von Waldheim 1840). Kutorga (1842) redescribed these species, which initially were attributed to the genus *Neuropteris* Brongniart, and published well-made pictures illustrating their morphology: *Neuropteris wangenheimii* Fischer (Kutorga 1842: Taf. I, Fig. 1), *Neuropteris salicifolia* Fischer (Kutorga 1842: Taf. I, Fig. 2), *Neuropteris rotundifolia* Brongniart (Kutorga 1842: Taf. I, Fig. 3).

Neuropteris wangenheimii Fischer and *N. rotundifolia* Brongniart, figured by Kutorga (1842) could be attributed to the genus *Permocallipteris* Naug., gen. nov. The species *N. salicifolia* Fischer has already been transferred to the genus *Compsopteris* Zalessky (Naugolnykh 1999).

In his third paper Kutorga (1844) described several new species of callipterids from the Permian deposits of the Urals (formal and now incorrect generic attribution is given following original Kutorga's determination): *Adiantites strogonowii* Fischer (Kutorga 1844: Taf. VIII), *Neuropteris*

wangenheimii Fischer (Kutorga 1844: Taf. VII, Fig. 1; holotype), *Pecopteris regalis* Kutorga (Kutorga 1844: Taf. III; Taf. IV, Figs 1–2), *Pecopteris principalis* Kutorga (Kutorga 1844: Taf. V, Figs 1–2), *Pecopteris neuropteroides* Kutorga (Kutorga 1844: Taf. IV, Fig. 3), *Odontopteris serrata* Kutorga (Kutorga 1844: Taf. VI, Figs 1a, b), *Odontopteris crenulata* Kutorga (Kutorga 1844: Taf. VI, Fig. 2), *Neuropteris dufresnoyi* Brongniart (Kutorga 1844: Taf. VI, Fig. 3).

The names *Adiantites strogonowii* Fischer, *Pecopteris neuropteroides* Kutorga, *P. regalis* Kutorga, *P. principalis* Kutorga, *Odontopteris serrata* Kutorga (in part.), together with a number of other related forms are assigned as synonyms of *Permocallipteris wangenheimii* (Fischer) Naug. in this paper (see below).

The names *Odontopteris crenulata* Kutorga and *O. serrata* Kutorga (in part.) were assigned as synonyms of *Compsopteris salicifolius* (Fischer) Naug. (Naugolnykh 2001: 12, 14).

In subsequent years many species of callipterids from the Permian deposits of Angaraland were described by the outstanding Russian palaeobotanist M. D. Zalessky (Zalessky 1918, 1927, 1929, 1934, 1937, 1939). Unfortunately, he didn't pay special attention to the questions of intraspecific variability of the callipterid leaves. As a result, some of the species established by Zalessky now can be regarded as junior synonyms.

Meyen & Migdisova (1969) published a synthesis of morphology and epidermal anatomy of some Angaran callipterids, mostly based on material from the Permian deposits of the Pechora Coal Basin. They established a new subgenus *Feonia* Meyen & Migdisova, but the incorrect notification of discriminative characters of this subgenus doesn't allow to accept this subgenus as valid.

The present author published several personal and cooperative works on Permian callipterids and their evolutionary derivates from the Urals and neighboring regions (Naugolnykh 1991, 1992; Naugolnykh & Kerp 1996; Naugolnykh & Oskolski 2010). The present paper is a continuation of previously published results and a proposal of the new genus *Permocallipteris* Naugolnykh, gen. nov. for callipterid foliages from the Permian of Angaraland.

Systematics and description

Class **Peltaspermopsida Cronquist, 1981**

Order **Peltaspermales Taylor, 1981**

Family **Peltaspermaceae Thomas, 1933**

***Permocallipteris* Naugolnykh, gen. nov.**

Etymology. From the city Perm (Russia), the Permian System and *Callipteris*, the generic name.

Type species. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov., Middle Permian, Kazanian, Pechora Cis-Urals and Pechora Coal Basin, Russia.

Generic diagnosis. Compound bipinnate to tripinnate, occasionally tetrapinnate leaves, with well-developed pecopteroid pinnules, with round to almost acute apices, distinct midvein, numerous lateral veins. Pinnules decurrent, veins come into decurrent part directly from pinna rachis. There are additional (intercalated) pinnules directly attached to frond rachis between bases of last order pinnae. Basal part of frond is naked. Frond apex is dichotomizing (overtopped).

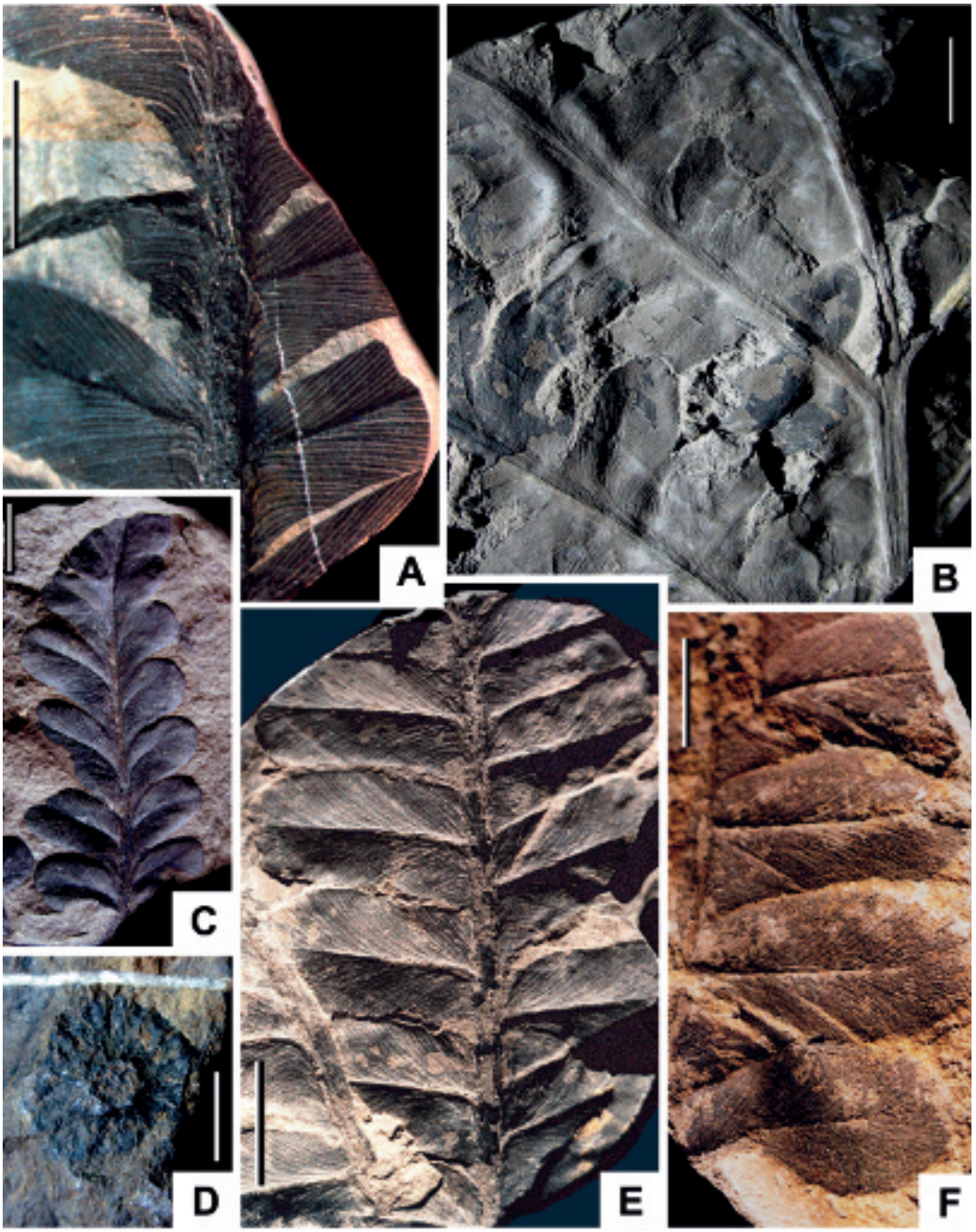

Figure 2. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov. General morphology of the leaves. A – middle part of the last order pinna, spec. 4851/239; B – middle part of the well-developed adult frond, which was macerated (see here Figs 5 and 6 for cuticle details), spec. 4851/219; C – apical part of the last order pinna, spec. 4851/243; D – isolated seed-bearing disc found in close association with the callipterid foliages of *P. adzvensis*, spec. 3005/10; E – last order pinna with relatively long, well-developed pinnules (see Fig. 5 for details of venation), spec. 5851/242; F – four relatively short pinnules with dense venation, spec. 3718/52.

Localities: the Pechora Cis-Urals and Pechora Coal Basin; A – Loc. 708-391; B – NSK-210, depth 158 m; C – NSK-218, depth 156.2 m; D – Pai-Khoi, Yangarei River, coll. N. V. Shmelev; E – NSK-218, depth 156.2 m; F – Pechora River, outcrop of T. A. Dobrolyubova 17(1). Scale bars = 1 cm.

Comparison. The new genus is different from the closest form-genus *Rhachiphyllum* Kerp (Kerp 1988) in considerably larger entire-margined pinnules, presumably more pecopteroid than alethopteroid pinnules, pseudodichotomizing (overtopped) frond apex, which is typical of *Permocallipteris*. Another close genus *Compsopteris* Zalessky is different from *Permocallipteris* in having monopinnate frond architecture and long lanceolated pinnules, alethopteroid in the middle and apical parts of the frond and with constricted bases in the basal part of the frond.

Composition. Formal introducing of new combinations see in descriptive part of this work. *Permocallipteris acutifolia* (Radczenko) Naug., *P. altaica* (Zalessky ex Neuburg) Naug., *P. adzvensis* (Zalessky) Naug. (type species), *P. artipinnata* (Zalessky) Naug., *P. bexellii* (Durante) Naug., *P. vancevia* (Gorelova) Naug., *P. lobata* (Gorelova & Drjagina) Naug., *P. mongoliense* (Neuburg) Naug., *P. orientalis* (Zalessky) Naug., *P. retensoria* (Zalessky) Naug., *P. sahnii* (Zalessky) Naug., *P. wangenheimii* (Fischer) Naug., *P. zeillerii* (Zalessky) Naug.

Distribution. Permian of the Angaraland and adjacent areas.

Permocallipteris adzvensis (Zalessky) Naug., comb. nov. (Figs 2 A–C, E–F; 3 A–D; 4; 5 A–E; 6 A–E)

Basionym. *Callipteris adzvensis* Zalessky (Zalessky 1927: 34, 51; Plate XL, Fig. 1).

Selected synonymy.

Callipteris adzvensis Zalessky (Zalessky 1927: 34, 51; Plate XL, Fig. 1; Zalessky 1934: 256–259, Figs 24–30; Zalessky & Tschirkova 1938: 36–37, Fig. 51; Gorelova & Radczenko 1962: 102–103, Plate XIV, Figs 8a, b; Pukhonto & Fefilova 1983: 50, Plate X; Naugolnykh & Oskolski 2010: 31, Fig. 1 D, F).

Callipteris adzvensis Zalessky f. *adzvensis* (Fefilova 1973: 109–111, Plate XXX, Figs 1–4).

Callipteris adzvensis Zalessky f. *micropinnata* Fefilova (Fefilova 1973: 111–113, Plate XXXI, Figs 1–2).

Callipteris septentrionalis Zalessky (Zalessky 1934: 262, Fig. 36; Pukhonto & Fefilova 1983: 50–51, Plate XII, Fig. 2).

Callipteris ? (*Feonia*) *lepidopteroides* S. V. Meyen (Meyen & Migdisova 1969: 65–67, Plate I, Figs 1–5; Text-Fig. 1a, b).

Callipteris ? (Feonia) aequabilis S. V. Meyen (Meyen & Migdisova 1969: 67–69, Plate II, Figs 1–6, Plate III, Figs 1–5; Text-Fig. 2).

Callipteris ? (*Feonia*) *sadovnikovii* S. V. Meyen (Meyen & Migdisova 1969: 69–70, Plate III, Figs 6–7, Plate IV, Figs 1–7; Text-Fig. 1a, b).

Holotype. Zalessky 1927: Plate XL, Fig. 1.

Diagnosis. Fronds large, up to 60–70 cm long, tripinnate, well-developed adult fronds can be tetrapinnate. Frond rachis robust, slightly thickening towards its base, longitudinally striated. There are intercalating additional pinnules directly attached to the frond rachis between bases of lateral last order pinnae. Last order pinnae are long, straight or slightly curved, up to 20 cm long and 6 cm wide. Pinnules attached to the last order pinna rachis under an angle 40–90°. Pinnules are lanceolate, pecopteroid, entire-margined, with parallel lateral margins and round apex. Midvein of pinnule is well-pronounced, rarely reduced, but normally reaches ¾ of pinnule

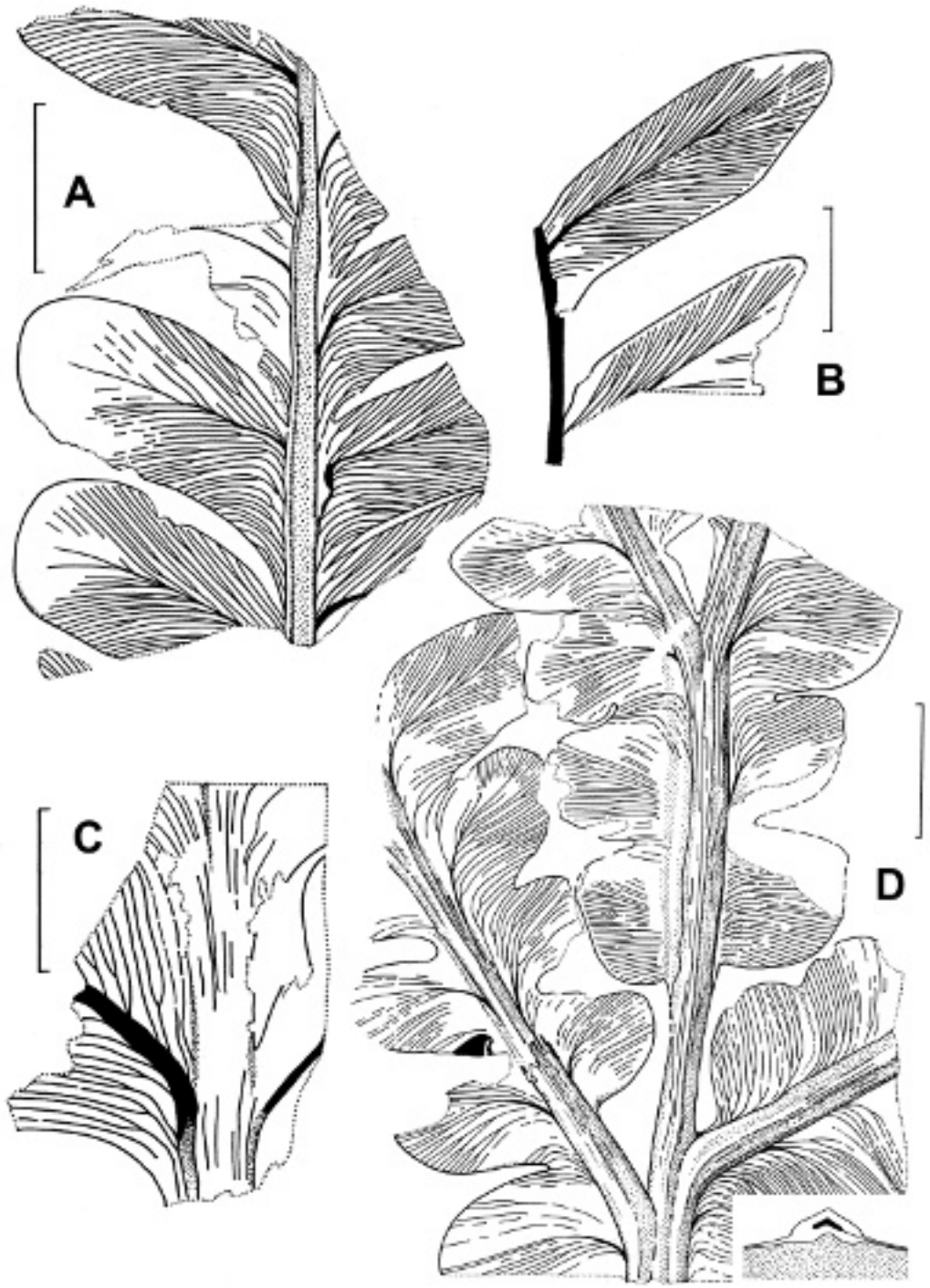

Figure 3. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov. Line tracings of general morphology of the leaves and details of their venation. A – middle part of the last order pinna, spec. 4851/239; B – part of pinna with relatively long lanceolate pinnules having slightly restricted bases, spec. 4851/241; C – details of venation in the basal part of the pinnule, spec. 4851/245; D – part of the large well-developed frond with pseudodichotomizing (overtopped) apex and intercalated pinnules, which are directly attached to the frond rachis and lack the clear midvein, spec. 4851/219.

Localities: the Pechora Cis-Urals and Pechora Coal Basin; A – Loc. 708-391; B – Loc. 42K-159; C – Adzva River; D – NSK-210, depth 158.0 m. Scale bars = 1 cm.

length. Lateral veins are once or twice dichotomizing. Leaves are amphystomatic. Functionally lower (abaxial) cuticle is slightly thinner and possesses more numerous stomata than adaxial cuticle.

Comparison. The most characteristic features of this species are its relatively large pinnules and fronds, which are bigger than the pinnules of the most closely related (probably, ancestral) species *Permocallipteris retensoria* (Zalessky) Naug., comb. nov., in average more than two times.

Remarks. The material in hands doesn't allow to distinguish forms as published by Fefilova (1973). The two main morphological modifications of *Permocallipteris adzvensis* (1) relatively

Figure 4. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov. Line tracing of the overtopped apical part of a frond with two neighboring last order pinnae, spec. 4851/242.

Localities: the Pechora Cis-Urals and Pechora Coal Basin; NSK-218, depth 156.2 m. Scale bar = 1 cm.

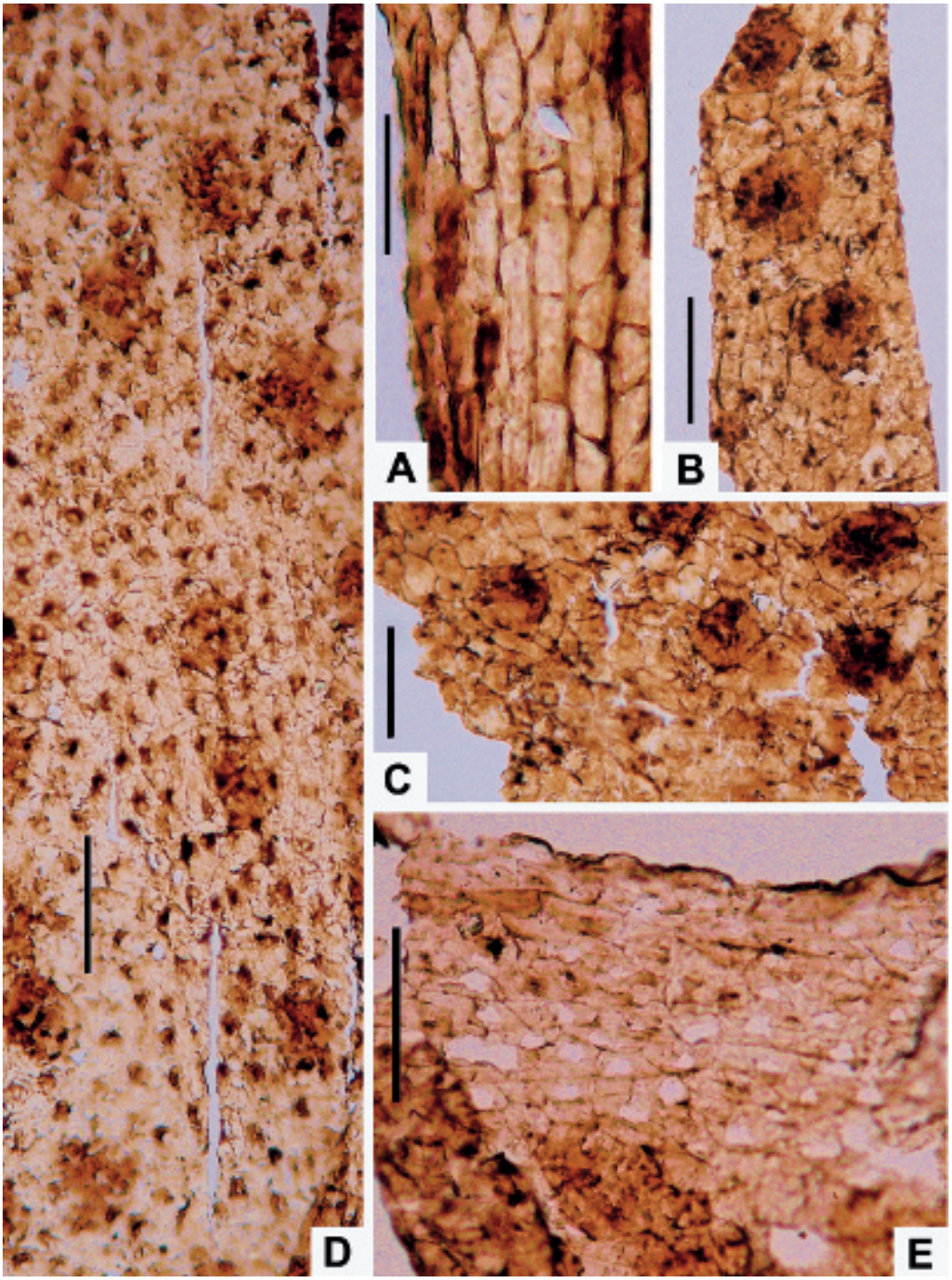

Figure 5. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov. Epidermal-cuticular structure, spec. 4851/219. A–C – cuticles of functionally upper (adaxial) side of the leaf: A – costal field with rectangular epidermal cells; B, C – intercostal fields with the stomata, which are arranged in unclear rows; D, E – cuticles of functionally lower (abaxial) side of the leaf; D – strongly papillate cuticle with the irregularly arranged stomata; E – part of the cuticle with detached papillae, which left round and ovoid perforations in the cuticle.

Localities: the Pechora Cis-Urals and Pechora Coal Basin; NSK-210, depth 158.0 m. Scale bars = 50 µm.

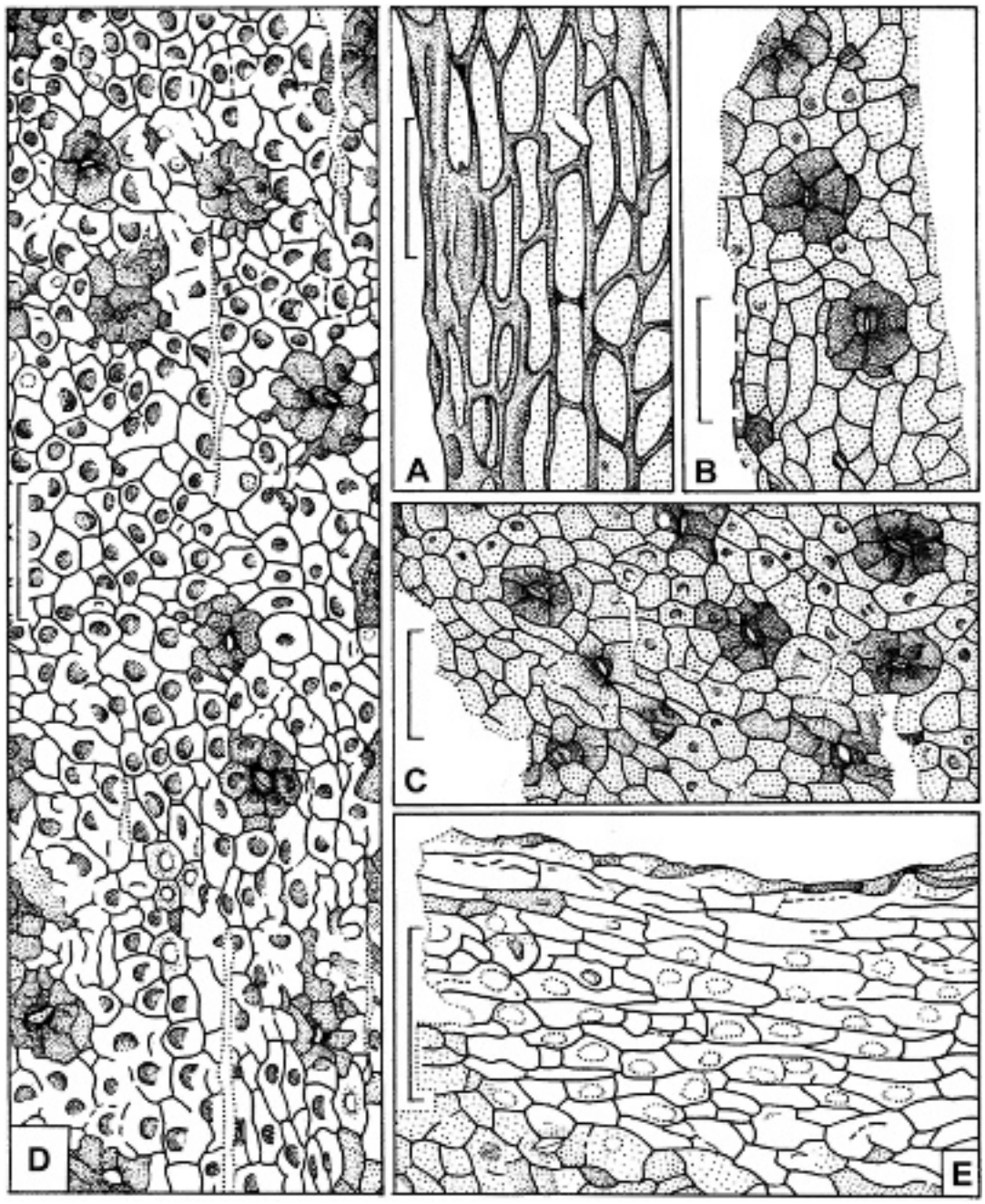

Figure 6. *Permocallipteris adzvensis* (Zalessky) Naug., comb. nov. Line tracing of the cuticles shown in Fig. 5, spec. 4851/219.

Localities: the Pechora Cis-Urals and Pechora Coal Basin. Scale bars = 50 µm.

short pinnules with round apices and (2) long and round to almost acute apices (see Fefilova 1973) were formed most probably by influence or effect of climatic factors, mostly season wetness and shadow or sun position of the pinnae.

Distribution. Middle Permian (Wordian; Kazanian and Urzhumian according to regional stratigraphic scale) deposits of the Pechora Cis-Urals and adjacent regions of Russia.

Permocallipteris retensoria (Zalessky) Naug., comb. nov. (Fig. 7 A–G)

Basionym. *Callipteris retensoria* Zalessky (Zalessky 1939: 342, Fig. 16).

Selected synonymy.

Callipteris retensoria Zalessky (Zalessky 1939: 342, Fig. 16).

Rhachiphyllum retensorium (Zalessky) Naug. (Naugolnykh 1991: 45–48, Fig. 3; 1992: 31–36, Figs 11–13).

Peltaspermum retensorium (Zalessky) Naug. & Kerp (Naugolnykh & Kerp 1996, in part.: 41–59, Plate I, 1–10; II, 1, 4; III, 1–9; IV, 1–8; V, 1–11; VI, 1–3; Figs 3–5, 6 A–C; Naugolnykh 1998, in part.: 90–97, Plates XI, 2–5, XII, 1, 4–6; XIII, XIV, XVI, 2; Text-Figs 47, 48 B, 49 A–C, 50–53 C–D; Naugolnykh 2007: Plates XVIII, Fig. 1; XIX, Fig. 1–2, 4; XXV, 4; Text-Fig. 57).

Holotype. Zalessky 1939: 342, Fig. 16.

Diagnosis. Fronds of middle size, about 30 cm long in average, sometimes slightly larger. Adult fronds bipinnate to tripinnate. Young juvenile fronds can be monopinnate; order of leaf dissection increases in process of ontogenetic development of the frond. Herontic or senile fronds in rare cases can be tetrapinnate. Frond apex is once or twice pseudodichotomizing (overtopping). Frond rachis of young fronds has a limb (wings); frond rachis of well-developed adult fronds has intercalated pinnules of subtriangular to lanceolate shape, disposed between bases of lateral pinnae. Lateral pinnae are straight, attached to the frond rachis in alternate order. Pinnules attached to the pinna rachis under an obtuse (wide) angle up to 90°. Pinnules, which are attached to the acroscopic (anadromic) side of lateral pinna, are almost always shorter. Pinnules are pecopteroid, relatively wide, up to 2 cm long and 1 cm wide, sometimes slightly bigger in the apical part of the frond. Pinnule lateral margins are subparallel, pinnule apex is round. Basal parts of the pinnules are coalescently fused. Pinnules of basal pinnae can be completely fused forming comiopteroid coherent venation. Midvein is always well-developed, reaches ¾ of pinnule length or even can come up to the pinnule apex. Lateral veins strong, from simple to twice dichotomizing. Leaves are amphystomatic, but most of the stomata are disposed on functionally lower (abaxial) leaf surface. Abaxial (lower) cuticle is thinner, strongly papillate, with numerous stomata. Stomata monocyclic, sunken, with strongly cutinized subsidiary cells having proximal papillae. Adaxial (upper) cuticle is thicker, with wide and strongly cutinized cell walls. There are numerous round to elliptical resin bodies located inside the mesophyllous tissue of the leaf.

Comparison. This species differs from similar *P. adzvensis* and *P. wangenheimii* in a considerably smaller leaf size and less dense venation; *P. retensoria* differs from *P. artipinnata* in a larger frond size, round pinnule apex and more obtuse (wider) angle of pinnule attachment.

Remarks. Seed-bearing discs associatively linked with the leaves *P. retensoria* had initially been reported by the present author as *Peltaspermum*-like fructifications *Lopadiangium* sp. (Naugolnykh 1991), but later it became clear that this material should be taxonomically reconsidered.

Distribution. Artinskian and Kungurian deposits of the Middle and South Urals. Typical localities of this species are: Molebka, Krutaya Katushka-1, Krutaya Katushka-2, Krasnaya Glinka, Matveevo, Taezhnoe-1, Taezhnoe-2, Chekarda-1, Yulaevo, Mazuevka (Naugolnykh 1998, 2007, etc.).

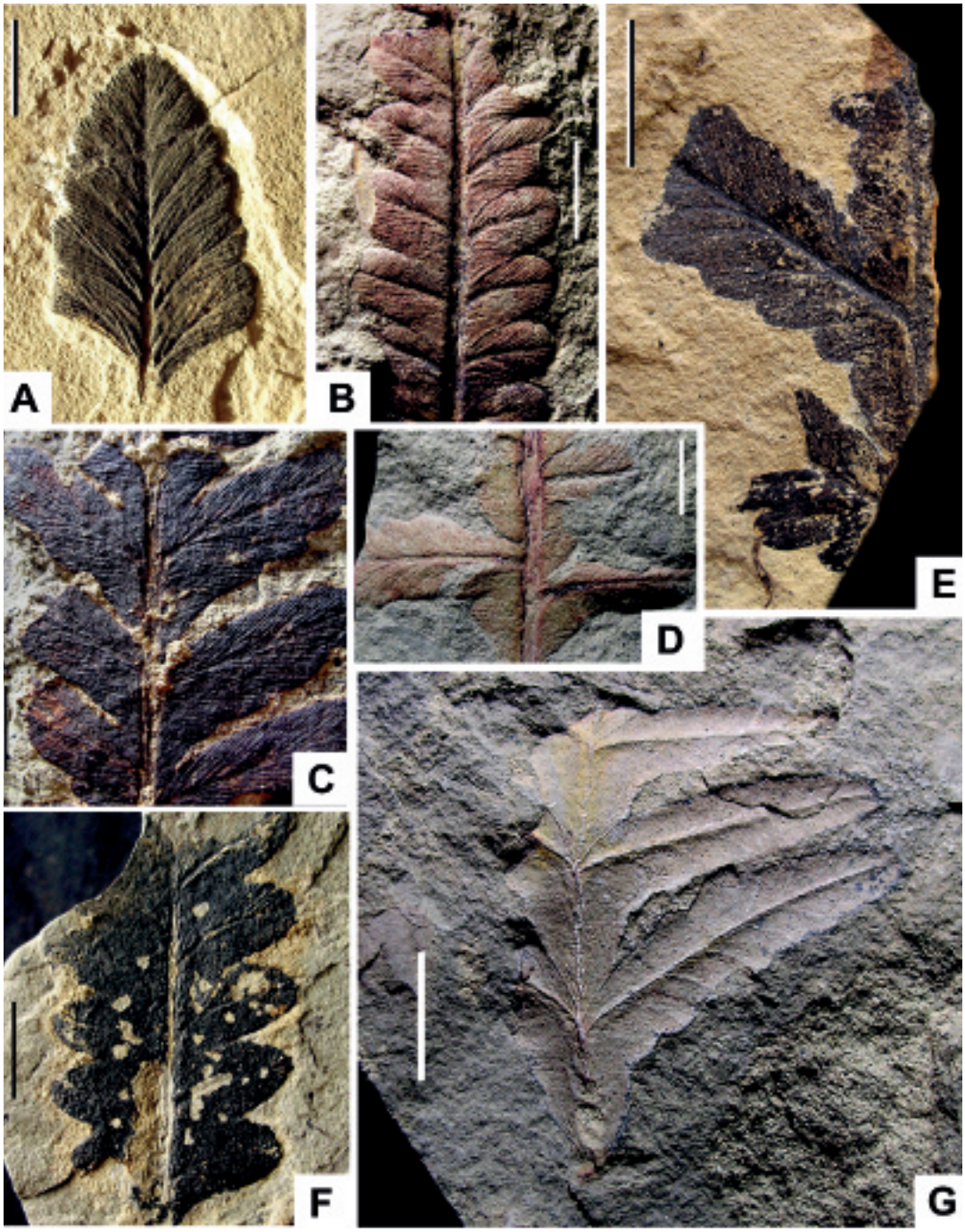

Figure 7. *Permocallipteris retensoria* (Zalessky) Naug., comb. nov. General morphology of the leaves. A – apical part of the last order pinna with the pinnules coalescently (coherently) connected by their lateral margins, spec. 3773(11)/351(93); B – middle part of the well-developed last order pinna, spec. KKM IK 9642/5; C – last order pinna of the well-developed adult frond, spec. KKM IK 9461/10; D – very young frond with winged rachis, spec. KKM IK 9462/1; E – middle part of fragmentary preserved, well-developed frond with the intercalated pinnules resembling normal (common) pinnules, spec. 3737/96; F – last order pinna with relatively short pinnules, spec. 4856/311; G – middle part of the young frond with juvenile last order pinnae having undeveloped pinnules with coalescently (coherently) fused lateral marging, spec. KKM IK 9576/11.

Localities: Chekarda-1 (A, E, F); Mazuevka (B–D, G). Scale bars = 1 cm.

Permocallipteris artipinnata (Zalessky) Naug., comb. nov. (Fig. 8 A–G)

Basionym. *Odontopteris artipinnata* Zalessky (Zalessky 1937: 56, Fig. 21).

Selected synonymy.

Odontopteris artipinnata Zalessky (Zalessky 1937: 56, Fig. 21).

Dicranopteris regia Zalessky (Zalessky 1937: 48–51, Figs 13–15).

Rhachiphyllum artipinnatum (Zalessky) Naug. (Naugolnykh 1998: 97–99, Figs 56, 57 C, 58; Naugolnykh 2002: Plate V, Figs 1–4; Naugolnykh 2007: Plate XIX, Figs 6, 8; XXII, Figs 1–6; Plate XXIII, Figs 1–6; Plate XXIV, Figs 1–5; Plate XXVIII, Fig. 5; Text-Figs 55, 56).

Holotype. Zalessky 1937: 56, Fig. 21.

Diagnosis. Fronds relatively small, about 20 cm long in average, from bipinnate to tripinnate. Frond rachis is well-developed, longitudinally striated, basally widened. Basal part of the frond is naked. Last order pinnae attached to the frond rachis in alternate to almost opposite order. Pinna rachis is slender, slightly curved toward the frond apex. Pinnules are lanceolate, prolonged, attached to the pinna rachis under an acute angle 45–55°. Pinnule base narrow, almost sphenopteroid in the middle and basal parts of the frond. Pinnule apex is acute. Venation is fun-shaped or rarely pinnate. Midvein is unclear or very short, strongly decurrent. Lateral veins run from the midvein under very acute angle, if the midvein is present. Intercalated pinnules attached to the frond rachis between bases of last order pinnae. The intercalated pinnules are identical to normal ones or can be slightly shorter.

Comparison. See above *P. retensoria.*

Distribution. Artinskian and Kungurian deposits of the Middle and South Urals. Most typical localities of this species: Molebka, Krutaya Katushka-1, Krutaya Katushka-2, Krasnaya Glinka, Matveevo, Taezhnoe-1, Taezhnoe-2, Chekarda-1, Yulaevo, Mazuevka.

Permocallipteris wangenheimii (Fischer) Naug., comb. nov. (Fig. 9 A–G)

Basionym. *Neuropteris wangenheimii* Fischer (Fischer von Waldheim 1840: 239).

Selected synonymy.

Neuropteris wangenheimii Fischer (Fischer von Waldheim 1840: 239; Kutorga 1842: 4, Plate I, Fig. 1; 1844: 79–80, Plate VII, Fig. 1).

Rhachiphyllum wangenheimii (Fischer) Naug. (Naugolnykh 1999: 86–87, Text-Fig. 4 d, e; Text-Fig. 5 a, b; Naugolnykh 2001: 10, 12, Plate I, Figs 1–4; Plate III, Fig. 1; Text-Fig. 4 B, E–G; Naugolnykh 2002: 10–18, Plate I, Figs 1–2, 4; Plate II, Figs 1–6; Plate III, Figs 1–6; Plate IV, Figs 1–2, 4; Plate VI, Fig. 3; Plate VII, Fig. 5; Text-Figs 4–5, 6 B, 14; Naugolnykh 2007: Plate LXIX, Figs 2–4, 6, 7; Plate LXX, Figs 1–6; Plate LXXI, Figs 1–6; Color Plate VI, 2; Color Plate VIII, Figs 1, 3–5).

For expanded synonymy see Naugolnykh (2001: 10).

Neotype. Kutorga 1844: Plate VII, Fig. 1; Wordian (Kazanian), the Santagulovsky copper mine, near Melchak Rivulet, Belebei area, Southern Urals.

Diagnosis. Fronds large, about 40 cm long, from bipinnate to tripinnate, with pseudodichotomizing apex. Frond rachis is well-developed, robust, covered by small scales of semi-lunar shape. There are

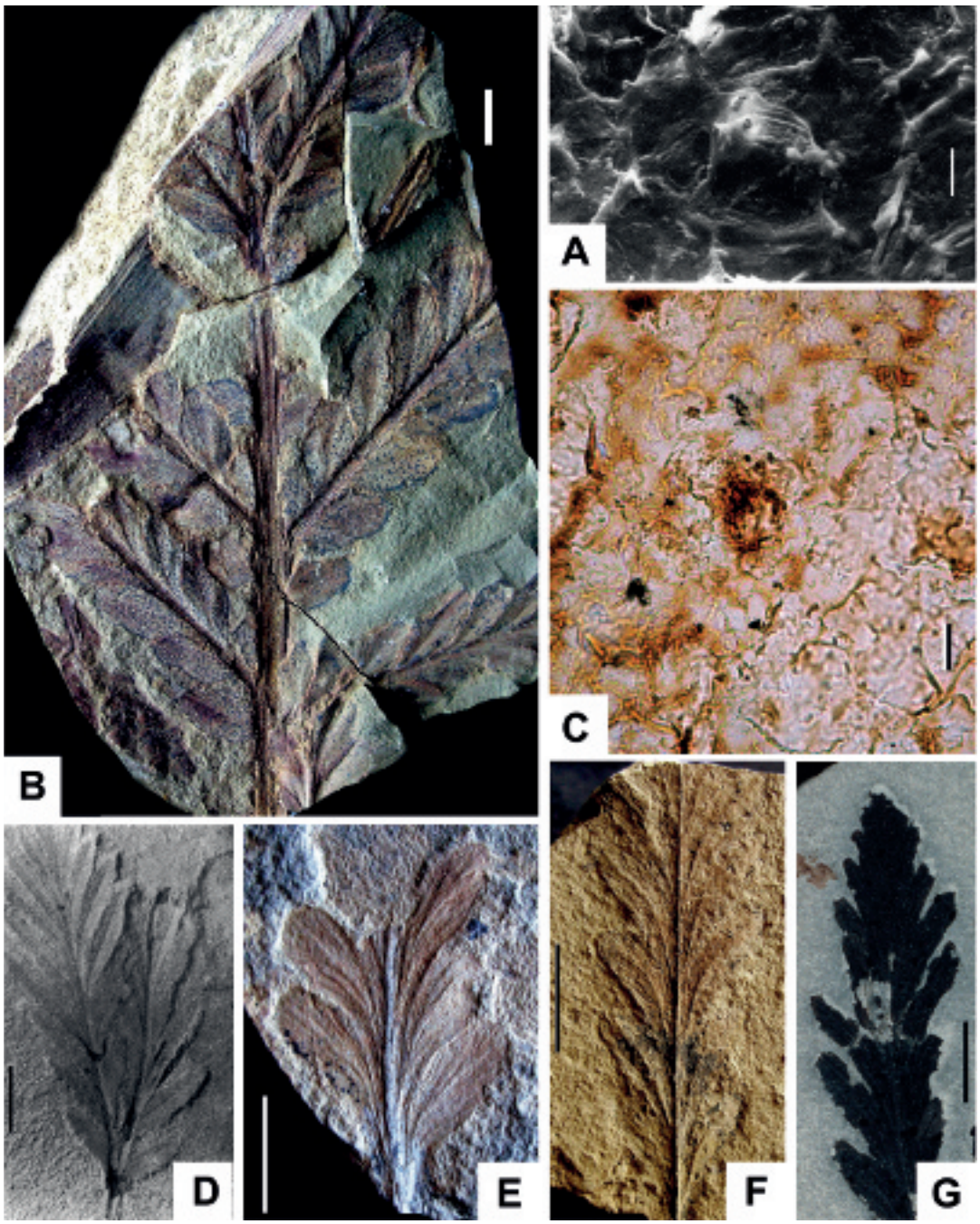

Figure 8. *Permocallipteris artipinnata* (Zalessky) Naug., comb. nov. Epidermal-cuticular structure (A, C) and general morphology of the leaves (B, D–G). A – the stoma with the well-visible lips-like guard cells, SEM, spec. 3773/368; B – middle part of the semi-adult frond with the intercalated pinnules, spec. UGM 2286; C – stoma with strongly cutinized guard cells, in light microscope, spec. 3773/368; D – apical part of the frond with pseudodichotomizing (overtopping) apex; spec. 3773/368, this specimen was macerated and used as a source of the cuticles shown here on Fig. 8 A, C, and other cuticular preparations figured and published in previous work (Naugolnykh 2007: Plates XXII–XXIV); E – middle part of the last order pinna with five completely preserved strongly decurrent pinnules, spec. 4856/508; F – almost completely preserved last order pinna, but without apex, spec. 4856/500; G – apical part of the last order pinna, spec. 3773(11)/328(92).

Localities: Chekarda-1, layer 10 (A–C, D–G); Rakhmangulovo (B). Scale bars = 1 cm (B, D–G); 10 µm (A, C).

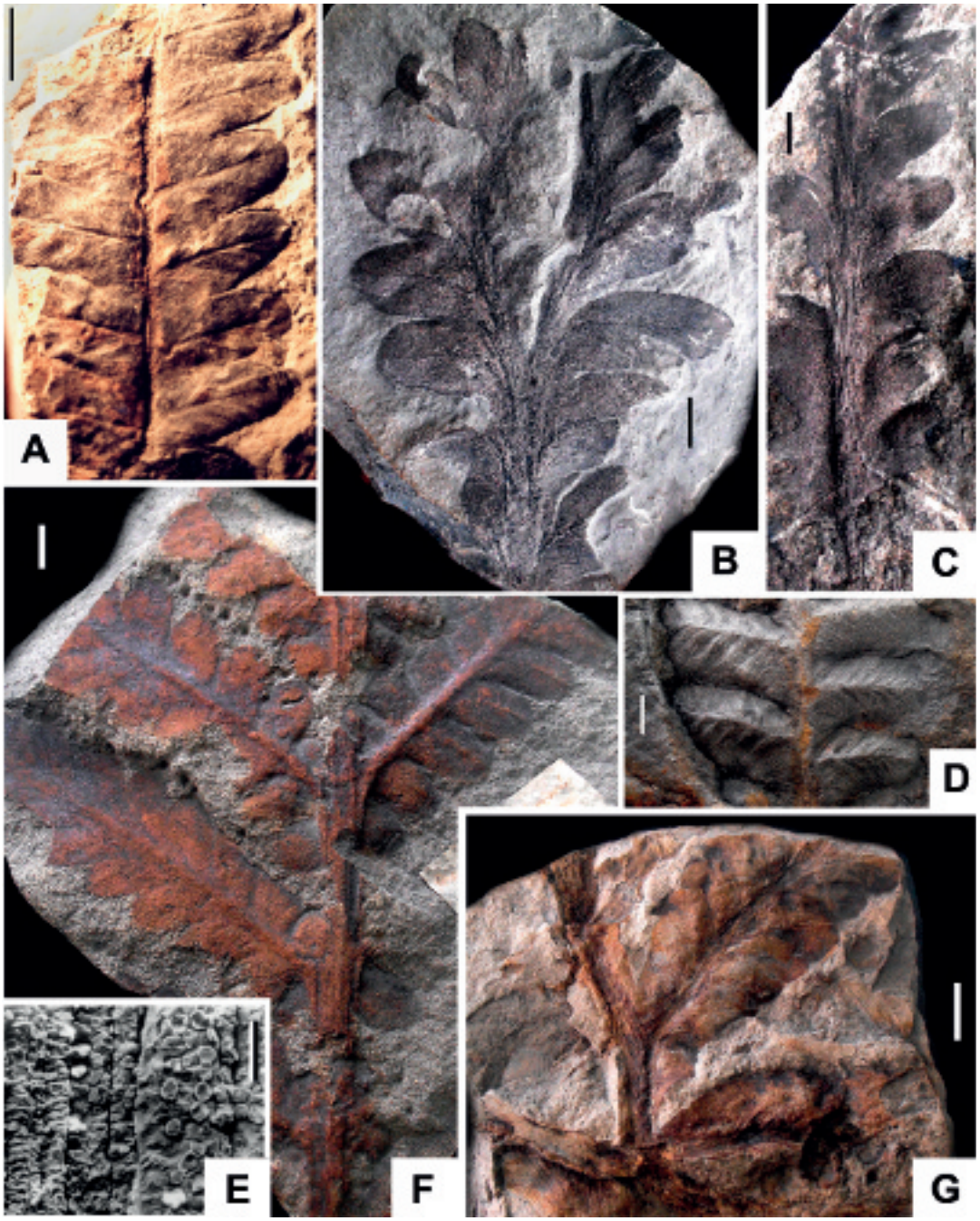

Figure 9. *Permocallipteris wangenheimii* (Fischer) Naug., comb. nov. A – the last order pinna, spec. GGM 469-1 FL-02589; B – the fork-shaped overtopped apex; same specimen was figured as *Odontopteris tatarica* Zalessky (Zalessky 1927: Plate XXXVII, Fig. 3, spec. TsNIGR 56/1543); C – the last order pinna, spec. TsNIGR 54/1543; counterpart of the same specimen – TsNIGR 55/1543; this specimen was figured as *Odontopteris tatarica* Zalessky (Zalessky 1927: Plate XXXVIII, Fig. 1); D – the young frond with unicoherent venation; same specimen was figured as *Callipteris uralensis* Zalessky (Zalessky 1927: Plate V, Fig. 1); spec. TsNIGR 10/1543; E – anatomy (tracheids) of the frond rachis, spec. GGM 469-30 FL-026118 (for details see: Naugolnykh 2002: Text-Fig. 5 A–D; Plates II–III); F – middle part of the well-developed frond, spec. TsNIGR 7/1543 (same specimen was figured by Kutorga 1844: Plate V, Fig. 1, as *Pecopteris principalis* Kutorga); G – lower part of the adult frond with unicoherent pinna, spec. TsNIGR 14/1543; same specimen was figured in Zalessky 1927: Plate VI, Fig. 4).

intercalated pinnules disposed on the frond rachis between bases of last order pinnae. Sometimes intercalated pinnules could be completely fused at their margins and form a limb-like structure (wing). Pinnules are lanceolate, large, pecopteroid, strongly decurrent; attached to the frond rachis under an angle 40–85°. Common pinnules are similar to intercalated pinnules, but larger. Pinnule apex is round. Developed pinnules have a strong, well-pronounced midvein, often going to the pinnule apex. Juvenile pinnules have less pronounced midvein, seen only at the pinnule's basal part. Venation pinnate. Some morphs of this species can have fun-shaped venation. Lateral veins are dichotomizing up to two or three times.

Conducting tissues of the frond rachis consist of primary and secondary xylem. Xylem includes tracheids of two types: (1) tracheids of metaxylem with ring-like and spiral thickenings; these tracheids are disposed closer to axial part of the rachis; (2) tracheids of secondary xylem with round pore-pairs located in one or two rows (numbers); tracheids of second type are disposed closer to peripheric part of the frond rachis.

Remarks. Presence of the secondary xylem in the frond rachis shows that the fronds of Angaran callipterids had cladoid origin (Naugolnykh 2009). High morphological variability of the leaves of *Permocallipteris wangenheimii* leads to a different extent of the development of the intercalated pinnules, which can be well-developed in the middle and upper parts of the frond, or considerably reduced in the basal part of the frond (see, for instance, Kutorga 1844: Plate V, Fig. 1). Weak development of the rachis wing, which was noted by the present author earlier (Naugolnykh 2002: 18), is only typical of basal parts of herontic or senile fronds of that species.

Comparison. The species *P. wangenheimii* differs from *P. adzvensis* in large and wider pinnules, and less dense venation. Comparison with similar but phylogenetically older species *P. retensoria* is given above in characteristics of *P. retensoria.*

Distribution. Middle Permian (Upper Roadian, Wordian, Lower Capitanian; or Kazanian and Urzhumian according to the regional stratigraphic scale) deposits of the Middle and Southern Urals.

Permocallipteris zeillerii (Zalessky) Naug., comb. nov. (Fig. 10 A–H)

Basionym. *Callipteris zeilleri* Zalessky ex Neuburg (Neuburg 1948: 122, Plate XXIV, Fig. 1).

Selected synonymy.

Callipteris zeilleri Zalessky (Zalessky 1918: Plate XLIV–XLVI, XLVII, Figs 1–2; Plate XLVIII, Fig. 2; Neuburg 1948: Plate XXIV, Fig. 1; Plate XXV, Figs 1–4, 6; Radczenko 1955: 127–128, Text-Figs 155–156).

Lectotype. Zalessky 1918: Plate XLIV, Fig. 1; selected by Neuburg 1948: 122, Plate XXIV, Fig. 1, spec. TsNIGR 72/573, figured here on Fig. 10 A.

Diagnosis. Fronds very large, up to 60 cm long, bipinnate to tripinnate. Frond rachis is well-developed, thick, robust, longitudinally striated. Pinnae long, narrow. There are intercalated pinnules attached to the frond rachis and disposed between bases of last order pinnae. Intercalated

◀ Localities: Orenburg region, Belebei district, Dioma River basin, Melchak rivulet, the Santagulovo Mine (A, D, F, G); Viatka (Kirov) region, Elabuga district, Bezjakinsky rivulet (B, C); Orenburg region, Belebei district, Karma River, the City of Nizhne-Troitsk, Nizhnetroitsky Mine (E). Scale bars = 1 cm (A–D, F, G); 30 μm (E).

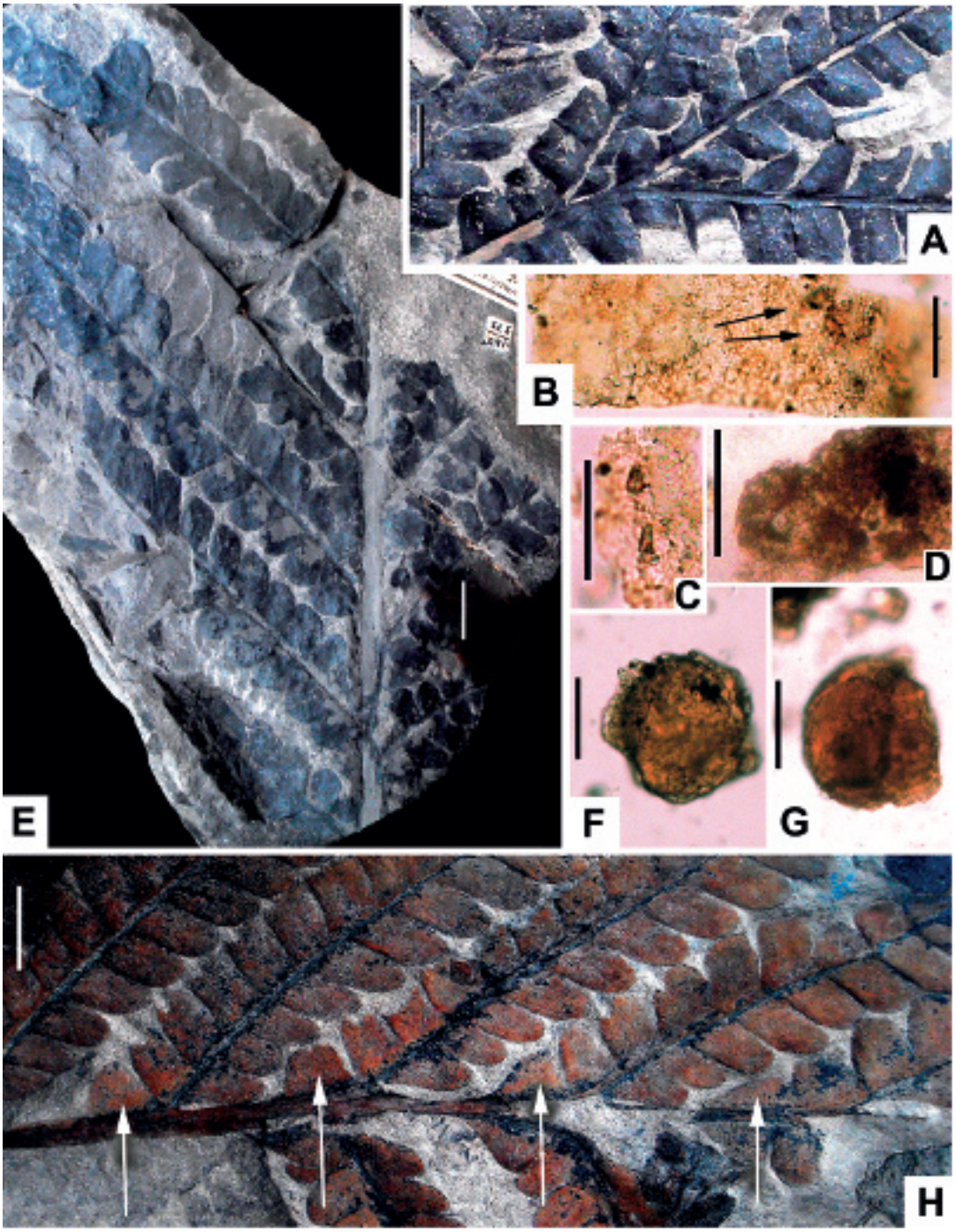

Figure 10. *Permocallipteris zeillerii* (Zalessky) Naug., comb. nov. A – apical part of the well-developed frond, lectotype, spec. TsNIGR 72/573 (figured in Zalessky 1918: Plate XLV, Fig. 2); B–D, F, G – cuticular structure, spec. TsNIGR 180/573; B – two neighboring resin bodies (marked by arrows); C – two unicellular hairs of conic shape; F, G – the resin bodies of round (F) and ovoid (G) shape; D – two neighboring stomata with thick proximal cutinization of the subsidiary cells; E – the specimen macerated (the cuticle preparations are shown here Fig. 10 B–D, F, G, TsNIGR 180/573); H – adult frond with well-developed intercalated pinnules (marked by arrows), spec. 73/572 (same specimen was figured in Zalessky 1918: Plate XLV, Fig. 1).

Localities: Kuznetsk basin, Kolchugino, Kolchuginskaya Mine (A–H). Scale bars = 1 cm (A, E, H); 50 µm (B–D, F, G).

pinnules are similar or almost identical to common ones, sometimes slightly shorter. Pinnules are pecopteroid, entire-margined, lanceolate, with rounded to acute apices. Pinnule midvein is short, weakly developed. Lateral veins come from the midvein under an acute angle. There are round resin bodies in the mesophyllous tissues of the leaf. Stomata practically unsunken, monocyclic, with proximal cutinization of the guard cells.

Comparison. This species differs from other species of Angaran callipterids in longer and narrower pinnae, smaller pinnules and weak-developed or almost completely reduced midvein.

Distribution. Middle Permian (Roadian to Guadalupian) deposits of Central Angaraland, Mongolia and Northern China.

Other new combinations

Permocallipteris acutifolia (Radczenko) Naug., comb. nov. Basionym: *Callipteris acutifolia* Radczenko (Radczenko 1955: 129–130, Plate XIII, Fig. 4 – holotype).

Permocallipteris altaica (Zalessky ex Neuburg) Naug., comb. nov. Basionym: *Callipteris altaica* Zalessky ex Neuburg (Neuburg 1948: 125, Plate XXVI, Fig. 2 – lectotype, designated by Neuburg 1948: 125).

Permocallipteris angustata (Zalessky) Naug., comb. nov. Basionym: *Callipteris angustata* Zalessky (Zalessky 1939: 344, Fig. 22 – holotype).

Permocallipteris bardensis (Zalessky) Naug., comb. nov. Basionym: *Callipteris bardensis* Zalessky (Zalessky 1939: 342, Fig. 17 – lectotype, designated by Naugolnykh 1991: 42).

Permocallipteris bella (Zalessky) Naug., comb. nov. Basionym: *Callipteris bella* Zalessky (Zalessky 1939: 339, Fig. 12 – holotype).

Permocallipteris bexellii (Durante) Naug., comb. nov. Basionym: *Callipteris bexellii* Durante (Durante 1992: 14–15, Plate II, Figs 3–4; Plate III, Figs 1–2; Plate X, Fig. 11; Plate XI, Fig. 4; Text-Figs 2, 3a, b.; Plate X, Fig. 11, Text-Fig. 2 – holotype.) [Incorrect citation of the holotype in the protologue: should be cited Plate X instead Plate XI.]

Permocallipteris confluens (Neuburg) Naug., comb. nov. Basionym: *Callipteris confluens* Neuburg (Bobrov & Neuburg 1957: 610, Fig. 1b – holotype).

Permocallipteris cuspidata (Zalessky) Naug., comb. nov. Basionym: *Callipteris cuspidata* Zalessky (Zalessky 1939: 341, Fig. 15 – holotype).

Permocallipteris elegans (Fefilova) Naug., comb. nov. Basionym: *Callipteris elegans* Fefilova (Fefilova 1973: 113–115, Plate XXXII, Figs 1–5; Fig. 1 – holotype).

Permocallipteris ivancevia (Gorelova) Naug., comb. nov. Basionym: *Callipteris ivancevia* Grelova (Gorelova 1960: 69–71, Plate 16, Figs 4, 5. Plate 16, Fig. 4 – holotype).

Permocallipteris karskianum (Tschirkova & Zalessky) Naug., comb. nov. Basionym: *Callipteris karskiana* Tchirkova & Zalessky (Tchirkova & Zalessky 1939: 315–316, Fig. 1 – holotype).

Permocallipteris lobata (Gorelova et Drjagina) Naug., comb. nov. Basionym: *Callipteris lobatus* Gorelova et Drjagina (Betekhtina et al. 1988: 125–126, Plate L, Figs 1, 1a – holotype).

Permocallipteris lobulata (Fefilova) Naug., comb. nov. Basionym: *Callipteris lobulata* Fefilova (Fefilova 1973: 115–117, Plate XXXIII, Figs 1–4; Figs 2, 4 – holotype).

Permocallipteris mongoliense (Neuburg) Naug., comb. nov. Basionyn: *Callipteris mongoliensis* Neuburg (Bobrov & Neuburg 1957: 610; Durante 1976: 150–151, Plate XLIII, Fig. 3 – holotype; Plate XLIV, Fig. 2–3).

Permocallipteris oranetzensis (Zalessky) Naug., comb. nov. Basionym: *Callipteris oranetzensis* Zalessky (Zalessky 1934: 261, Fig. 35 – holotype).

Permocallipteris orientalis (Zalessky) Naug., comb. nov. Basionym: *Callipteris orientalis* Zalessky (Zalessky 1929: 129–130, Fig. 10 – holotype).

Permocallipteris patula (Zalessky) Naug., comb. nov. Basionym: *Callipteris patula* Zalessky (Zalessky 1939: 343, Fig. 19 – lectotype, designated by Naugolnykh 1991: 42).

Permocallipteris plumosa (Zalessky) Naug., comb. nov. Basionym: *Callipteris plumosa* Zalessky (Zalessky 1939: 344, Fig. 21 – holotype).

Permocallipteris polyneura (Zalessky) Naug., comb. nov. Basionym: *Callipteris polyneura* Zalessky (Zalessky 1937: 51–52, Fig. 16 – holotype).

Permocallipteris pubescens (Zalessky) Naug., comb. nov. Basionym: *Callipteris pubescens* Zalessky (Zalessky 1939: 340, Fig. 13 – lectotype, designated by Naugolnykh 1991: 42).

Permocallipteris rarinervis (Zalessky) Naug., comb. nov. Basionym: *Callipteris rarinervis* Zalessky (Zalessky 1934: 259, Fig. 32 – holotype).

Permocallipteris sahnii (Zalessky) Naug., comb. nov. Basionym: *Callipteris sahnii* Zalessky (Zalessky 1929: 128–129, Figs 8–9. Fig. 9 – lectotype, designated here).

Permocallipteris tatianaeana (Zalessky) Naug., comb. nov. Basionym: *Callipteris tatianaeana* Zalessky (Zalessky 1934: 260, Fig. 33, right specimen – lectotype, designated by Naugolnykh 1991: 43).

Permocallipteris uralensis (Zalessky) Naug., comb. nov. Basionym: *Callipteris uralensis* Zalessky (Zalessky 1914: 64–67, Plate I, Fig. 1 – holotype).

Permocallipteris vuktylensis (Zalessky) Naug., comb. nov. Basionym: *Callipteris vuktylensis* Zalessky (Zalessky 1934: 259, Fig. 31 – holotype).

Acknowledgements

This work was funded by the subsidy of the Russian Government of the Program of Competitive Growth of Kazan Federal University among World's Leading Academic Centers. I want to express my deep gratitude to colleagues W. DiMichele (Smithsonian Institution, Washington, USA), Sun Yuewu and Zhang Dejun (Research Center of Paleontology & Stratigraphy, Jilin University, Changchun, China) for discussion of the peltasperm taxonomy and systematics. Colleagues N. M. Kadlets and T. V. Vinogradova from the Tchernyshev Central Scientific-Research Geological Museum (TsNIGR Museum, St. Petersburg) are acknowledged for their kind and helpful assistance in working with the callipterid specimens, which are kept in storage of TsNIGR Museum. The author is sincerely grateful to all persons who allowed to study their specimens and Roland Eberwein is gratefully acknowledged for his valuable editor's help and suggestions.

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