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Kizelopteris, a new genus of climbing pteridosperms from the Lower Carboniferous of the Urals, Russia

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Summary: The present article deals with the new liana-like pteridosperm attributed to the new genus and species *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. The material studied originated from the Lower Carboniferous (Visean) deposits of the Perm region, the Urals, Russia. The new pteridosperm is described both macromorphologically and in terms of epidermal-cuticular structure. *Kizelopteris* has at least bipinnate fronds with small alternate pinnae of last order. Pinnules are of subtriangular shape, semi-adult pinnules are sphenopteroid to pecopteroid, margins of pinnules are lobate. Adult pinnules become almost entire-margined. Bases of pinnules are coalescently fused and form a limb (wing) of pinna rachis. Apical part of pinna rachis and apical lobes of pinnules can be modified into terminal tendrils or climbing hooks. General thoughts on the ecology of Early Carboniferous vegetation of the Urals are given as well.

Keywords: pteridosperms, Carboniferous, Callystophytales, lianas, new taxa, Urals, *Kizelopteris flexuosa*, gen. et sp. nov.

The first ecologically sophisticated plant communities began to develop in low latitudes as early as in Carboniferous (Bertrand & Corsin 1950; Gothan & Remy 1957; Scott 1989; DiMichele & Phillips 1996; DiMichele et al. 2002, 2006, 2007). The tropical Carboniferous forests, as they are understood and reconstructed now (Scott 1977; Van Amerom & Pagnier 1990; Wagner 2001; Greb et al. 2006; Oplustil et al. 2009; Naugolnykh & Jin Jianhua 2014), show a large number of ecological niches and evolutionary possibilities for various adaptations of terrestrial plants.

Practically, all the Carboniferous plant groups used many different evolutionary strategies for adaptation and surviving in conditions of high competition, which took place in so-called Carboniferous 'coal-swamps'. The plants developed several types of growth forms, such as self-supporting trees and shrubs, small grassy plants scrambling on the ground or partly submerged in water, and lianas.

As it was unequivocally proved by recent researchers (Steur 1995; Kerp & Krings 1998; Krings et. al. 2001, 2003), various Carboniferous lianas were represented by pteridosperms, a gymnosperm group rapidly evolved during the Late Palaeozoic (Zalessky 1907; Gothan & Remy 1957; Dunn et al. 2003; Wagner 2001; etc). But most of the pteridosperms, which had liana-like growth forms, were typical of the Late Carboniferous (*Mariopteris* Zeiller, *Karinopteris* Boersma) or latest Carboniferous and early Permian (*Pseudomariopteris* Danzé-Corsin; see for further discussion: Krings et al. 2003). Very scarce evidence is present on more ancient liana-like pteridosperms existing before the Late Carboniferous time.

The present study deals with an Early Carboniferous pteridosperm with a clear adaptation for climbing and which is representing one of the most ancient cases of appearance of liana-like

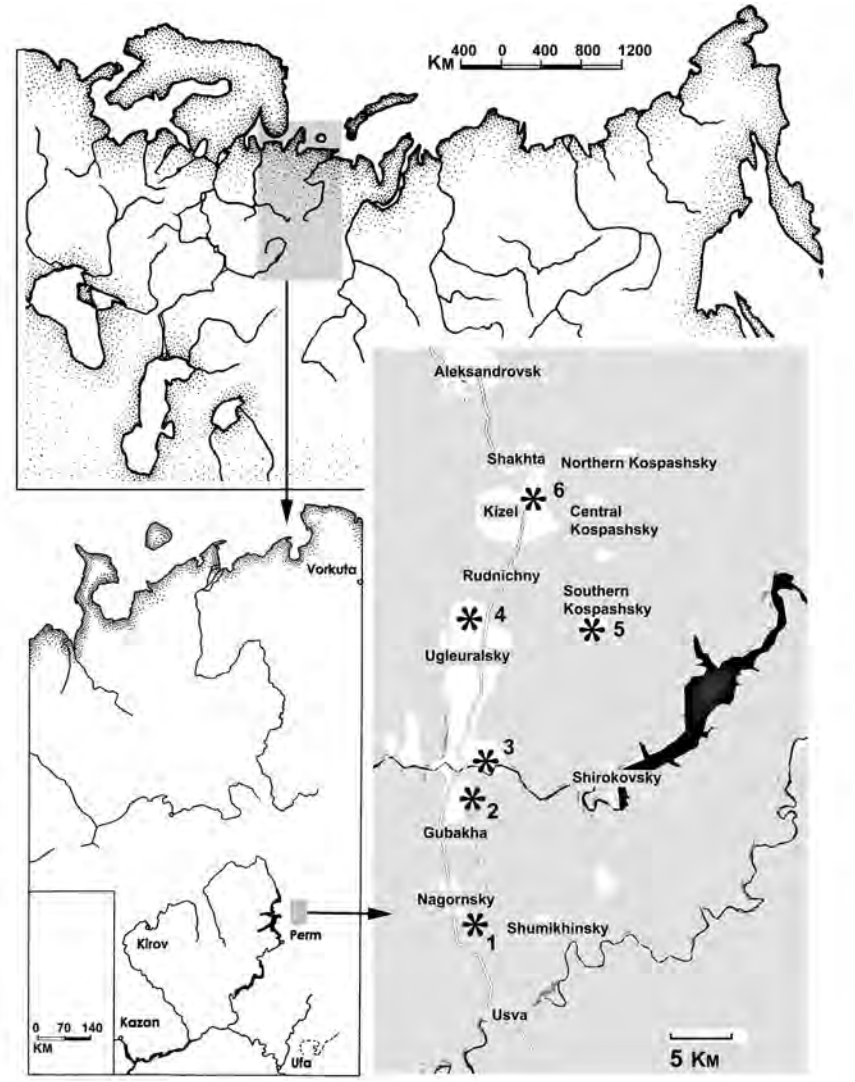

Figure 1. The geological sections cited in the present paper (from south to north). 1 – Nagornsky; 2 – Krestovaja Mountain; 3 – Gubakha-Stary Most; 4 – Polovinka; 5 – Southern Kospashsky (the Mine No. 33, 'Kapitalnaya'); type locality of *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov.; 6 – Kizel.

plants in the history of the earth. This pteridosperm is attributed to the new genus and species *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov.

Materials and methods

The collection studied originated from the Lower Carboniferous (Visean) deposits of the Western Urals, outcropped in several sections in the Perm region, Russia, nearby the City of Kizel, in the Kizel Coal Basin. The type locality of *Kizelopteris flexuosa*, gen. et sp. nov., is disposed nearby the South Kospashsky mine settlement, eastwards of the City of Kizel (Fig. 1 No. 5). Other localities studied and cited in the text (discussion of *Kizelopteris* paleoecology; i.e. Krestovskaya Mountain, Gubakha-Stary Most, Polovinka, Kizel: Fig. 1 Nos. 1–4, 6) give a good basis for the general considerations on the early Carboniferous flora of the Kizel Coal basin. Stratigraphically, all the localities studied belong to the coal-bearing deposits of the Visean stage, Lower Carboniferous.

The geological sections and exact positions of the localities (from south to north, Fig. 1):

1) *Nagornsky*. The Nagornsky Mine is disposed in 300 m eastwards from the village of Nagornsky, 4 km south from the City of Gubakha. 58.781 N; 57.552 E.

2) *Krestovaja Mountain*. The outcrop of the quartz sandstones are disposed on the top of the Krestovaja Mountain, in meridional direction on the distance of 4 km; 500 m east from the eastern suburb of the City of Gubakha. 58.837 N; 57.584 E.

3) *Gubakha-Stary Most*. The right bank of the Kosva River in 2 km upstream the new city road bridge, opposite to the old bridge. 58.867 N; 57.589 E.

4) *Polovinka*. The outcrop of the intercalating quartz sandstones, alevrolithes, siltstones, and coals in the rail-road trench in the distance between the station '150 km' and the Kluchevskaya Mine, the rail-road Perm–Ugleuralskaya. 58.978 N; 57.560 E.

5) *Southern Kospashsky* (the Mine No. 33, 'Kapitalnaya'). 58.970 N; 57.749 E. The type locality of *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov.

6) *Kizel*. The coal mine on the left bank of the River Poludenny Kizel, 100 m east from the road bridge on the P343 road, 200 m north-east from the post-office of the city of Kizel. 59.057 N; 57.661 E.

The plant fossils are preserved as impressions/compressions. Compressions were macerated in concentric nitric acid for three days. Products of oxidation were removed by concentric solution of ammonia. The cuticles obtained were washed by distilled water and then mounted into permanent preparations (slides) with glycerin-jelly medium. The cuticles were studied with Carl Zeiss Axiostar digital optical microscope in the Geological Institute of the Russian Academy of Sciences, Moscow (GIN).

Some of the cuticular details are shown with different focuses and in different light (lateral or frontal) for a more adequate characteristic of their structure. The collection studied is kept at the Geological Institute of Russian Academy of Sciences, Moscow, Russia.

General habit of the flora

The Early Carboniferous (to be precise, Visean) flora of the western slope of the Urals can be regarded as a typical tropical flora of Euramerian appearance. The Kizel flora includes numerous arborescent lycopodiopsids which certainly dominated there and can be considered as edificators of hygrophilous vegetation. It should be underlined that this kind of vegetation took place in the studied area in Early Carboniferous time. The lepidodendrid species *Lepidodendron veltheimii* Stur is reported from practically all the localities studied and listed above. This species was a dominating taxon in this flora and formed a more or less dense canopy and was used as support for some other plants which grew in the same plant communities and were adapted for scrambling or climbing life strategy (see discussion part of this paper).

High evolutionary competition in this low latitude tropical vegetation gave an advantage for some plants for developing a new type of adaptation for surviving. This adaptation was aimed at combining the possibilities to reach sources of fresh water from the swampy ground and at the same time to reach the sun light for effective insolation by means of raising the stem and leaves above the ground as high as possible. This task was not simple in the dense canopy of other tropical plants, mostly the lepidodendrid *Lepidodendron veltheimii* Stur.

This adaptation lead to the formation of a new growth form of plants with long, narrow and flexible stems possessing leaves armed with the modified segments shaped as hooks or tendrils for fixing on or attaching to other plants serving as support. This ecological strategy was realized in liana-like plants. The liana-like growth forms were rare in Early Carboniferous vegetation, but abundant and even flourished in the Late Carboniferous (Krings et al. 2001, 2003).

One of the most ancient lianas in the history of the plant world was a mariopterid pteridosperm *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov., which is described here.

Systematics and description

Division Gymnospermae (= Pinophyta)
Subdivision Pteridospermae Scott, 1899
Order Callystophytales Rothwell, 1981
Family Callistophytaceae Stidd & Hall, 1970

Genus *Kizelopteris* Naugolnykh, gen. nov.

Type species. *Kizelopteris flexuosa* Naugolnykh, sp. nov.; Lower Carboniferous (Visean) deposits of the Western Urals.

Diagnosis. Same as for the type species.

Comparison. The new genus *Kizelopteris* is different from the close mariopterid genera *Mariopteris* Zeiller (Fig. 2), *Karinopteris* Boersma and *Pseudomariopteris* Danzé-Corsin in deeper dissection of the young pinnules, simpler venation, wider spaced pinnules and longer adult pinnules of the well-developed pinnae. The new genus differs from the genus *Karinopteris* in amphistomatic leaves in contrast to hypostomatic leaves of *Karinopteris*.

Distribution. Lower Carboniferous, Visean of the Urals, Russia.

Kizelopteris flexuosa Naugolnykh, sp. nov. (Figs 3–9, 12)

Etymology. From flexible character of the frond and pinna rachises.

Holotype. Spec. No. 4856/730; Kizel Coal Basin; the Southern Kospashsky locality; figured here on Fig. 3B, C, E and Fig. 5A. [Geological Institute of Russian Academy of Sciences, Moscow, Russia]

Diagnosis. Fronds at least bipinnate. Pinnae of last order small, alternately pinnate. Pinnules of subtriangular shape. Adult pinnules sphenopteroid to pecopteroid. Margins of pinnules lobate; adult pinnules become almost entire-margined. Bases of pinnules coalescently fused and form limb (wing) of pinna rachis. Apical part of pinna rachis and apical lobes of pinnules can

Figure 2. The pinna of *Mariopteris muricata* Schlotheim after Zalessky (1907: Plate XIII, Fig. 19). Donetsk Coal Basin, village Nizhny Srebryakov, Golubinnaya ravine. Scale bar = 1 cm.

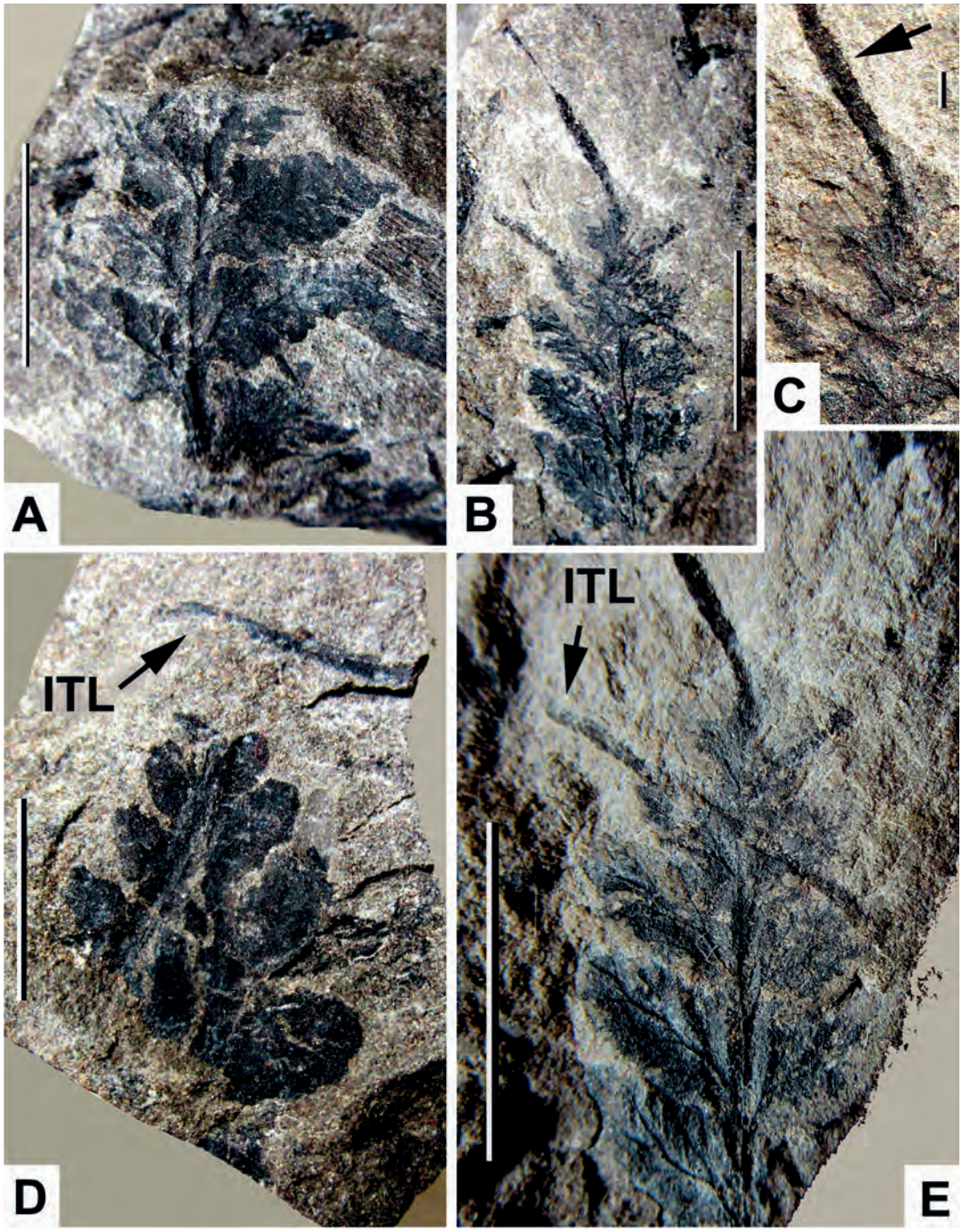

Figure 3. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Diversity of the leaves. A – spec. 4856/732; B, C, E – holotype spec. 4856/730; D – spec. 4856/729. ITL – isolated terminal lobe (tendril). Locality: Southern Kospashsky (the Mine No. 33, 'Kapitalnaya'). Scale bars = 1 cm (A, B, D, E); 1 mm (C).

be modified into terminal tendrils or climbing hooks. Midvein of pinnules slightly waving, undulating or straight. Lateral veins once to twice dichotomizing. Leaves amphistomatic. Common cells of epidermis long, of trapezioid to rectangular shape, with straight to slightly curved radial (centriclinal) walls. Long unicellular hairs (trichomes) present. Stomata monocyclic

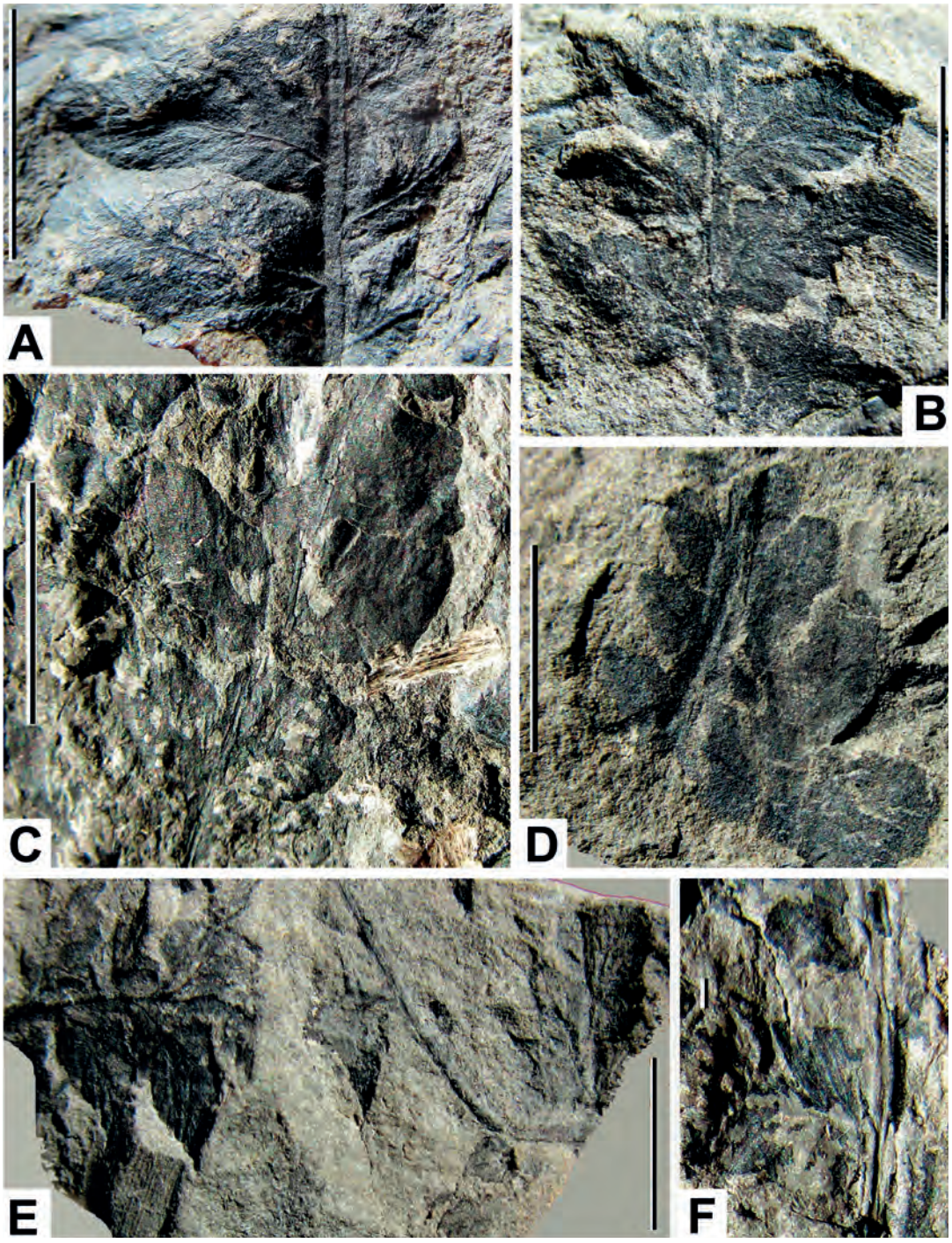

Figure 4. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Diversity of the leaves. A – spec. 4856/733; B – spec. 4856/732; C – spec. 4856/731; D – spec. 4856/729; E – spec. 4856/732; F – spec. 4856/733. Locality: Southern Kospashsky (the Mine No. 33, 'Kapitalnaya'). Scale bars = 1 cm (A–E); 1 mm (F).

to incompletely dicyclic, with two proximal papillae disposed opposite to each other on opposite subsidiary cells. Periclinal walls of subsidiary cells slightly thicker than periclinal walls of common epidermal cells.

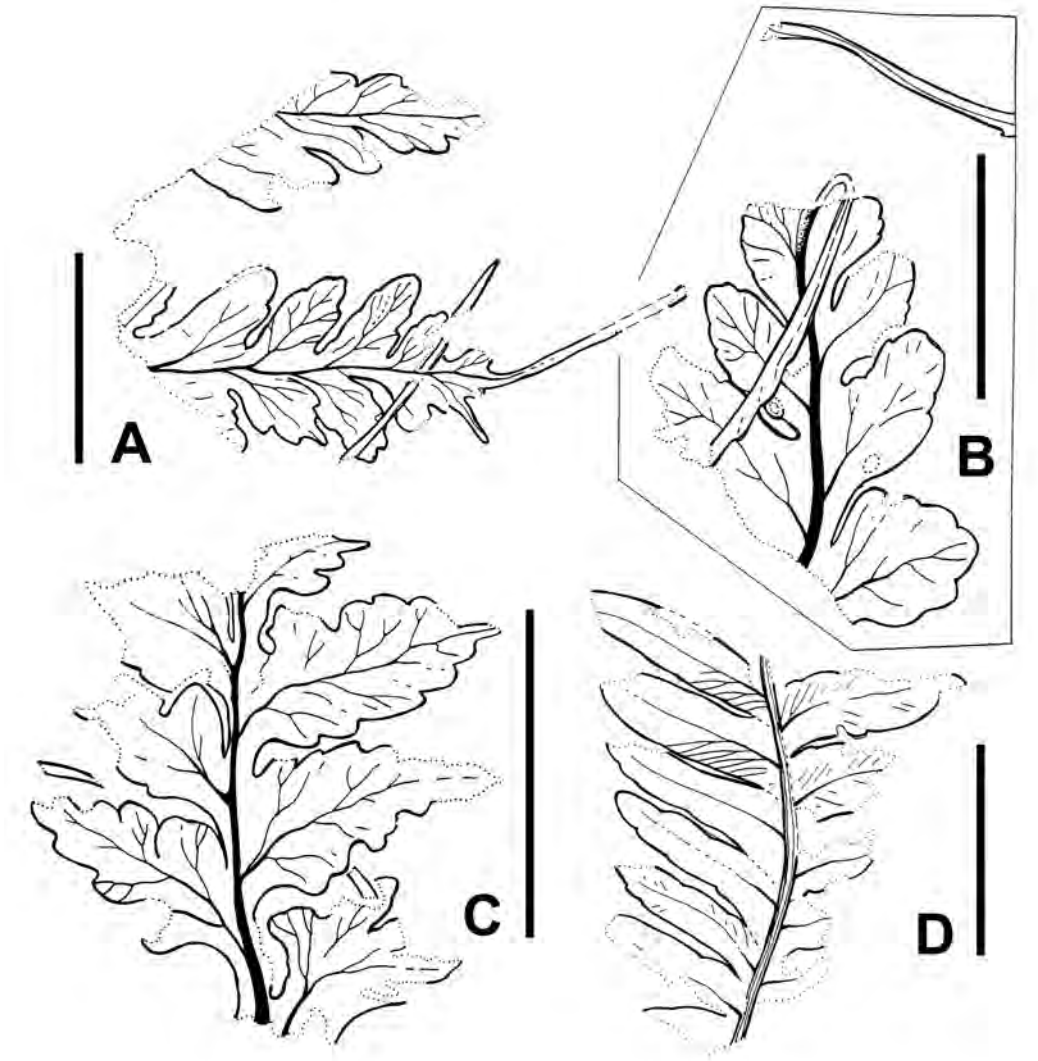

Figure 5. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Diversity of the leaves. A – holotype spec. 4856/730; B – 4856/729; C – 4856/732; D – spec. 4856/733. Locality: Southern Kospashsky (Mine No. 33, 'Kapitalnaya'). Scale bars = 1 cm.

Description. *Macromorphology.* The collection studied includes two fragmentarily preserved parts of bipinnate fronds and five pinnae of last order (penultimate segments). All the specimens came from one and the same locality and show a gradual transition in macromorphological characters between different specimens. Therefore, these differences between the specimens should be interpreted as intraspecific variations and can be explained in terms of natural variability of leaves belonging to one and the same species.

Judging from the most well-preserved specimens, the species *Kizelopteris flexuosa* Naugolnykh, sp. nov. had at least bipinnate fronds consisting of a slender and most probably flexible rachis, which the pinnae of last order (penultimate segments) were attached to. The frond rachis is smooth, lacking additional morphological structures (sculpture). The pinnae of last order are attached to the frond rachis in alternate (not-opposite) order. Basis of the pinnae is wedge-like, practically not decurrent. The pinnae are attached to the frond rachis under an angle of 60–80°.

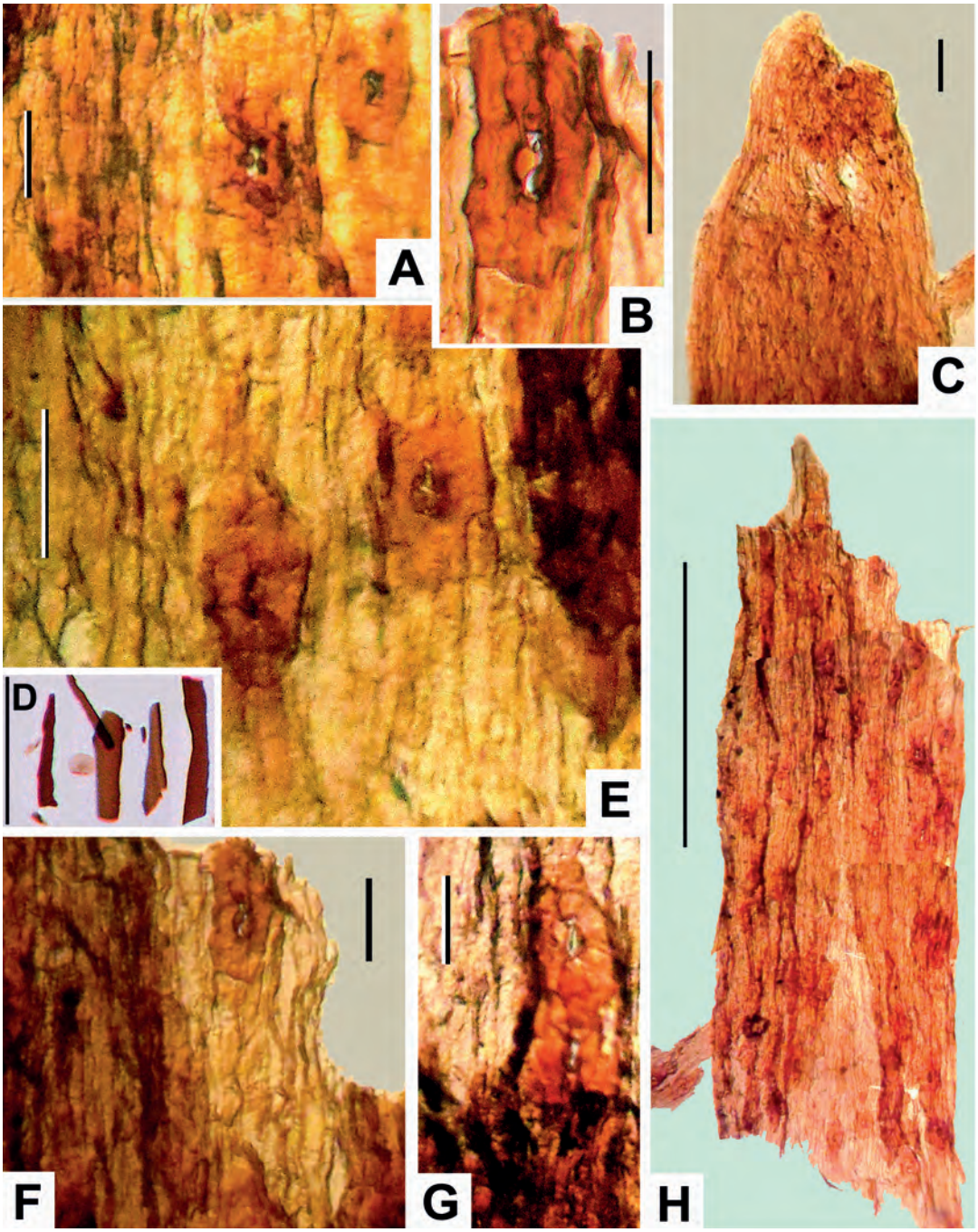

Figure 6. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Epidermal cuticular structure. Detailed description see in the text. Spec. 4856/731. Locality: Southern Kospashsky (Mine No. 33, 'Kapitalnaya'). Scale bars = 50 µm (A, B, E, F, G); 100 µm (C, D); 500 µm (H).

The pinna rachis is thin, slender, undulated in young pinnae, but more robust and straight in well-developed adult pinnae. Maximal observed wideness of the pinna rachis is 1 mm.

The pinnules (ultimate segments) are of subtriangular shape, mostly sphenopteroid in young pinnae with the exception of its apical part, where the pinnules are fused in basal parts by their

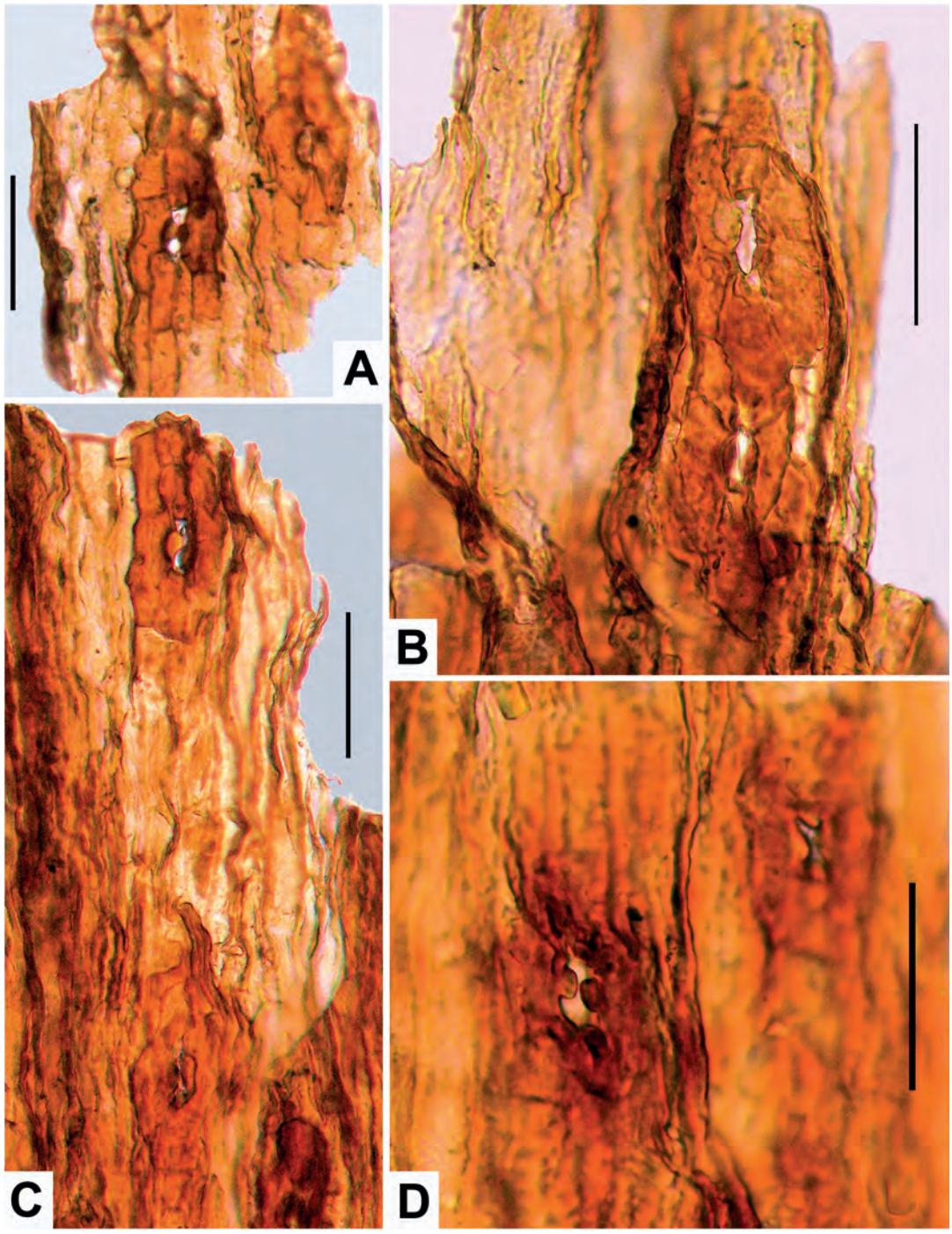

Figure 7. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Epidermal cuticular structure. Spec. 4856/731. Detailed description in the text. Locality: Southern Kospashsky (Mine No. 33, 'Kapitalnaya'). Scale bars = 50 µm.

margins. The pinnules of well-developed adult pinnae are more or less pecopteroid. The pinnules are always coalescently fused in different extent and form the clear limb (or wing) of the pinna rachis. The pinnules of the young pinnae have always lobate margins, with the three to five distinct marginal lobes disposed on each side of the pinnule.

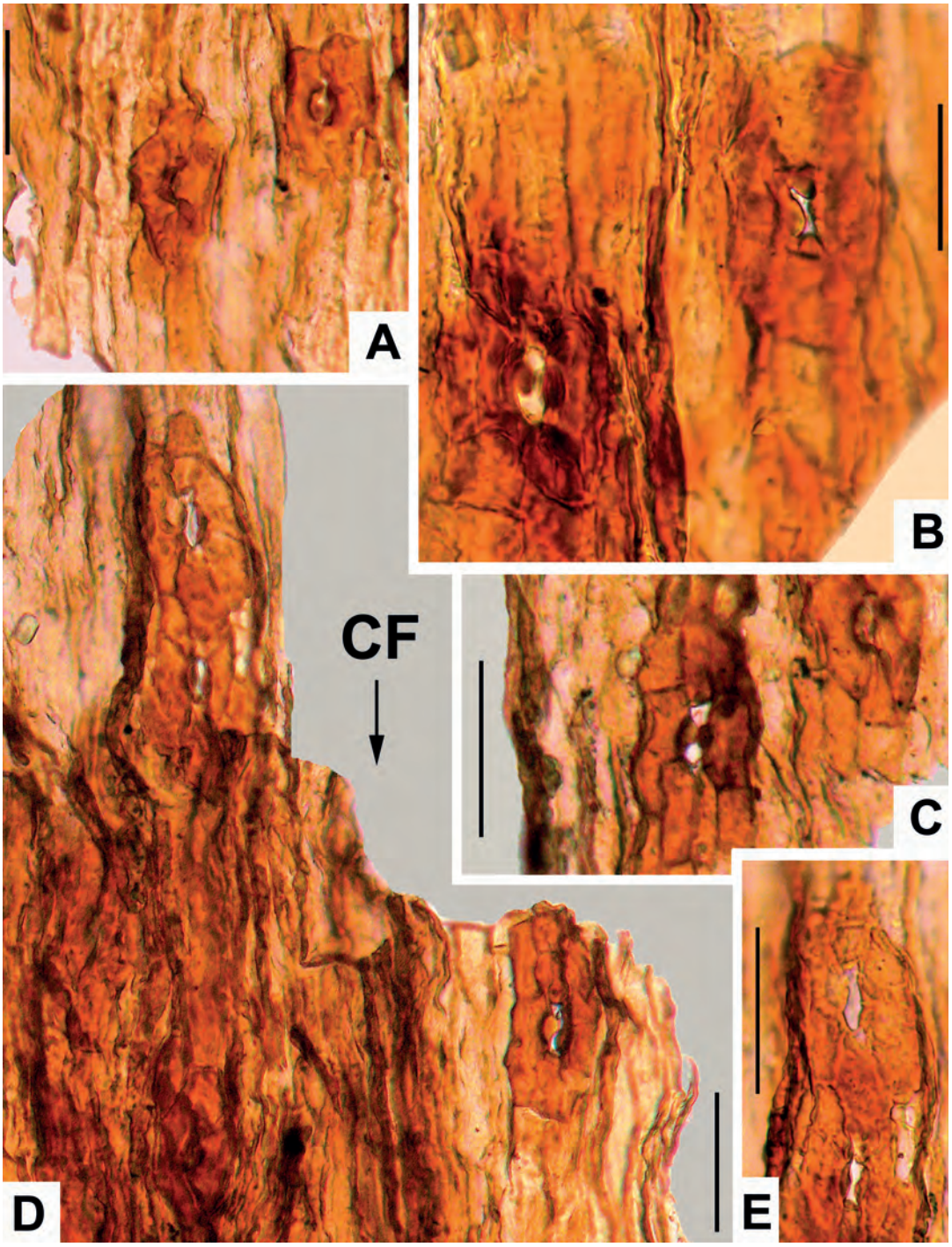

Figure 8. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Epidermal cuticular structure. Spec. 4856/731. Detailed description in the text. Locality: Southern Kospashsky (Mine No. 33, 'Kapitalnaya'). Scale bars = 30 µm (B); 50 µm (A, C–E).

The venation is pinnate. The midvein is undulating in the young pinnules, but more straight in the well-developed adult pinnules. Each pinnule bears three to five pairs of lateral veins disposed in alternating order. The lateral veins are once or twice dichotomizing.

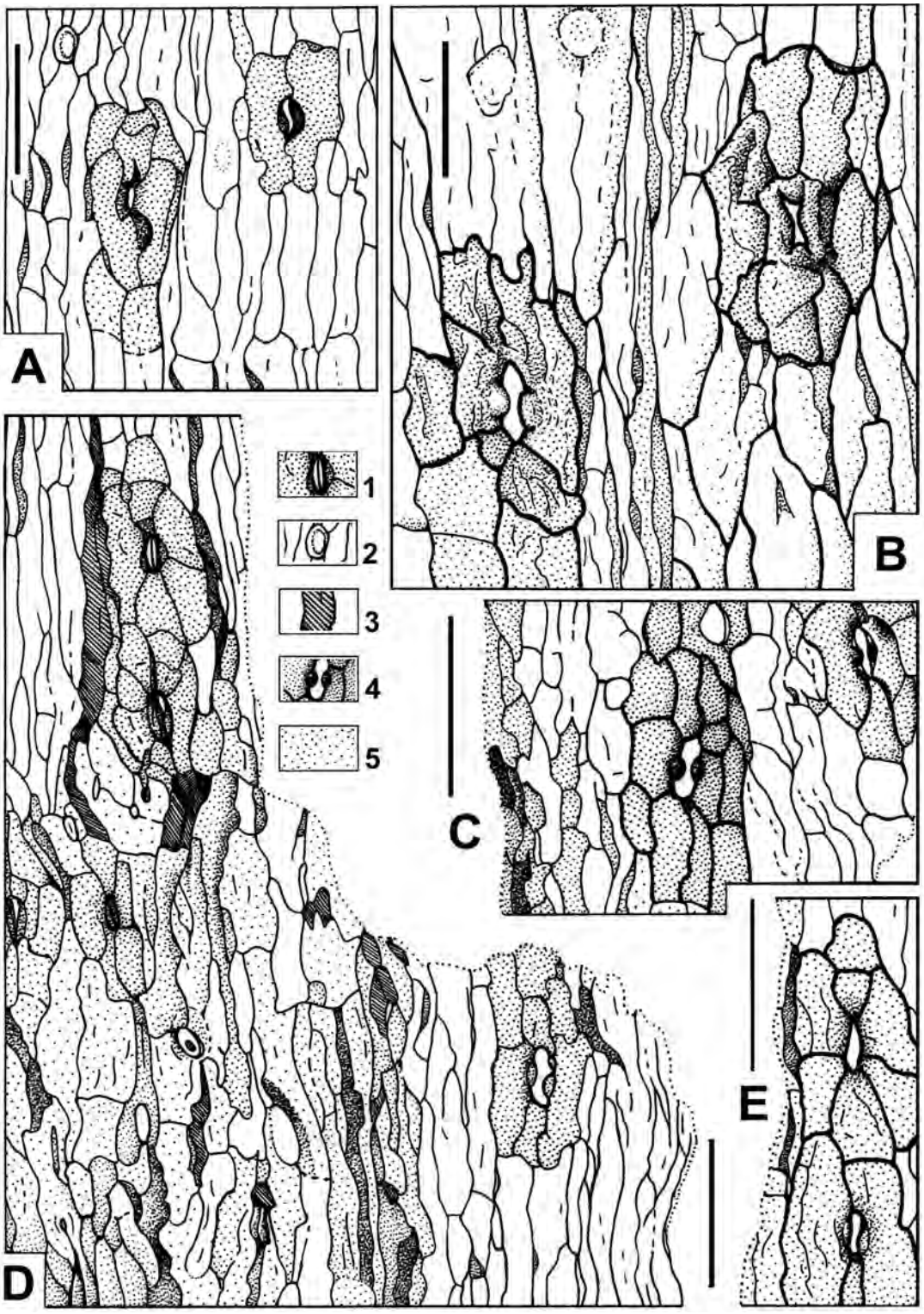

Figure 9. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Epidermal cuticular structure. Line-tracings. 1 – lip-like thickenings of the guard cells; 2 – trichoma base; 3 – areas with the dense cuticle; 4 – proximal papillae of subsidiary cells; 5 – strong cutinisation of the periclinal walls. Locality: Southern Kospashsky (Mine No. 33, 'Kapitalnaya'). Scale bars = 30 μm (B); 50 μm (A, C–E).

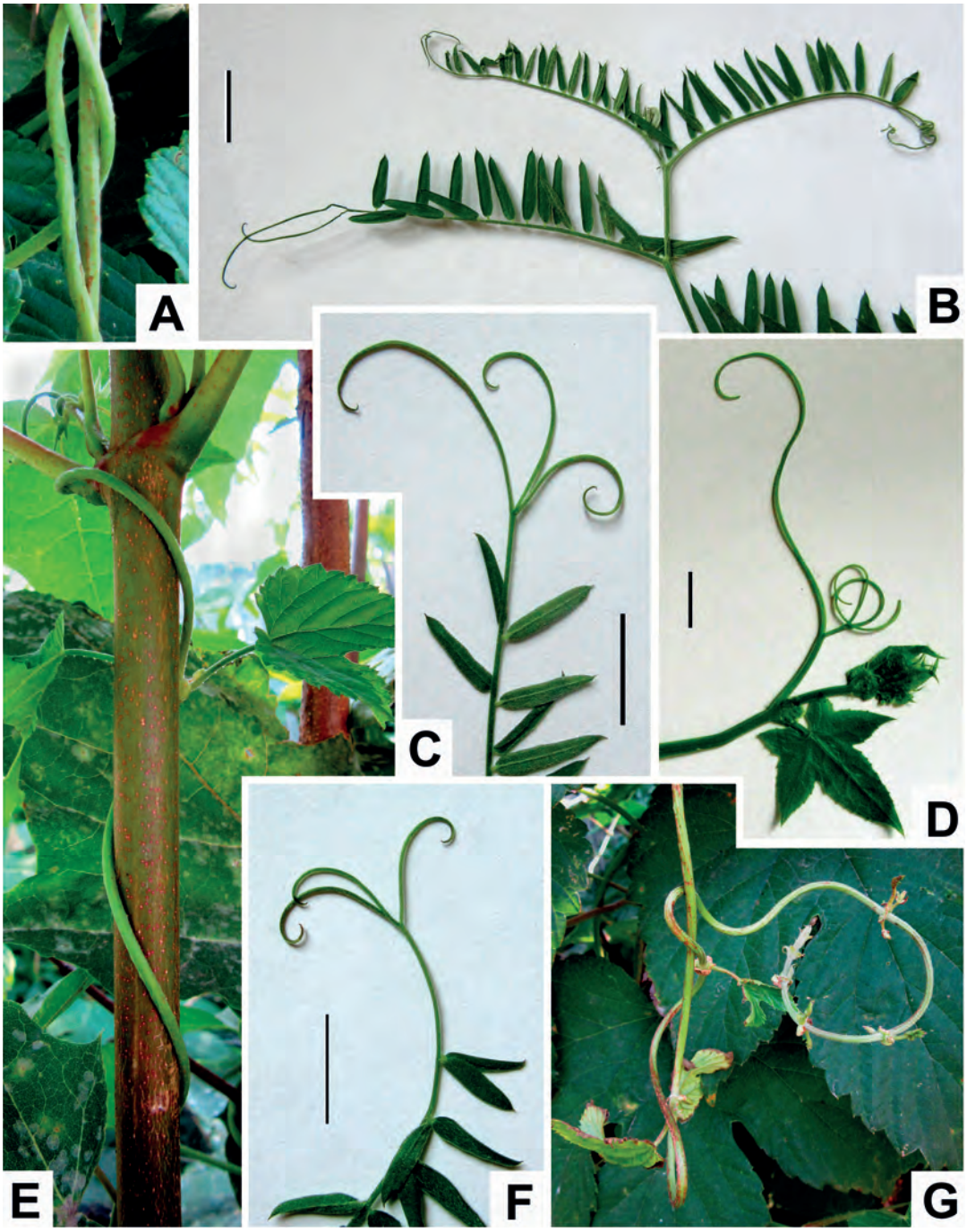

Figure 10. Recent ecological and morphological analogues of *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. A, E, G – *Humulus lupulus* L.; B, C, F – *Vicia cracca* L.; D – *Bryonia alba* L. Specimens from the City of Ramenskoe, station '47 km'; leg. *S.V. Naugolnykh* 2016. Scale bars = 1 cm.

Length of the pinnules varies from 5–15 mm with the average width 3–7 mm. One pinnule (Fig. 5B) has two small (1 mm in diameter) round scars of uncertain nature, which can be preliminarily interpreted as scars of seed attachment. The same seed/ovule position is typical of other mariopterid pteridosperms (see, for instance: Krings et al. 2001: Figs 9, 10).

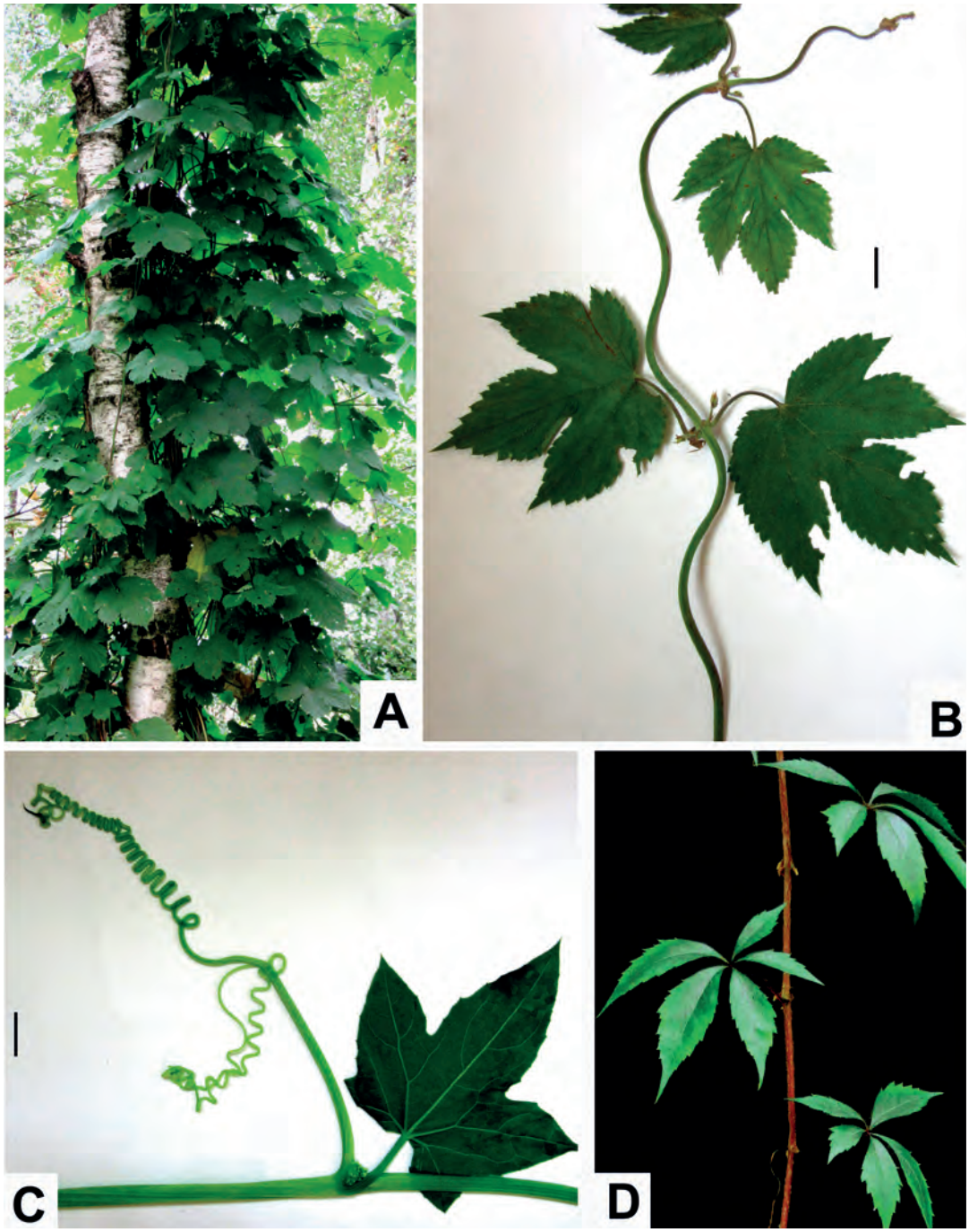

Figure 11. Recent ecological and morphological analogues of *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. A, B – *Humulus lupulus* L.; C – *Bryonia alba* L.; D – *Parthenocissus quinquefolia* (L.) Planch. Specimens from the City of Ramenskoe, station '47 km'; leg. *S.V. Naugolnykh* 2016. Scale bars = 1 cm.

Apical part of the last order pinnae as well as apical segments of some apical pinnules possess long terminal extensions which should be interpreted as tendrils and/or climbing hooks. Such morphological structures are typical of many mariopterid pteridosperms from the Upper Carboniferous and Lower Permian of the Euramerian palaeofloristic realm (Fig. 2; see discussion

Figure 12. *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov. Reconstruction of the frond. Scale bar = 1 cm.

below). Length of the tendrils can reach 10 mm, average width is 1 mm. Proximal pinnules are normally lacking tendrils or other well-pronounced extensions and are terminated only by one small apical lobe.

Epidermal-cuticular structure. The cuticles are obtained from different parts of leaves including apical extended lobes (tendrils). Cuticles of both leaf sides are similar to each other. Leaves are amphistomatic. Common epidermal cells are prolonged, trapezoid to rectangular. There are bases of trichomes disposed in places of contact of the neighboring common epidermal cells. Several isolated unicellular trichomes were found in the preparations (Fig. 6D). These trichomes apparently were detached from the cuticles during processing of maceration. Periclinal walls of common epidermal cells are smooth, but could be slightly thickened in some areas of the cuticle (Fig. 9D). Radial (centriclinal) walls are more or less straight, thin, but can rarely be slightly thickened (Fig. 9A, left).

The stomata are monocyclic to incompletely dicyclic with three to eight subsidiary cells. Two opposite subsidiary cells are orientated along the stoma aperture (or along the leaf axis). These subsidiary cells bear small but distinct round proximal papillae. This character is also known for some other mariopterid pteridosperms, for example, *Karinopteris* sp. from the Indiana Paper Shale (DiMichele et al. 1984; Kerp & Barthel 1993: Plate VI, Figs 5, 6).

There are bases of long unicellular hairs (trichomes) located mostly at the basal part of tendrils. Most probably these trichomes served for mechanical protection of tendrils in the places, where they could be damaged by dynamic pressure between tendril and the plant, which the tendril was attached to.

Material. Seven specimens of good preservation from the type locality.

Distribution. Same as for the genus.

Discussion

Early Carboniferous low latitude vegetation of the Urals compared to some recent plants

Ecological and morphological models for reconstruction of the growth form of *Kizelopteris flexuosa* Naugolnykh, gen. et sp. nov., are based on several general considerations.

The morphological peculiarities of *Kizelopteris flexuosa*, i.e. tendrils, hook-like extended lobes of the pinna rachis and slender and flexible tips of ultimate segments (pinnules) allow to compare this plant to recent plants having same or similar adaptations for a liana-like life style (Figs 10, 11).

The most typical representative of the present day lianas having tendrils and other specialized organs of attachment to other plants are *Humulus lupulus* L. (Fig. 10A, E, G), *Vicia cracca* L. (Figs 10B, C, D, F; 11A, B), *Bryonia alba* L (Fig. 11C) and *Parthenocissus* spp. (Fig. 11D) figured here for instance, as well as some others, which are very well-known and used as basis for detailed biomechanical studies (Darwin 1867; Lisk 1924; Jaffe & Galston 1968; Menninger 1970; Levin 1973; Givnish & Vermeij 1976; Jacobs 1976; Putz 1980; Stevens 1987; Hegarty 1989, 1991; Holbrook & Putz 1996). Practically, all of these plants have tendrils very similar or even identical to that of *Kizelopteris flexuosa*.

Most of the reconstructed pteridosperms which are biologically unequivocally interpreted as lianas, are typical of the Late Palaeozoic vegetation and reported from the localities reflecting low latitude tropical and equatorial hygrophilous floras belonging to the Euramerian palaeophytogeographical realm (Kerp & Krings 1998; Krings et al. 2001). Dense canopy of these swampy forests allowed growth of different lianas which need to use other plants from the same community for supporting their bodies.

The Lower Carboniferous floras of the Urals and the flora of the Kizel Coal basin belonged to the Euramerian palaeofloristic realm and grew in warm and wet humid climatic conditions. The flora of the Kizel Coal basin includes such typical Euramerian elements as *Archaeocalamites* (=*Asterocalamites*) sp., *Lepidodendron veltheimii* Stur, *L. acuminatum* Goeppert, *L. volkmannianum* Sternberg, *Bothrodendron* sp., *Stigmaria ficoides* (Sternberg) Brongniart, *S. rugulosa* Gothan, *S. arenaria* Ludwig, *S. cochleata* Ludwig, etc., which are also typical of other Lower Carboniferous floras of the world (Gothan & Remy 1957).

Ecologically and regarding its gross morphology, *Kizelopteris flexuosa* should be interpreted as a liana which was adapted for growing in dense canopy of other plants (apparently, mostly lepidodendrids which were absolute dominant in the Visean vegetation of the Kizel Coal basin).

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