Late Permian Phylloclades of the New Genus *Permophyllocladus* and Problems of the Evolutionary Morphology of Peltasperms

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Abstract—Phylloclades from the Upper Permian (Tatarian) deposits of the Sokovka locality, Vladimir Region, showing gradational transformation of a planate scale-leaved shoot into a foliar organ, are assigned to the new genus *Permophyllocladus* (Peltaspermales?). The phylloclades are distinctly dorsoventral: scaly leaves and their rudiments are developed on the lower side and are only marked by suture lines on the cuticle of the opposite side. In epidermal characteristics, the phylloclades are similar to the leaves of peltasperms from coeval deposits. It is supposed that peltasperm leaves are of phylloclade origin and were formed by cohesion of units of a coniferoid scale-leaved shoot that resembles shoots of the Mesozoic family Hirmerellaceae (Cheirolepidiaceae), which also tend to develop phylloclades.

INTRODUCTION

The Late Permian Subangarian flora of the Russian Platform and Cis-Urals is dominated by gymnosperms with small scaly and large pinnate leaves, conventionally assigned to conifers and peltasperms. It was named the Tatarina flora, emphasizing the abundance of leaf remains of the *Pursongia–Tatarina* group (Gomankov and Meyen, 1986). However, the systematics of Subangarian peltasperms is insufficiently developed. Their phylogenetic relationships both with the older European callipterids and the younger *Lepidopteris–Scytophyllum* group, which became common in the terminal Permian and Triassic, are still unclear. Some so far unexplained morphological peculiarities (e.g., the axial scales of *Lepidopteris*) imply that the leaf of peltasperms may be of phylloclade nature, and this may be true for all pteridosperms. Meyen (1987) hypothesized that peltasperms might have been related to some Permian scale-leaved gymnosperms of coniferoid aspect. The phylloclades found in the Sokovka locality are relevant to these topical problems of the systematics and evolutionary morphology of Permian gymnosperms.

MATERIAL AND METHODS

The Sokovka locality is situated on the northwestern boundary of the town of Vyazniki (Vladimir Region), in the gully between the town and the quarry opposite the village of Sokovka. In 1841, an expedition led by Murchison first found Permian ostracodes and bivalves near the town of Vyazniki. In 1951, 1952, 1955, and 1956, expeditions of the Paleontological Institute of the Academy of Sciences of the USSR led by V'yushkov gathered a collection of fossil fishes, amphibians, and reptiles. In 1999–2003, Sennikov, Golubev, and Bulanov rediscovered two localities named Bykovka and Sokovka corresponding to the Vyazniki II locality of Efremov and V'yushkov (1955), where plant macrofossils, spores and pollen grains, and bivalves and ostracodes were recorded. In 2005, additional material was collected by a paleoentomological group led by D.E. Shcherbakov. Afonin (2005) and Naugolnykh (2005) contributed to the study of the Vyazniki flora.

The Vyazniki fauna includes typical Late Tatarian bivalves, conchostracans, and fishes. Insect, tetrapod, and plant assemblages are transitional between the typical Permian and Triassic assemblages. The ostracode assemblage is of the Triassic aspect with the presence of some Permian elements (Golubev et al., 2005; Sennikov and Golubev, 2005).

The plant remains are preserved as impressions with compression fragments. The fragments of compressions were removed from the rock and studied with a CAMSCAN scanning electron microscope. In addition, cleared compressions and macerated cuticles were studied with MBS-10 and Axioplan 2 light microscopes. Photographs were taken with a Nikon Coolpix 4500 digital camera.

The stomatal index (SI) was determined by the equation $E = I + SC$; $SI = [SD/(E + SD)] \times 100$, where SD is the number of stomata per mm^2; E is the number of epidermal cells per mm^2; I is the number of ordinary epidermal cells per mm^2; and SC is the number of guard cells per mm^2 (Woodward, 1987).

MATERIAL

The present study used material collected by S.A. Afonin (2004), D.E. Shcherbakov, and A.C. Bashkuev (2005); the most important specimens were provided by Shcherbakov. The collection no. 5139 is housed in the Paleontological Institute of the Russian Academy of Sciences (PIN).

SYSTEMATIC PALEOBOTANY

Order Peltaspermales?

Genus *Permophyllocladus* Karasev et Krassilov, gen. nov.

E t y m o l o g y. From the Permian Period and the genus *Phyllocladus*.

T y p e   s p e c i e s. *P. polymorphus* sp. nov.

D i a g n o s i s. Planate branching shoots of variously connate scale leaves, gradationally transformed into imparipinnate phylloclades by extensive leaf cohesion. Leaves typically distinct on lower (abaxial) side, but reduced to coalescent leaf cushions or marked by suture lines alone on the opposite (adaxial) side. Lateral branches opposite or subopposite spreading at open angle, decurrent, forming pinnae or lobed pinnules of pinnate phylloclades. Ultimate units short elliptical or obovate branchlets with transverse sutures of adherent leaf pairs, distally leaflike, rounded or notched at the apex, reduced to phylloclade pinnules. Phylloclades strongly cutinized, amphistomatic, papillate. Stomata scattered, more numerous abaxially, irregularly oriented, monocyclic. Subsidiary cells, 4–7(6), radial, with proximal papillae. Florin ring distinct. Guard cells small, sunken.

S p e c i e s   c o m p o s i t i o n. Type species.

C o m p a r i s o n   a n d   r e m a r k s. In gymnosperms, phylloclades are known in the modern families Cupressaceae, Phyllocladaceae, and Sciadopityaceae and in the Mesozoic Hirmerellaceae (= Hirmerelliaceae, Cheirolepidiaceae). Among the latter, there are forms with dorsoventral shoots in which a facial leaf is only developed on one side (Watson, 1988). A pinnate phylloclade formed from a flattened scale-leaved shoot is described in detail in the Cretaceous genus *Androvettia* Hollick et Jeffrey, which belongs either to the Cupressaceae or Cheirolepidiaceae (Hueber and Watson, 1988). Although a certain general resemblance to *Permophyllocladus* gen. nov. exists, significant dissimilarities are observed, related to different directions of phylloclade morphogenesis. In the Permian genus, the maximal coalescence of leaves is observed in ultimate branches of limited growth, terminating with an imparipinnate foliar apex, whereas in *Androvettia* the terminal branchlets and the apices of the penultimate branches often retain the alternate arrangement of leaves and look like shoots of unlimited growth. The modern genus *Phyllocladus* L.C. et A. Rich apparently combines both modes of phylloclade formation: with branches of limited and unlimited growth (Hueber and Watson, 1988).

In Permian gymnosperms, phylloclades have not been found (or recognized) up to now. The most leaflike variants of polymorphic phylloclades of the new genus are similar to pinnate leaves of peltasperms having entire or lobed alethopteroid pinnules. Permian leaves of this type were traditionally referred to as *Callipteris* Brongniart; however, this generic name was found to be preoccupied and has so far not been conserved in accordance with the rules of botanical nomenclature.

A recent approach to the taxonomy of Permian peltasperms permits generic names for reproductive organs (*Autunia* F. Krasser, *Peltaspermum* T. Harris, and *Autuniopsis* Poort et Kerp) being applied to associated leaves (*"Callipteris", Lepidopteris* Schimper, and *Meyenopteris* Poort et Kerp, respectively), considered in such cases as belonging to a natural genus. However, we do not support this approach in the present paper, since genera based on both reproductive organs and leaves belong to morphotaxa of various degrees of naturalness and are recognized by their morphological characters rather than by their supposed taxonomic affinities.

Axial scales or swellings of uncertain morphological nature were recorded in the Triassic *Lepidopteris* and *Meyenopteris*, which have bipinnate leaves with interstitial pinnules (Harris, 1932; Poort and Kerp, 1990). Comparison with the new genus *Permophyllocladus* suggests that these structures are rudiments of the scaly leaves of the initial phylloclade. In this context, the callipteroid Permian leaves of *Lepidopteris* (*"Peltaspermum"*) *martinsii* (Germar) Poort et Kerp, which were described as bi- or tripinnate, with a forked rachis, are of particular interest. Pinnules are alethopteroid, subopposite or alternate, decurrent, finely toothed in the upper part of the leaf. Venation is pinnate, the midvein is relatively thin (or indistinct) and decurrent; lateral veins are rare, loosely arranged, simple or forked. This species is characterized by highly polymorphic leaves, some of which have well-defined "blisters" on rachises of the first and second orders (Poort and Kerp, 1990). The possible phylloclade interpretation was not considered in the original description. Unlike *Permophyllocladus*, scales are lost from the ultimate segments, and the dorsoventral orientation is expressed only in the thickness of the cuticle and the density of stomata.

Naugolnykh (2005) described, from the "Bykovka" locality near the town of Vyazniki, leaves of cf. *Lepidopteris* (al. *Callipteris*) *martinsii* Townrow, which are devoid of axial scales, and have triangular basal pinnules that become longer toward the acute apex. Therefore, the material from the Bykovka locality is significantly different from *Permophyllocladus polymorphus* sp. nov., although the cuticular characters are largely identical.
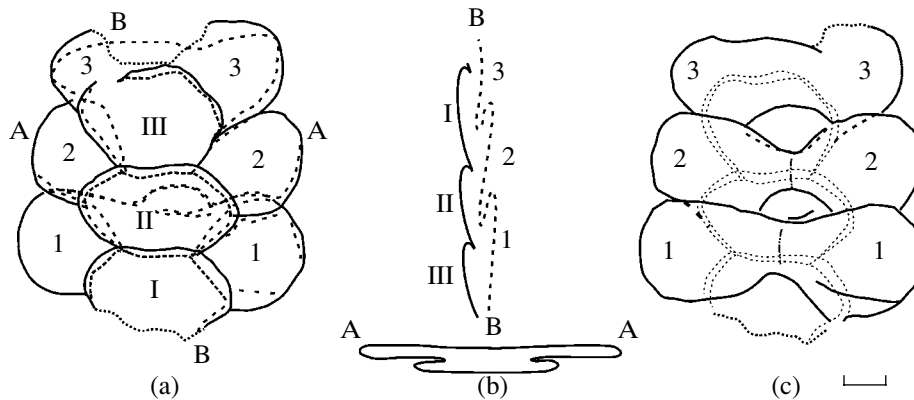
Plate 10

1   1000 μm

2   1000 μm

3   1000 μm

4   1000 μm

5   1000 μm

6   1000 μm

7   1000 μm

8   1000 μm
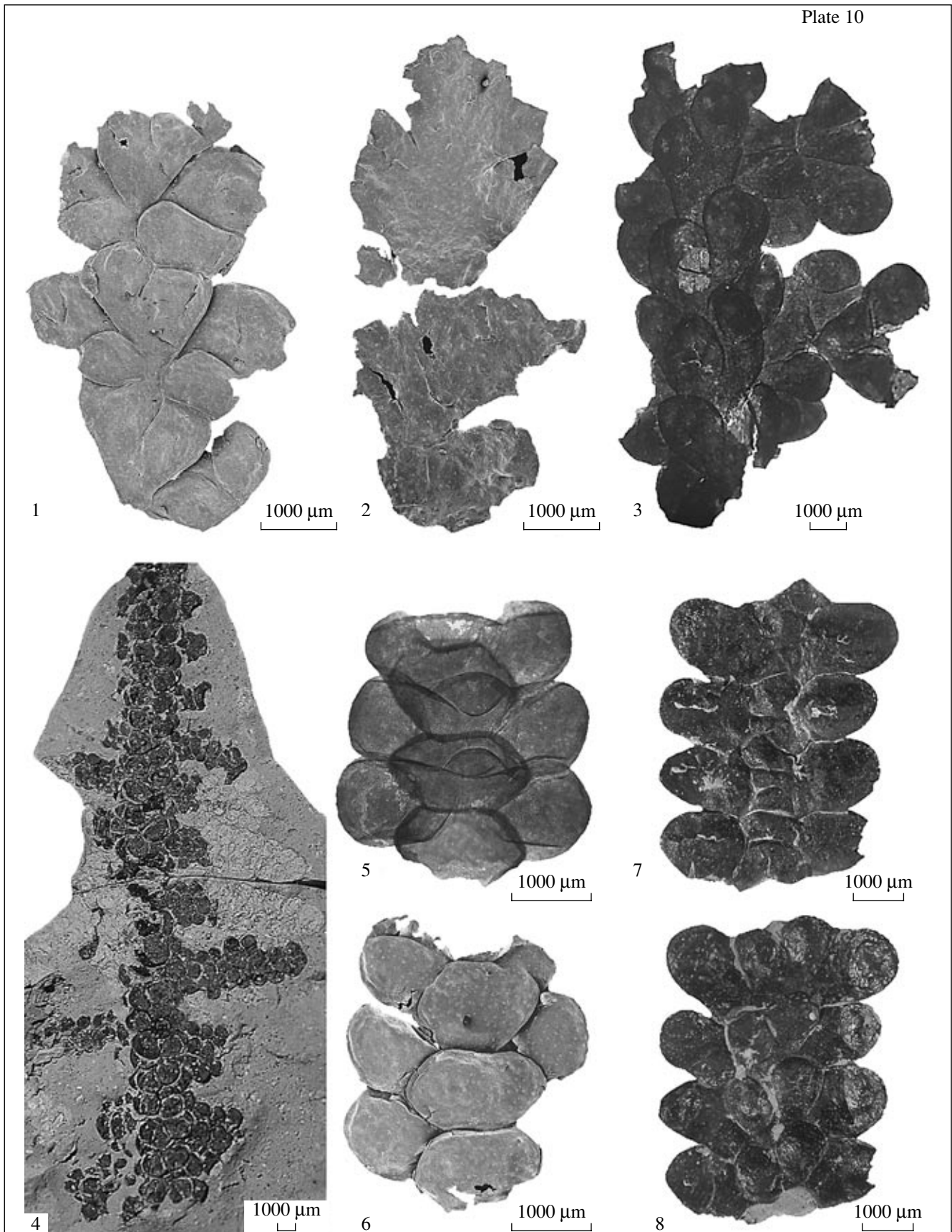
Fig. 1. *Permophyllocladus polymorphus* gen. et sp. nov., holotype PIN, no. 5139/1: (a) abaxial side of a lateral branchlet; (b) abaxial side of a lateral branchlet, schematic sections along the lines A–A and B–B; (c) adaxial side of a lateral branchlet; (I, II, III) facial row of leaf cushions; (1, 2, 3) lateral lobes corresponding to reduced terminal branchlets with fused leaves. Scale bar 500 μm.

Permophyllocladus polymorphus **Karasev et Krassilov, sp. nov.**

Plate 10, figs. 1–8; Plate 11, figs. 1–6

E t y m o l o g y. From the Greek *polymorphus* (of variable shape).

H o l o t y p e. PIN, no. 5139/1, Vladimir Region, Vyazniki district, right bank of the Klyaz'ma River, gully between the town of Vyazniki and Bykovskii quarry, Sokovka locality, Upper Permian, Tatarian (Pl. 10, figs. 4–6; Pl. 11, figs. 1, 2; Figs. 1, 2b, 2c).

D i a g n o s i s. As for the genus.

D e s c r i p t i o n (Figs. 1–4). The phylloclade consists of a planate axis 4–4.5 mm wide and lateral branches. The most complete specimen is a shoot 50 mm long (Pl. 10, fig. 4). The axis is covered with scaly leaves that partially belong to the decurrent bases of lateral branches. Leaves supporting the lateral branches are relatively large, variously connate, elliptical, 1.4–1.6 mm wide, alternate, the step of the spiral is about 1 mm.

The compression shows a dorsoventrally differentiated shoot: the supposed lower (abaxial) side has more or less distinct leaves and a higher stomatal index, whereas the opposite (upper, adaxial) side is more flattened, and the leaves are no longer distinct.

Lateral branches are placed 5–7 mm apart on the main axis of the shoot, at an angle about 90°. They are subopposite, flattened-cylindrical, apically rounded, straight or reflexed, about 12 mm long and 2–3 mm wide in the middle of the shoot, rapidly tapering toward the apex. The leaves are obovate, decurrent, and variously fused and reduced. The cohesion of the leaves increases from the base of the branch toward the apex and is more complete on the flattened adaxial side. The abaxial leaves are fused in pairs basally (Pl. 10, fig. 6, Fig. 1a) or along their entire length; they form a facial row of slightly convex, transversely elongated leaf cushions of elliptical, trapezoidal, or polygonal outlines, 1.5 mm wide, giving the branch an articulate aspect (Pl. 10, fig. 8). On the flattened side, these variants are matched by transverse leaf cushions (Fig. 1b) or transverse sutures that in the extreme case are distinguishable only on the cuticle (Pl. 10, figs. 5, 7).

The branchlets of the last order are axillary, adnate to their supporting leaves, mostly reduced to rounded-elliptical or subspherical lobes that may appear as lateral scaly leaves, the opposite leaves of the lateral pairs being directly fused with each other (connected by a concave suture) on the flattened foliar side of the shoot (Fig. 1c).

The phylloclades are amphistomatic, the cuticle is thick (6–8 μm), resistant to maceration. The cuticles of the lower and upper epidermises are of approximately equal thickness (Fig. 2a). The ordinary epidermal cells are pentagonal to heptagonal, with straight, smooth anticlinal walls, 15–30 μm across (Pl. 11, fig. 1). In the basal region of the leaf, they become slightly larger, and the degree of cutinization decreases. The periclinal wall bears a median papilla that is basally 7–8 μm in diameter and up to 3 μm high. The largest papillae are situated in the marginal regions of the leaf; in the central part, papillae are sometimes lacking (Pl. 11, figs. 3, 5). The densities of stomata are different on the opposite leaf surfaces: on the side with more distinct leaf scales (the

Explanation of Plate 10

Figs. 1–8. *Permophyllocladus polymorphus* gen. et sp. nov.: (1) paratype PIN, no. 5139/4, abaxial side of the apical region of a flattened dorsoventral scale-leaved shoot; (2) the same, adaxial side; (3) paratype PIN, no. 5139/3, abaxial side of a shoot with two lateral branchlets; (4) holotype PIN, no. 5139/1, compression of the middle portion of a phylloclade with lateral branchlets; (5) holotype PIN, no. 5139/1, adaxial side of a lateral branchlet; (6) holotype PIN, no. 5139/1, abaxial side; (7) paratype PIN, no. 5139/2, adaxial side of the compression of a lateral branchlet with two rows of scales on the rachis; (8) the same, abaxial side; (1, 2, 6) SEM; (3, 5) LM.
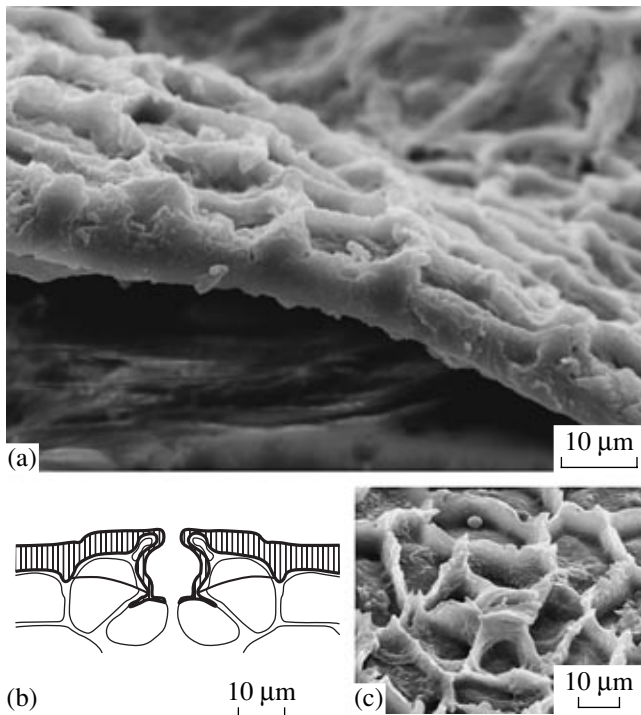
Plate 11
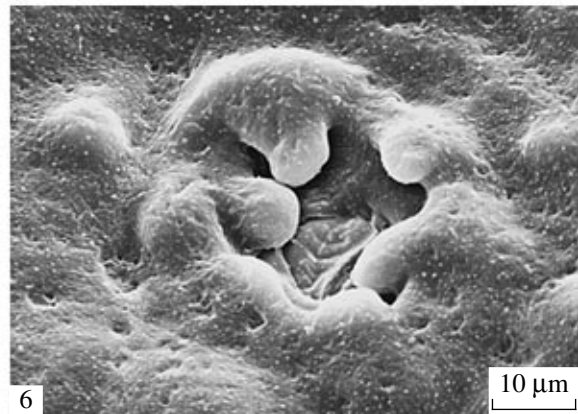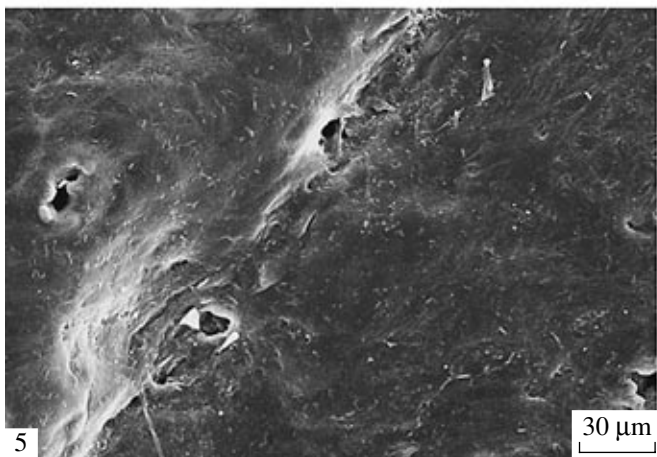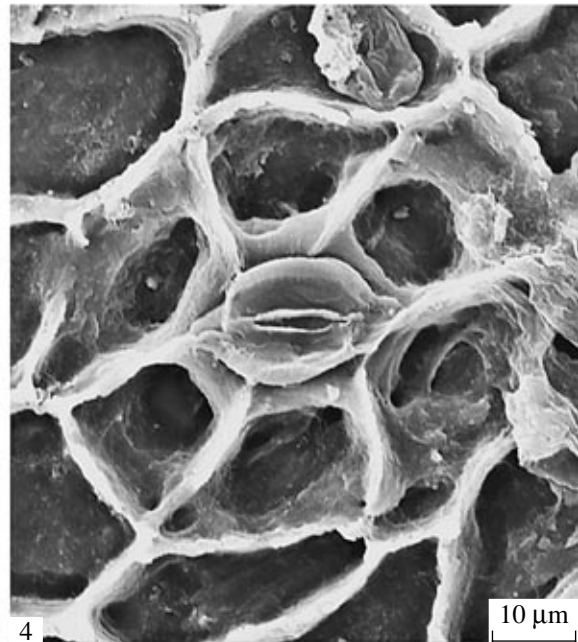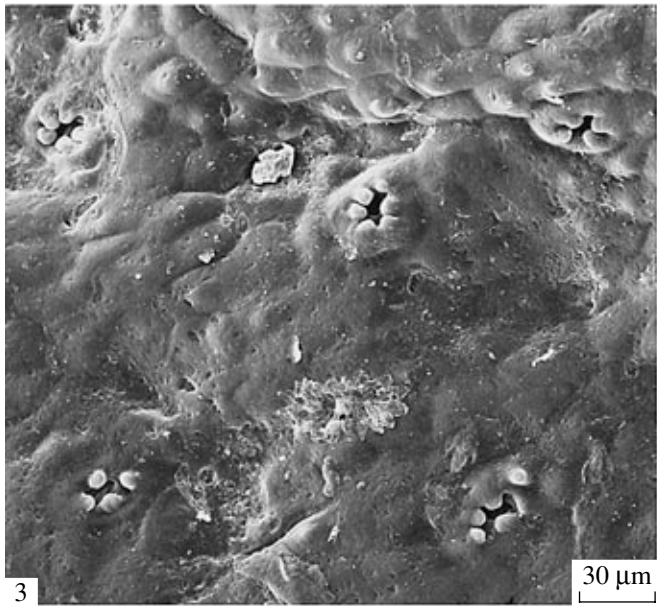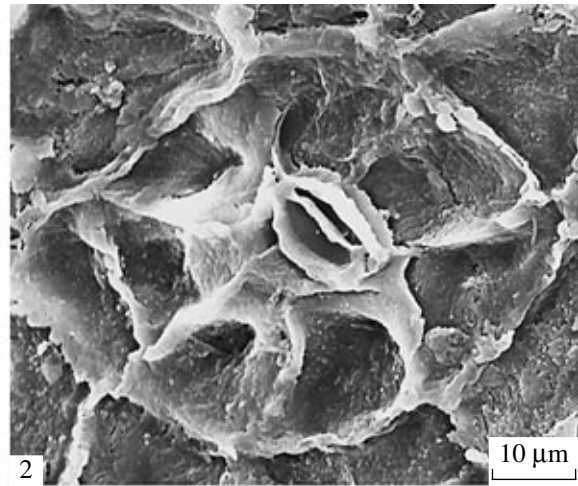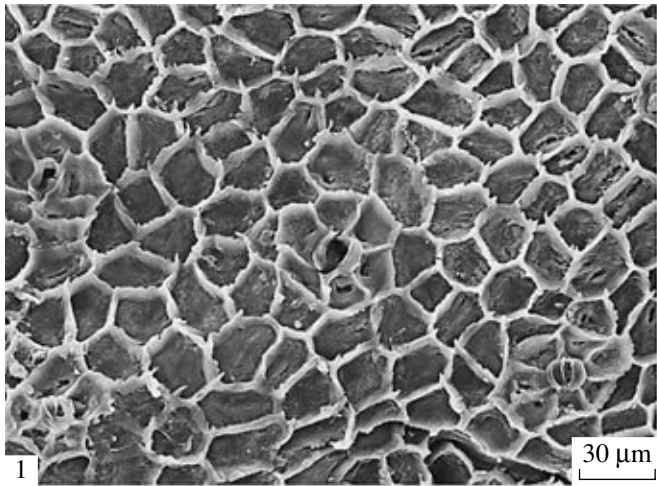
Fig. 2. *Permophyllocladus polymorphus* gen. et sp. nov., holotype PIN, no. 5139/1: (a) thickness of the lower cuticle, SEM; (b) schematic reconstruction of stomatal apparatus; (c) stomatal apparatus at an angle of 45°, SEM; (a, c) Vladimir Region, vicinity of the town of Vyazniki, Sokovka locality, Upper Permian, Tatarian.

abaxial side) the stomata are twice as frequent as on the other side (table), they are regularly arranged and do not form rows. The stomatal apertures are irregularly orientated.

Stomata are monocyclic, encyclocytic, or, less commonly, actinocytic. Usually, there are six subsidiary cells, or, more rarely, four, five, or seven. They are radially arranged around the stoma, their distal walls form a ring or an irregular contour 38–56 μm across. The proximal walls are strongly cutinized, papillate, the papillae are hollow, sometimes apically thickened, or, more rarely, solid. The base of papilla is about 5–8 μm in diameter, the height is up to 6 μm (Pl. 11, fig. 6). The guard cells are sunken at a depth of 5–10 μm below the leaf surface. They are 10–13 μm long, 3.8–5.5 μm wide (Pl. 11, fig. 2, Figs. 2b, 2c).

There are phylloclades with the leaves that are only basally connate on the penultimate axis, forming a wide inversely wedge-shaped bilobed scale. In such speci-
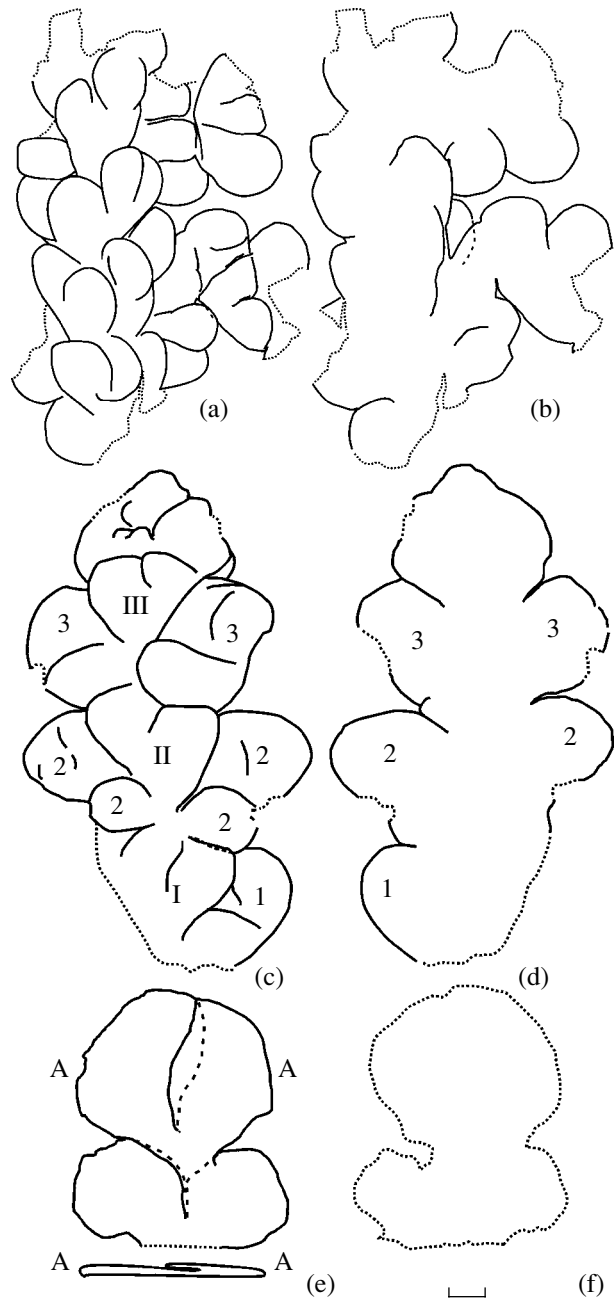

Fig. 3. Polymorphism of phylloclades of *Permophyllocladus polymorphus* gen. et sp. nov.: (a, b) PIN, no. 5139/3, phylloclade with two lateral branchlets; (c, d) paratype PIN, no. 5139/4, apical region of a branch with pinnule-like ultimate branchlets; (e, f) paratype PIN, no. 5139/7, apical portion of a leaflike branchlet and schematic section along the line A–A; (a, c, e) abaxial side; (b, d, f) adaxial side; (1, 2, 3) pinnule-like lateral branchlets; (I, II, III) facial rows of leaf cushions. Scale bar 500 μm.

E x p l a n a t i o n   o f   P l a t e   11

Figs. 1–6. *Permophyllocladus polymorphus* gen. et sp. nov., cuticle, SEM: (1, 2) holotype PIN, no. 5139/1; (1) lower cuticle of a scaly process of a lateral branchlet; (2) encyclocytic stomatal apparatus; (3) paratype PIN, no. 5139/4, external surface of the cuticle with distinct papillae on ordinary epidermal cells; (4) paratype PIN, no. 5139/7, stomatal apparatus of a leaflike branchlet; (5) paratype PIN, no. 5139/3, external surface of the upper cuticle with occasional papillae on ordinary epidermal cells; (6) paratype PIN, no. 5139/4, stomatal apparatus with large proximal papillae overhanging the stoma.
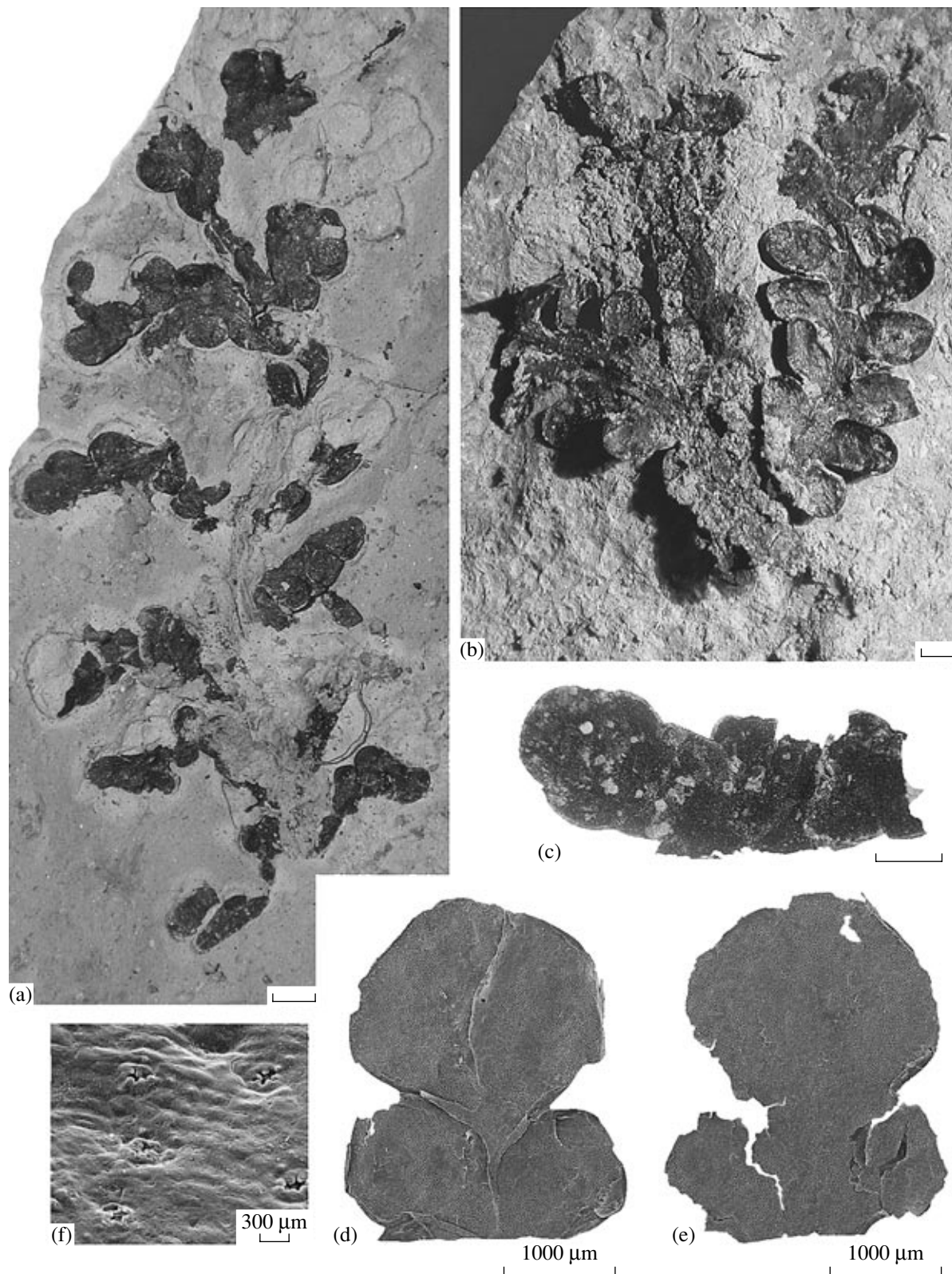
Fig. 4. Polymorphism of phylloclades of *Permophyllocladus polymorphus* gen. et sp. nov.: (a) paratype PIN, no. 5139/6, compressed shoot with lobed pinnule-like lateral branchlets; (b) paratype PIN, no. 5139/5, compressed shoot with entire pinnule-like lateral branchlets; (c) paratype PIN, no. 5139/6, adaxial side of a compressed pinnule-like branch; (d, e) paratype PIN, no. 5139/7, two sides of a compressed apex of pinnule-like branchlets, SEM; (f) PIN, no. 5139/4, external side of lower cuticle, SEM; (a–f) Vladimir Region, vicinity of the town of Vyazniki, Sokovka locality, Upper Permian, Tatarian; (c) LM; (d–f) SEM. Scale bar (a–c) 1000 μm.

mens, the terminal branchlets are better developed, with distinct scaly leaves (Pl. 10, figs. 1–3). On the abaxial side of the penultimate axis, facial leaves are tear-shaped or obovate, 1.0–1.8 × 1.2–1.7 mm. On the adaxial side, they are reduced to cuticular folds (Figs. 3a, 3b). The branchlets of the ultimate order are elongate or conical, up to 2 mm long, with one or two pairs of proximal leaves and a subspherical leaflike apex (Figs. 3c, 3d). The leaves are adnate, fused for their entire length, separated by a transverse fold, or else they have free triangular tips. The cohesion of basal leaves of lateral branchlets with their subtending leaf on the penultimate axis results in a large (0.7–1 mm wide) irregular leaf cushion at the base of the branchlet. Occasionally, the ordinary epidermal cells are smooth-walled and without papillae (Pl. 11, fig. 5).

The most leaflike specimens (Figs. 3e, 3f, 4a–4e) have elongate pinnae (modified lateral branches) with two rows of contacting pinnules (modified ultimate branchlets), abaxially fused, and with an apical pinnule. The lateral pinnules are obovate, spatulate, or rhomboidal, decurrent, usually measuring about 1.6 × 1.6 mm. The apical pinnule, which is formed of completely fused distal scaly leaves, is larger and rounded. Abaxially, it is divided by a median longitudinal fold, and adaxially it is entire. Epidermal cells along the pinnule margins are distinctly elongate, the stomata are larger, the contour of subsidiary cells is 50–60 μm across, the guard cells are longer, up to 20 μm (Pl. 11, fig. 4, Fig. 4d). SI on the abaxial (divided) side is 3.46, whereas on the adaxial (entire) side it is 2.72.

M a t e r i a l. Seven impressions of phylloclades with preserved compressions, including four fragments of the middle region with lateral branches and three detached lateral branchlets.

DISCUSSION

The polymorphism of *Permophyllocladus* gen. nov. allows the transitions to be traced from a scale-leaved shoot with incipient dorsoventral differentiation to a pinnate phylloclade having variously reduced scaly leaves. The comparison with leaves of peltasperms shows that some callipterids (e.g., *Lepidopteris martinsii*) also betray phylloclade characteristics, although they are less distinct. Phyllocladization is even more advanced in the foliar organs assigned to *Lepidopteris* and *Meyenopteris*, which are usually considered as fernlike foliage, typical of pteridosperms. Axial scales or swellings recorded in such "leaves" have formerly been interpreted as analogous to petiolar scales of ferns or as glands. Our data support the hypothesis that they are reduced leaves of an initial scale-leaved shoot.

Therefore, we have obtained evidence of the phylloclade nature of the leaves of the dominant Permian gymnosperms, peltasperms. While in *Permophyllocladus* the initial shoot with scaly leaves has not yet lost its morphological distinctness showing successive phases

Density of stomata and stomatal indices for different sides. Lower surface denotes the lower surface of phylloclade, upper surface denotes the upper surface of phylloclade. (SD) number of stomata per mm^2, (SI) stomatal index

No.	Lower surface		Upper surface	
	SD	SI	SD	SI
1	103	3.62	75	2.47
3	70	3.46	44	2.72
5	113	4.44	38	1.82

of cohesion, dorsoventral differentiation, and leaflike flattening, in more advanced forms traces of phylloclade origin occur as the axial scales only or are altogether lacking.

Peltasperms are usually assigned to pteridosperms, a vast group of Late Paleozoic gymnosperms with large planate or more or less fernlike leaves. However, the difference between typical pteridosperms and peltasperms is that in the former group the ovules develop on the foliar organs, whereas in the latter group they are in cones.

Our data show that Permian gymnosperms with scale-leaved branching shoots ("conifers"), on the one hand, and with large pinnate leaves ("pteridosperms"), on the other, might have belonged to one natural plant group; this is supported both by the presence of transitional forms of phylloclades, described in this paper, and by similarity in epidermal characters.

However, the phyllocladization processes might have been differently orientated in peltasperms and coniferoids. In the former group, fusion of the leaves progresses from terminal branchlets towards branches of lower orders; in the latter, this process was directed oppositely, although a combination of both modes is conceivable.

In terms of morphogenesis, the difference between typical pteridosperms and cycads, which also contain forms with compound fernlike leaves, is that in pteridosperms the ovuliphores were comprised in phyllocladization, which led to the development of seeds on fernlike leaves, whereas in cycads only vegetative shoots were influenced by phyllocladization, and ovuliphores were variously strobilized. On account of the latter distinction, peltasperms are closer to cycads and may be considered as a possible ancestral group of Mesozoic cycadophytes.

When this paper was in press, Gomankov (2006) established a new species, *Lepidopteris archaica* Gomankov, including specimens from the Sokovka locality. However, the holotype of *L. archaica* from the

Fore-Urals has little in common with our species. Moreover, we see no confirmation of a phyllodial nature (developed from a petiole) of the leaf of *Lepidopteris*; according to our data, this is a homologue of the phylloclade rather than phyllode.

REFERENCES

1. S. A. Afonin, "Latest Permian Palynological Assemblage from Vyazniki, European Russia: Stratigraphic and Palaeoecological Significance in Relation to the Permo-Triassic Boundary," in *The Nonmarine Permian*, ed. by S. G. Lucas and K. E. Zeigler, New Mexico Mus. Nat. Hist. Sci. Bull., No. 30, 5–8 (2005).

2. V. K. Golubev, A. G. Sennikov, and S. V. Naugolnykh, "New Data on the Geology and Paleontology of Permian Deposits in the Vicinity of the Town of Vyazniki (Vladimir Region)," in *Paleostrat-2005. Annual Meeting of the Section of Paleontology of the Moscow Society of Nature Explorers and the Moscow Division of the Paleontological Society, Moscow, February 14–15, 2005* (Paleontological Inst. Ross. Akad. Nauk, Moscow, 2005), pp. 14–15.

3. A. V. Gomankov, "A New Species of the Genus *Lepidopteris* (Peltaspermaceae, Peltaspermales) from the Upper Permian of the Russian Platform," Botan. Zh. **91** (12), 1906–1914 (2006).

4. A. V. Gomankov and S. V. Meyen, *Tatarinovo Flora (Composition and Distribution in the Late Permian of Eurasia)* (Nauka, Moscow, 1986) [in Russian].

5. T. M. Harris, "The Fossil Flora of Scoresby Sound, East Greenland, Pt. 3," Medd. Grønl. **83**, 1–114 (1932).

6. F. M. Hueber and J. Watson, "The Unusual Upper Cretaceous Conifer, *Androvettia* from Eastern U.S.A.," Bot. J. Linn. Soc. **98**, 117–133 (1988).

7. S. V. Meyen, *Fundamentals of Paleobotany* (Chapman and Hall, London–New York, 1987).

8. S. V. Naugolnykh, "Upper Permian Flora of Vyazniki (European Part of Russia), Its Zechstein Appearance, and the Nature of the Permo-Triassic Extinction," in *The Nonmarine Permian*, ed. by S. G. Lucas and K. E. Zeigler, New Mexico Mus. Nat. Hist. Sci. Bull., No. 30, 226–242 (2005).

9. R. J. Poort and J. H. F. Kerp, "Aspects of Permian Palaeobotany and Palynology XI. On the Recognition of True Peltasperms in the Upper Permian of Western and Central Europe and a Reclassification of Species Formerly Included in *Peltaspermum* Harris," Rev. Palaeobot. Palynol. **63**, 197–225 (1990).

10. A. G. Sennikov and V. K. Golubev, "Unique Vyazniki Biotic Complex of the Terminal Permian from the Central Russia and the Global Ecological Crisis at the Permo-Triassic Boundary," in *The Nonmarine Permian*, ed. by S. G. Lucas and K. E. Zeigler, New Mexico Mus. Nat. Hist. Sci. Bull., No. 30, 302–304 (2005).

11. J. Watson, "Cheirolepidiaceae," in *Origin and Evolution of Gymnosperms*, Ed. by C. B. Beck (Columbia Univ. Press, New York, 1988), pp. 382–447.

12. F. I. Woodward, "Stomatal Numbers are Sensitive to Increases in CO Concentration from the Pre-industrial Levels," Nature **327**, 617–618 (1987).