

Basic reproductive strategies of glossopterids: supraidoadaptive divergence from the viewpoint of a non–Gondwana palaeobotanist

SERGE V. NAUGOLNYKH

Geological Institute of Russian Academy of Sciences, Pyzhevsky per. 7, 119017, Moscow, Russia.
Contract affiliation–Kazan Federal University, Kremlyovskaya St. 18, Kazan, 420008, Republic of
Tatarstan, Russia.
Email: naugolnykh@list.ru

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ABSTRACT

Naugolnykh SV 2016. Basic reproductive strategies of glossopterids: supraidoadaptive divergence from the viewpoint of a non–Gondwana palaeobotanist. The Palaeobotanist 65(1): 1–17.

The paper deals with two main tendencies in the reproductive adaptations of the glossopterids (order Glossopteridales Pant, 1982, class Glossopteridopsida Banerjee, 1984). The life conditions in densely inhabited communities compelled the glossopterids to use two considerably different reproductive strategies. The glossopterids with the ovuliferous reproductive organs similar to *Scutum* Plumstead, i.e. the large number of closely related genera, such as *Bifaria* Prevec *et al.*, *Dictyopteridium* Feistmantel ex Zeiller, *Hirsutum* Plumstead, *Homevaleia* Nishida *et al.*, *Lanceolatus* Plumstead, *Ottokaria* Zeiller emend. Pant & Nautiyal, *Pluma* Plumstead, *Plumsteadia* (= *Cystella*) Rigby, *Plumsteadiostrobus* Chandra & Surange, *Venustostrobus* Chandra & Surange, etc. were barochorous and produced very many small unwinged seeds. The seeds of that type of glossopterid fructifications fell down due to gravitation nearby the parent plant, after they detached from the reproductive organ. The chance for successful germination was minimal for these plants because of high density of plant population, and it was compensated by large amount of the produced seeds. The plants with the female reproductive organs of the genus *Partha* Surange & Chandra and similar genera *Denkania* Surange & Chandra, *Lidgettonia* Thomas, *Rusangea* Lacey *et al.* produced small numbers of relatively large seeds with well–developed wings. These plants were anemochorous. Their seeds were dispersed by wind over long distances, far away from the parent plant, and because of this the chance for successful germination of those plants was much higher. The direct result of this was the reduction of seed numbers on the fructifications of the second type.

Such diversification of reproductive strategies expressed in different styles of propagate dissemination (i.e. type of seed dispersal) was characteristic of glossopterids in all the Gondwana regions. This process agrees well with the concept of supraidoadaptive effects proposed by the present author.

Key–words—Glossopterids, *Glossopteris*, Evolution, Reproductive biology, Upper Palaeozoic, Gondwana.

ग्लोसोप्टेरिडों के आधारी पुनरुत्पादक कौशल : गैर–गोंडवाना पुरावनस्पतिविज्ञानी के दृष्टिकोण से
सुपरैडायोएडप्टिव भिन्नता

सर्ज वी. नौगॉल्लीख

सारांश

शोध–पत्र ग्लोसोप्टेरिडों (ग्लोसोप्टेरीडेल्स पंत, 1982 क्रम, ग्लोसोप्टेरीडॉप्सिडा बनर्जी 1984 वर्ग) के पुनरुत्पादक रूपांतरों में दो मुख्य प्रवृत्तियों से संबंधित है। सघन आवासित समूहों में जीवन स्थितियों ने दो यथेष्टता से भिन्न पुनरुत्पादक युक्तियों का आदी होने को बाध्य किया। स्कुटम प्लमस्टीड के सदृश बीजांडधर पुनरुत्पादक अवयवों सहित, अर्थात् निकटता से संबंधित वंश की व्यापक संख्या जैसे कि *बिफरिला* प्रेवेक और अन्य, *डिक्टीओप्टेरिडियम* फीस्टमेंटल एक्स ज़ील्लर, *हिरसुटम प्लमस्टीड*, *होमेवेलीआ* निशीदा और अन्य, *लेन्सिओलेटस प्लमस्टीड*, *ओटोकोरिया* ज़ील्लर एमैंड. पंत और नौटियाल, *प्लुमा प्लमस्टीड*, *प्लमस्टीडिया* (= *सिस्टेला*) रिग्बी, *प्लमस्टीडियोस्ट्रोबस* चंद्रा और सुरंगे,

वेगुस्टोट्रोबस चंद्रा और सुरंगे इत्यादि वायुस्थायी थे तथा पूर्णतः अति सूक्ष्म पररहित बीज उत्पन्न किए। पुनरुत्पादक अवयव से उनके विलग्नोपरांत मूल पादप के समीप गुरुत्वाकर्षण के कारण ग्लोसोप्टेरिड फलनों के उस प्रकार के बीज गिर गए। पादप जनसंख्या की उच्च सघनता की वजह से इन पादपों के फलते-फूलते अंकुरण के मौके न्यूनतम थे तथा इसकी क्षतिपूर्ति बड़ी संख्या में उत्पन्न हुए बीजों से हो गई। *पार्थ* सुरंगे और चंद्रा वंश के मादा पुनरुत्पादक अवयवों सहित इन पादपों तथा सदृश वंश *डॅकनिया* सुरंगे और चंद्रा, *लिजेट्टोनिया* थॉमस, *रसंगिया* लेसी और अन्य ने सुविकसित परों सहित तुलनात्मक रूप से विशाल बीजों की कम संख्या उत्पन्न की। ये पादप पवनस्थायी थे। पवन से उनके बीज मूल पादप से बहुत दूर लंबी दूरी तक फैल गए, तथा इस वजह से उन पादपों के फलते-फूलते अंकुरण के अवसर अति प्रबलतर थे। दूसरे प्रकार के फलनों पर इसका सीधा असर बीज संख्या में कमी थी। प्रचार-प्रसार (अर्थात् बीज बिखराव का प्रकार) की विभिन्न विशिष्टताओं में व्यक्त पुनरुत्पादक कौशलों का ऐसा विविधरूपण समस्त गोंडवाना अंचलों में ग्लोसोप्टेरिडों का वैशिष्ट्य था। मौजूदा लेखक द्वारा प्रस्तावित सुपरैडायोएडप्टिव प्रभावों की संकल्पना से यह प्रक्रम भली-भांति अनुकूल है।

सूचक शब्द—ग्लोसोप्टेरिड, *ग्लोसोप्टेरिस*, उद्भव, पुनरुत्पादक जीवविज्ञान, ऊपरी पुरानूतन, गोंडवाना।

INTRODUCTION

PALAEOZOIC gymnosperms are represented by exceptionally high diversity in the Carboniferous and Permian, which at family level far exceeds the diversity of the extant representatives of this group. The glossopterids, a morphologically distinct group of gymnosperms, still remain enigmatic with respect to their phylogenetic links and taxonomic rank (Taylor & Taylor, 2009; McLoughlin, 2011).

During my visit in 2011 to the City of Lucknow, India, as an invited scientist of the Birbal Sahni Institute of Palaeobotany (BSIP), I had a very valuable opportunity for studying the original specimens of various reproductive organs of glossopterids, mostly from the famous Handapa locality, which are kept at the Palaeobotanical Museum of the BSIP (Chandra & Surange, 1977; Surange & Chandra, 1974a, b). After short time in Moscow I received several interesting specimens of fertile glossopterids from Upper Permian deposits of Australia, which were provided to me by colleague A.A. Razumovsky. All these materials, as well as personal impressions after work at the BSIP, were used as the basis of my considerations about possible reproductive strategies of glossopterids, which are summarized below.

Regarding general diversity of the gymnospermous fructifications, which are known from Gondwana, we should

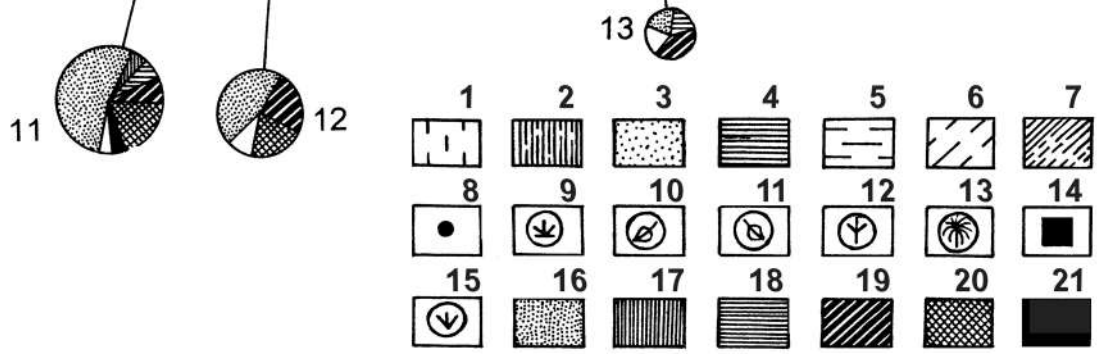
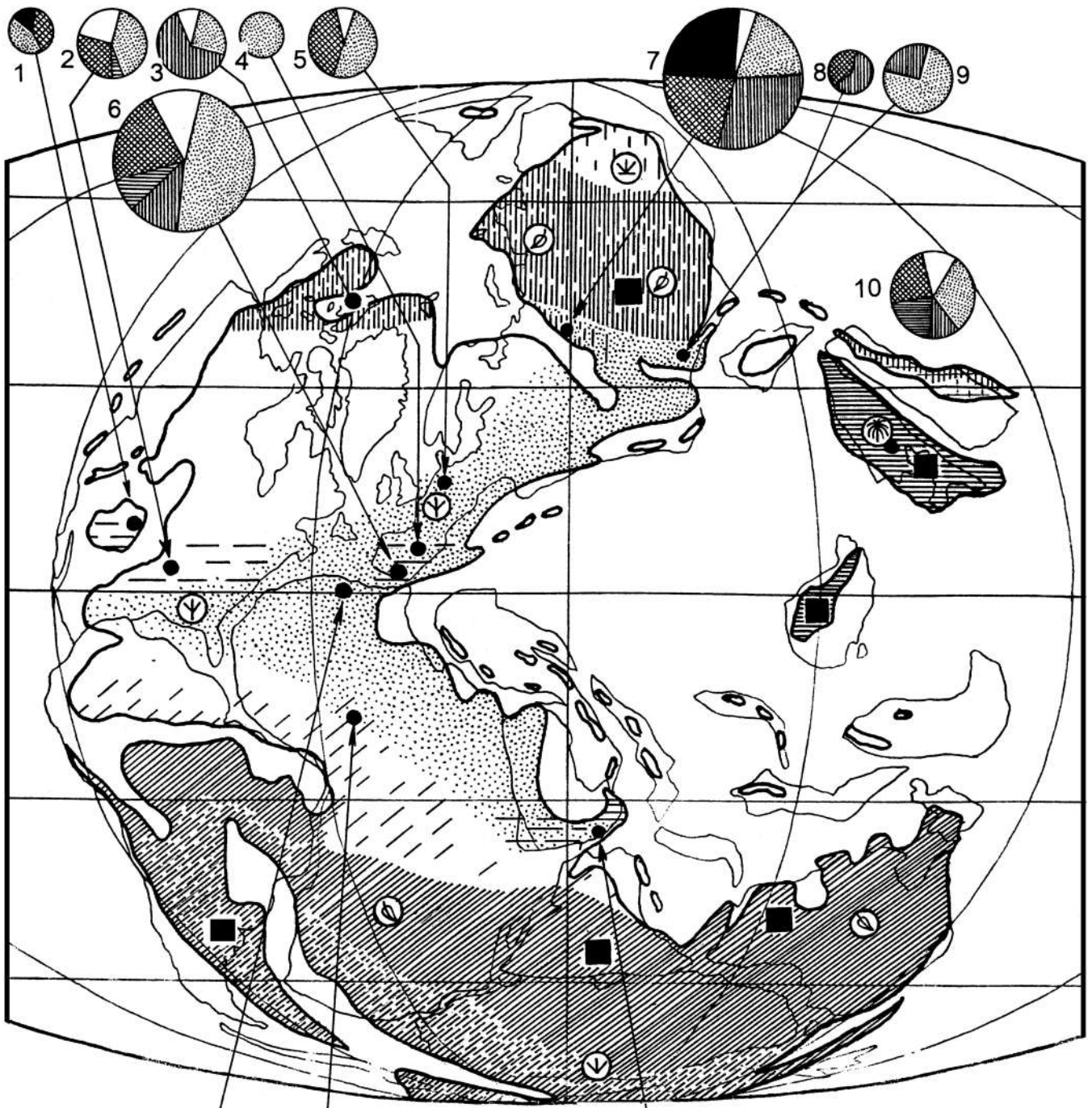
state that some of them still cannot be assigned with certainty to the higher taxa of gymnosperms (Chandra, 1984; Rigby & Chandra, 1990; Bajpai & Maheshwari, 1991), but others can be attributed to the glossopterids with confidence.

Glossopterids, the gymnosperms of the order Glossopteridales Pant, 1982 (class Glossopteridopsida Banerjee, 1984) were and still are in focus of many morphological, morphogenetical and anatomical studies (reviews and new data see in: Chandra & Surange, 1977; Rigby, 1978; Pant, 1987; McLoughlin, 1995; Pigg & Nishida, 2006; Nishida *et al.*, 2007; Prevec *et al.*, 2008; Prevec, 2011; Ryberg, 2009; Cariglini *et al.*, 2009). The most widely-accepted classification of glossopterids was proposed by J. Anderson and H. Anderson (Anderson & Anderson, 1985) and includes four families (Ottokariaceae, Rigbyaceae, Arberiaceae and Lidgettoniaceae) of one order Glossopteridales (Ottokariales). Some of the glossopterid plants are reconstructed on the basis of plexus-taxa, established on different parts belonging to one and the same parent plant (e.g. female fructifications *Dictyopteridium sporiferum* Feistmantel, produced ovules *Stephanostoma crystallinum* (Pant) Pant & Nautiyal, pollen-bearing organs *Eretmonia cf. hinjridaensis* Surange & Maheshwari, with microsporangia (“pollen sacs”) *Arberietta africana* Pant & Nautiyal, produced pollen *Protohaploxylinus limpidus*

Fig. 1—Permian World and selected Permian floras. 

Floristic assemblages: 1—Hermit (Read & Mamay, 1964); 2—Clear Fork (Read & Mamay, 1964); 3—Axel Herber Island (LePage *et al.*, 2003); 4—Pena Sagra (Gand *et al.*, 1997); 5—Elmshorn (Mädler, 1992); 6—Guadal canal (Broutin, 1974, 1977, 1985, 1986); 7—Kungurian flora of the Middle Cis-Urals (Naugolnykh, 1998); 8—Kyzylkiin flora (Salmenova, 1978, 1979); 9—Karmyz flora (Salmenova, 1978, 1979); 10—Taiyuan (Wang, 1996); 11—Tiddas (Broutin *et al.*, 1987); 12—Niger (Broutin *et al.*, 1990); 13—Ghariff (Broutin *et al.*, 1995).

Legend: 1–7—the biomes (1—boreal vegetation of tundra—or forest–tundra type with the low taxonomical diversity; 2—typically Angaran deciduous vegetation, Permian analogue of the present–day boreal forest, or “taiga”); 3—tropical to equatorial semi–arid zones; vegetation of the winter–wet Mediterranean ecological type; 4—equatorial and tropic evergreen vegetation, ecologically similar to the recent rain forests; 5—xerophilous vegetation of the playa depressions; 6—mix–zone of the Euramerian vegetation and vegetation of Southern moderate to cold–moderate biomes (Gondwana vegetation); 7—notal deciduous vegetation with the dominant glossopterids; 8—geographical position of the selected localities of fossil plants; regional floras. Life–forms or growth–forms of higher plants and types of the landscapes (9–13, 15): 9—chamephytes and hemicryptophytes, shrubs, tundra and forest–tundra; 10—phanerophytes, arborescent deciduous plants of the Northern Hemisphere (vojnovskyopsids); 11—phanerophytes, arborescent deciduous plants of the Southern Hemisphere (glossopterids); 12—xerophytes, represented by phanerophytes and chamephytes; semi–arid landscapes, colonized or inhabited by peltasperms and conifers; 13—equatorial rain forests; 14—zones of peat accumulation; 15—chamephytes and hemicryptophytes, supposed tundra zone of the Southern Hemisphere (notal area, Gondwana). Circle–diagrams (16–21); phytogeographically important genera: 16—Euramerian; 17—Angaran; 18—Cathaysian; 19—Gondwanan; 20—cosmopolitan; 21—endemic. Continent position is after A. Ziegler (Ziegler *et al.*, 1998). Size of the circle–diagrams corresponds to the degree of taxonomical diversity of the floras on generic level: I–1–5; II–6–19; III–20–39; IV–40–60.



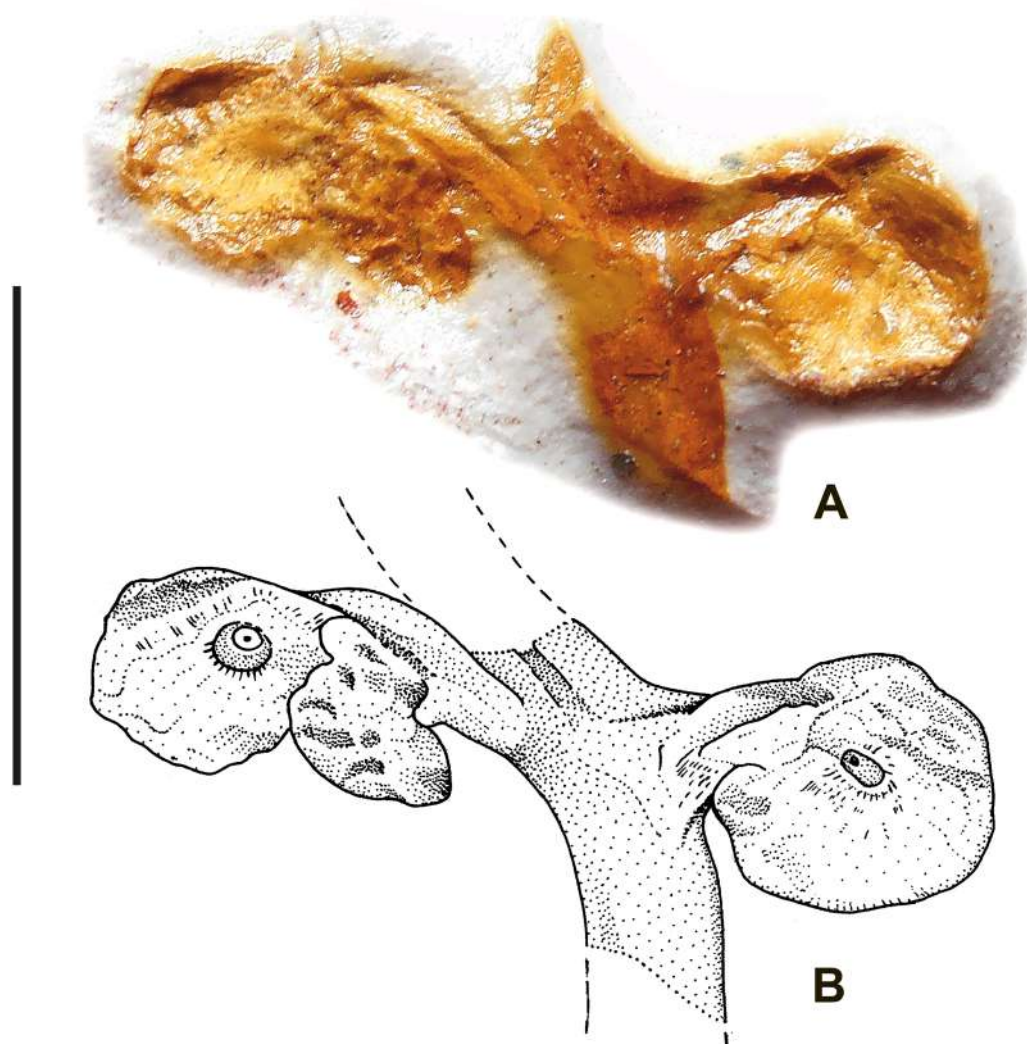


Fig. 2—*Partha* sp., female reproductive organ with two open seed-bearing capsules with the seed-scars; the seeds are detached. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. Spec. D–NSW–5A. Scale is 1 cm.

(Balme & Henelly) Balme & Playford, leaves *Glossopteris communis* Feistmantel, woods *Araucarioxylon bengalense* (Holden) Maheshwari, rootlets *Vertebraria australis* McCoy; Retallack & Dilcher, 1988).

The reproductive organs definitely affiliated with glossopterids have been studied in all possible details. Now it is even known that the glossopteris were zooidogamic plants (Nishida *et al.*, 2004).

Organic connection between several glossopterid fructifications and *Glossopteris* leaves has been proven by many well-preserved specimens (for instance, Plumstead,

1952, fig. 1, a, b; figs 2–4, 6, 7; Pl. XLIII, 1, 2; Pl. XLV, 1; Pl. XLVI, 1, 2; Pl. XLVII, 1; etc; Plumstead, 1958, Pl. VIII, 1; Pl. IX, 1, 2; Pl. X, 1, 3; Pl. XI; etc; *Ottokaria zeilleri* Pant & Nautiyal with the ovules in attachment: Pant & Nautiyal, 1984, text-fig. 1, A–C, E, F, Pl. 2, figs 9–13; Pl. 3, figs 20, 22; *Austroglossa walkomii* Holmes: Holmes, 1995, figs 22, 23, 25, 47).

Glossopterids played a dominant role in the most late Palaeozoic plant communities of the Southern Hemisphere (fig. 1), and thus were incorporated in the complex trophic structure of Gondwana ecosystems. The leaves of *Glossopteris*

PLATE 1

Glossopteris spp., diversity of the leaves. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. Scale is 1 cm. ➔

1. D–NSW–6D.
2. D–NSW–4D.
3. D–NSW–6G (morphotype *Glossopteris ampla* Dana).

4. D–NSW–7B.
5. D–NSW–7A (morphotype *G. elongata* Dana).

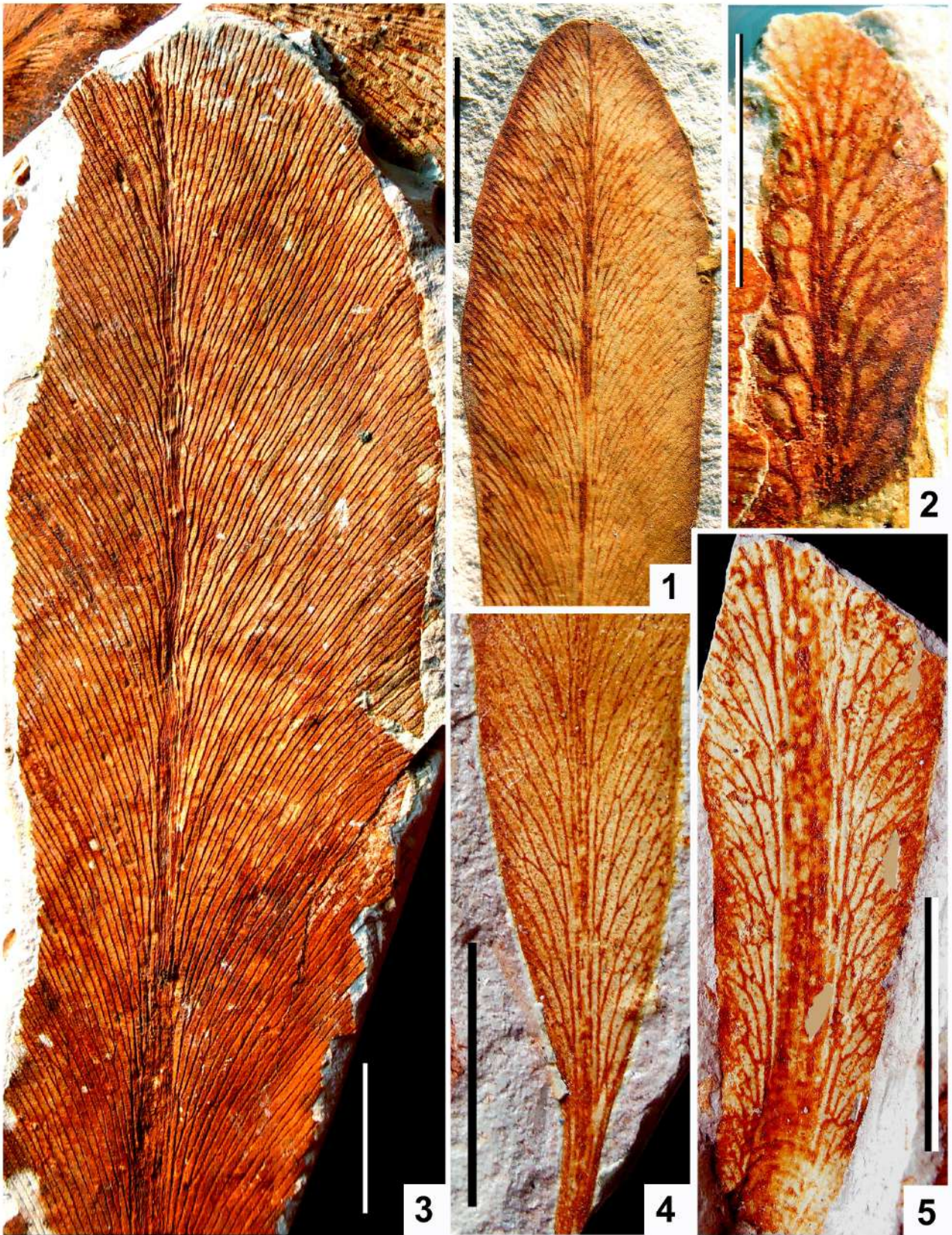


PLATE 1



Fig. 3—Digital remountage of the *Partha* sp. female fertiliger sitting on the leaf *Glossopteris browniana* Brongniart; the reconstruction on basis of the specimens D-NSW-5A (the fertiliger) and D-NSW-5B (the leaf). Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. Scale is 1 cm.

PLATE 2

Glossopteris spp., diversity of the leaves. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. Scale is 1 cm. ➔

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| 1. | D-NSW-1B. | 4. | D-NSW-1E (morphotype <i>Glossopteris leptoneura</i> Bunbury). |
| 2. | D-NSW-6A (morphotype <i>Glossopteris</i> cf. <i>ampla</i> Dana). | 5. | D-NSW-6C (morphotype <i>Glossopteris ampla</i> Dana). |
| 3. | D-NSW-6A. | | |

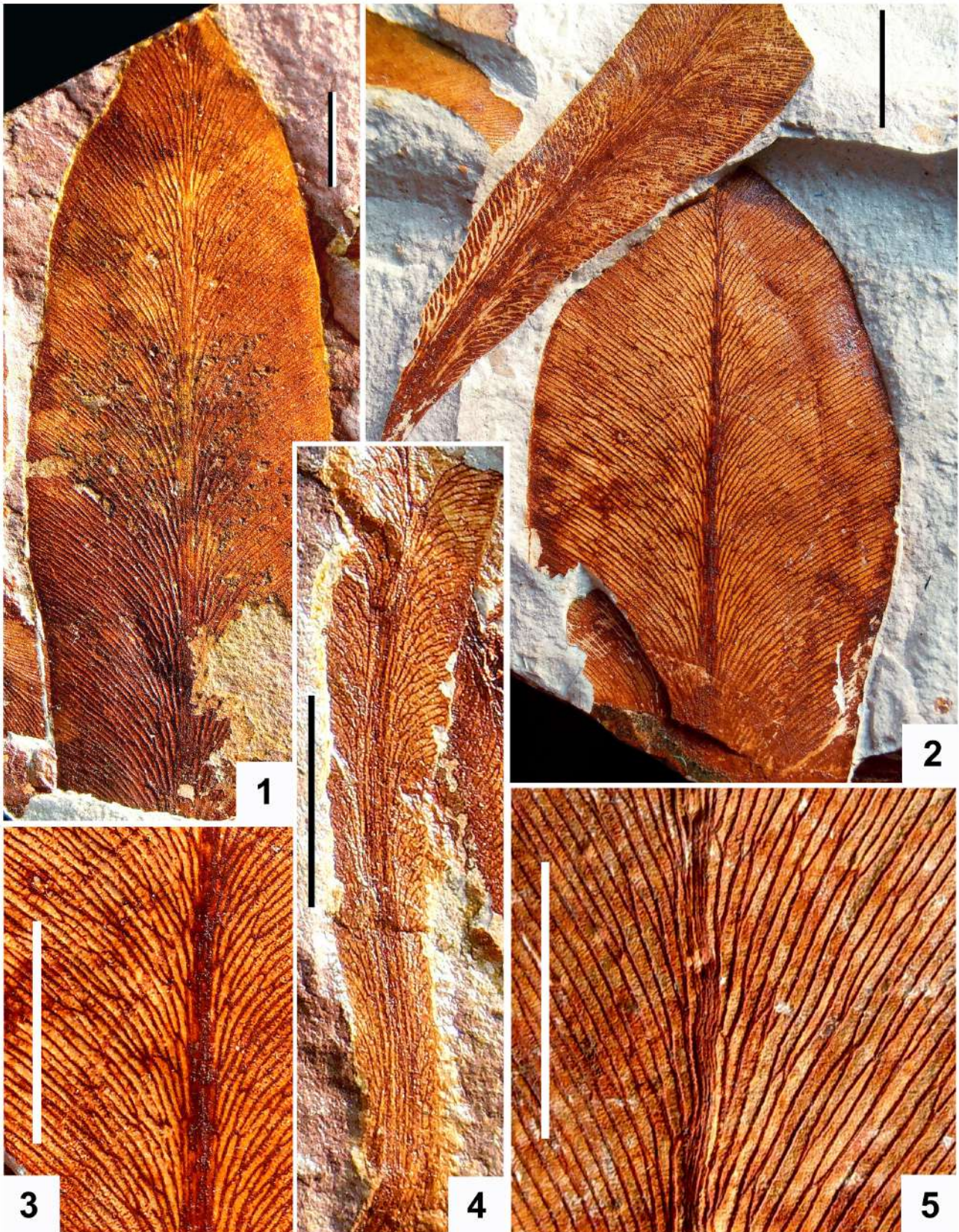


PLATE 2

were the trophic substrate for insects (Holmes, 1995, Fig. 54) and a place for their oviposition (Prevec *et al.*, 2009; McLoughlin, 2011; also see here Pl. 6.4).

The importance of the glossopterids is much higher than just at regional level, therefore I think that it is useful to discuss the morphology and systematics of that plant group internationally. My own thoughts on the glossopterids in general and their reproductive strategies are summarized in this paper.

MATERIAL

The specimens, which are kept at the Geological Institute of RAS (Moscow) and some of glossopterid fructifications, which are stored at the Repository of the Palaeobotanical Museum of the BSIP are used as the material for the present study. Bibliographical sources were used as well.

The collection of glossopterid remains, including leaves of *Glossopteris browniana* Brongniart from the Upper Permian deposits of the Illawarra Coal Measures, Dunedoo, New South Wales, Australia was provided to the author by A.A. Razumovsky (Figs 2, 3; Pl. 1–5), who officially obtained them from the distributive company “Crystal World & Prehistoric Journeys” (<www.crystal-world.com>). Additional specimens from the Handapa locality, Orissa State, India, which were used as the comparative material, were provided to the present author by K.J. Singh (Birbal Sahni Institute of Palaeobotany, Lucknow, India). The author expresses his sincere gratitude to all the persons who helped him with study of the Gondwana material.

SUPRAIDIOADAPTIVE EVENTS AND EFFECTS

The biological nature of supraadaptive events and effects should be explained in strict evolutionary terms. Some morphologically and taxonomically closely related organisms, which live together in one and the same communities ought to diverge physiologically, morphologically or behaviourally into separate adaptive spaces to avoid excessive competition.

The adaptive space effects are seen not only on the morphological architecture or fine structural peculiarities of the organisms, but also on their ethology. Changing and modifying the ethological features are very effective mechanisms of decreasing the competitive pressure within densely populated communities.

The most widespread expression of such changes and modifications is the adjustment of reproductive cycles, for example, changing the time of germination of spores or seeds, different types of pollination, etc. In other words, the most common ways to avoid excessive competition are to modify reproductive mechanisms in terms of ethological preferences. Thus, dividing of the ethological space allows the organisms to survive, especially when these organisms are coeval and exist in the same densely spaced communities.

The supraadaptive events and effects were reported and illustrated for the first time by the present author on the peltasperm s.l. and angaropeltian material from the lower Permian and uppermost Permian and lowermost Triassic deposits of the Cis-Urals and European part of Russia, or palaeophytogeographically from the Western Angaraland (Naugolnykh, 2007). In the case of angaropeltians two closely related genera *Sylvocarpus* Naug. and *Permoxylocarpus* Naug., which grew together in the same vegetation, were analyzed. These genera are basically similar, but differed strikingly in the extent of seed protection.

This difference most probably was also reflected in the speed and time of ovule germination, and in such a way the parent plants could divide their ethological space by one and the same idioadaptive process.

Practically the same supraadaptive pattern was characteristic of the Upper Permian and Lower Triassic genera *Navipelta* Karasev (Karasev, 2009) and *Vetlugospermum* Naugolnykh (Naugolnykh, 2012c). I sincerely think that just the same processes of diversification of the ethological space were and still are typical of many plants. We have many such examples among the fossil taxa, which grew together in one and the same communities. A good example is the Jurassic and Lower Cretaceous genera *Czekanowskia* and *Phoenicopsis* (Vakhrameev & Doludenko, 1961).

Coming back to the glossopterids it is worth saying that these plants existed in a taxonomically low-diversity vegetation. But this vegetation certainly was densely populated, what can be proved by palaeoecological and taphonomical observations (Taylor & Ryberg, 2007; Naugolnykh & Lunev, 2009). The glossopterid vegetation was commonly a source of peat accumulation, for example in the Antarctic Upper Permian Weller Coal Measures with predominant small to medium leaves of *Glossopteris* and the associated fructifications *Dictyopteridium*, *Rigbya*, *Senotheca* and *Squamella* (Retallack *et al.*, 2006), and namely the

PLATE 3

Glossopterids: female reproductive organs and details of morphology. Scale is 1 cm.



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| <ol style="list-style-type: none"> 1. Partly broken seed-bearing capsule, spec. D–NSW–3E. 2. Complete but not adult seed-bearing capsule probably belonging to the <i>Partha</i>-like reproductive organ, spec. D–NSW–4B. 3. seed-bearing capsule figured here on the Pl. III, fig. 2 in close association with the leaves <i>Glossopteris browniana</i> Brongniart, spec. D–NSW–4A, B. | <ol style="list-style-type: none"> 4. <i>Glossopteris</i> leaf with the juvenile seed-bearing capsule, spec. D–NSW–3C. 5. Net-venation of the leaf <i>Glossopteris</i>, spec. D–NSW–7A. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. |
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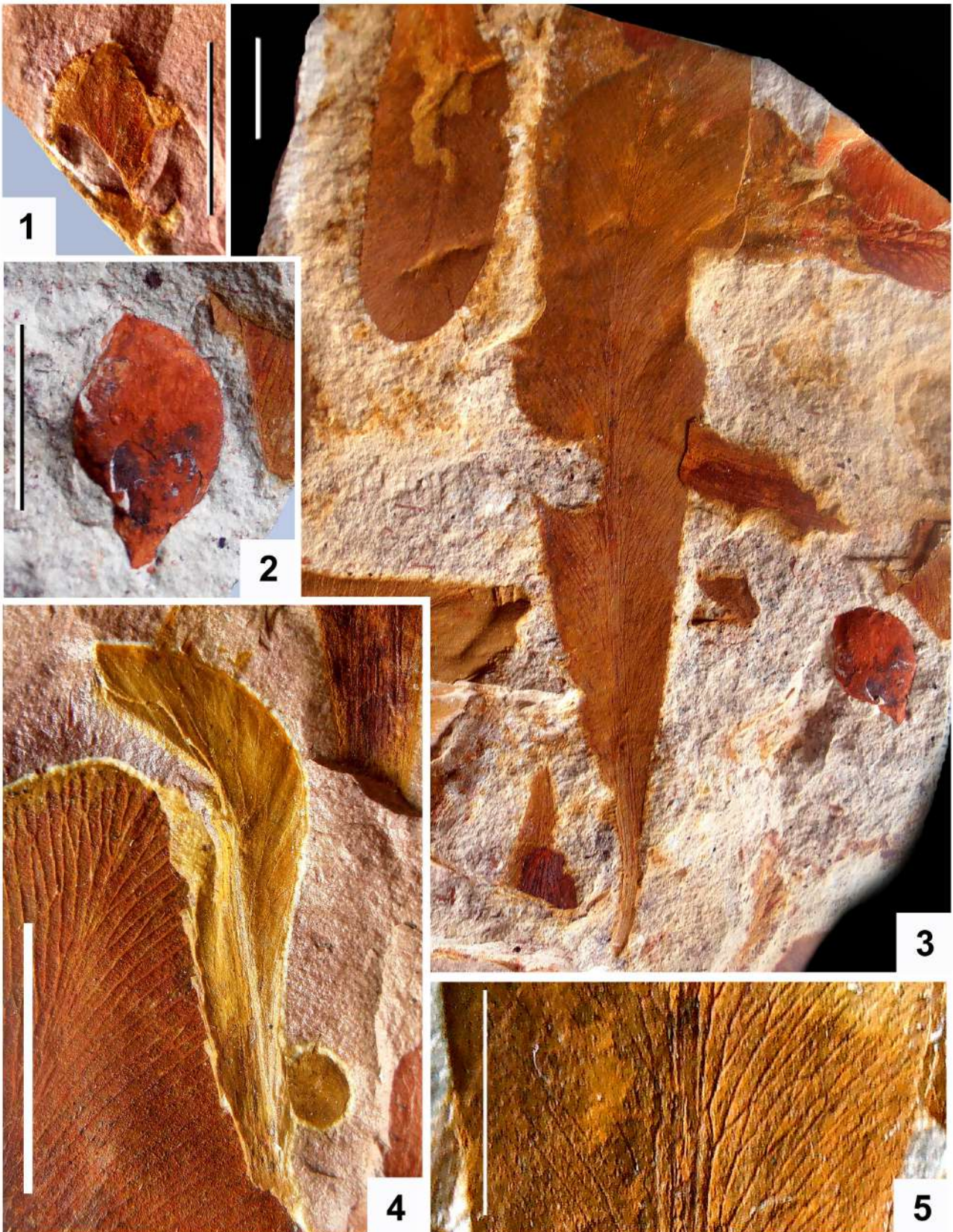


PLATE 3



Fig. 4—Reconstruction of the leafy shoot *Glossopteris* with the *Partha* sp. female reproductive organs. Late Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. Scale is natural size.

PLATE 4

Glossopterids: female reproductive organs and details of morphology. Scale is 1 cm. →

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| 1. <i>Partha</i> sp. (left up) in association with the leaf base <i>Glossopteris browniana</i> Brongniart, spec. D-NSW-5A. | 4. Net-venation of the <i>Glossopteris</i> leaf (see here figs 2, 5), spec. D-NSW-5B. |
| 2. General view on taphonomic association of glossopterid leaves and <i>Partha</i> reproductive organ (right up; same specimen is shown with more details on Pl. IV, figs 1, 3), spec. D-NSW-5A, B. | 5. <i>Glossopteris browniana</i> Brongniart, spec. D-NSW-5B. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia. |
| 3. <i>Partha</i> sp., detailed macromorphology, spec. D-NSW-5A. | |

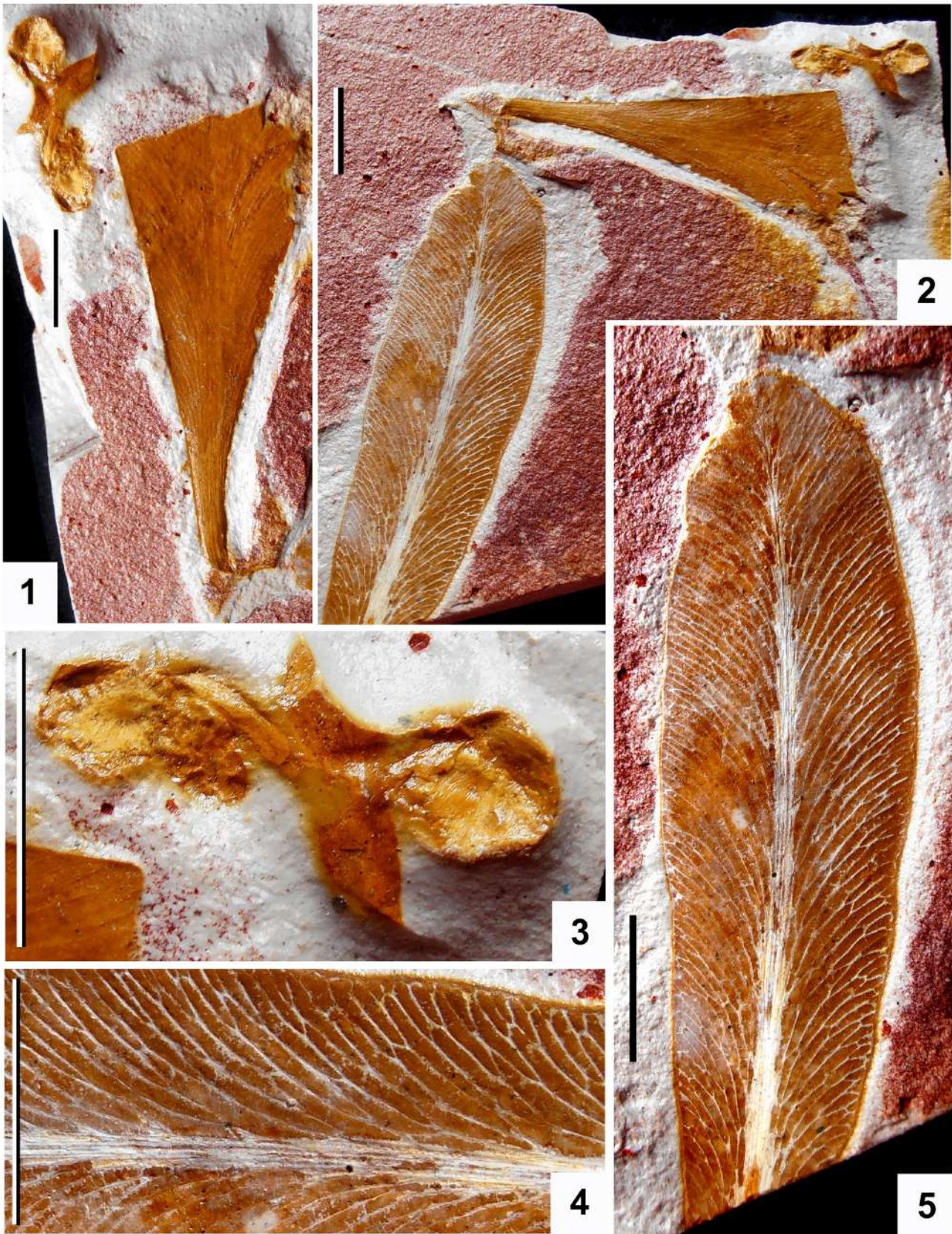


PLATE 4

glossopterids had largest potential in these peat-forming processes (Holdgate *et al.*, 2005).

To my viewpoint, these circumstances lead to supraidoadaptive events and processes in the glossopterid evolution. These plants certainly had to solve the problem of overpopulation, and could do it by means of supraidoadaptation by the diversification of their reproductive strategies.

OBSERVATIONS

The most abundant plant remains in the collection studied are leaves of the genus *Glossopteris*, which demonstrate several forms or morphotypes, normally assigned to different species, but linked by intermediate forms (Pl. 1–5). Thus, most of them were attributed here to the single species *Glossopteris browniana* Brongniart. Other similar “morpho-species” (*G. ampla* Dana, *G. angustifolia* Brongniart, *G. elongata* Dana, *G. communis* Feistmantel; see for details: Rigby *et al.*, 1980; Chandra & Singh, 1992) are cited here as conditional morphotypes.

The collection studied includes several fertile specimens, i.e. a fragment of fertiliger bearing two open bilobate seed-bearing capsules (Fig. 2; Pl. 4.1–3), four closed isolated capsules of the same type (Pl. 3.1–4; Pl. 5.2), and one open isolated capsule with the seed of *Samaropsis*-type just detached from it (Pl. 5.1, 4).

All the female seed-bearing capsules listed above were attributed with some doubts to the genus *Partha* Surange & Chandra (Surange & Chandra, 1973). The most representative specimen in the collection studied (Fig. 2; Pl. 4.1–3) is a part of the axis with two lateral appendages bearing open bilobate capsules. Width of the axis is 2 mm; observed length of the axis is 10 mm, but certainly it was somewhat longer when the plant was alive. Length of the lateral appendages is 4 mm each, width is 0.8 mm. Seed-bearing capsules have ovate outlines, with the length 4.5 mm and width 4 mm.

Each lateral appendage bears ovoid megasporophyll with a small seed scar disposed on its abaxial surface. The scar is not of central position, but located slightly asymmetrically closer to the proximal margin of the sporophyll. The seed scars are ovoid, 0.9 mm in maximal measurement, with the point-like exit of the conductive strand. The seed scar is surrounded by fine radial striation. When the ovules/seeds were immature, the capsule was closed or covered by second valve, which is preserved on the left megasporophyll on the Fig. 2 A, B. The

collection studied includes several isolated seed capsules of the same type, but of larger size (up to 10 mm long and 8 mm wide (Pl. 3.3). One of the capsules was just opened (Pl. 5.1, 4), and one can see a seed of *Samaropsis* type, which is preserved nearby the valves of the capsule. Judging from the megasporophylls with the single seed scar per megasporophyll shield and the specimen with the single seed nearby the opened capsule we can state that one megasporophyll produced only one winged *Samaropsis*-type seed. Since one fertiliger of *Partha* sp. has two megasporophylls, the fructification normally produced two seeds, in contrast to the multiovulate fructifications of *Ottokaria* and other related forms (see below).

The associated plant remains preserved together with the fructifications *Partha* sp. are represented exclusively by the leaves of *Glossopteris*, mostly assignable to the species *Glossopteris browniana* Brongniart, as it was already noted above, but with some exceptions represented by less frequent morphotypes. I am far from certain that all these leaf morphotypes of *Glossopteris* belonged to one and the same natural or botanical species, but certainly some of them are linked to each other by intermediate forms and can be no more than just ecological morphs or varieties of one parent plant. I think it is not too difficult to prove it by means of comparative analysis of rather large collection, but this task is not a subject of the present paper.

REPRODUCTIVE STRATEGIES OF GLOSSOPTERIDS

There are two basic types of female fructifications of glossopterids in the most localities of glossopterids around the world. Both types are fertiligers, i.e. reproductive structures attached to the vascular cluster of medial veins of the unspecialized or weakly specialized glossopterid leaf.

Fertiligers of the first type are relatively large, normally assigned to the genus *Scutum* Plumstead and several morphologically similar genera. They bear a large number (several dozens) of small spherical to ovoid, normally unwinged seeds or seeds with a very slender wing. The similar genus *Ottokaria* Pant & Nautiyal bears many small ovules of round to ovoid shape, with weakly-developed wings (Pant & Nautiyal, 1984, text-fig. 1, A–D, text-fig. 2, D, I, F; text-fig. 3, A–F).

PLATE 5

Glossopterids: female reproductive organs and details of morphology. Scale is 1 cm.



1. The open seed-bearing capsule *Partha* sp. with the detached seed (right) of *Samaropsis*-type, spec. D–NSW–2C.
2. Seed-bearing capsule *Partha* sp. nearby the leaf *Glossopteris browniana* Brongniart, spec. D–NSW–2A.
3. *Glossopteris browniana* Brongniart, venation in the basal part of the leaf, spec. D–NSW–3A.
4. The open seed-bearing capsule *Partha* sp. (details see here on the Pl. V, fig. 1) in close taphonomic association with the leaves *Glossopteris browniana* Brongniart, D–NSW–2C. Upper Permian; Illawarra Coal Measures, Dunedoo, New South Wales, Australia.

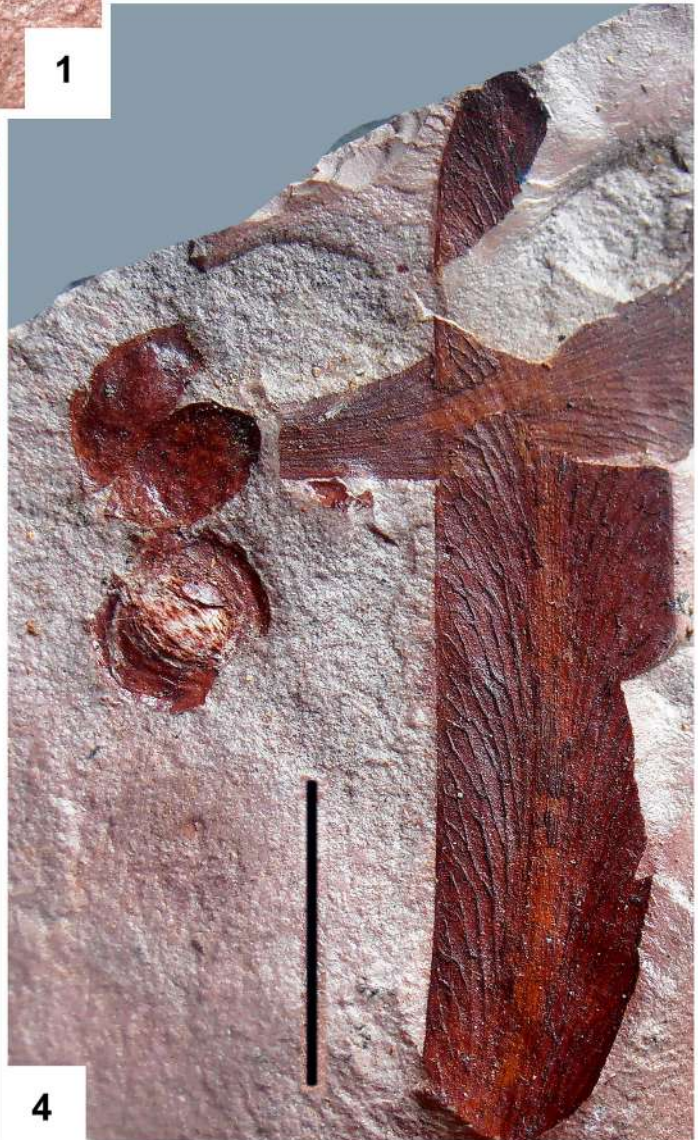
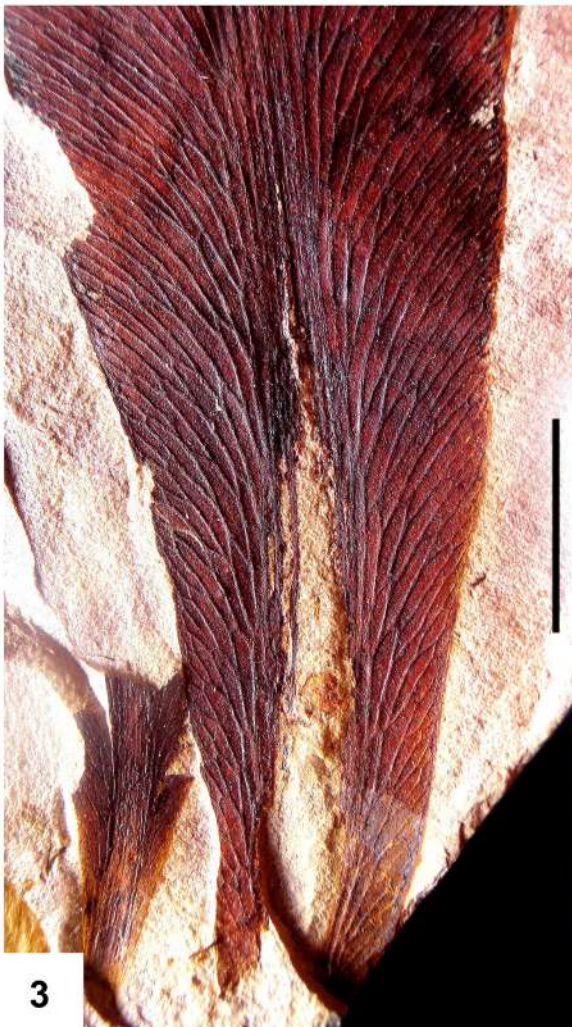


PLATE 5

Fertiligers of the second type, in contrast, are relatively small. Fructifications of that type from the Handapa locality are assigned to the genera *Partha* and *Denkania*. A single organ of this (second) type of fertiligers produced one to ten seeds of larger size and with the well-developed wings. Perhaps the genus *Cometia* McLoughlin from the Permian deposits of Australia (McLoughlin, 1990b) also belongs to the second type of the glossopterid fertiligers.

The glossopterids or at least some of them grew in near-water habitats and were peat-forming plants (McLoughlin, 1993). This has been shown in a great number of palaeobotanical and palaeoecological works; but for me this fact became unequivocal during study of material from the Upper Permian deposits of the Amery Group in the Beaver Lake and Radok Lake area, Antarctica (Naugolnykh & Lunev, 2009). We can consider the conditions of existence of the glossopterids as more or less similar. I think that these plants lived in the same palaeophytocoenoses, and most probably the life conditions in densely inhabited communities provoked the glossopterids to use two considerably different reproductive strategies.

The glossopterids with the female reproductive organs like *Scutum* Plumstead and a large number of closely related genera, such as *Bifariata* Prevec *et al.*, *Dictyopteridium* Feistmantel ex Zeiller, *Hirsutum* Plumstead, *Homevaleia* Nishida *et al.*, *Lanceolatus* Plumstead, *Ottokaria* Zeiller emend. Pant & Nautiyal, *Pluma* Plumstead, *Plumsteadia* (= *Cystella*) Rigby, *Plumsteadiostrobos* Chandra & Surange, *Venustostrobos* Chandra & Surange, *Senotheca* Banerjee (see for details: Banerjee, 1969; McLoughlin, 2012) were barochorous and produced a large number of small unwinged seeds. The seeds of *Plumsteadia* and similar types of fructifications were borne on the surface of the megasporophyll lamina, that faced the leaf-like bract (McLoughlin, 1990a, text-fig. 3), in contrast to other version of ovules disposition of *Ottokaria zeilleri* Pant & Nautiyal (Pant & Nautiyal, 1984, text-fig. 6, A), which probably was misinterpreted by observation on twisted specimen (personal communication by S. McLoughlin to the present author).

The seeds of that type of glossopterid fructifications fell down due to force of gravitation nearby the parent plant,

after they were detached from the reproductive organ. The chance for successful germination was minimal for these plants because of high density of plant population, and it was compensated by the large numbers of produced seeds.

The plants with the female reproductive organs of the genus *Partha* Surange & Chandra, as well as other related genera *Denkania* Surange & Chandra, *Lidgettonia* Thomas, *Rusangea* Lacey *et al.*, and probably *Cometia* McLoughlin produced small numbers of relatively large seeds with well-developed wings. The genera *Partha*, *Rusangea* and *Denkania* probably are synonyms of *Lidgettonia* (Anderson & Anderson, 1985; and personal communication of S. McLoughlin). Certainly, those plants were anemochorous. Their seeds were dispersed by wind for long distances, far away from the parent plant, and because of this the chance for successful germination of those plants was much higher. The direct result of this was the reduction of the number of seed per fertiliger of second type.

I contend that this diversification of reproductive strategies expressed in different modes of dissemination (i.e. type of seed dispersal) was characteristic of glossopterids in all Gondwana regions. This process is in good agreement with the concept of supraidiadaptive effects proposed by the present author (see above; details are in: Naugolnykh, 2012a, b).

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PLATE 6

Glossopterids: female reproductive organs and details of morphology. Scale is 1 cm.



1. *Glossopteris browniana* Brongniart, the leaf damaged (eaten) by an insect, marked by an arrow, spec. I-HND-3A.
2. Multiovulate reproductive organ *Scutum sahnii* Surange & Chandra, one small unwinged seed is marked by an arrow (original description of the specimen is published by: Surange & Chandra, 1974a).
3. *Partha spathulata* Surange & Chandra (original description of the specimen is published by: Surange & Chandra, 1973).
4. The leaf of *Glossopteris browniana* Brongniart with the traces of insect activity (feeding?), spec. I-HND-1.
5. Almost complete young leaf of *Glossopteris browniana* Brongniart, with partly damaged apex, spec. I-HND-2A. Upper Permian, Handapa. Orissa, India.

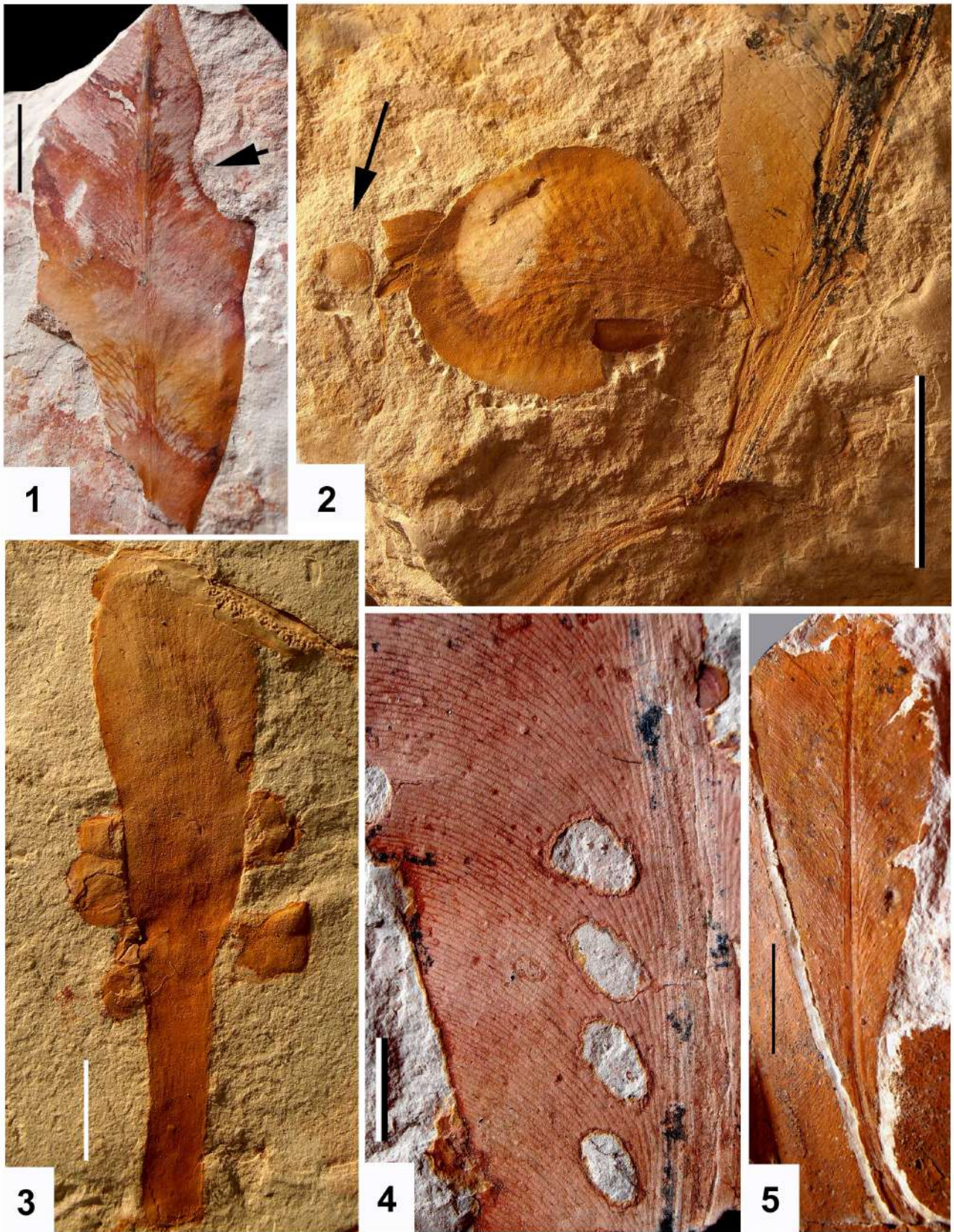


PLATE 6

REFERENCES

- Anderson JM & Anderson HM 1985. Palaeoflora of South Africa. Prodrum of South African megaflores: Devonian to Lower Cretaceous. A.A. Balkema, Rotterdam.
- Bajpai U & Maheshwari HK 1991. On two enigmatic infructescences from Permian Gondwana of the Rajmahal Basin. *Palaeobotanist* 39: 9–19.
- Banerjee M 1969. *Senotheca murulidihensis* a new glossopteridean fructification from India associated with *Glossopteris taeniopteroides* Feistm. Sen Memorial Volume, Botanical Society of Bengal, Calcutta: 359–368.
- Banerjee M 1984. Fertile organs of the *Glossopteris* flora and their possible relationship in the line of evolution. Proceedings of a Symposium on Evolutionary Botany and Biostratigraphy, AK Ghosh Commemoration Volume: 29–59, Today and tomorrow's Printers and Publishers, New Delhi.
- Broutin J 1974. Sur quelques plantes fossiles du bassin Autun–Stephanien de Guadalcanal (province de Seville, Espagne). *Lagasalia* 4: 221–237.
- Broutin J 1977. Nouvelles données sur la flore des bassins Autun–Stephaniens des environs de Guadalcanal (province de Seville–Espagne). *Guaderns Gelogia Iberica* 4: 91–98.
- Broutin J 1985. *Ginkgophyllum boureaui*, nouvelle espèce de ginkgophyta du Permien inférieur du Sud–Ouest de l'Espagne. Bulletin de la section des sciences, Tome. VIII, Paléobotanique recherches nouvelles sur l'évolution végétale: 125–132.
- Broutin J 1986. Etude paléobotanique et palynologique du passage Carbonifère–Permien dans le Sud–Oest de la Peninsula Ibérique. Paris: Ed. CNRS. 165 p.
- Broutin J, Doubinger J, El Hamet MO & Lang J 1990. Palynologie comparée du Permien Nigérien (Afrique occidentale) et Peritethysen. Implications stratigraphiques et phytogéographiques. *Review of Palaeobotany and Palynology* 66: 243–261.
- Broutin J, El Wartiti M, Freyret P, Heyler D, Lazhrib M & Morel J–L 1987. Nouvelles découvertes paléontologiques dans le bassin détritique carbonate Permien de Tiddas (Maroc Central). *C.R. Acad. Sci. Paris* 305(Ser. 2): 143–148.
- Broutin J, Roger J, Platel JP, Angiolini L, Baud A, Bucher H, Marcoux J & Al Hasmi H 1995. The Permian Pangea. Phytogeographic implications of new paleontological discoveries in Oman (Arabian Peninsula). *Comptes Rendus de l'Académie des Sciences* 321: 1069–1086.
- Cariglino B, Gutiérrez PR & Manassero M 2009. *Plumsteadia pedicellata* sp. nov.: a new glossopterid fructification from La Colondrina Formation (Guadalupian–Lopingian), Santa Cruz Province, Argentina. *Review of Palaeobotany and Palynology* 156: 329–336.
- Chandra S 1984. *Utkalia dichotoma* gen. et sp. nov.–a fossil fructification from the Kamthi Formation of Orissa, India. *Palaeobotanist* 31: 208–212.
- Chandra S & Singh KJ 1992. The genus *Glossopteris* from the Late Permian beds of Handapa, Orissa, India. *Review of Palaeobotany and Palynology* 75: 183–218.
- Chandra S & Surange KR 1977. Cuticular studies of the reproductive organs of *Glossopteris*. 2. *Cistiella* type fructification *Plumsteadiostrabus ellipticus* gen. et sp. nov. attached on *Glossopteris taenioides* Feistmantel. *Palaeobotanist* 23: 161–175.
- Gand G, Kerp H, Passons C & Martínez–García E 1997. Palaeoenvironmental and stratigraphic aspects of animal traces and plant remains in Spanish Permian red beds (Pena Sagra, Cantabrian Mountains, Spain). *Geobios* 30: 295–318.
- Holdgate GR, McLoughlin S, Drinnan AN, Finkelman RB, Willett JC & Chiehowsky LA 2005. Inorganic chemistry, petrography and palaeobotany of Permian coals in the Prince Charles Mountains, East Antarctica. *International Journal of Coal Geology* 63: 156–177.
- Holmes WBK 1995. The Late Permian megafossil flora from Cooyal, New South Wales, Australia. *Birbal Sahni Centenary Volume*: 123–152.
- Karasev EV 2009. A new genus *Navipelta* (Peltaspermales, Pteridospermales) from the Permian/Triassic Boundary deposits of the Moscow Syneclise. *Paleontological Journal* 43: 1262–1271.
- LePage BA, Beachamp B, Pfefferkorn HW & Utting J 2003. Late Early Permian plant fossils from the Canadian High Arctic: a rare paleoenvironmental/climatic window in northwest Pangea. *Palaeogeography, Palaeoclimatology, Palaeoecology* 191: 345–372.
- Mädler KA 1992. Die Rotliegend–Zechsteinflora von Lieth bei Elmshorn, Schleswig–Holstein. *Geologisches Jahrbuch, Reihe A* 133: 3–31.
- McLoughlin S 1990a. Late Permian glossopterid fructifications from the Bowen and Sydney basins, Eastern Australia. *Geobios* 23: 283–297.
- McLoughlin S 1990b. Some Permian glossopterid fructifications and leaves from the Bowen Basin, Queensland, Australia. *Review of Palaeobotany and Palynology* 62: 11–40.
- McLoughlin S 1993. Glossopterid megafossils in Permian Gondwanic non–marine biostratigraphy. *Gondwana 8, Assembly, Evolution, and Dispersal*. Rotterdam: A.A. Balkema. pp. 253–264.
- McLoughlin S 1995. New records of *Bergiopteris* and glossopterid fructifications from the Permian of western Australia and Queensland. *Alcheringa* 19: 175–192.
- McLoughlin S 2011. New records of leaf galls and arthropod oviposition scars in Permian–Triassic Gondwanan gymnosperms. *Australian Journal of Botany* 59: 156–169.
- McLoughlin S 2012. Two new *Senotheca* (Glossopteridales) species from the Sydney Basin, Australia, and a review of the genus. *Review of Palaeobotany and Palynology* 171: 140–151.
- Naugolnykh SV 1998. Kungurian flora of the Middle Cis–Urals. Moscow: Geos. 201 p. (Transactions of Geological Institute of Russian Academy of Sciences, Vol. 509) [in Russian, with English and French summaries].
- Naugolnykh SV 2007. Permian floras of the Urals. Moscow: Geos. 322 p. (Transactions of the Geological Institute of RAS, Iss. 524) [in Russian, with English and French summaries].
- Naugolnykh SV 2012a. How two genera were supplied by one ecological niche. *Priroda* 4: 31–38 [in Russian].
- Naugolnykh SV 2012b. Symbol of Gondwana. *Priroda* 12: 49–59 [in Russian].
- Naugolnykh SV 2012c. *Vetlugospermum* and Vetlugospermaceae: a new genus and family of peltasperms from the Lower Triassic of Moscow syncline (Russia). *Geobios* 45: 451–462.
- Naugolnykh SV & Lunev PI 2009. Palaeoecology of hygro–and hydrophilic palaeophytocoenoses as exemplified by the Permian plants in the Northern Prince Charles Mountains, East Antarctica. *Russian Earth Science Research in Antarctica*. Collection of papers. Vol. 2 (Ed. e.V. Mikhalsky, A.A. Laiba). Saint–Petersbourg: Okeanologia. P. 26–41.
- Nishida H, Pigg KB, Kudo K & Rigby JF 2004. Zooidogamy in the Late Permian genus *Glossopteris*. *Journal of Plant Research* 117: 323–328.
- Nishida H, Pigg KB, Kudo K & Rigby JF 2007. New evidence of reproductive organs of *Glossopteris* based on permineralized fossil from Queensland, Australia. I. Ovulate organ *Homevaleia* gen. nov. *Journal of Plant Research* 1209: 539–549.
- Pant DD 1982. The Lower Gondwana gymnosperms and their relationships. *Review of Palaeobotany and Palynology* 37: 55–70.
- Pant DD 1987. Reproductive biology of the Glossopterids and their affinities. *Bulletin de la Société botanique de France* 134: 77–93.
- Pant DD & Nautiyal DD 1984. On the morphology and structure of *Ottokaria zeilleri* sp. nov.–a female fructification of *Glossopteris*. *Palaeontographica Abt. B* 193: 127–152.
- Pigg KB & Nishida H 2006. The significance of silicified plant remains to the understanding of *Glossopteris*–bearing plants: an historical review. *Journal of the Torrey Botanical Society* 133: 46–61.
- Plumstead EP 1952. Description of two new genera and six new species of fructifications borne on *Glossopteris* leaves. *Transactions of the Geological Society of South Africa* 55: 281–328.
- Plumstead EP 1958. Further fructifications of the Glossopteridae and a provisional classification based on them. *Transactions of the Geological Society of South Africa* 61: 51–96.
- Prevec R 2011. A structural reinterpretation and revision of the type material of the glossopterid ovuliferous fructification *Scutum* from South Africa. *Palaeontologia Africana* 46: 1–19.
- Prevec R, McLoughlin S & Bamford MK 2008. Novel double wing morphology revealed in a South African ovuliferous glossopterid fructification: *Bifariaia intermittens* (Plumstead 1958) comb. nov. *Review*

- of Palaeobotany and Palynology 150: 22–36.
- Prevec R, Labandeira CC, Neveling J, Gastaldo RA, Looy CV & Bamford M 2009. Portrait of a Gondwanan ecosystem: A new late Permian fossil locality from KwaZulu–Natal, South Africa. *Review of Palaeobotany and Palynology* 156: 454–493.
- Read CB & Mamay SH 1964. Upper Paleozoic floral zones and floral provinces of the United States. Geological Survey Professional Paper 454–K. USA Government Printing Office. pp. 1–35.
- Retallack GJ & Dilcher DL 1988. Reconstructions of selected seed ferns. *Annales of Missouri Botanical Garden* 75: 1010–1057.
- Retallack GJ, Metzger CA, Greaver T, Jahren AH, Smith RMH & Sheldon ND 2006. Middle–Late Permian mass extinction on land. *Geological Society of America Bulletin* 118: 1398–1411.
- Rigby 1978. Permian glossopterid and other cycadopsid fructifications from Queensland. Geological Survey of Queensland Publication 367. *Palaeontological Paper* 41: 1–21.
- Rigby JF & Chandra S 1990. The Late Permian sporangiate fructification *Nesowalesia edwardsii* Pant, 1977, from Katoomba, New South Wales, Australia. *Review of Palaeobotany and Palynology* 65: 175–178.
- Rigby JF, Maheshwari HK & Schopf JM 1980. Revision of Permian plants collected by J.D. Dana during 1839–1840 in Australia. Queensland Department of Mines, Geological Survey of Queensland, publication 376, palaeontological paper 47. Brisbane. 25 p.
- Ryberg PE 2009. Reproductive diversity of Antarctic glossopterid seed–ferns. *Review of Palaeobotany and Palynology* 158: 167–179.
- Salmenova KZ 1978. Permian flora of the Northern Cis–Balkhash area. *Paleontological journal* 4: 122–127.
- Salmenova KZ 1979. Peculiarities of the Permian flora of Southern Kazakhstan and its links with the adjacent floras. *Paleontological journal* 4: 119–127.
- Surange KR & Chandra S 1973. *Partha*, a new type of female fructification from Lower Gondwana of India. *Palaeobotanist* 20: 356–360.
- Surange KR & Chandra S 1974a. Fructifications of Glossopteridae from India. *Palaeobotanist* 21: 1–17.
- Surange KR & Chandra S 1974b. Morphology of the gymnospermous fructifications of the *Glossopteris* flora and their relationships. *Palaeontographica. Abt. B* 149: 153–180.
- Taylor EL & Ryberg PE 2007. Tree growth at polar latitudes based on fossil growth ring analysis. *Palaeogeography, Palaeoclimatology, Palaeoecology* 255: 246–264.
- Taylor EL & Taylor TN 2009. Seed ferns from the late Paleozoic and Mesozoic: Any angiosperm ancestors lurking there? *American Journal of Botany* 96: 237–251.
- Vakhrameev VA & Doludenko MP 1961. Upper Jurassic and Lower Cretaceous flora of the Bureja Basin and its significance for stratigraphy. Moscow; Academy of Sciences of the USSR Press. 136 p. (Transactions of the Geological Institute of RAS, iss. 54) [in Russian]
- Wang Z–Q 1996. Past global floristic changes: the Permian great Eurasian floral interchange. *Palaeontology* 39: 189–217.
- Ziegler AM, Gibbs MT & Hulver ML 1998. A mini–atlas of oceanic water masses in the Permian Period. Proceedings of the Royal Society of Victoria. Thematic issue: Strzelecki International Symposium on Permian of eastern Tethys: *Biostratigraphy, Palaeogeography and Resources* 110: 323–343.