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New Jurassic protocycadalean ovuliphores and the origins of the Cycadales

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ABSTRACT

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Ovuliferous spikes with two lateral rows of ovules are described from the Callovian of Georgia. The ovules are large, orthotropous, oblique to the stout rachis, with a scar of subtending bract at the base. They show a relatively thin integument and a bulky nucellus topped by a broad nucellar beak. This find constitutes a new genus *Baruligyna* gen. nov. closely related to the previously described *Semionogyna* Krassilov et Bugdaeva from the Lower Cretaceous of Transbaikalia. Both are associated with pteridosperm-like foliage. In the case of *Baruligyna*, the associated leaves are of a *Pachypteris* morphotype, bipinnate with thick leathery pinnules similar to the ovules in shape and dimensions. This group of Mesozoic plants is considered as transitional between the Permian callipterids and the Mesozoic cycads indicating the origin of *Cycas*-type ovuliphores ("macrosporophylls") form planated bracteate strobili.

Key-words—Cycadales, Jurassic, Plant Morphology, Phylogeny.

नवीन जुरासिक प्रोटोसाइकेडेलियन बीजांडधर तथा साइकेडेलीस की उत्पत्ति

वेलनटीन ए. क्रासीलोव एवं मया पी. डोलुडेंको

सारांश

जियोरजिया के केलोवियन से प्राप्त दो पार्श्व पंक्तियों में विन्यासित बीजांड के बीजांडधर स्पाइक्स का वर्णन किया गया है। ये बीजांड गुरु ऋजु, तिरक्षे से पुष्ट प्राक्ष तथा आधार पर कक्षांतरकारी सहपत्र के क्षत चिन्ह के साथ हैं। वे परस्पर पतले अध्यावरण तथा स्थूल बीजांडकाय जिसके शीर्ष पर चौड़ी बीजांडकायी चोंच है, के द्वारा प्रदर्शित है। इस खोज के द्वारा नया वंश *बारुलीगाइना* नव वंश बनाया गया जो कि पहले वर्णित ट्रॉंसबाइकेलिया के निम्न क्रिटेशस से प्राप्त *सेमियोनोगाइना* क्रासीलोव एवं बुगदेवा से नजदीकी संबंध रखता है। ये दोनों टेरिडोस्पर्म के समान पर्णसमूह सी दिखती हैं। *बारुलीगाइना* के सन्दर्भ में सहयोगी पत्तियाँ *पैकिप्टेरिस* के चित्ररुप, आकार एवं विस्तार में बीजांडों से मिलती-जुलती द्विपच्छिका मोटी चर्मिल पिच्छिका के साथ है। मीसोजोइक वनस्पति का यह समूह परमियन कैलिप्टेरिडस तथा मीसोजोइक साइकेड के मध्य संक्रामी की तरह माना गया है और *साइकस*-टाइप बीजांडधर की उत्पत्ति समतल सहपत्री शंकु बनाने का संकेत करती है।

संकेत शब्द—साइकेडेलिस, जुरासिक, पादप आकारिकी, जातिवृत।

INTRODUCTION

Mesozoic is described as an Era of Cycads, having their origin in the Palaeozoic. The Mesozoic cycadophytes include the orders Bennettitales, Pentoxylales, Nilssoniales and possibly also some plants with a fern-like foliage, such as the peltasperms and corystosperms, which are more commonly conceived of as "Mesozoic pteridosperms" on account of their leaf morphology (which is essentially like in *Bowenia*, an extant cycad). Their phylogenetic affinities to cycads remain an open question at the moment.

The senior author has touched upon the intriguing problem of cycad origins in connection with the finds of protocycadalean ovuliferous spikes in the Lower Cretaceous of Transbaikalia (Krassilov & Bugdaeva, 1988) and a giant pollen cone from the Callovian of the Caucasus (Krassilov *et al.*, 1996). These structures present a challenge to the widely held view of cycadalean origins from the Palaeozoic plants with leafy ovuliphores ("megasporophylls"). New morphotype of ovulate organ described below provides an additional argument for revision of this concept.

MATERIAL AND METHODS

The material was collected by Doludenko and Svanidze during their field work on the Jurassic floras of Georgia, Caucasus, from many localities in the Rioni Basin (Doludenko & Svanidze, 1968). The richest locality occurs on the Barula River, a tributary of the Rioni. Here the shallow marine Late Jurassic sandstones and shales rest unconformably upon the mid-Jurassic volcanites. The plant-bearing shales contain also a rich assemblage of Callovian ammonites along with Bennettitales and conifers. The Barula plant assemblage includes also ferns, cycadophytes, *Sagenopteris* and *Pachypteris*. In addition, the Marattialean fern *Angiopteris* (Delle *et al.*, 1986) and a giant cycadalean pollen cone *Cycandra* (Krassilov *et al.*, 1996) have been described from the same locality.

The ovuliphores are preserved as mineralised compressions that do nct yield to maceration. Yet we could reveal some microscopic details by removing few ovules from the rock and mounting them for SEM. The leaves of *Pachypteris* that are associated with the ovuliphores were studied in the same way for comparison.

The material is deposited in the Geological Institute of the Russian Academy of Sciences (GIN), collection no. 3326.

SYSTEMATICS

Genus—BARULIGYNA Krassilov and Doludenko gen. nov.

Name—after *Barula* River and -gyna (Gr.) means female.

Type species—Baruligyna disticha sp. nov. from the Callovian of Barula River (described below).

Diagnosis—Ovuliphores pinnate, stalked, base expanded, axis flat, ovules in two lateral rows in one plane, at acute angle to the axis. Ovules elongate-elliptical, keeled, with protruding micropyle, base constricted, with a transverse scar slightly above the point of attachement. Seed coat ridged, containing small rounded resin bodies. Epidermis has longitudinally elongated cells with trichome bases, lacking stomata. Nucellus bulky, with a broad beak over a circular pollen chamber.

Comparison—The ovuliphores resemble that of *Cycas* which however are much more leaf-like. The only fossil genus standing for comparison is *Semionogyna* from the Early Cretaceous of Transbaikalia (Krassilov & Bugdaeva, 1988). In general morphology the ovuliphores are similar to *Semionogyna* but in the latter the ovules are subtended by linear bracts, unlike the basal scars on the ovules of *Baruligyna*. In *Semionogyna* the subtending bracts are persistent and fairly conspicuous even in mature ovuliphores. Distal portion of the ovuliferous axis is sterile, with only bracts. Due to these distinctions, *Baruligyna* is here considered as a genus phylogenetically allied but taxonomically separate from *Semionogyna*.

BARULIGYNA DISTICHA Krassilov and Doludenko sp. nov.

(Pl. 1.1-6, Pl. 2.1-5)

Name—refers to the arrangement of ovules in two lateral rows.

Holotype—GIN 3326-1, the Callovian of the Barula River, the Rioni River Basin, Western Georgia.

PLATE 1 →

(Baruligyna disticha sp. nov., ovuliphores from the Callovian of Barula, Georgia)

1. Holotype GIN 3326-1, middle part of ovuliphore with a broad axis bearing two lateral rows of ovules. x 2.
2. Paratype GIN 3326-3, stalked ovuliphore. x 1
3. Paratype GIN 3326-2, ovuliphore with a broad rachis and the relatively small ovules. x 1
4. Paratype GIN 3326-4, ovuliphore with a slender rachis and large ovules. x 2.
5. Holotype GIN 3326-1, ovules showing scars of subtending bracts at the base. Tubercles on the upper ovules are marks of resin bodies upon the through the cuticle. x 6.
6. Holotype GIN 3326-1, ovule that was removed from the rock and studied in SEM (Pl. T. 1-5).

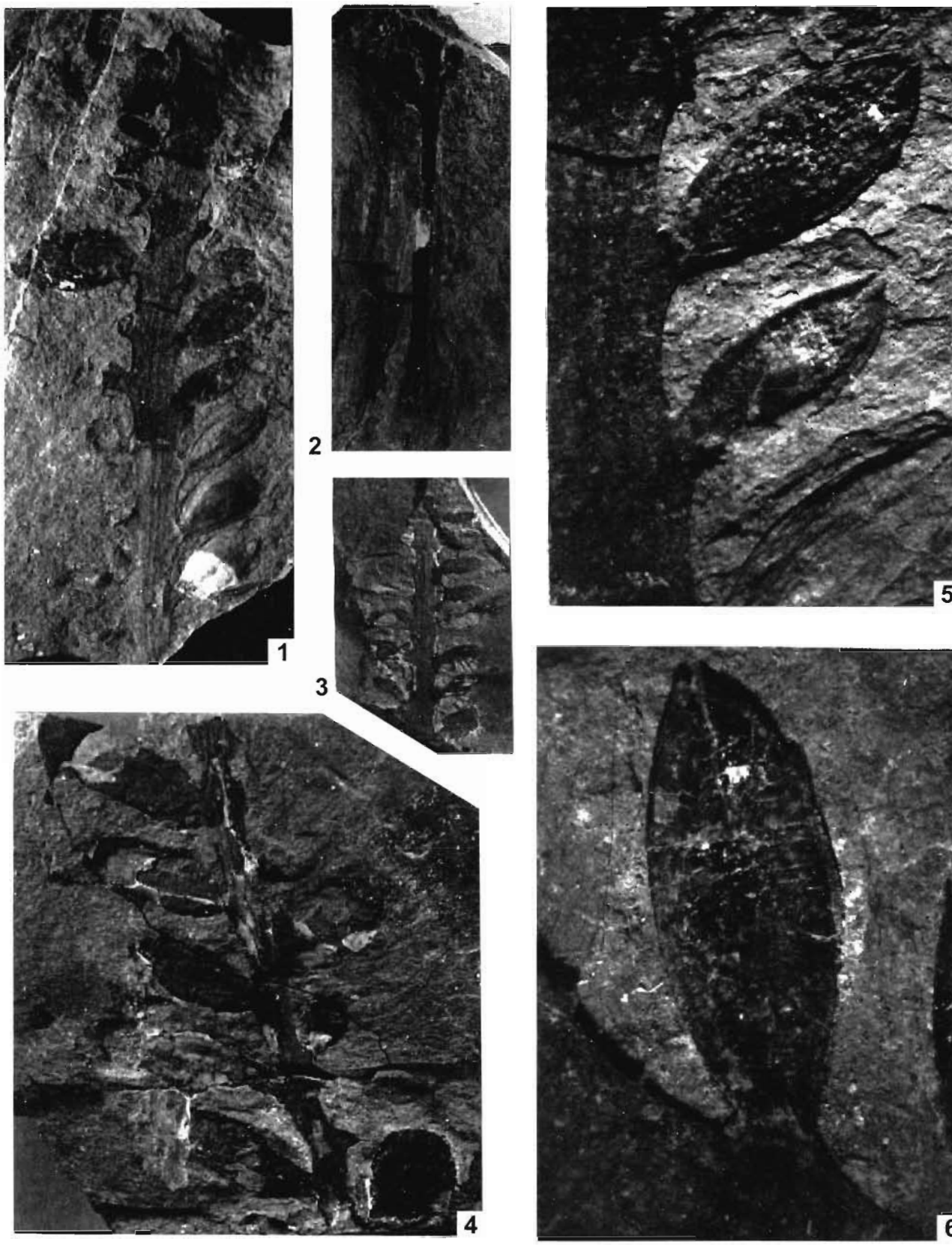


PLATE 1

Diagnosis—As for the genus.

Material—In addition to the holotype, specimens nos 3326-2 - 3326-7 from the same locality.

Description—There are seven fragments of ovuliphores, one of which represents a proximal portion with only two pairs of ovules, stalk is 50 mm long, expanded at the base and shows a straight line of abscission. Fragments of middle part do not exceed 60 mm in length. The megasporophylls are parallel-margined, scarcely tapering to either base or apex, indicating that the whole length might have been about 120 mm or more. There is no correlation between the stoutness of the axis (rachis) and dimensions of the ovules. A relatively thin axes 3 mm wide bears larger ovules (about 14 mm long, 5–6 mm broad (Pl. 1.2), while a broader axis, 5 mm thick, supports much smaller ovules (8–10 mm long, 3–4 mm broad)) (Pl. 1.1, 3). The thicker axis, in particular appears flat, conspicuously expanded at the nodes, and coarsely longitudinally striated. The ovules are attached in two lateral rows, alternate or subopposite, apparently spreading in one plane, but because many of them are broken at base, they might have been slightly inclined to the plane of the rachis before compression. The angles of attachment are 45° to 60°, uniform over a leaf fragment, and the ovules are well and uniformly spaced, never overlapping.

The ovules are elongate-elliptical with maximum width in the middle, occasionally somewhat obovate, broader in the distal portion and gradually tapering to the base, stalk absent and attached directly to the nodal expansions of the rachis. In the ovules turned by their abaxial face to the observer there is a transverse slightly arched scar or a flap of tissue at the base (Pl. 1.5, 6; Pl. 2.2), marking the attachment of a subtending bract which was shed before the maturation of an ovule. The distal portion is smoothly tapering to the acute apex which occasionally shows a shortly protruding micropyle, commonly splited in the plane of the micropyle. The split is extending down to the abaxial face as a more or less prominent keel (Pl. 2.1).

The surface of an ovule shows at a low magnification small rounded structures corresponding to resin bodies of the seed coat (Pl. 1.5). Under SEM, the surface is traversed by interlocking ridges forming irregular polygonal patterns (Pl. 2.4). The epidermal cells are irregular-polygonal to elongate, slightly swollen or indistinctly papillate, longitudinally aligned, encircling hair bases (Pl. 2.4). The latter are scattered, represented by a single elliptical cell with a thickened border. Neat holes lacking encircling cells, such as shown in Pl. 2.5 are here interpreted as piercing marks of an ovulivorous insect. They suggest, among other things, a fleshy seed coat. In the laterally compressed ovules the integument is only 0.5 mm thick, the bulk of the body being filled with nucellar tissue (Pl. 2.3). Broad nucellar beak with a perfectly circular pollen chamber is occasionally seen where the integument was split and pilled off at the apex (Pl. 2.1). No pollen grains were found in the chamber and the condition of the nucellus, is obviously unexhausted, which suggests that the embryogenesis had not yet commenced. However, occasionally the ovules are shrinked, and show a median swelling indicative of a developing embryo.

ASSOCIATED ORGANS

The ovuliphores of *Baruligyna disticha* are associated with bipinnate leaves. Earlier these were described by Doludenko and Svanidze (1969) as *Pachypteris lanceolata* Brong. Fragments of pinnae with their thick, leathery, obliquely spreading pinnules are fairly similar to the ovuliphores in their general aspect and can even be confused with the latter at the first sight, except that the pinnules are broadly decurrent, with obtuse apices (see Pl. 3). SEM of the ovule shows a broad marginal flange of small swollen cells aligned along the margin. In the central portion, the epidermal cells are larger, with undulate anticlinal walls, and papillate (see Pl. 3). The papillae leave small circular scars when detached. Scattered hair bases are much as on the ovules of *Baruligyna disticha*. The stomatal openings are not easily discernible from the hair bases in surface view being only slightly larger and of a more regularly elliptical outline than the latter.

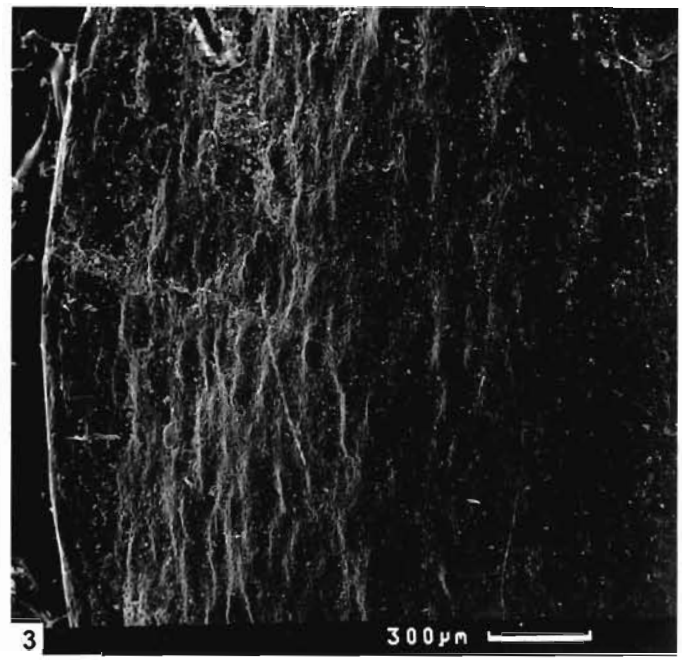
Pachypteris is known to have been associated with a different type of ovulate organs belonging to peltasperms. However, this leaf morphotype might have occurred in more than one group of extinct gymnosperms. Since the most probable progenitors of both the Mesozoic peltasperms and the *Baruligyna – Semionogyna* type protocycadalean plants were the Palaeozoic callipterids with the *Autunia*-type ovulate structures (Krassilov, 1997), a conservative callipteroid leaf morphotypes might have been retained in the both clades.

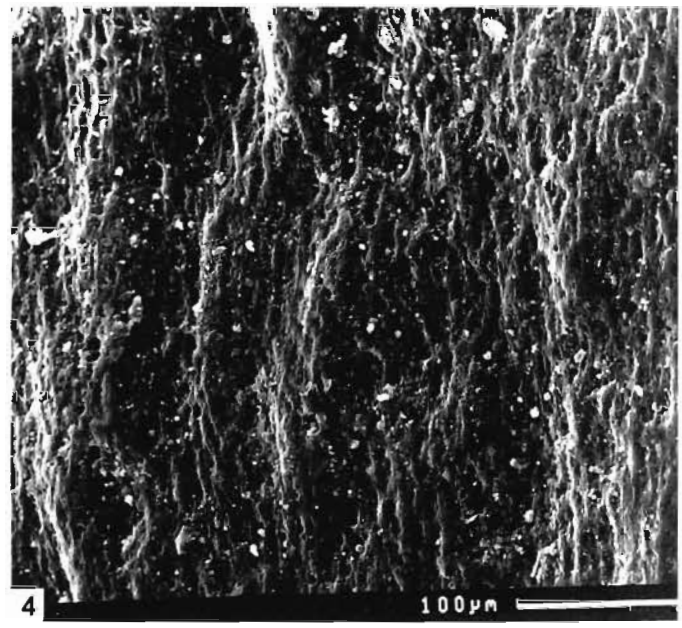
From the same locality comes a giant pollen cone *Cycandra* that resembles a widespread nilssonialean morphotype *Androstrobus*, but differs in the vertical align much of synangia made up of partly fused sporangia similar to some Palaeozoic pteridospems (Krassilov *et al.*, 1996). In the

PLATE 2 →

[Baruligyna disticha sp. nov., ovuliphores from the Callovian of Barula, Georgia, SEM of an ovule from the holotype (Pl. 1.6)].

1. Distal part of the ovule with a split micropyle showing nucellar beak.
2. Proximal part of the ovule showing scar of subtending bract.
3. Margin of the ovule showing integument as a flat fringe surrounding a bulky nucellus.
4. Ridge pattern and hair bases on the surface of the ovule.
5. Perforations supposedly inflicted by an ovulivorous insect.





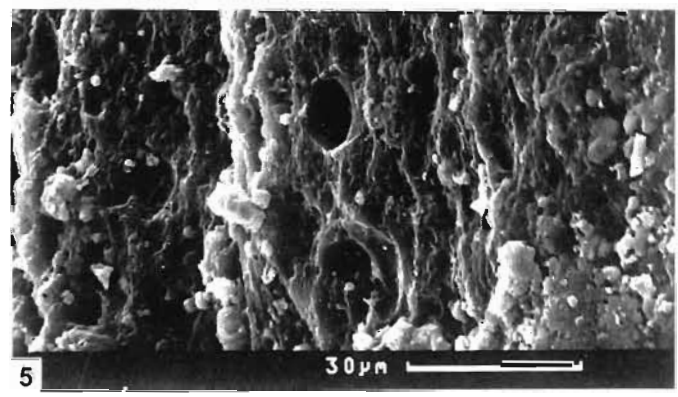
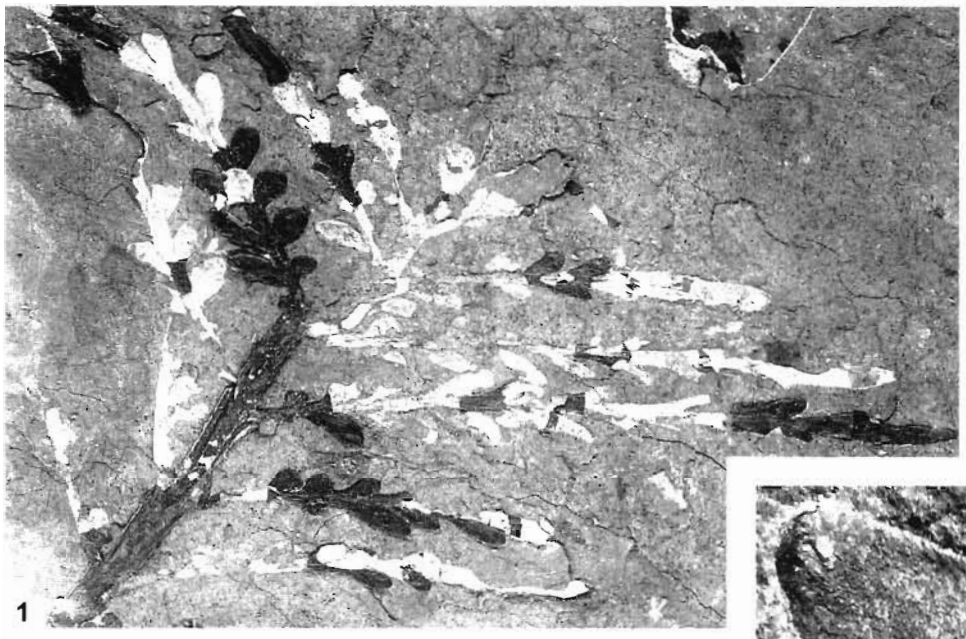
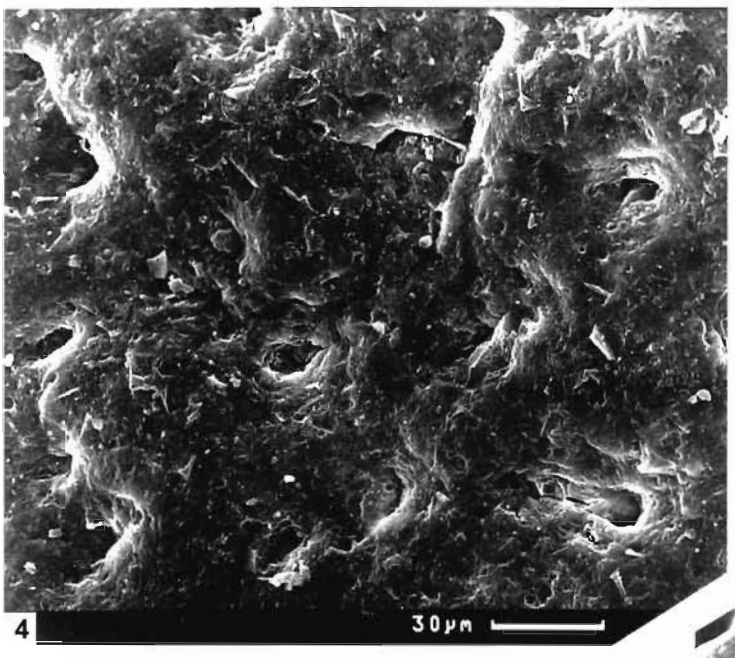
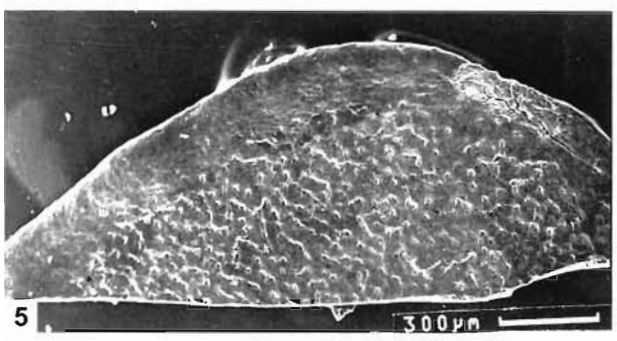


PLATE 2







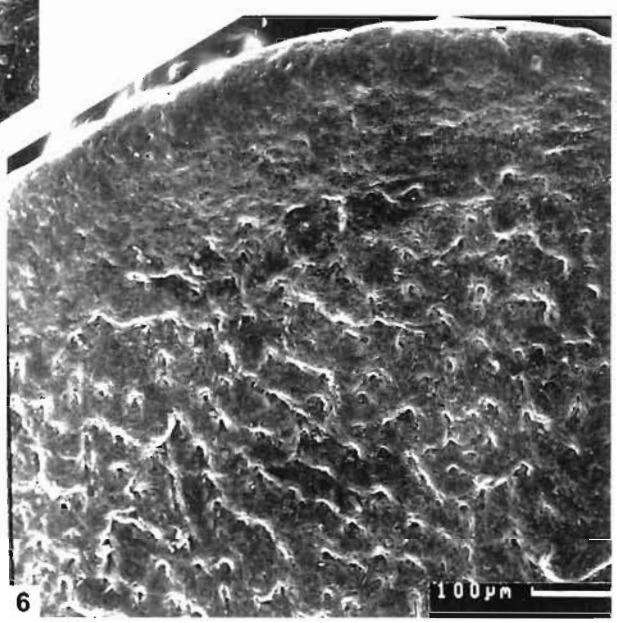


PLATE 3

absence of morphological evidence, *Cycandra* and *Baruligyna* belonging to one and the same plant, as its male and female organs can also be considered.

DISCUSSION

It has become a text-book notion that cycads had their origins with the Late Palaeozoic plants with marginal ovules on leafy ovuliphores of the type described from the Pennsylvanian and Permian of North America (Mamay, 1976) and China (Mei *et al.*, 1992). Yet the modern-type cycads with leaf-like ovuliphores has appeared not earlier than the Late Cretaceous (e.g., *Cycas* from the Senonian of Sakhalin: Krassilov, 1978). Even if, ignoring the ambiguities of morphological interpretation (e.g., Meeuse, 1963), one complies with the opinion that *Cycas*-type ovuliphores are directly derivable from leaves with marginal ovules, there remains the difficulty of enormous time-gap between the supposed Permian prototype and the Cretaceous appearance of true cycads. All the cycad-like plants in-between, such as nilssonias, had strobilate ovuliphores. In particular, the *Beania*-type ovulate organs of nilssonias (Harris, 1964) with their loosely arranged biovulate cone-scales are closely comparable with *Autunia*, an ovulate organ of Permian callipterids (Krasser, 1921) and can be considered, both on morphological and chronological grounds, as direct descendants of the latter (Krassilov, 1997).

Baruligyna is more *Cycas*-like but ovules show basal scars that cast some doubts on its derivation from a leafy prototype. The comparison with *Semionogyna*, another *Cycas*-like Mesozoic form (Krassilov & Bugdaeva, 1988) explains the scars suggesting that they were left by subtending bracts, but persistent in mature ovuliphores in *Semionogyna*. A next morphologically conceivable step suggested is further planation of ovuliphores accompanied by a complete reduction of subtending bracts resulting in a secondary leaf-like ovuliphore.

REFERENCES

Doludenko MP & Svanidze TI 1968. Late Jurassic flora of Georgia. Nauka, Moscow : 116 (in Russian).

Delle GV, Doludenko MP & Krassilov VA 1986. First find of Jurassic *Angiopteris* Hoffman (Marattiaceae) in the USSR. In Problems in Paleobotany, Nauka, Leningrad · 38-44 (in Russian).

Harris TM 1964. The fossil Yorkshire Jurassic Flora. II Caytoniales, Cycadales and Pteridosperms. London, British Museum (Natural History): 191 p.

Krasser LM 1921. Studien uber die fertilen Region der Cycadophyten aus der Lunzer Schichten. Makrosporophyle. Kgl. Akad. Wiss. Wien Denkschr. 97 : 1-32.

Krassilov VA 1978. Late Cretaceous gymnosperms from Sakhalin and the terminal Cretaceous event. Palaeontology 21 : 893-905.

Krassilov VA 1997. Angiosperm origins : morphological and ecological aspects. Pensoft, Sophia : 270.

Krassilov VA & Bugdaeva EV 1988. Protocycadopsid pteridosperms from the Lower Cretaceous of Transbaikalia and the origin of cycads. Palaeontographica B201 · 27-32.

Krassilov VA, Delle GV & Vladimirova HV 1996. A new Jurassic pollen cone from Georgia and its bearing on cycad phylogeny. Palaeontographica B238 · 71-75.

Mamay SH 1976. Paleozoic origin of the cycads. U.S. Geological Survey Professional Paper 934.

Meeuse ADJ 1963. The so-called "megasporophyll" of *Cycas* – a morphological misconception. Its bearing on the phylogeny and the classification of the Cycadophyta. Acta botanica neerlandica 12 : 119-128.

Mei Meitang, Dilcher DL & Wan Zhi-hui 1992. A new seed-bearing leaf from the Permian of China. Palaeobotanist 41 · 98 -109.

←

PLATE 3

[Leaf associated with the ovuliphores *Baruligyna disticha* sp. nov. (Pl. 1, 2)].

1 Leaf, GIN 3326-160, general habit. x 1

2 Pinna with pinnules similar to the ovules of *Baruligyna disticha* sp. nov. in shape and dimensions (compare Pl. 1.3), GIN 3326-7. x 1

3. Pinnule of the pinna shown in fig. 2.

4. Surface view of the cuticle with hair bases, SEM.

5. Margin of pinnule, SEM.

6. Enlargement of marginal flange and intramarginal part of the lamina, SEM.