

Ginkgoales: Some Problems of Systematics and Phylogeny

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Received December 19, 2013

Abstract—The rudimentary outgrowths in fixed positions on the collars of *Nagrenia samylinae* Nosova (plant closely related to *Ginkgo biloba* L.) and similar rudiments in extant *Ginkgo* suggest that the collar of *Ginkgo* was initially a bilateral structure with directional growth, which bore ovule on its abaxial side. The collar of *Ginkgo* is interpreted as a vestigial organ. In the light of the data obtained, the origin and phylogeny of Ginkgoales are discussed; the most probable ancestors of Ginkgoales are Umkomasiales (Corytospermales) and allied plants. Thus, the new data confirm the interpretation of the collar of *Ginkgo* proposed by Meyen (1984) and are consistent with his hypothesis of the origin of Ginkgoales.

Keywords: Ginkgoales, *Ginkgo*, *Grenana*, *Nagrenia*, Umkomasiales, evolution, systematics, phylogeny, Jurassic

DOI: 10.1134/S0031030115050068

INTRODUCTION

The early stage of Ginkgoales evolution up to the Middle Triassic is a subject of heated discussions until the present time. Several hypotheses concerning the origin of this plant group have been developed. The point of view of Florin (1949), according to which Ginkgoales evolved directly from Trichopityales by reduction of the number of ovules is most widely accepted. In his opinion, Trichopityales are close to conifers or Dicranophyllales and their ovules are interpreted as terminal. An alternative point of view was developed by Meyen (1984), who regarded Ginkgoales as descendants of Peltaspermales sensu lato. Meyen interpreted ovules of Trichopityales as abaxial, assigning this group to primitive Ginkgoopsida, which are ancestral to Peltaspermales. Supporters of the latter hypothesis are mostly Russian paleobotanists; however, it also finds acceptance among foreign researchers (Anderson and Anderson, 2003).

The key point of both hypotheses is the interpretation of the collar of *Ginkgo* or, in a broader sense, of the structure bearing single ovule (pedicel + collar); extant *Ginkgo biloba* usually has two structures of this kind on the ovuliphore axis. Florin regarded the collar as a swelling of the pedicel at the base of terminal ovule; Meyen believed that the collar is a reduced, hooked upward peltoid of Peltaspermales. Other researchers also regard the collar of *Ginkgo* as a rudiment of megasporophyll or bract, cupule, second integument, etc. (for review, see Douglas et al., 2007). Krassilov (1972) derives the collar of *Ginkgo* from a seed scale of *Umaltolepis* Krassilov, which he considered as a “fertile cladode” or “fertile bract” resembling the seed scale of conifers. In support of this hypothesis, Krassilov refers to similar conclusions, obtained

on the material of aberrant ovuliphores of extant *Ginkgo biloba* (Emberger, 1954).

There are several points of view on the evolution of Ginkgoales and diversification within this plant order. In particular, Krassilov believes that Ginkgoales evolved from Karkeniaceae to Pseudotorelliaceae Krassilov (=Umaltolepidaceae Stanislavsky) and Ginkgoaceae (Krassilov, 1972), but does not exclude that Karkeniaceae and Ginkgoaceae are early diverging evolutionary lineages (Krassilov, 1989). Naugolnykh (2007) depicts the lineage leading to the genus *Ginkgo* as the reduction series *Karkeniania*–*Yimaia*–*Ginkgo*; the family Umaltolepidaceae he considers as an independent lineage derived from Karkeniaceae. Zhou, in his last review, derives from Karkeniaceae two independent families, Yimaiaaceae and Ginkgoaceae (Zhou, 2009). The two families are distinguished by the presence–absence of collar or its homologues. In his opinion, the family Umaltolepidaceae evolved from Yimaiaaceae. Zhou (1991, 2009) does not homologize bract and collar; the scale of *Umaltolepis* he considers as a bract, and collar as a swelling of the pedicel at the ovule base.

Recently, the interpretation of the collar as a novel structure has received wide acceptance. This interpretation is supported by the fact that the collar is initiated relatively late with reference to the nucellus and integument of the ovule and that the collar of *Ginkgo* is formed as a radial structure with circumferential growth (Pankow and Sothmann, 1967; Douglas et al., 2007).

Naugolnykh (2007) developed a hypothesis of the origin of the collar in *Ginkgo* as a result of recapitulation of characters of pre-karkeniaceous ancestors, which possessed foliar ovuliferous organs. This hypothesis is intended to explain the absence of collar or its homologues in supposed closest ancestors of

Ginkgo: *Karkenian* and *Yimaia*. Aberrant ovuliphores of *Ginkgo* are often interpreted as an atavistic manifestation of characters of an ancestral group, which possessed leaflike ovuliphores (Fujii, 1896; Seward and Gowan, 1900; Sakisaka, 1929; Naugolnykh, 2007; Fischer et al., 2010; etc.).

In our opinion, the most important for gaining an understanding of the nature of *Ginkgo* collar is a fossil plant described by Samylina (1990) as *Grenana angrenica* Samylina from the Middle Jurassic of Angren (Uzbekistan) and initially interpreted by her as a seed fern. *Grenana angrenica* was described on the basis of association of leaves, seeds, and ovuliphores. After publishing this material, other researchers began to point out to the fallacy of Samylina's interpretation and to relationship of *Grenana* Samylina to the family Ginkgoaceae (Zhou, 1997; Kvaček et al., 2005; etc.). Samylina designated a leaf as the holotype of this plant; therefore, the name was reserved for leaves (Nosova and Gordenko, 2012; Nosova, 2013). The ovuliphores previously assigned to the genus *Grenana* Samylina were described under a new generic and specific name, *Nagrenia samylinae* Nosova (Nosova, 2013); in the same publication, general description of their morphology and epidermal–cuticular characters is provided. The genus *Nagrenia* Nosova was proposed by Nosova for ginkgoalean ovuliphores which possess collars and for which the organic connection with seeds was not established. We regard *Nagrenia samylinae* as a representative of the genus *Ginkgo* sensu lato; the combination of characters, such as nearly completely reduced pedicel at the collar base and small number of ovules on the ovuliphore makes this plant most similar to extant *G. biloba* among known Mesozoic species included in the genus *Ginkgo*: *Ginkgo yimaensis* (Zhou and Zhang, 1989) from the Middle Jurassic of Henan Province, *G. apodes* (Zheng and Zhou, 2004) from the Lower Cretaceous of Liaoning Province of China, *G. ginkgoidea* Yang, Friis et Zhou from the Middle Jurassic of southern Sweden (Yang et al., 2008), etc. Probably, the ovuliphores from Angren bore associated seeds of *Allicospermum budantsevii* Gordenko (Gordenko, 2015), which resemble in epidermal structure the ovuliphores under discussion, and show the morphology characteristic of seeds of *Ginkgo*. The pollen found in the pollen chamber of these seeds is closely similar to that of *Ginkgo biloba* (Zavialova et al., 2014). Nosova assumed that the variant of ovuliphores of *Nagrenia samylinae* with long pedicels could bear seeds *A. angrenicum* Nosova (Nosova, 2013), but the latter show the morphology which is not typical for seeds of representatives of the genus *Ginkgo* and they differ significantly from seeds *A. budantsevii* (Gordenko, 2015). The present paper is not intended to resolve the nomenclature questions; therefore, hereinafter we use the combination "*Nagrenia samylinae*", implying, however, that we are talking about a fossil representative of the genus *Ginkgo*.

According to our observations, the collars of *Nagrenia samylinae* possess marginal outgrowths in fixed structural position (Figs. 1a–1d, 2, 3). These outgrowths are subtriangular, with slightly rounded tips, to which cell rows converge (Figs. 1d, 1e). The largest outgrowths are up to 0.9 mm long, that is, approximately one-fourth of the collar diameter. The outgrowths are usually paired (Figs. 1a–1d, 2; see also figures provided by Samylina (1990, pl. III, figs. 1, 7–9, 11) and Nosova (2013, pl. VI, figs. 1, 2, 10, 11, 20–22). In some instances, the outgrowths are single (Fig. 1e; Samylina, 1990, pl. III, figs. 7–9; Nosova, 2013, pl. VI, figs. 16, 18). These outgrowths are situated approximately (exact correspondence is impossible to establish because of the absence of detailed data on the morphology and anatomy of ovuliphores) on the side of (and directed to) the main axis of the ovuliphore, although this is not always clearly visible because of distortion of specimens during fossilization (Figs. 1a–1d, 2, 3a). In particular, the collar with paired outgrowths of the specimen shown in Figs. 1, 2 was turned for approximately 90° (clockwise in Fig. 1a), as indicated by the character of distortion of its pedicel. The presence of these outgrowths suggests bilateral rather than radial structure of the collar in *Nagrenia samylinae*. The bilateralism of collars can be accentuated by their asymmetrical development. The collar is frequently narrower from the side opposite to the outgrowths. This feature is most pronounced in the specimen shown in Fig. 1 (in the work of Samylina, 1990, pl. III, figs. 7–9), where one of the collars not completely embraces the ovule base; it is not developed in the area opposite to single outgrowth (Fig. 1b, indicated by white arrow; Fig. 2, indicated by gray arrow).

On the collars of extant *G. biloba* (approximately in the same position as the outgrowths in *Nagrenia samylinae*) one or two small marginal tubercles are often observed at early developmental stages (Fig. 3b); they are clearly visible, for example, in the figures provided by Jin et al. (2012, p. 4, text-figs. 2i, 2k; p. 6, text-fig. 3i). At later developmental stages, these tubercles are often masked by nonuniform development of the collar. In a similar structural position, extant species also has a small lobe ("flap" after Douglas et al., 2007) between the ovule base and collar. Anatomically, this is an adaxial position, corresponding to the upper side of collateral V-shaped vascular bundle (which vascularizes the structure bearing single ovule) near the place of arms of "V" fusion (Shaw, 1908). If the collar possessed any vestigial structure, this is the most probable position, in which it could have been vascularized either via emission from the arms of this bundle or by two larger bundles of the collar vascular system connected with them; the latter is uncertain, since Shaw (1908) suggests that the collar vascular system in extant *G. biloba* includes only secondary tissues.

The data obtained suggest that the collar of *Ginkgo* was initially a bilateral structure with directional

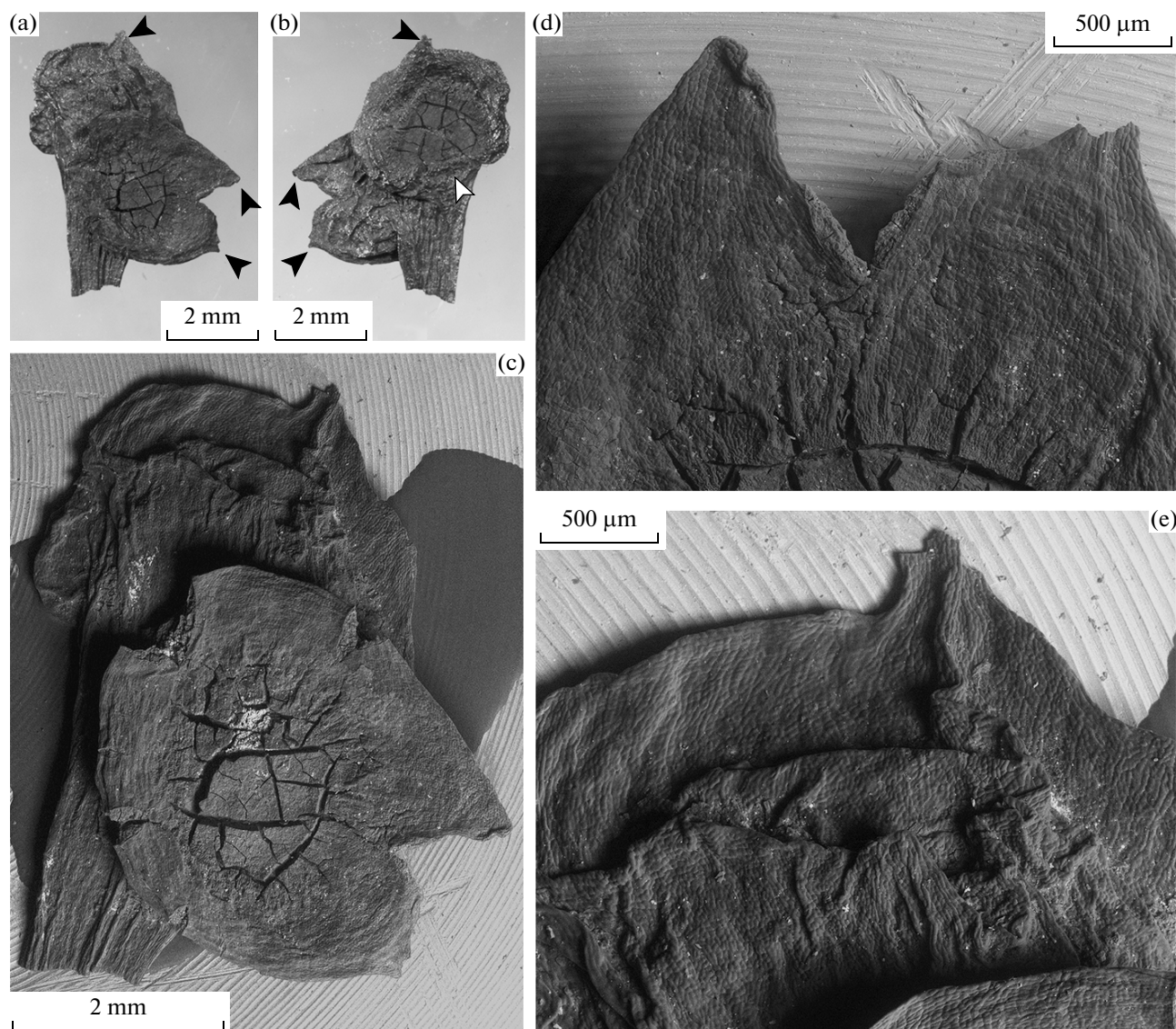


Fig. 1. *Nagrenia samylinae* Nosova, BIN 813/1N41, ovuliphore fragment: (a) general view of the side of the collar with paired outgrowths; black arrows pointing to the outgrowths on collars; (b) general view of the side of the collar with a single outgrowth; black arrows pointing to outgrowths on collars and white arrow pointing to the area free of collar; (c) area of ovule attachment visible on the upper surface of the collar, SEM; (d) detail of the collar with paired outgrowths, cell rows directed towards the outgrowth apices are visible, SEM; (e) detail of the collar with single outgrowth, SEM.

growth, which bore an ovule on its abaxial side. The adaxial (distal) part of this structure disappeared almost completely in *G. biloba*, but its rudiments are still present in *Nagrenia samylinae*. Evidently, the collar of *Ginkgo* is not a novel structure, but was inherited from ancestors of Ginkgoales. The abaxial position of ovule excludes the possibility that the collar corresponds to a bract or structure like a seed scale of conifers or its derivatives.

Based solely on the rudiments present in *Nagrenia samylinae* and *Ginkgo biloba*, it is impossible to infer the nature of their initial organ; the outgrowths may have corresponded to a lobe (or lobes) of a cupule, leaf lamina, distal part of the second order axis, etc. This

situation has its specific counterpart in the problem with microsporophylls of *Ginkgo*, which possess similar outgrowths (see, for example, Bierhorst, 1971); the nature of these outgrowths has different variants of explanation, although at present researchers are inclined to their interpretation as rudiments of additional sporangia (Mundry and Stützel, 2004). In the context of possible correspondence of the collar of *Ginkgo* to a leaf lamina, it should be noted that the leaf lamina, which develops on aberrant seed-bearing organs of *G. biloba*, occurs in different structural position. The presence of these aberrations in *Ginkgo* is often considered as an atavistic manifestation of ancestral characters, which suggest that seed-bearing

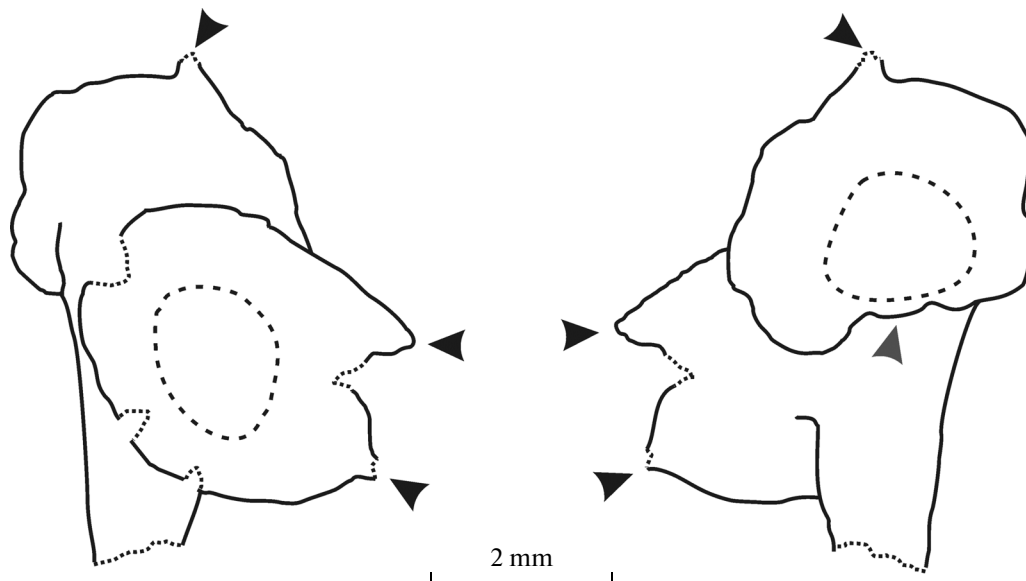


Fig. 2. *Nagrenia samylinae* Nosova, BIN 813/1N41, ovuliphore fragment, drawing of Figs. 1a and 1b (dotted lines are damaged areas, stippled lines are outlines of seed attachment areas, black arrows point to marginal outgrowths; gray arrow, the area free of collar).

organs of ancestral forms were initially leaflike (Fujii, 1896; Seward and Gowan, 1900; Sakisaka, 1929; Naugolnykh, 2007; Fischer et al., 2010; etc.). Naugolnykh regards aberrant leaflike seed-bearing organs of *Ginkgo* as a proof of the presence of a leaflike ovuliphore in the pre-karkeniaceous ancestors of *Ginkgo* and considers aberrant funnel-shaped leaves as a model for the collar formation in *Ginkgo* (Naugolnykh, 2007). At the same time, in aberrant forms, among which both ovule-bearing leaves and aberrant ovuliphores proper are noted (Bierhorst, 1971), the leaf lamina is initiated proximally relative to the collars, which are borne by this structure, and, therefore, it represents a modification not of single collar, but of the whole distal part of the ovuliphore. The collars themselves do not transform into a leaf lamina or its segments (see Fujii, 1896, p. 106, pl. 1, fig. 1; Xing et al., 2011; etc.); in the case that collars are absent, this is probably caused by their underdevelopment (underdeveloped are often also ovules themselves: see, for example, Soma, 1999). If the collar had been transformed into a leaf or leaf segment, the ovule of aberrant forms would have never been accompanied by a collar. Under formation of a collar from a funnel-shaped leaf, the ovule would have occurred on its adaxial side (the inner side of the funnel-shaped leaf is adaxial), while the inner side of the collar of *Ginkgo* is abaxial, as indicated, among other, by its vascularization (Shaw, 1908) and also the position of the rudimentary outgrowths.

To draw homologies between ovuliferous organs of *Ginkgo* and *Umaltolepis*, available data are insufficient. Since the ovuliferous organ of *Umaltolepis* bears a single ovule (presumably adaxial: Krassilov, 1972), it is difficult to establish whether its lamina is homologous to the collar of *Ginkgo* or to a whole ovuliphore; the

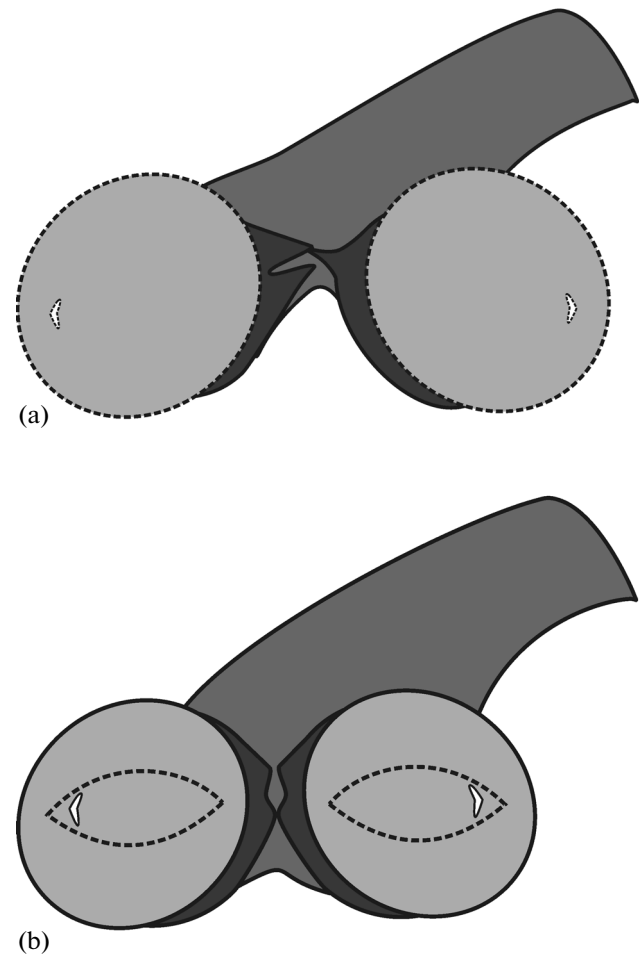


Fig. 3. Schematic reconstruction showing the position of marginal outgrowths on collars: (a) in *Nagrenia samylinae* Nosova (ovules are designated by stippled lines); (b) in juvenile specimens of *Ginkgo biloba* L. (orientation of “stones” relative to tubercles is designated by stippled lines).

homologies proposed by Zhou (1991, 2009) are also possible.

Although the possibility of reappearance in descendants of lost features of remote ancestors cannot be excluded, in authors opinion, more probable is the direct inheritance of traits from ancestral forms; the structures preserved in *Ginkgo* as rudiments should be present in its immediate ancestors. In *Yimaia* and *Karkenian*, collars or their homologues are absent and, consequently, they do not fit in direct ancestors of Ginkgoaceae. Thus, *Ginkgo* cannot be placed at the end of the reduction series *Karkenian*—*Yimaia*—*Ginkgo*, which was proposed by Naugolnykh (2007); most probably, Karkeniaceae, Yimaiceae, and Ginkgoaceae evolved parallel to each other. The assumption that the collar of Ginkgoaceae represents a progressively expanding structure (Zhou, 2009) is not supported by our data.

Among forms supposedly ancestral to Ginkgoales, distinguishing characteristics of the structure bearing single ovule (presence of sterile distal part, abaxial position of ovule, its bilateral symmetry and radial orientation: Meyen, 1984, 1987) with *Ginkgo* share some representatives of the so-called “Mesozoic seed ferns” complex. Within this complex, there are plants with *Ginkgo*-like leaves, characteristic of Ginkgoales peculiarities of the architecture (differentiation of the shoot system into auxiblasts and brachyblasts, pycnoxyly) and vascularization (Meyen, 1984, 1987; Anderson and Anderson, 2003; Taylor et al., 2006, 2009; Decombeix et al., 2014; etc.). These plants demonstrate mosaic distribution of features characteristic of Ginkgoales, which indicates noncontemporaneous manifestation of general trends of the group evolution. Hence, it is difficult to reveal a particular taxon that could be ancestral to Ginkgoales. Among plants most closely related to Ginkgoales, the Umkomasiales (Corystospermales) are the first to be mentioned. Krassilov (1975, 1997) and Meyen (1984, 1987) pointed to probable origin of Ginkgoales from Umkomasiales. Meyen (1984, p. 61) suggested that the collar of *Ginkgo* correlated with the peltoid of Peltaspermales sensu lato, but strongly reduced and hooked upward; therefore, the ovule of *Ginkgo* appears apical, but it is morphologically abaxial. As an example of probable ancestral form, Meyen cited the umkomasialean *Pilophorosperma* Thomas known from the Triassic of Gondwana. Thus, the data obtained here support the hypothesis of Meyen, arguing for the abaxial position of ovule in *Ginkgo*; the outgrowths in *Nagrenia samylinae* and their analogues in *Ginkgo biloba* may represent rudiments of that structure, about which Meyen wrote, just being in that position, in which they most likely can be expected to occur.

In extant *Ginkgo biloba*, there are normally two structures, bearing single ovule, on the axis of ovuliphore. However, the presence of a greater number of such structures in aberrant forms and some fossil representatives of the family Ginkgoaceae (Fujii, 1896; Rothwell, 1987; Zhou and Zhang, 1989; Zheng and

Zhou, 2004), peculiarities of vascularization of multi-ovulate aberrant forms (Rothwell, 1987), and also the axillary position of the ovuliphore suggest that the strobilus, similar to pollen strobili of *Ginkgo*, may be the initial form of ovuliphore of Ginkgoales, and the ovuliphore of extant *Ginkgo* is a result of its simplification. The trend towards simplification of ovule-bearing organs was manifested in different representatives of Ginkgoales and allied plants. Among the Umkomasiales, ovule-bearing organs were strongly reduced in *Umkomasia uniramia* Axsmith, E.L. Taylor, T.N. Taylor et Cuneo (Axsmith et al., 2000); there are plants with multiovulate fertile structures which correspond in the degree of reduction to the ovuliphore of *Ginkgo biloba* (for example, *Avatia* Anderson et Anderson and *Hamshawia* Anderson et Anderson and Anderson, 2003). Seed-bearing laminae of the type observed in *Avatia* could be transformed into structures bearing single ovule of the same type as in *Ginkgo* via a decrease in the number of ovules and recurvation of the lamina onto the abaxial side; in this case, bundles of vascularization of *Ginkgo* collar (Shaw, 1908) could have represented rudiments of vascularization of disappearing ovules.

Previously, based on the similarity of integument of Ginkgoales and composite capsule of Vladimariales (plants allied with Umkomasiales), in particular, abundance of stomata on the surface of *Ginkgo* integument, as well as the integument complex structure and vascularization, and also on presence in *Vladimaria* Gordenko of similar collar, Gordenko (2010) proposed that the integument of *Ginkgo* is possibly homologous to the cupule of Umkomasiales. This assumption disagrees with the hypothesis discussed above; at the same time, the above-mentioned peculiarities of *Ginkgo* integument represent one of the main difficulties in this hypothesis. To test the hypotheses concerning the origin of Ginkgoales, further study of the entire complex of characters of putative ancestral forms of this order is necessary (primarily, investigation of structures, which occur in the position of the outgrowths of *Nagrenia samylinae* and *Ginkgo biloba*) as well as additional study of morphology and anatomy of normal and aberrant ovuliphores of extant *Ginkgo*.

ACKNOWLEDGMENTS

We are grateful to employees of the Laboratory of Paleobotany of the Botanical Institute of the Russian Academy of Sciences for providing possibility to study the material published in the paper of Samylin (1990). We also thank R.A. Rakitov (Borissiak Paleontological Institute, Russian Academy of Sciences) for his helpful assistance with a scanning electron microscope, and to the reviewers for constructive discussion.

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Translated by G. Rautian