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Emendation of *Sorosaccus gracilis* Harris 1935, a gymnospermous pollen cone

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Abstract Study of gymnospermous pollen cones, identified with *Sorosaccus gracilis* Harris 1935, from the Yangcaogou Formation, Late Triassic of China, has led to the identification of new and significant characteristics of the species. The new specimens show distinct variations in the morphology of the distal laminar portions of the microsporophylls. These well-preserved fossils are helpful in elucidating, reconstructing and revising the diagnostic features of *S. gracilis*. After comparing the characteristics of the specimens from China with those of *S. sibiricus* Prynada 1962, and of the pollen cones which were respectively assigned to *Baiera longifolia* (Pom.) Heer 1876 from Siberia, Russia, *S. minor* Harris 1935 from Greenland, and *S. umaltensis* Krassilov 1972 from Bureya River of Russia, we consider that these four names should be reduced to the synonymy of *S. gracilis*. Thus we revise the diagnosis of *Sorosaccus*. The significance of *Sorosaccus* in evolution of pollen cones is discussed. We consider that *Sorosaccus* is possibly basic to the evolution of the genus *Ginkgo* by the reduction of the number of microsporangia and of microsporophylls. *Ginkgo liaoningensis* Liu, Crane, Li & Wang 2005 from the Early Cretaceous of Liaoning Province, China represents likely one of morphologically intermediate steps between *Sorosaccus* and *G. biloba* in evolution.

Key words *Sorosaccus gracilis*, pollen cone, evolution, Late Triassic, Liaoning.

The genus *Sorosaccus* was established by Harris in 1935, based on pollen cones initially found from the Neil Cliff, Liverwort Bed belonging to the *Thaumatopteris* Zone, in the fossil flora of Scoresby Sound East Greenland (Harris, 1935). The pollen cones were always associated with ginkgoalean leaves in East Greenland, and "their microspores were of a type which occurred in the Ginkgoales and many Gymnosperms" (Harris, 1935). But the genus is dubious in taxonomic position or is unknown in evolutionary trends. So far, only four species have been contained in *Sorosaccus*: *S. gracilis* Harris 1935, *S. minor* Harris 1935, *S. sibiricus* Prynada 1962 and *S. umaltensis* Krassilov 1972.

In this paper, the specimens of pollen cone *Sorosaccus gracilis* from Yangcaogou Formation (Late Triassic) in Beipiao County, Liaoning Province, China, were studied, and its likely taxonomic affinity and evolutionary trends were considered. The Late Triassic flora from Yangcaogou Formation contains *Thallites, Neocalamites, Annulariopsis, Danaeopsis, Dictyophyllum, Todites, Cladophlebis, Nilssonia, Pterophyllum, Sphenobaiera, Baiera, Ginkgoites, Glossophyllum, Podozamites, Pityophyllum, Cycadocarpidium, Taeniopteris, Stenorachis* (Zhou, 1981).

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1 Material and methods

The specimens were collected from Yangcaogou Formation in Zhaomagou Village, Beipiao County, Liaoning Province, China (Fig. 1). Yangcaogou Formation is regarded as Late Triassic in age (Zhou, 1981; Zhang & Zheng, 1987). They are preserved as impressions in a matrix of gray to yellow mudstone. The specimens were observed under a stereomicroscope Stemi SV 11 and photographed using a Nikon FM2 camera. All specimens are housed in the National Museum of Plant History of China, Institute of Botany, the Chinese Academy of Sciences, Beijing, China.

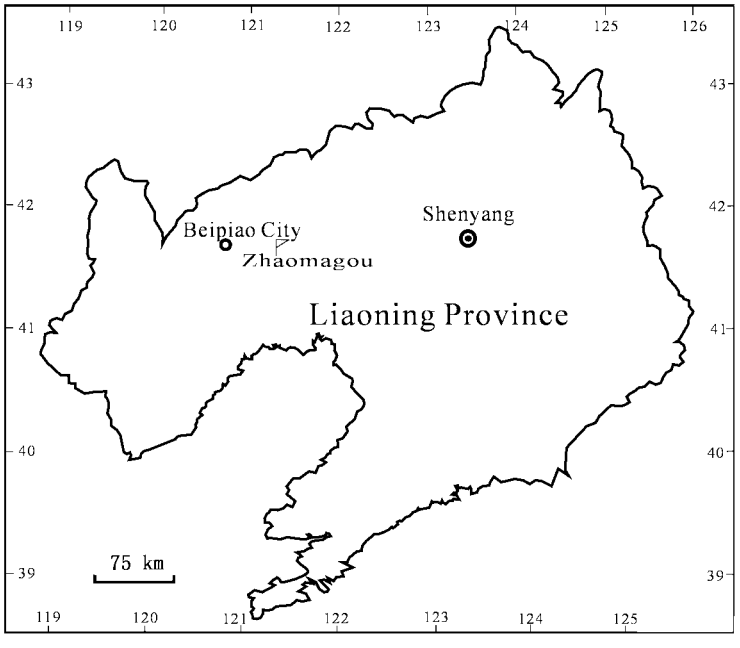
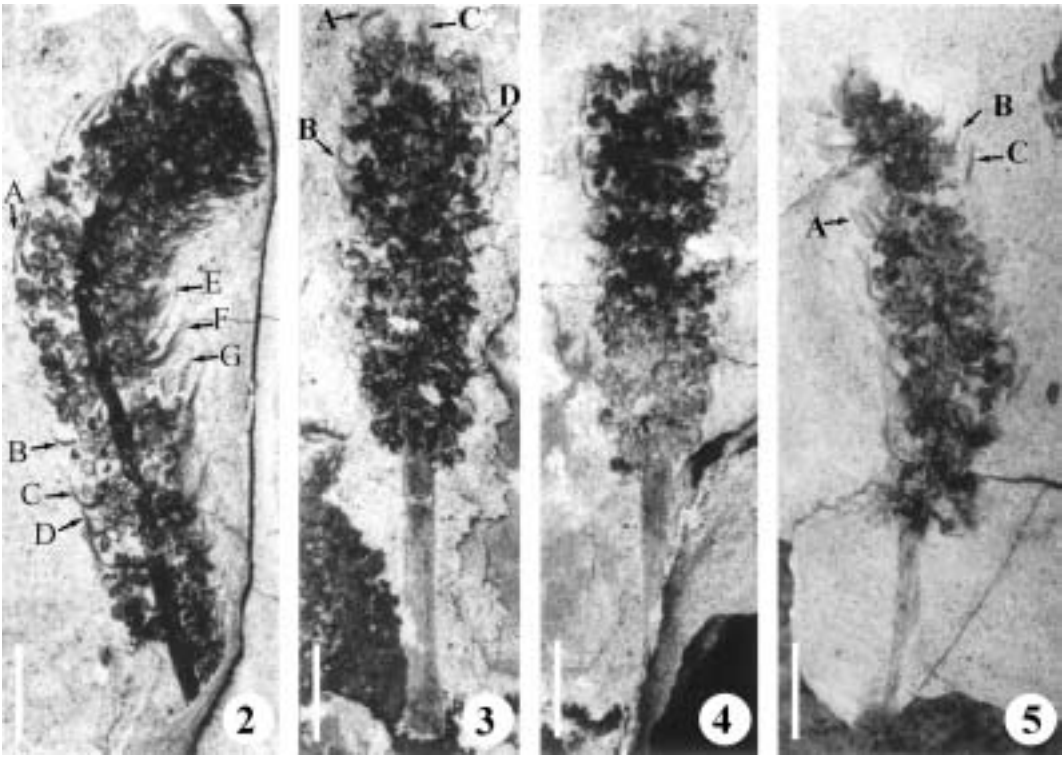


Fig. 1. Map showing fossil locality.

2 Description

Cones are roughly catkin-like (Figs. 2-5), cylindrical (Figs. 3, 4, 10), 35-45 mm in length, 6-10 mm in diameter. They consist of a main axis with microsporophylls arranged helically (Fig. 6). Some specimens (Figs. 2, 6-9) clearly show the microsporophylls with their arrangement and microsporangia. The main axis, 1-2 mm in diameter, possesses faintly striated surface (Figs. 3, 4). Microsporophylls, 30-40 in number, arise and are directed upwardly at acute or obtuse angles to the main axis. The distance from the base of the axis to the lowest microsporophyll is 10-15 mm. The interval between microsporophylls is 1-1.5 mm. Microsporophylls consist of a lamina bearing microsporangia on the abaxial surface. The microsporophyll is divided into two parts: a petiole and an upwardly bending, expanded lamina. The petiole is 2-3 mm long and 0.1-0.5 mm wide. The lamina is 2-5 mm long and 0.2-2.5 mm wide, bending upward and exhibiting considerable variation in outline from linear-lanceolate to oval (Fig. 11). Some laminae are broken from their petioles away from the main axis (Fig. 2). Microsporangia, in clusters of 6 to 8, are attached to the lateral and the abaxial sides of the petiole. Each microsporangium is oval, 1-1.5 mm long and 0.5-1 mm wide, and dehisces longitudinally.



Figs. 2-5. Hypotypes of *Sorosaccus gracilis*. The specimen in Fig. 4 is the counterpart of the specimen in Fig. 3. The numbers (2A, 2B, 2C, 2D, 2E, 2F, 2G; 3A, 3B, 3C, 3D; 5A, 5B, 5C) show the microsporophylls with microsporangia. Scale bar = 5 mm.

3 Systematic palaeobotany

DIVISION GYMNOSPERMOPHYTA
ORDER INCERTAE SEDIS
FAMILY INCERTAE SEDIS

Sorosaccus Harris 1935 emend. Liu, Hueber, Li & Wang

Emended generic diagnosis: Pollen cone consisting of a main axis with microsporophylls arranged helically. Microsporophyll consisting of petiole and lamina bearing microsporangia. Microsporophyll arising to the axis; lamina bending upward. Microsporangia attached in a cluster on the lateral and abaxial sides of the petiole. Microsporangium oval, dehiscing longitudinally.

Type: *Sorosaccus gracilis* Harris 1935.

Sorosaccus gracilis Harris emend. Liu, Hueber, Li & Wang 1935. *Sorosaccus gracilis* Harris, pl. 24, figs. 3-7, 11, 12; pl. 28, fig. 11; text-fig. 50, E, F, H.

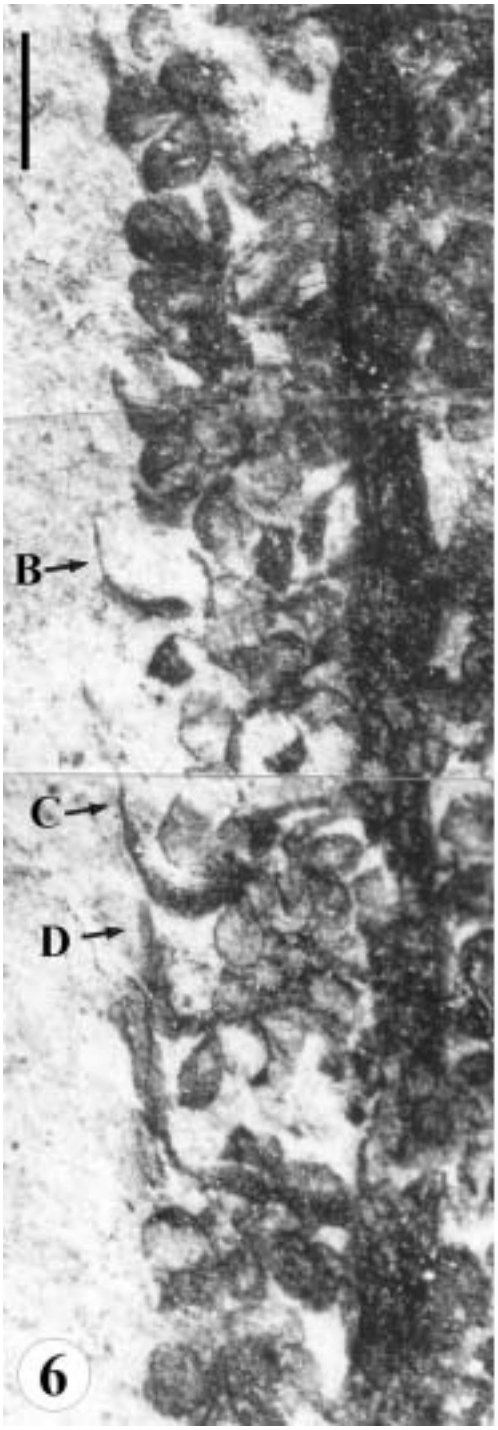
Synonyms:

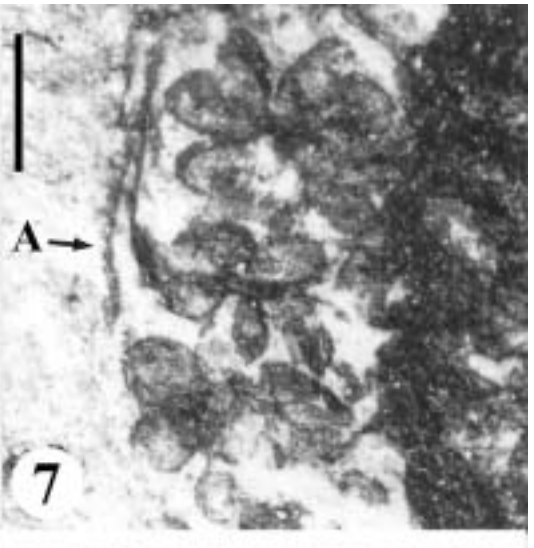
1876. *Baiera longifolia* Heer, Pars. 53, pl. IX, figs. 8, 9.

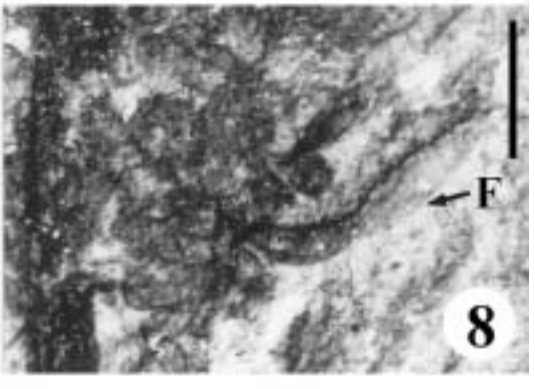
1935. *Sorosaccus minor* Harris, pl. 27, fig. 2.

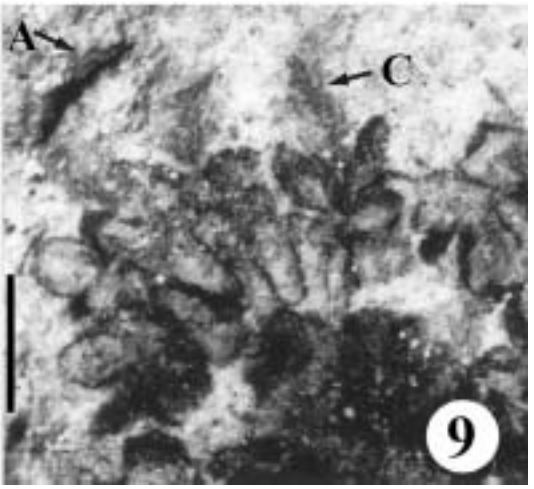
1962. *Sorosaccus sibiricus* Prynada, pl. XIII, figs. 7, 8; pl. XVIII, figs. 4a, 5-7; pl. XXI, fig. 5.

1972. *Sorosaccus umaltensis* Krassilov, pl. XIX, figs. 1, 2, 4-7, 9.









Figs. 6-9. Magnification of the hypotypes of *Sorosaccus gracilis* Harris 1935 emend. Liu, Hueber, Li & Wang. **6.** Magnification of the part of the specimen of Fig. 2 and the numbers are corresponding to those in Fig. 2. **7.** Magnification of the left side of the specimen in Fig. 2 and the letter A is corresponding to that in Fig. 2. **8.** Magnification of the middle part of the right side of the specimen in Fig. 2 and the letter F is corresponding to that in Fig. 2. **9.** Magnification of the top of the specimen in Fig. 3 and the letters A and C are corresponding to those in Fig. 3. Scale bar=2 mm.

Fig. 10. Reconstruction of *Sorosaccus gracilis* Harris 1935 emend. Liu, Hueber, Li & Wang.

1972. *Sorosaccus* ex. gr. *sibiricus* Prynada 1962, in Krassilov, Mesozoic Flora of Bureya River (Ginkgoales and Czekanowskiales), pl. XIX, figs. 3, 8. Nauka, Moscow.

Emended specific diagnosis: Pollen cone elongate-cylindrical, catkin-like, 20-45 mm long and 5-10 mm wide. Main axis with microsporophylls arranged helically, cylindrical, 1-2 mm in diameter, surface faintly striated. Microsporophyll divided into two parts: horizontal petiole and an expanded lamina. Lamina linear, lanceolate to oval in outline, bending upward. Microsporangia attached to lateral and abaxial sides of petiole, 6-8 in number. Microsporangium oval, 0.7-1.5 mm long, 0.5-1.0 mm wide and longitudinal in dehiscence.

Holotype: *Sorosaccus gracilis* Harris, 1935. pl. 24, figs. 5, 6.

Type locality: Scoresby Sound East Greenland, Denmark.

Horizon: Neil Cliff Formation, Liverwort Bed of Rhaetic (Late Triassic) and Lower Liassic (Early Jurassic) (Harris, 1937).

Epitypes: Figs. 2-5. LN-8486, LN-8487, ZMG-8488, ZMG-8489.

Locality: Zhaomagou Village, Beipiao City, Liaoning Province, China.

Horizon: Yangcaogou Formation, Late Triassic (Zhou, 1981; Zhang & Zheng, 1987).

Repository: National Museum of Plant History of China, Beijing, China.

Distribution: East Greenland, Denmark; Siberia, Russia; Liaoning, China.

4 Comparison

We compare four species in *Sorosaccus*: *S. gracilis* Harris 1935, *S. minor* Harris 1935, *S. sibiricus* Prynada 1962 and *S. umaltensis* Krassilov 1972.

Harris (1935) separated *Sorosaccus minor* from *S. gracilis* stating that the former was “differing in being more slender owing to its smaller sporophylls (basal region 2 mm long) and smaller sporangia (0.7×0.5 mm)”. The sporangium of *S. gracilis*, 1.1×0.8 mm, is bigger than that of the type specimen of *S. minor* (Harris, 1935, pl. 27,

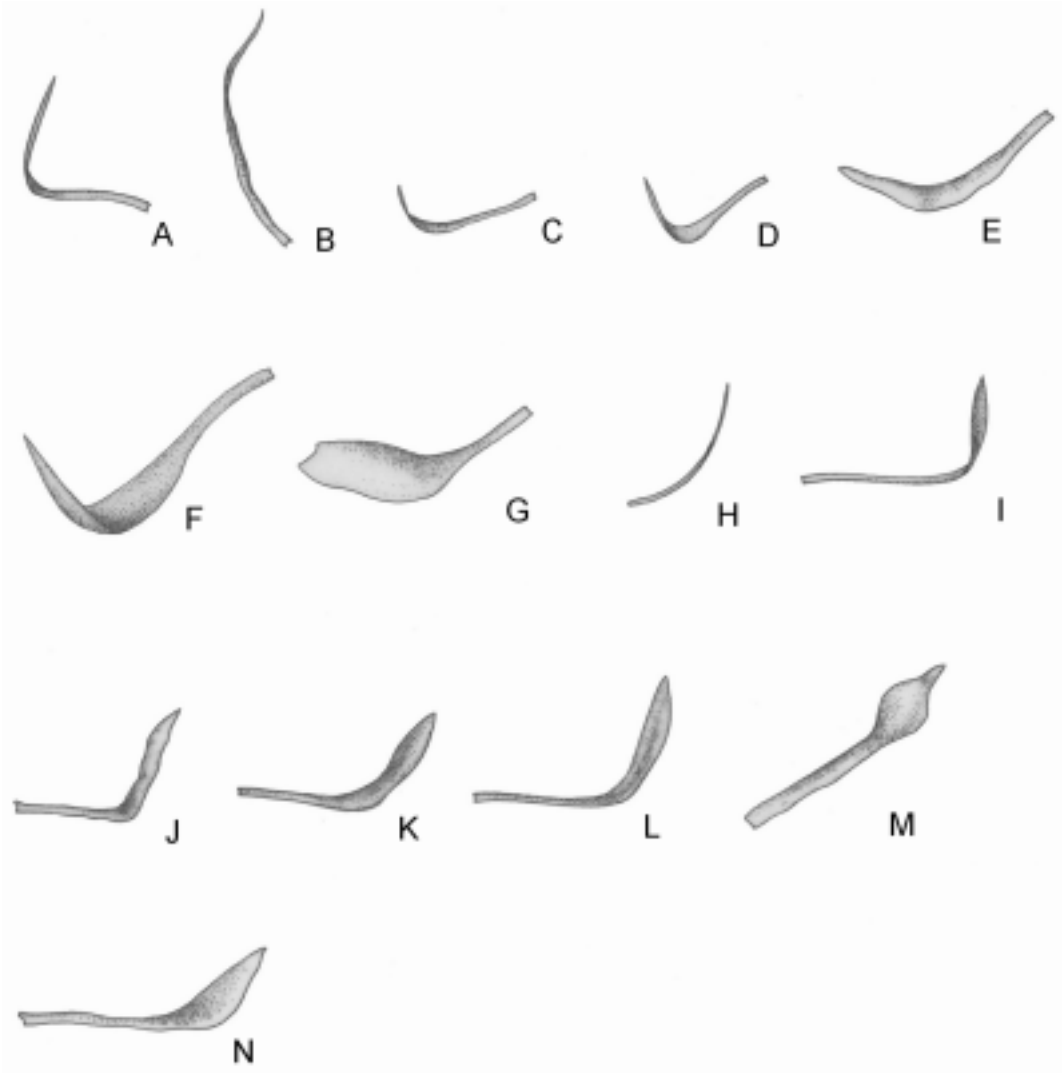


Fig. 11. Variation of microsporophylls without microsporangia of *Sorosaccus gracilis* in outline. The letters A-N show respectively the drawings of the microsporophylls without microsporangia in Fig. 3A, Fig. 2A, Fig. 2B, Fig. 2D, Fig. 3B, Fig. 2C, Fig. 5A, Fig. 2E, Fig. 3D, Fig. 5B, Fig. 2G, Fig. 5C, Fig. 3C, and Fig. 2F.

fig. 2), 0.7×0.5 mm (Table 1). But the size of the sporangium in our specimens, 1-1.5× 0.5-1 mm, covers that of *S. minor*. We consider that the different sizes show the specimens in different phases of development. The size of sporophylls in *S. minor*, with the petiole 2 mm long, is similar to that in *S. gracilis* based on Harris' description, which is 2-4 mm, and the size is in the range of that of *S. gracilis* based on our collections, which is 1-3 mm long. It is very difficult to differentiate *S. minor* from *S. gracilis* based only on the size of basal stalks and microsporangia. We transfer therefore the specimens assigned to *S. minor* to *S. gracilis*.

Table 1 Comparison of specimens assigned to *Sorosaccus gracilis* Harris 1935 emend. Liu, Hueber, Li & Wang

Specimen*	Locality	Age	Size of male cone (mm)	Diameter of axis (mm)	Length of petiole* (mm)	Angle of petiole* with axis	Number of MIC	Size of MIC (mm)	Size of pollen grain (μm)	Reference
S. gracilis	Greenland, UK	LT, EJ	30×8	1	2-4	right angle	6	1.1×0.8	90×60	Harris, 1935
S. minor	Greenland, UK	LT, EJ			2			0.7×0.5		Harris, 1935
S. sibiricus	Siberia, Russia	MJ	20×5-7			right angle	8			Prynada, 1962
S. umaltensis	Bureya River, Russia	LJ	18×8 (Not intact)	0.5	3.5-4.5	right angle	8	1.0×0.8	40×27-50×36	Krassilov, 1972
Specimen from China	Liaoning, China	LT	35-45×6-10	1-2	3	right or obtuse angle	6-8	1-1.5×0.5-1		In this paper

Notes: Specimen*=Specimens assigned to *Sorosaccus gracilis* Harris 1935 emend. Liu, Hueber, Li & Wang in this paper; Petiole*=Petiole of microsporophyll; MIC=Microsporangium; LT=Late Triassic; EJ=Early Jurassic; MJ=Middle Jurassic; LJ=Late Jurassic.

Specimens of *Sorosaccus sibiricus* was collected from the Middle Jurassic of eastern Siberia (Prynada, 1962). Prynada discussed that "the sporophylls of Ust'-Baley specimens are similar with those from the Lower Jurassic deposits of Greenland but differing from them in the size of the whole cones and close arrangement of sporophylls". In fact, the sporophylls of Ust'-Baley specimens are similar to those of Greenland in the size of the entire cones and arrangement of sporophylls. Firstly, the size of the specimens assigned to *S. sibiricus*, 20×5-7 mm, is covered in that of *S. gracilis* based on new materials from China, 35-45×6-10 mm (Table 1). The number of microsporangia in *S. sibiricus* (8 in number) is similar to that of *S. gracilis* (6-8 in number). Krassilov (1972) thought that dimensions of pollen cones ascribed to *S. sibiricus* by Prynada were insignificantly distinguished from those by Harris. Thus we move the specimens assigned to *S. sibiricus* to *S. gracilis*.

The specimens of *Sorosaccus umaltensis* were collected from the sediments of the Upper Jurassic at the right bank of Bureya River, Russia (Krassilov, 1972). Krassilov (1972) considered that the reproductive organs from Bureya River coincide almost completely with those of *S. gracilis* in dimensions of the pollen cones, microsporophylls and microsporangia. But the pollen grain size of *S. umaltensis*, 40×27-50×36 μm, is smaller than that of *S. gracilis* (90×60 μm) (Harris, 1935). It is uncertain to describe a new species based on the size of pollen grains since the size of pollen grains varies distinctly in different phases of development. We also transfer the specimens assigned to *S. umaltensis* to *S. gracilis*.

Four specimens (Heer, 1876, pl. IX, figs. 8-11) were described as the pollen cones of *Baiera longifolia* based on their general agreement with the pollen cones of *Ginkgo* and on their association with the leaves. Harris (1935) considered that they were exactly is the same nature of *Sorosaccus gracilis*. After our observation, two specimens (Heer, 1876, pl. IX, figs. 8, 9) from the four show that the cone axis bears the bracts with extended laminae that bend upward and bear microsporangia. Therefore, we considered that the two belong to *Sorosaccus gracilis*.

5 Discussion

We are trying to relate the genus *Sorosaccus* with ginkgoaleans and deduce its evolution based on the oval microsporangia dehiscing longitudinally and the pollen like that in Ginkgoales. Comparing the whole pollen cone of *Sorosaccus gracilis* with the pollen cone of *Ginkgo biloba* (the only extant species of the order Ginkgoales) and *Ginkgo liaoningensis* (a pollen cone collected from the Yixian Formation of Early Cretaceous, Liaoning, China) (in our another paper which is accepted by *Botanical Journal of the Linnean Society*, "The pollen cones of *Ginkgo* from the Early Cretaceous of China, and its bearing on the evolutionary significance"), it is found that 6-8 microsporangia per cluster are attached to lateral and abaxial sides of microsporophyll in *Sorosaccus gracilis*, and 3-4 pendulous microsporangia are attached to the abaxial side of microsporophylls in *Ginkgo liaoningensis* and 2 in *G. biloba*. As these pollen cones are quite similar in outline, we consider that *Sorosaccus* could have evolved to *Ginkgo* through the reduction of the number of sporangia and shortening the distal portion of the lamina at the distal portion of the microsporophyll (Fig. 12). *Ginkgo liaoningensis* from the Early Cretaceous could represent one of morphologically intermediate steps between *Sorosaccus* and *Ginkgo biloba* in the evolutionary course of the ginkgoalean pollen cones. Another transitional type between *Sorosaccus* and *Ginkgo* (*G. liaoningensis*), probably occurring in the period of the Middle-Late Jurassic (Fig. 12), is interpreted to contain a shortened and narrowed lamina at the distal portion of the microsporophyll. It suggests that the number of sporangia may have decreased in the evolutionary process, and the length of the lamina at the distal portion of the microsporophyll may have shortened. The hypothesis of the evolutionary trend of the pollen cones needs further confirmation after obtaining specimens of pollen cones in organic connection with foliar axes.

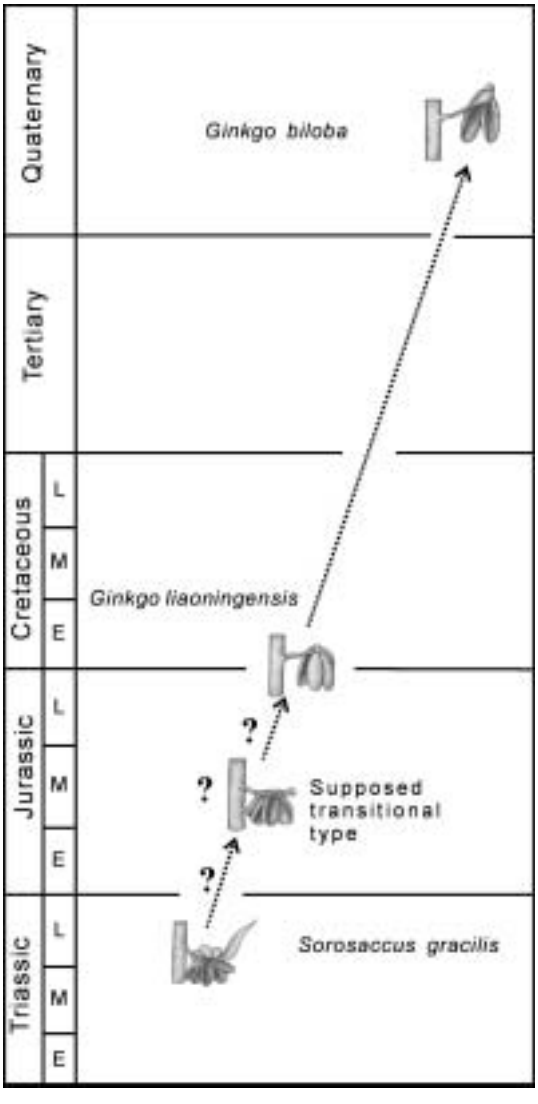


Fig. 12. Schematic drawing showing the evolutionary lineage of several pollen cones from *Sorosaccus gracilis* to *Ginkgo biloba*.

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裸子植物雄球花——纤细堆囊穗的修订

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摘要 研究了采自中国东北晚三叠世羊草沟组的一种裸子植物雄球花——纤细堆囊穗。通过对新材料的研究,发现这种雄球花小孢子叶末端的裂片在形态上差异很大,这是原来没有发现的十分重要的特征。这些保存精美的化石对于纤细堆囊穗特征的阐明和修订以及物种复原很有帮助。将中国的标本与西伯利亚堆囊穗、小堆囊穗、乌尔马堆囊穗和被定为长叶拜拉的雄球花进行了比较,发现它们与纤细堆囊穗在特征上一致,故将它们处理为纤细堆囊穗的异名。修订后的纤细堆囊穗包括上面所提到的所有种。同时,也讨论了堆囊穗属可能的演化意义。它可能是银杏属的远祖,经过小孢子囊数目的减少和小孢子叶长度的缩短而演化到现在的银杏,而产自辽西早白垩世的辽宁银杏可能代表了堆囊穗和现代银杏在形态演化上的一个中间步骤。

关键词 纤细堆囊穗; 雄球花; 演化; 晚三叠世; 辽宁