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Early Cretaceous sarraceniacean-like pitcher plants from China

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Abstract.- This paper reports fossil plants of *Archaeamphora longicervia* gen. et sp. nov. Li from the Early Cretaceous Yixian Formation, northeastern China. The plants are herbaceous and similar to modern sarraceniaceans in having spirally arranged developed/underdeveloped pitchers and phyllodia-like leaves that have parallel major veins and reticulate meshes, distinctive honey-spoon-like structures and porous glands. The intimately associated seeds are reticulate-tuberculate and winged, resembling sarraceniacean seeds. The unique pitcher and characteristic seed suggest a relationship to Sarraceniaceae. The relationship to Angiosperms is also supported with fossil molecule oleanane found from *Archaeamphora*, using GC-MS. *Archaeamphora* demonstrates the earliest carnivorous plant and the only fossil record of pitcher plants. Also, as the third genus of the oldest Angiosperms, the existence of such a derived taxon suggests that flowering plants should have originated much earlier.

Key words : carnivorous plants - Early Cretaceous - fossil pitcher plants - origin of Angiosperms - Sarraceniaceae.

Résumé.- Cet article présente des plants fossiles d'*Archaeamphora longicervia* gen. et sp. nov. Li du Crétacé inférieur du Yixian, Chine du Nord-Est. Les plantes sont herbacées et semblables aux sarracénies actuelles avec des urnes développés/sous-développées organisées en spirale, des phyllodes à nervures principales parallèles, un réseau réticulé, des structures semblables à une cuillère à nectar et des glandes ouvertes. Les graines intimement associées sont réticulées-turberculées et ailées comme les graines de sarracénies. La parenté avec les Angiospermes est aussi établie par des molécules fossiles d'oléanane détectées sur *Archaeamphora* par GC-MS. *Archaeamphora* se présente comme la plus ancienne des plantes carnivores et le seul fossile de plante à urnes connu. Aussi en tant que troisième genre des plus vieilles Angiospermes, l'existence d'un taxon si évolué suggère une apparition des plantes à fleurs beaucoup plus ancienne.

Mots clés : plantes carnovores - Crétacé inférieur - plantes à ascidies fossiles - origine des Angiospermes - Sarraceniaceae.

I. INTRODUCTION

With the carnivorous pitchers and beautiful flowers, sarraceniacean plants are found with three genera separately distributed in South and North Americas (Juniper *et al.*, 1989; Albert *et. al.*, 1992; Bayer *et al.*, 1996). They are considered neither related to the monospecific Cephalotaceae in Australia, nor the monogeneric Nepenthaceae in the Old World tropics (including southern China). For lacking fossil record, whether sarraceniacean genera originated from South Africa or alternately within North America has been uncertain (Juniper *et al.*, 1989; Albert *et. al.*, 1992; Bayer *et al.*, 1996; Schnell, 2002; Lloyd, 1942). Here I briefly report a new fossil plant taxon, *Archaeamphora longicervia*, from the Jianshangou Formation (Sun *et al.*, 1998, 2001), Low Cretaceous, at Beipiao, western Liaoning, China. The fossil-bearing beds are considered to be the lower part of the Yixian Formation that is about 124.6 mya (Swisher *et al.*, 1999). Currently, the two oldest fossil Angiosperm genera, *Archaefructus* (Sun *et al.*, 1998, 2001, 2002) and *Sinocarpus* (Leng & Friis, 2003), are found from the Yixian Formation. For lacking typical bisexual flowers, *Archaefructus* is debated as either a sister taxon of all extant Angiosperms (Sun *et al.*, 2002) or a crown-group Angiosperm (Friis *et al.*, 2003). However, a recently reported new species, *Archaefructus eoflora*, based on an entire fossil plant (from root, stem, to reproductive axes in various stages), indeed demonstrates bisexual flowers and suggests an attribution to dicots (Ji *et al.*, 2004). *Sinocarpus*, from the same formation, is proposed to be a basal Eudicot (Leng & Friis, 2003). However, no core eudicot Angiosperm has been found from the formation yet.

The fossil plants of *Archaeamphora longicervia* are presented here as the earliest carnivorous sarraceniacean-like pitcher plants of core Eudicots, and they are discovered in Sun's fossil collection from the site of *Archaefructus liaoningensis* (Sun *et al.*, 1998, 2001). On the same rock specimens, the intimately associated, reticulate-tuberculate seeds resemble those of sarraceniaceans. These specimens are embedded in yellowish gray claystone that has none or very little fine-sized quartz or mica, suggesting a very low hydrodynamic taphonomic condition, possibly as that in modern bogs.

II. TAXONOMY AND DESCRIPTION

Archaeamphora longicervia gen. et sp. nov. Li
Holotype: CB00220 (Fig. 1 to 4); paratypes: CB00754 (Fig. 5 to 12).
Etymology. *Archaeamphora* is named for the ancient pitcher plant, while *longicervia* for its neck between the tank and mouth.

Diagnosis

Plant herbaceous, about 50 mm tall with pitchers and underdeveloped pitchers or phyllodia-like leaves spirally arranged on stem that has vertical ridges and grooves. Pitcher composed of a tubular base, tank, neck, and spoon-shaped lid, with a thickened wing/ridge along the abaxial side of the pitcher, and a short wing (ala) with reticulate veins along the adaxial side of the tank. Pitcher with 3-5 parallel major veins, a few anastomosing intercostal veins, and extensive veinlet meshes around a thick honey-spoon-like structure (hereafter HSLS) that is round (3-5 mm in diameter) and convexly protruded outwards on each lateral side of the tank. A similar but semicircular HSLS found on a lateral margin of the upright lid. HSLS exhibiting strong yellow-green intrinsic fluorescence, excited with a

500 nm wavelength light. Same fluorescence found in cuticularized porous glands that partially embedded along veins in the tank.

Description

Here is a brief description based on the holotype (Fig. 1 to 4) and paratype (Fig. 5 to 12), and seven additional specimens. A report with more details will be published separately.

The plants are herbaceous, with the remained part up to 50 mm in height (Fig. 5). Stem (at least 21 mm long and 1.2 mm wide) has vertical ridges and grooves (Fig. 6) and bears with spirally arranged pitchers and phyllodia-like tubular leaves that have 3-5 parallel major veins (Fig. 1, 4, 5). Pitchers are ascidiate (baglike), 30-40 mm long (Fig. 1, 5), consists of a convex tubular basal section (Fig. 6), an expanded tank (Fig. 1, 4, 5), a long narrow neck (Fig. 1), and an upright, spoon-shaped lid (Fig. 2). Each pitcher curves upwards, with a thick flat ridge buttered on the abaxial side of the whole pitcher (Fig. 1, 2, 4, 5) and a small wing (ala) on the adaxial side of the tank (Fig. 4, 5). Reticulate veinlets develop on the wing and in the intercostal areas on the expanded tank and on the lid (Fig. 2 to 4).

Splitting a fusiform tank, a thick concave (up to about 1 mm deep) round area (3-5 mm in diameter) is found with more or less, darker brown debris in the cavity on each side (Fig. 1, 5, 7). No fruit/seed structure has been found in the expanded area. Excited with a 500 nm wavelength light, the thick round areas exhibit very strong golden-yellow fluorescence, observed under a Nikon or Olympus fluorescence microscope. On one marjin of the lid, a similar thick, sinuate area (Fig. 2) is also found with the same strong golden-yellow fluorescence.

The inner surface of the tank is relatively flat (Fig. 7) and some part still has a cuticle covered on small bump-like structures (Fig. 8). Glands (about 4 μm in diameter) are found laid on the inner surface (Fig. 8 to 10), or partially embedded in the grooves along the veins. Some glands are twisted (Fig. 12) and some have droplet-like structures (< 2 μm in diameter; Fig. 11). These glands also have very strong golden-yellow fluorescence.

Associated seeds

On the counterpart of the holotype (Fig. 1b), less than 1 cm away from the pitcher, a well-preserved seed (Fig. 13) is found in an oval shape (0.9 x 1.25 mm), covered with black-brown warts (each is about 80μm in diameter) that are reticulate-tuberculate (Fig. 14). The seed has a lateral wing/ridge (the right side in Fig. 13) that is tuberculate too. The seed has an inconspicuous, tuberculate ridge on the other lateral side. Another tuberculate seed is broken and in a clavate shape (0.7 x 1.25 mm) found aside a pitcher plant on another specimen.

III. DISCUSSION

Oleanane analysis was applied to test if the fossil plants could belong to Angiosperms. Oleanane has been considered to be a biomarker of Angiosperms (Moldowan *et al.*, 1994) because it has not been found in extant Gymnosperms but in most Angiosperm families. If oleanane can be found in *Archaeamphora*, then the plants can be suggested belong to Angiosperms. Chemical extracts were directly leached off from three fossil pitcher samples and several other fossil plants and sedimentary specimens from the same forma-

tion, treated with zeolite molecular sieve to remove non-oleanane isomers, and finally analyzed with GC-MS to screen for oleanane peaks. Oleanane has not been found from other specimens, but from the three pitcher plant specimens, suggesting the fossil plants belong to Angiosperms and thus *Archaeamphora* becomes the third earliest Angiosperm genus from the Yixian Formation.

The fossil pitchers are obviously different from those of Nepenthaceae (which has the pitcher originated from a leaf apical tendril, two separated wings along the pitcher tube and a ribbed peristome around the mouth opening) and Cephalotaceae (which has the petiole of the pitcher between the tube and the lid, four distinct pitcher wings, and a coarsely clawed peristome), but identical to Sarraceniaceae in having pitchers directly extended out upwards from the top of a short petiole, one or two pitcher wings and a smooth peristome (Juniper *et al.*, 1989; Schnell, 2002; Lloyd, 1942).

The *Archaeamphora* plants are morphologically similar to modern *Sarracenia purpurea* in having spirally arranged pitchers and phyllodia-like tubular leaves with parallel major veins. They also resemble *Heliamphora* in having pitchers/leaves spirally arranged on stems and pitchers with a long neck and upright lid. Especially, the thick semicircular structure on the lid margin is comparable to the honey spoon on *Heliamphora heterodoxa* var. exappendiculate (based on Andrea Wistuba's material). The round thick concave areas on each side of the tank also resemble the concave honey spoon. The strong golden-yellow fluorescence suggest the cavity area could have produced some cuticular or waxy substance like that found in modern pitcher plants. The *Archaeamphora* glands with droplet remnants are identical with the carnivorous plant digestive glands that have innumerous microscopic pores (cuticular gaps) to secret mucilaginous drops with enzyme and cuticularized material, and also absorb nutrients from the digested insects (Juniper *et al.*, 1989). So, morphologically *Archaeamphora* resemble to both *Sarracenia purpurea* and *Heliamphora* very much. All of the above evidence suggests that *Archaeamphora* could be a sarraceniacean-like pitcher plant.

Another type of pitcher is found (not reported here) without an expanded tank and a narrow neck, but simply gradually expanded from the petiole tip upwards into a hollow trumpet-like shape. It should be a different species. An intermediate type (with a wider neck) between the trumpet-like like species and *Archaeamphora longicervia* is also found from the same flora. These suggest that the pitcher plants were diversified during the Early Cretaceous already.

The existence of sarraceniacean-like pitcher plants in the Yixian Formation is also supported by the associated seeds that have their unique reticulate-tubercles exclusively identical to seeds of Sarraceniaceae (McDaniel, 1971; Maguire, 1978), especially the seeds of *Sarracenia* (Fig. 15). Both have the same size range (1.1-2.2 mm), similar sized warts on surface, and a lateral inconspicuous ridge (McDaniel, 1971; Maguire, 1978).

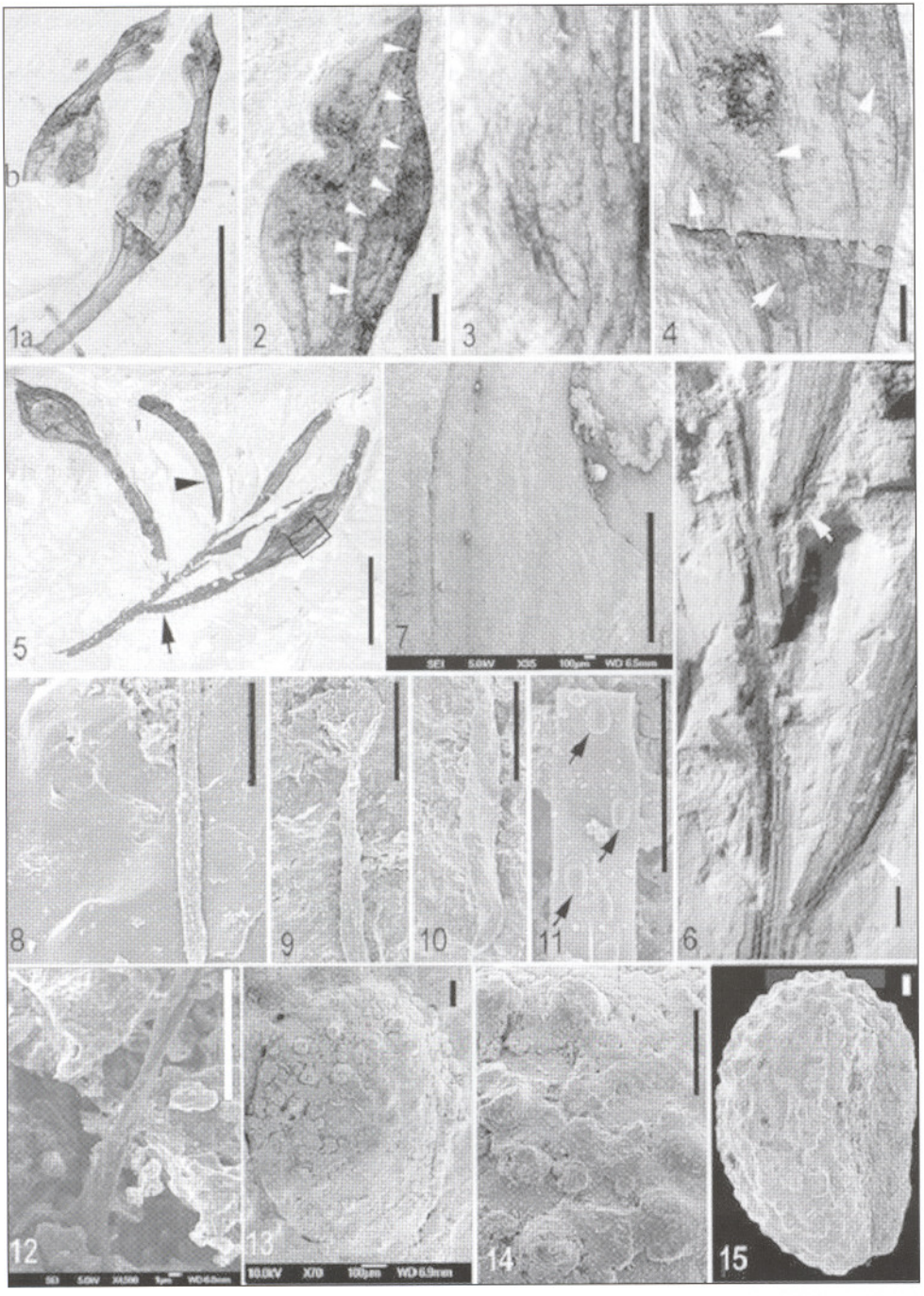
Fossil record of carnivorous plants can be only traced back to some Cenozoic fossil pollen and seeds, with the oldest record (the seeds of aquatic *Aldrovanda* and *Palaeoaldrovanda*) back to Senonian (85-87 mya) of Late Cretaceous (Degreef, 1997). Thus, *Archaeamphora* does not represent the only fossil pitcher plant but also predated the oldest carnivorous plants.

Sarraceniaceae is currently classified as a family of Ericales is plotted in a clade of Asterids, one of two major groups of the core crown Eudicots (Anderberg *et al*, 2002; Walters & Olmstead, 2004). Thus, sarraceniacean-like *Archaeamphora* appear to be earliest representative of the crown Angiosperms. The existence of a so highly derived Angiosperm in the Early Cretaceous suggests that Angiosperms should have originated

much earlier, maybe back to 280 mya as the molecular clock studies suggested (Sanderson *et al.*, 2004).

China does not have living sarraceniacean plants, but very few species of Nepenthaceae. Obviously, *Archaeamphora* from China also provides us significant data in study of the origin, evolution and phylogenetic relationships of pitcher plants.

An artist restoration of *Archaeamphora longicervia* by Diana Li.
Représentation artistique de *Archaeamphora longicervia* par Diana Li.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Figs. 1 to 12.- *Archaeamphora longicervia* gen. et sp. nov. Li. 1 - The holotype (CB00220). 2 - The spoon-shaped upright lid with a honey-spoon-like structure on the left margin and the right margin (arrowhead) curved inwards, to make the whole lid in a spoon shape. 3 - The ala with reticulate venation. 4 - The tank with intercostal veins (arrows) and reticulate veinlets (arrowheads). 5 - Paratype (CB00754); two pitchers and three incomplete phyllodia-like leaves spirally arranged on the stem. 6 - Showing the stem (of Fig. 5) with grooves and ridges, bearing a pitcher (lower) and a phyllodium-like leaf (upper), both with a tubular base and a flat ridge on abaxial side (arrowheads). 7 - SEM photo of the counterpart of the insert portion in Fig. 5, showing the concave cavity (in the upper right corner) of the honey-spoon-like structure where contains debris. 8 - A cuticularized gland on the inner surface that has bump-shaped structures. 9 - A gland and its possible basal part on the inner surface. 10 - A gland tip. 11 - A cuticularized gland with droplet-like structures (arrows) secreted from microscopic pores. 12 - A twisted gland partially embedded in a groove along a vein.

Fig. 13-14.- An intimately associated, reticulate-tuberculate seed with an inconspicuous ridge on the right side; Fig. 14 - Magnification of the reticulate-tubercles of Fig. 13.

Fig. 15.- A seed of *Sarracenia* with a ridge on the right.

Fig. 1 à 12.- *Archaeamphora longicervia* gen. et sp. nov. Li. 1 - Holotype (CB00220. 2 - Capuchon en forme de cuillère avec une structure de cuillère à nectar sur le bord gauche et sur le bord droit (flèche) courbée vers l'intérieur formant le couvercle complet en forme de cuillère. 3 - Aile à nervation réticulée. 4 - Urne avec nervures intermédiaires (flèches) et vaisseaux capillaires réticulés (pointes de flèche). 5 - Paratype (CB00754) ; deux urnes et trois phyllodes incomplètes organisés en spirale sur la tige. 6 - Tige (de la Fig. 5) avec cannelures et arêtes, portant une urne (inférieure) et une phyllode (supérieure), à base tubulaire et arête plate du côté abaxial (pointes de flèche). 7. - Photo SEM du carré inséré dans la fig. 5, montrant la cavité concave (dans le coin droit supérieur) de la cuillère à nectar contenant des débris. 8 - Glande cuticulisée sur la surface interne de structures bombées. 9 - Glande et son éventuelle partie inférieure sur la surface interne. 10 - Fragment de glande. 11 - Glande cuticulisée avec des structures en forme de gouttelettes (flèches) sécrétées des pores microscopiques. 12 - Glande partiellement tordue incorporée dans une cannelure le long d'une nervure.

Fig. 13-14.- Graine tuberculée réticulée avec arête peu visible sur la droite ; Fig. 14 - Agrandissement des tubercules réticulés de la figure 13.

Fig. 15.- Graine de *Sarracenia* avec arête sur la droite.

Bar = 1 cm on 1 and 5; 1 mm on 2 to 4 and 6, 7; 100 µm on 13 to 15; 10 µm on 8 to 12.
Barre : 1 cm sur 1 et 5 ; 1 mm sur 2 à 4 et 6, 7 ; 100 µm sur 13 à 15 ; 10 µm sur 8 à 12.

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REFERENCES

Albert V.A., S.E. Williams & M.W. Chase, 1992.- Carnivorous plants: phylogeny and structural evolution. *Science*, **257**, 1291-1494.

Anderberg A.A., C. Rydin & M. Kallersjo, 2002.- Phylogenetic relationships in the order Ericales s.l.: analyses of molecular data from five genes from the plastid and mitochondrial genomes. *Am. J. Bot.* **89**, 677-687.

Bayer R.J., L. Hufford & D. E. Soltis, 1996.- Phylogenetic relationship in Sarraceniaceae based on rbcL and ITS esequences. *System. Bot.*, **21**, 121-134.

Degreef J.D., 1997.- Fossil *Aldrovanda*. *Carniv. Plant Newslett.* **26**, 93-97.

Friis E.M., J.A. Doyle, P.K. Endress & Q. Leng, 2003.- *Archaefructus*, Angiosperm precursor or specialized early Angiosperm? *Trends in Plant Sci.*, **8**, 369-373.

Ji Q., H. Li, L.M. Bowe, Y. Liu & D. W. Taylor, 2004.- Early Cretaceous *Archaefructus eoflora* sp. nov. with bisexual flowers from Beipiao, western Liaoning, China. *Acta Geol. Sinica*, **78**, 883-896.

Juniper B.E., R.J. Robbins & D.M. Joel, 1989.- *The Carnivorous Plants*. Academic Press, San Diego, 353 p.

Leng Q. & E.M. Friis, 2003, *Sinocarpus decussatus* gen. et sp. nov., a new Angiosperm with basally syncarpous fruits from the Yixian Formation of Northeast China. *Plant Syst. Evol.*, **241**, 77-88.

Lloyd F.E., 1942.- *The Carnivorous Plants*. Chronica Bot. Co., Waltham, Mass., 352 p.

Maguire B., 1978.- Botany of the Guyana Highland: Sarraceniaceae. *Memoirs New York Bot. Gard.*, **29**, 36-62.

McDaniel S., 1971.- The genus *Sarracenia* (Sarraceniaceae). *Bull. Tall Timbers Research Station*, **9**, 1-36.

Moldowan J.M., J. Dahl, B.J. Huizinga, F.J. Fago, L.J. Hickey, T.M. Peakman & D.W. Taylor, 1994.- The molecular fossil record of oleanane and its relationship to Angiosperms. *Science*, **265**, 768-771.

Sanderson M.J., J.L. Thorne, N. Wikström & K. Bremer, 2004.- Molecular evidence on plant divergence times. *Am. J. Bot.*, **91**, 656-1665.

Schnell D.E., 2002.- *Carnivorous Plants of the United States and Canada*, 2nd ed. Timber Press, Portland, Oregon, 468 p.

Sun G.G., S.-L. Zheng, D.L. Dilcher, Y.D. Wang & S.W. Mei, 2001.- *Early Angiosperms and their Associated Plants from Western Liaoning, China*. Shanghai Scientific and Technological Education Publishing House, 227 p.

Sun G., D.L. Dilcher, S.-L. Zheng, & Z.-K. Zhou, 1998.- In search of the first flower: a Jurassic Angiosperm, *Archaefructus*, from Northeast China. *Science*, **282**, 1692-1695.

Sun G., Q. Ji, D.L. Dilcher, S.-L. Zheng, K.C. Nixon & X. Wang, 2002.- Archaefructaceae, a new basal Angiosperm family. *Science*, **296**, 899-904.

Swisher III C.C., Y.-Q. Wang, X.-L. Wang, X. Xu & Y. Wang, 1999.- Cretaceous age for the feathered dinosaurs of Liaoning, China. *Nature*, **400**, 58-61.

Walters J. & R. Olmstead, 2004.- A survey of tricolpate (eudicot) phylogenetic relationships. *Am. J. Bot.*, **91**, 1627-1644.