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New juglandaceous fruit morphotype from the Palaeocene of Amur Province, Russian Far East*

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ABSTRACT. *Amurcarya lobata* gen. et sp. nov. from the Lower Palaeocene of Arkhara, the Amur Province, Russian Far East represents a new combination of involucral characters that are used in classification of juglandaceous fossil fruits. It has an orbicular wing consisting of the laterally fused bract and two bracteoles, which are discernible owing to their conservative venation patterns. The new fruit type is similar to the Engelhardiae in incorporation of the bract in the wing as a substantial part of it, and to the Platycaryae in the transverse (oblique transverse) orientation of the wing. However, on account of its constituent involucral organs, the wing is not homologous to those of the other juglandaceous fruits.

KEY WORDS: fruit morphology, Juglandaceae, combinatorial variation, Palaeocene, Russian Far East.

INTRODUCTION

The Juglandaceae appeared in the Late Cretaceous and experienced an explosive diversification in the Palaeocene (Knobloch & Mai 1986, Manchester & Dilcher 1982, Manchester 1987, 1989, Wing & Hickey 1984). The most distinctive organs of the family are fruits that develop from an inferior bicapellate ovary variously enveloped in the calyx, bracteoles and the adaxial bract (Manning 1940, Stone 1993) The diversity of fruits described from the Palaeocene of western – central Europe and North America is due primarily to various involvement and relative contribution of these components to the involucre and, in samaroid fruits, to the involucral wing (other taxonomically significant characters, such as septation of the locule or lacunas in the nutshell, are scarcely correlated with involucral characters). The variation can be described as combinatorial, with the involucral components alternatively prominent at the expense of the others, forming the distinctive wing morphologies. Further variants are added by the components being partly or completely reduced or being involved in homologous fusion (of bracteoles or sepals to each other), non-homologous fusions (of bract to bracteoles, sepals to bracteoles, etc.) and combinations of such, their morphological distinctiveness preserved or lost. Theoretically, the number of such combinations can be of the order of hundreds, but not all are realized. In fact, only eight combinations are represented in the extant genera of the family, but more are known as fossils and the potentials of new discoveries are far not exhausted.

Here we describe a new fruit genus representing a new kind of combinatorial variation in the involucre characters. We also suggest that some variants currently considered as intrageneric, represent non-homologous structures and deserve to be promoted to generic rank in the fossil fruit taxonomy.

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MATERIAL AND METODS

The material was collected by Kodrul in the Arkhara-Boguchan brown coal quarry approximately 15 km south-east of Arkhara Village, the Amur Province, Russian Far East (GIS 49°18′780 N, 130°12′808 E). Plant remains from the non-marine clastic deposits of Arkhara have been described by Kryshtofovich (in the 1930s, published in Kryshtofovich 1966) and Krassilov (1976) who assigned them to the Middle Tsagayan Subformation of the early Palaeocene (Danian) age. The area has been extensively quarried since and new plant localities appeared in the course of coal mining. The plant-bearing sequence of the quarries comprises the upper part of the Middle Tsagayan and the lower part of the Upper Tsagayan subformations (Akhmetiev et al. 2002).

Three juglandaceous fruits preserved as ferruginous impressions were recovered from the bluish grey mudstones of the Middle Tsagayan Subformation at the bottom of the quarry 10 cm above the coal seam "Nizhniy" ("Lower"). The associated plant megafossils are fern leaves, shoots of taxodiaceous and cupressaceous conifers, and angiosperm remains, none of which seem belonging to the same plant as the fruits (Kodrul 2004). However, leaves of juglandaceous morphology were found in an adjacent quarry approximately 200 m south of the fruit locality. On palynological evidence, the plant-bearing deposits of Arkhara-Boguchan are dated as the Early Danian (Markevich et al. 2004) or mid-Palaeocene (Nichols Douglas, written communication, 2004).

The collection is deposited in the Geological Institute, Russian Academy of Science, Moscow. The fruit impressions were studied with stereomicroscope LEICA MZ6 and digital camera LEICA DFC320.

SYSTEMATIC DESCRIPTION

Amurcarya Kodrul & Krassilov **gen. nov.**

Type. *Amurcarya lobata* sp. nov.

Derivation of the name. From the Amur Province and caryon (Gr.) nut.

Diagnosis. Winged fruit with an ellipsoid nutlet. Tepals connate, marked by radial ridges. Wing involucral, transverse or oblique-transverse, orbicular, indistinctly trilobed, with broad shallow incisions. The larger lobe bract-like, with a midrib anked by looping laterals. The smaller (bracteolate) lobes with digitate forking veins, criss-crossed over the lobe junction. Free-ending veinlets and glands frequent all over the wing.

Age and geography. Early Palaeocene of the Amur Province, Russia.

Amurcarya lobata Kodrul & Krassilov **sp. nov.**

Fig. 1: 1–4

Holotype. Fruit, AB1-101 (Fig. 1: 1, 2).

Type locality. Coal quarry at 49°18′780 N, 130°12′808 E, Arkhara-Boguchan mining area, the Amur Province, Russian Far East.

Type horizon. The Middle Tsagayan Subformation above the coal seam "Nizhniy", Early Palaeocene.

Derivation of the name. Lobata (Lat.), lobed.

Diagnosis. As for the genus.

Description. The holotype is the adaxial impression of a broadly triangular nearly isosceles samara 7.5 × 7.1 mm. The nutlet is marked as an elliptical depression in the middle, with faintly marked radial ridges and a somewhat eccentric pedicel scar 2 mm in diameter. The wing is orbicular, transverse or somewhat oblique to the nutlet (hence the eccentric position of the attachment scar), atly spreading, with three distinct or somewhat irregular radial lobes divided by shallow sinuses. The lobes differ in shape and venation. The larger (central) lobe encompasses about half of the circumference of the wing. The anks are slightly concave, converging to the shortly acuminate apex, basally forming broad shoulders that appear as vestigial lateral lobes. The venation consists of a prominent midrib anked by two series of somewhat angular loops decreasing to the apex. The tertiary veins arise on the outside of the loops arching toward the margin, forming a reticulate pattern of somewhat irregular polygonal areoles. The larger areoles are filled with free-ending veinlets that terminate in a minute swelling, perhaps glandular.

Two smaller basal lobes appear as somewhat unequal prominences opposite the central lobe, diverging at about 60°, narrowly pointed, connected by a broadly convex web. The venation is digitate, of repeatedly forking veins forming a criss-cross pattern over the web between the lobes. Their ultimate branches are free-ending, approaching each other or anastomosing, but scarcely forming a regular reticulate pattern.

A paratype AB1-102a (Fig. 1: 3) is the abax-

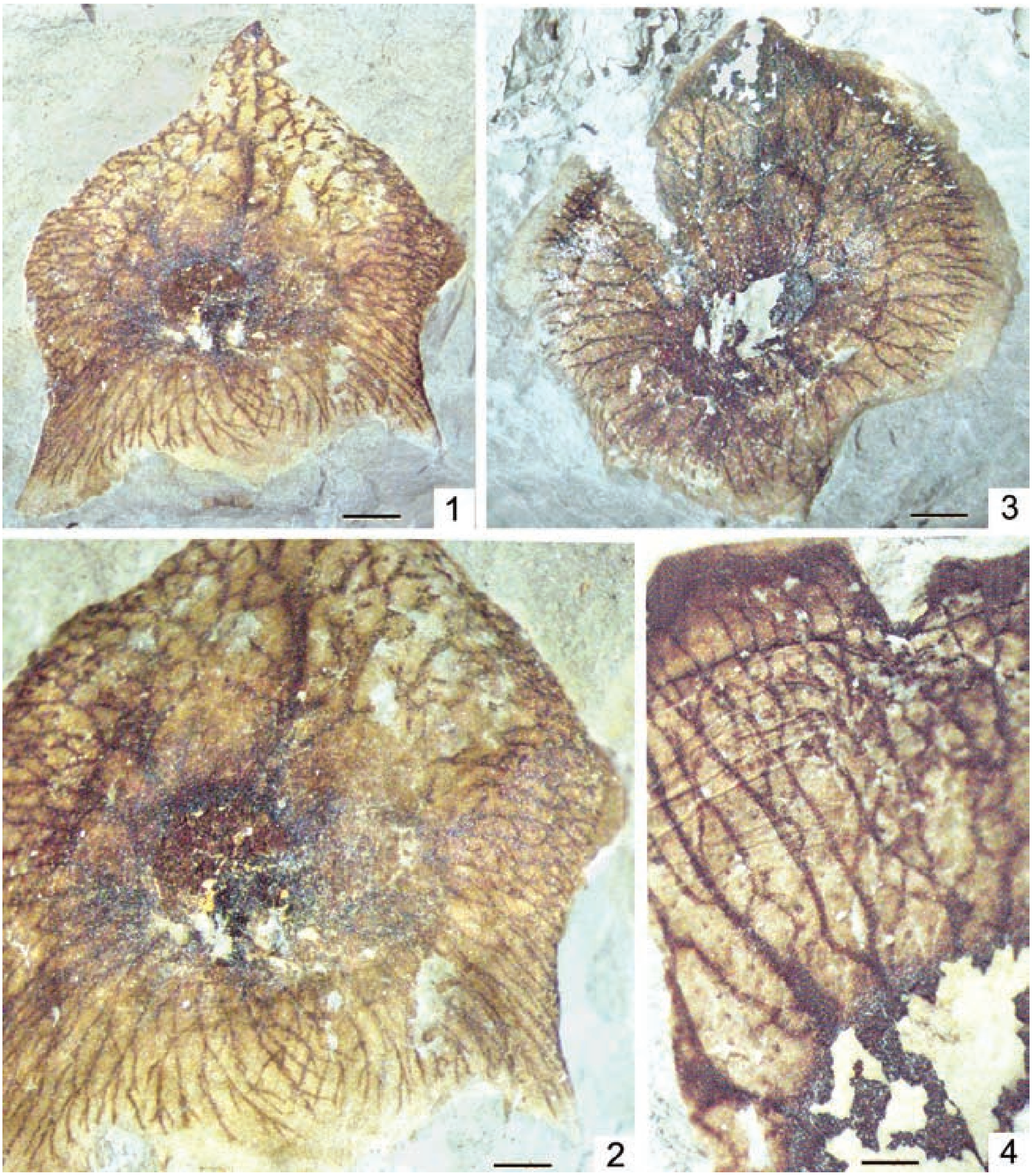

Fig. 1. *Amurcarya lobata* gen. et sp. nov. form the Lower Palaeocene of the Amur Province: **1** – holotype, adaxial aspect showing the attachment scar; **2** – part of holotype enlarged to show the difference in venation between the lobes; **3** – paratype AB1-102a, abaxial aspect with a shallowly lobed wing and with distinct commissural ridges of connate sepals; **4** – paratype AB1-102b, detail of venation showing glands as minute dots in the areoles. Scale bars 1 mm (1), 0.4 mm (2), 1 mm (3), and 0.1 mm (4)

ial impression of a somewhat squarish samara 8 mm across, with a less prominent central lobe than in the holotype, bluntly pointed central lobe and the broadly rounded basal lobes. The wing shows a smooth membranous rim devoid of veins. The venation is essentially as in the holotype, including the criss-cross pattern between the basal lobes, but the midrib and its anking loops are less clearly marked. The nutlet is 4.5 × 4 mm, clasped by the wing, with the commissural ridges of the calyx lobes which are connate for the whole length, bordering an elliptical apical area. No evidence of a style remained. Glands are well developed in this and the other paratype AB1-102b (Fig. 1: 4, and Fig. 2).

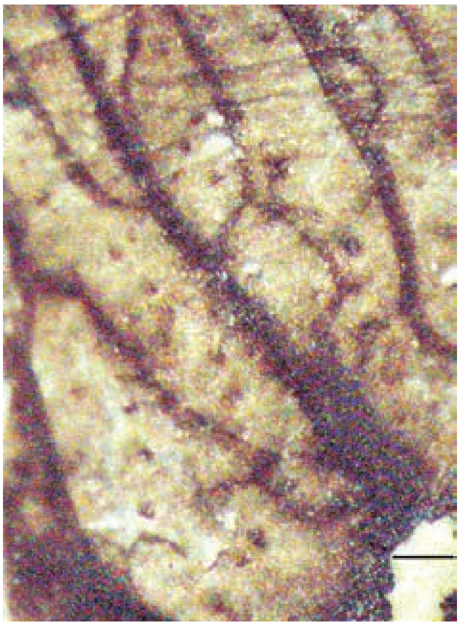

Fig. 2. Close-up of glands in paratype AB1-102b. Scale bar 1 mm

C o m p a r i s o n. The juglandaceous affinities of new genus are surmised from the shape of orbicular involucral wing, resembling extant genus *Cyclocarya* (Il'inskaya 1994), its characteristic venation and glands. The main distinguishing features of *Amurcarya* gen. nov. are the transverse (obliquely transverse) orientation of the lobed orbicular wing and the markedly different venation patterns of the larger lobe on the one hand and the two smaller lobes on the other betraying their origin from non-homologous involucral organs. In distinction from *Cyclocarya*, these much smaller fruits have a prominent central lobe showing midrib and ascending laterals, as in the involucral bracts of the extant and fossil engelhardioid fruits (Manchester 1987), whereas the smaller lobes with digitate venation resemble the bracteolate wing lobes of platycaryoid (*Hooleya*) and pterocaryoid fruits (Manchester 1987).

Conservatism of venation is a well-known feature of evolutionary plant morphology, typically manifested in composite organs formed by fusion of homologous, as well as non-homologous, components. The original venation patterns can be maintained even after the shapes of the components are lost in fusion. Thus, in simple leaves derived from compound leaves with marginally fused lea ets or pinnules, the latter are sometimes recognizable due to their conservative venation patterns (Krassilov 1997). A situation in *Amurcarya* is here considered as a further example of conservative venation betraying the components of a compound wing otherwise barely marked by the vestigial lobes.

Major groups of juglandaceous genera, the subfamilies and tribes, differ in the relative contributions of bracts and bracteoles to the involucres and their derived wings. In extant *Engelhardia* and *Oreomunnea* and in fossil *Palaeocarya* Saporta (the Engelhardieae: Manchester 1987, 1989) the wing is formed of the involucral bract with a prominent midrib anked by two series of loops formed by the ascending lateral veins. The bracts are typically three-lobed in this group, but in the fossil fruit-genera *Paraengelhardia* Berry and *Palaeooreomunnea* Dilcher, Potter & Crepet the lobes are divided by shallow sinuses only, whereas in *Casholdia* Crane & Manchester the bract is entire. In our fossil fruit, the broad shoulders of the central bract-like lobe may represent vestigial lateral lobes. However, in the engelhardioid fruits, the wing is median rather than transverse, and the bracteoles (sometimes vestigial) are fused into a valve ("prophyllum") folded over the nutlet rather than spread in the plane of the bract and incorporated in the orbicular wing, as in *Amurcarya*.

The transverse or oblique orientation of the bilobed or orbicular wing incorporating the bracteoles is characteristic of the pterocaryoid fruits, in particular of *Cyclocarya* with a transverse orbicular wing. However, in both *Pterocarya* and *Cyclocarya* the bract is reduced to an inconspicuous scale and in the latter genus is shed from the fruit, a condition fairly different from how it is maintained in the transverse wing of *Amurcarya*. We believe, that our new genus represents a fruit morphology derivable from that of the *Paraengelhardia* – *Palaeooreomunnea* group, but with the wing re-oriented transversely to the nutlet, on account of which the bracteoles are spread in the plane of the bract and are fused with it into an embracing wing, rather than being folded over the nutlet opposite to the bract.

DISCUSSION

Classification of juglandaceous fruit remains is based on the external features of the involucre, as well as on the internal septation of the locule and the structure of the nutshell

(Manchester 1987, 1989). The involucre is formed of the bract, bracteoles and perianth lobes variously transformed into the lobed or entire, one-sided, bilateral or circular wing or incorporated into the wingless husk. The oral and peri oral organs involved may lose or only partly maintain their identity (Stone 1993). The nutlet is either transverse (*Platycarya*, *Cyclocarya*) or median (*Pterocarya*, *Engelhardia*, *Oreomunnea*) or oblique (*Pterocarya*) in respect to the wing. The bracteoles are variously fused and juxtaposed to the bract in the involucre, or fused to the bract, or occasionally intermixed with the sepals, sometimes reduced (*Alfaroa*). One or more sepals may be lacking or they all are reduced (*Carya*), fused for the whole length or free at the tips (*Pterocarya*), the lateral ones sometimes fused to bracteoles (*Platycarya*). The dispersal units include the bract or this remains on the in orescence axis (*Platycarya*). In the samaras, the wing is 3-lobed, 2-lobed or entire, formed of bract, with the bracteoles fused in a basal valve ("prophyllum"), as in *Engelhardia* and *Oreomunnea*, or of bracteoles mostly (*Pterocarya*, *Cyclocarya*), sometimes with participation of the lateral sepals fused to the bracteoles (*Platycarya*).

Among the fossil fruit genera, *Paleoplatycarya* Manchester differs from *Platycarya* in having distinct median sepals. In the type species *Hooleya hermis* (Unger) Reid & Chandler, sepals are lost, perhaps in fusion (Reid & Chandler 1926), whereas in *H. lata* Wing & Hickey all the sepals are developed, and only the lateral ones are partly fused to bracteoles. In *Polyptera* Manchester & Dilcher, the transverse wing consists of eight to ten lobes, probably derived of bracteoles and sepals. *Casholdia* Crane & Manchester resembles *Engelhardia* and *Oreomunnea* in the well developed bracteolate valve ("prophyllum"), but the bract is simple rather than trilobate as in the other Engelhardiae. *Palaeoengelhardia* and *Palaeooreomunnea* with shallowly divided lobes represent the intermediate morphologies.

Fossil fruits with transverse orbicular wing are commonly included in the extant genus *Cyclocarya*, although at least in some of them sepals are lacking, whereas in the living species they are connate, with free tips. In a paratype of *C. brownii* Manchester & Dilcher from the Palaeocene of North Dakota, courteously provided by Manchester for comparison with the Amur material, we observed a differentiation of venation patterns suggesting a vestigial bract incorporated in the orbicular wing. The wing is, therefore non-homologous to that of the living *Cyclocary*a, where it consists of the bracteoles alone. We believe that such features justify separation at the generic level.

In respect to the contribution of bract to the involucre or lack of such, the Juglandaceae can be divided into two broad groups: (1) with the subtending bract forming the larger wing lobe (the Engelhardiae) and (2) with the bract exempt from the wing (the Platycaryae and Pterocaryae). In the group (1) the position of the wing is median; in the group (2) it is transverse. *Amurcarya* gen. nov. (probably also *Cyclocarya brownii*) is similar to group (1) in its bract being incorporated in the wing. It is at the same time closer to the group (2) in the orientation of the wing, thus forming a morphological link between the two groups in the essentially continuous combinatorial variation of juglandaceous fruits. Our interpretation of *Amurcarya* also implies that the relative contribution of involucral organs depends on the orientation (and changes with re-orientation) of the wing.

CONCLUSION

The diversity of fruit morphology in the fossil and extant Juglandaceae is due to a combinatorial variation of the oral and peri oral structures contributing to the involucre, which are the bract, bracteoles and sepals. Each of these components can be excessively developed at the expense of the others. Functionally such differences are scarcely significant. Whatever the constitutive elements, the involucre can be transformed into a one-sided, bilobed or orbicular wing. In effect, the superficially similar wings can be non-homologous, representing different combinations of involucral organs.

Just this seems to have been the case in *Cyclocarya*, an extant genus of the pterocaryoid tribe supposedly appearing in the Palaeocene, and *Amurcarya* gen. nov. from the Palaeocene of the Amur Province, Russian Far East. The latter has an orbicular transverse wing, as in *Cyclocarya*, yet the wing is lobed, and the lobes show different venation patterns, one resembling the wing-forming bract of the engelhardioid fruits, the two others corresponding to the wing-forming bracteoles of the pterocaryoid fruits. Thus, in the new genus, the wing is non-homologous to that of the typical *Cyclocarya*.

Our material adds to the combinatorial variation of juglandaceous fruits. It also confirms conservatism of venation patterns that are recognizable even after the shapes of connate organs are lost in fusion.

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