

Meeusella and the origin of stamens

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Meeusella gen. nov. is a strobilate pollen organ from the Lower Cretaceous of Transbaikalie (east of the Lake Baikal); the branched lateral branches (paracladia), if fully developed, bear a subterminal pair of stalked synangial heads. In some cases the latter are reduced to a pair of sessile heads or the paracladia are sterile. It is suggested that the synangial heads might be further reduced to a pair of bisporangiate thecae, while the paracladium apex between them might form a prominent connective of a typical stamen.

□ *Androeceum*, *androclade*, *angiosperms*, *proangiosperms*, *stamen*, *evolutionary morphology*.

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Problems of evolutionary morphology, such as the origin of stamens, are conventionally addressed from the viewpoint of morphological variation in extant plants (Stebbins 1974). But it is at least as important to know the ranges of morphological diversity in fossil plants of relevant geological age. Here we describe a new pollen organ which has, in our opinion, some bearing on this particular problem.

Locality, material and methods. – Recently, a number of new plant macrofossil localities were discovered in the non-marine Lower Cretaceous of Transbaikalie (east of the Lake Baikal). They yielded some peculiar fossils showing transitional gymnosperm–angiosperm characters (Krassilov & Bugdaeva 1982; Bugdaeva 1983; Krassilov 1986). One of the richest localities is situated in the Semion Valley 40 km south of Chita, the provincial capital. It is an outcrop of pale gray lacustrine shales about 20 m thick containing molluscs, conchostracans, fishes, aquatic and terrestrial insects and plants which indicate an upper Lower Cretaceous age (Bugdaeva 1984). The plant megafossils are confined to several plant beds each about 10 cm thick. A pollen organ came from the upper plant bed together with *Baikalophyllum* leaves described earlier (Bugdaeva 1983). It is an impression and its counterpart with a few coaly crumbs on it. Parts buried

in the rock matrix were uncovered using hard and flexible entomological needles. Coaly crumbs were treated in HNO_3 for several minutes (we found longer treatment not necessary because of the strong natural oxidizing) and then in an alkali solution. Transfer preparations were obtained from the counterpart and studied using SEM. Unfortunately no pollen masses were observed – a few scattered bisaccate pollen grains on transfers may come from the rock matrix. Other plant fossils from the same bed are cycadophyte, ginkgoalean and czekanowskialean leaves as well as the cone scales and seeds of the pinaceous conifers.

Meeusella gen. nov.

Derivation of name. – After A. J. D. Meeuse, a distinguished plant morphologist and originator of new ideas in the field of angiosperm evolution.

Diagnosis. – Loose androclade of a thin axis bearing spirally disposed lateral branches (paracladia) which are sterile, undivided, showing expanded apices or otherwise with a subterminal pair of stalked or sessile heads of four proximally connate sporangia.

Type species. – *Meeusella proteiclada*, sp. nov.

Meeusella proteiclada sp. nov.

Diagnosis. – As for genus.

Holotype. – Repository of the Institute of Biology and Pedology, Vladivostok, N 325/8222. Semion Valley 40 km south of Chita, Transbaikalie, Lower Cretaceous, Turginian horizon, upper plant-bearing bed.

Description. – The type specimen is a portion of a shoot 45 mm long with a straight longitudinally striated axis 1 mm thick bearing 14 paracladia in a loose spiral (Figs. 1–3). The latter are slightly decurrent, bent into two rows. Of the completely preserved paracladia, designated by letters in Fig. 1, the two lowermost, a, b, and the three uppermost, e, f, and j are sterile. They arise at an acute angle curving slightly toward the shoot apex, 6–7 mm long, and 0.4 mm thick but apically expanded to 0.8–1.0 mm. The apices seem flat, leafy, with a median groove and divergent striation (Fig. 3D).

A fully developed fertile paracladium (c) on the left side of the axis is 6 mm long, of the same shape as the sterile ones, with a similarly expanded apex. Subterminal on both sides of the apex there are two stalks of unequal length, 4 mm and 2.6 mm, diverging at an acute angle, bearing recurved sporangial heads about 2.6–2.8 mm wide. The heads seem massive in comparison with their slender stalks (Fig. 3A). They are rounded in plane, subconical in profile, slightly knobbed at the point of attachment, with four pendant sporangia. The sporangia are ovate, 2 mm long, fused about one third of their length. Paracladium (i) abutting the shoot axis shows the left hand branch of nearly the same length as the longer branch of (c). However, the paracladium (d) distal to the above described and in the same phyllotaxic position as (c), fully exposed on the rock surface (Fig. 3B) differs in having sessile adpressed sporangial heads, each showing adnate portion of its stalk which does not or only slightly extends below the head. On the opposite side of the main axis there is a somewhat shorter paracladium (h), 4 mm long, with even more

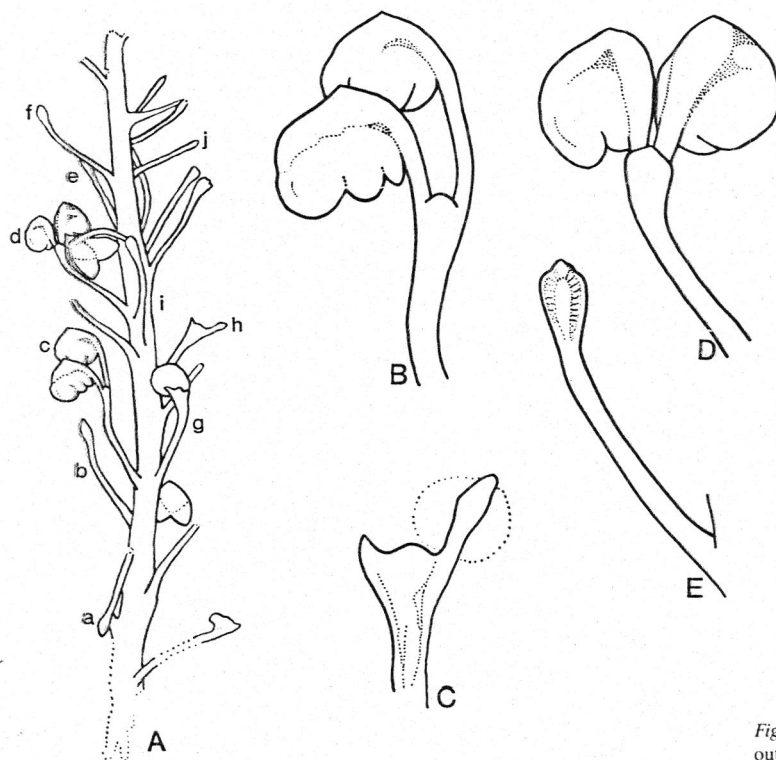


Fig. 1. *Meeusella proteiclada* sp. nov., outlines of a cone (A), $\times 3$, and its paracladia (B–E), $\times 10$.



Fig. 2. *Meeusella proteiclada* sp. nov., pollen cone, $\times 3$.

reduced stalks which have shed their sporangial heads (Fig. 3C). The same structure could be inferred for (g) below but its apical portion is somewhat crumpled.

Comparison and remarks. — The sporangial heads of *Meeusella* are similar to those of the peltasperms and corystosperms such as *Antevsia*, *Pteruchus*, *Townrowia* and *Pteroma* (Harris 1937, 1964; Townrow 1965; Retallack 1983), among which the first three have elongate sporangial heads while in the fourth one they are rounded,

with proximally fused sporangia of the same shape and dimensions as in *Meeusella*, but the sporangia are more numerous. *Meeusella* differs from these and all other gymnosperm pollen organs in the structure of paracladia, which have two subapical arms, while in the comparable androclades they are either simple or forked. Further peculiarities of the new genus are the wide range of variation in the paracladia arm lengths, from definitely stalked to sessile sporangial heads, and the sterile paracladia among the fertile ones. We considered the possibility that sporangial heads have been shed from the sterile paracladia but found it unlikely because in the case of shedding the head stalks persist as in Fig. 3C.

No other organs were found in organic connection with *Meeusella* but we suggest that the *Baikalophyllum* leaves may belong to the same plant (Fig. 4). They were repeatedly found in the same thin plant bed. Other associated leaves are shown to belong to plants with pollen organs which are quite different from *Meeusella*.

Discussion

The stamen is one of the most controversial structures in the morphology of angiosperms. While traditionally considered as modified fertile leaves, microsporophylls, stamens or some of them show certain cauline features, such as deep initiation, amphicribal vascular bundles and occasional branching. Profusely branched stamens are known in several members of the Euphorbiaceae, while forked filaments are occasionally observed in *Myrica*, *Ulmus* and *Fagus* (Sporne 1974). Fasciculate stamens born on a common primordium occur in several Dilleniidae families. They often develop in centrifugal succession — a supposedly derived feature. However, the fasciculate androecia can also be centripetal (Pauzé & Sattler 1978).

In some flowers with many single stamens the androecial traces are fasciculate, or dendroid, as in Paeoniaceae, one of the most ancient angiosperm families (Krassilov *et al.* 1983). Moreover, the fasciculate nature of the stamens, though apparent on early developmental stages, may be no longer recognizable in mature androecia. Stebbins (1974) has suggested a derivation of the cortical vascular bundles in some primitive Magnolialean genera from dendroid traces. He also pointed to vestigial fasciculate structures in the androecia of Degeneriaceae, Annonaceae,

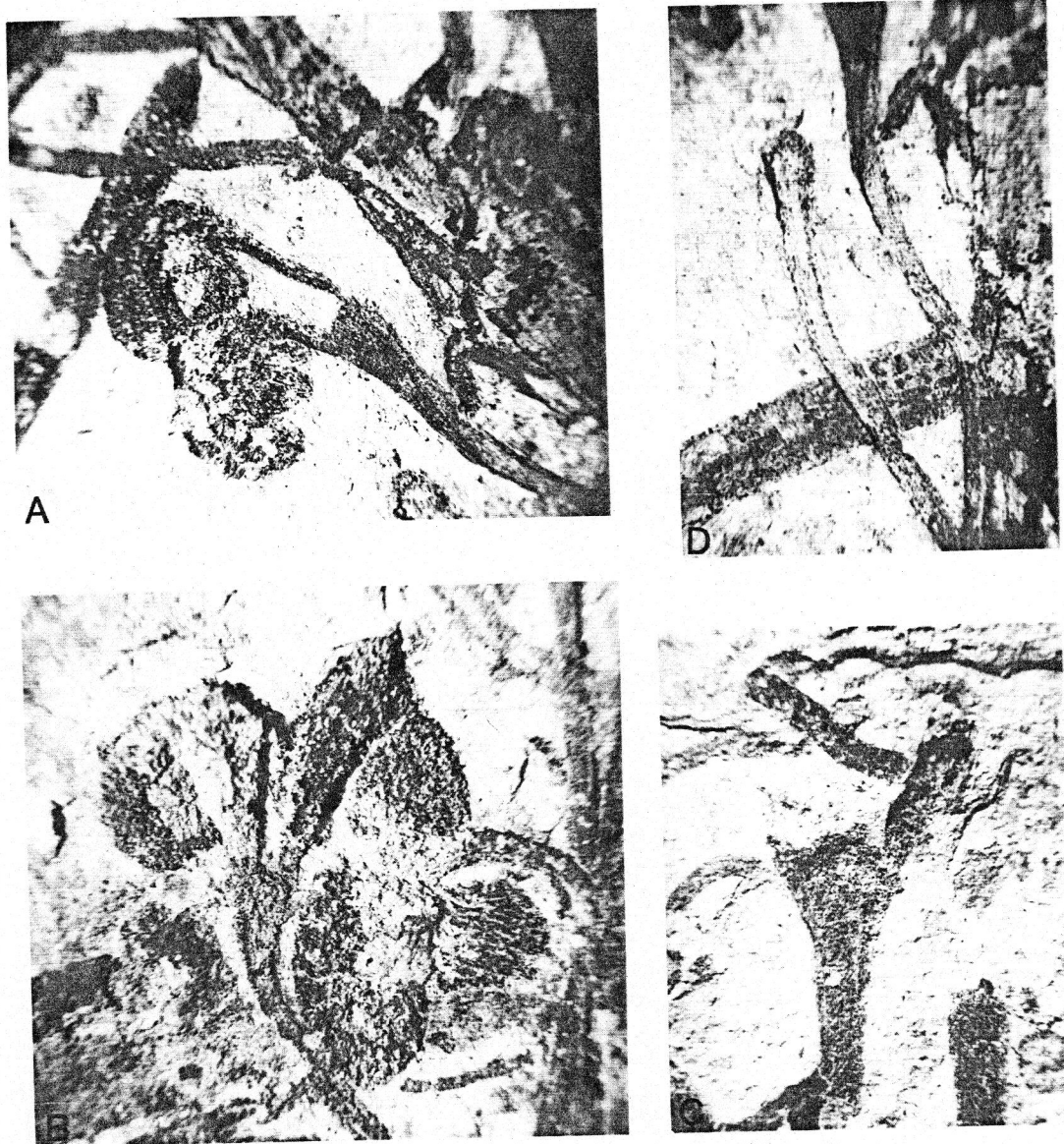


Fig. 3. Paracladia of *Meeusella proteiclada* sp. nov. □ A. With stalked sporangial heads, $\times 10$. □ B–C. With subsessile heads, $\times 12$. □ D. Sterile, $\times 10$.

Ranunculaceae, Papaveraceae, Rosaceae and Myrtaceae (see also Uhl 1976 on the arecoid palms). It follows that simple androecia of many single stamens may be derived rather than primitive (Meeuse 1972).

The laminar stamens of the Magnoliales and Nymphaeales, a cornerstone of the phyllome theory, differ from each other in vascularization (a single stellar and two cortical bundles in

Degeneria, two fused stellar bundles in *Austrobaileya*, etc.) and disposition of anthers and, therefore, might derive from different prototypes. Their produced connectives (characteristic also of the primitive Hamamelidoid genera) show a relatively high degree of specialization (Canright 1952). Some flattened petaloid stamens receive additional vascular supply from the cortical vascular system, and particularly in the *Nelum-*

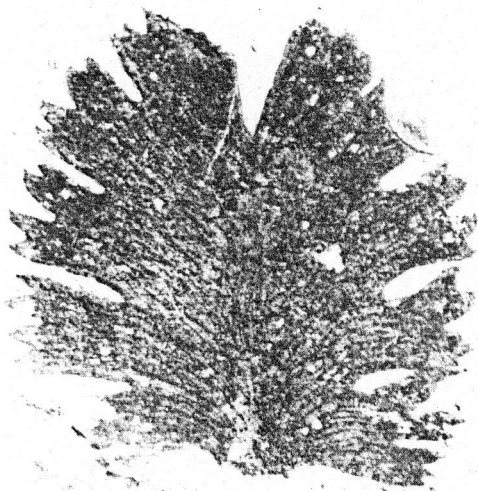


Fig. 4. *Baikalophyllum lobatum* Bugdaeva, a possible leaf of *Meeusella*, $\times 3$.

bonaceae a staminal pseudostele is formed by stellar and cortical bundles (Moseley & Uhl 1985).

In the Laurales, and especially Monimiaceae, stamens have two lateral vascularized append-

ages, often glandular, the nature of which is controversial. They have been interpreted as remnants of fused stamens, proliferated glands or vestigial branches (Singh & Singh 1985).

It was suggested that primitive stamens were cauline (Wilson 1937), derived from hypothetical branched microsporangiate shoots – androclades – or from such shoots fused to their supporting bracts – and androphyls of a dual caulome–phyllome nature (Melville 1963). Accordingly, the petaloid stamens of Magnoliaceae and Nymphaeaceae are conceived of as secondary flattened showy structures evolved in connection with beetle-pollination, or cantarophily. The so-called primitive flowers are specialized cantarophilous flowers similar to but not necessarily derived from the bennettitalean anthoid strobili with flattened pollen organs, also cantarophilous (Endress 1986). Because in primitive flowers stamens carried most of the display function, they were subjected to various adaptive modifications which obscured their prototypic features.

Attempts to reduce all the diversity of angiosperm stamens to a single prototype may prove futile, especially because different prototypic structures existed among the Mesozoic gym-

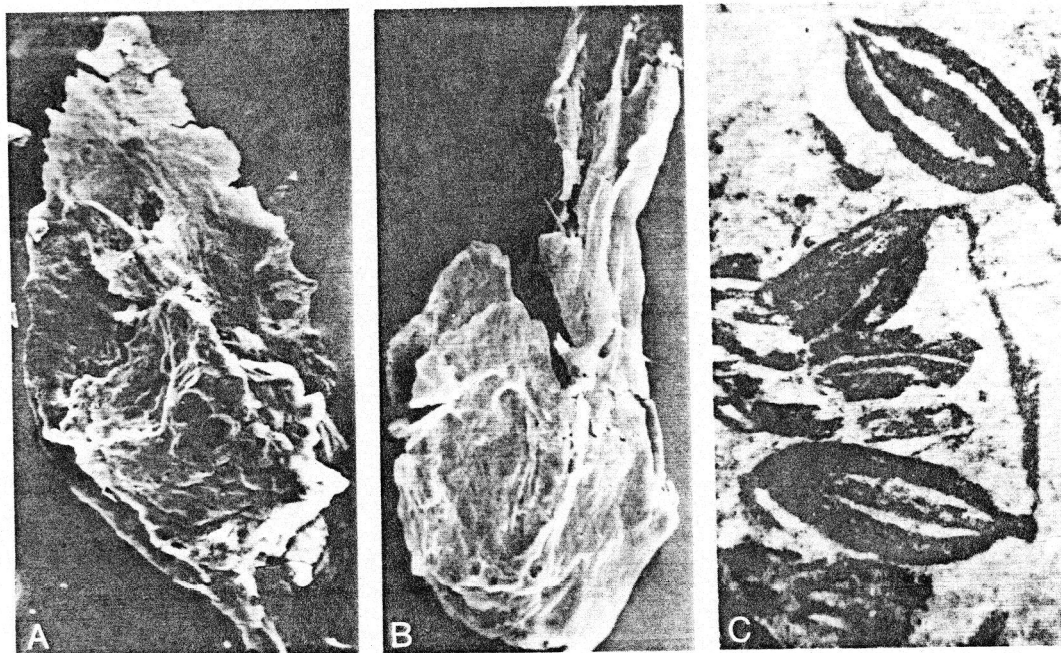


Fig. 5. Possible progenitors of a stame. □ A–B. Pollen organs of *Dinophyton spinosum* Ash, adaxial and lateral views showing sporangium fused proximally to a subtending bract. SEM, $\times 110$. □ C. *Caytonanthus tyrnensis* Krassilov, branched sporangiophore, $\times 8$.

nosperms and proangiosperms. According to the currently held views, pollen organs of gymnosperms have derived from the fertile syntelomic branching systems of progymnosperms subjected to various kinds of planation and fusion. Among the Palaeozoic pteridosperms, calamopityaleans and lyginopterids still retained a transitional caulome-phyllome organization of their branching pollen organs, the terminal branchlets of which bore radially disposed sporangia, sometimes proximally fused as in *Feraxotheca* (Millay & Taylor 1979). Slightly modified versions of this type of androclade occur in the Mesozoic peltasperms, corystosperms, ginkgoaleans, conifers and caytonialeans. In particular, *Caytonanthus*, a pollen organ of the latter (Fig. 5C) had branched sporangiophores bearing synangia of four fusiform sporangia which split apart when ripe (Harris 1964; Krassilov 1977). Normally the synangia are radial, but occasionally they become bilateral due to underdevelopment of one pair of sporangia (Krassilov 1977). The branching pattern in *Caytonanthus* resembles dendroid staminal traces of the Dillenioid angiosperms and *Paonia*.

In other evolutionary lines a stronger tendency to planation of the original syntelomic system or part it might produce a laminar sporangiophore as in the Permian gigantopterids (Li & Yao 1983) or Mesozoic bennettites. However, this type of pollen organ might derive also from androclades fused to their supporting bracts, as in the glossopterids. In the issuing dual structure the original androclades either partially retained their morphological identity as branching organs or were reduced to a single stalked or even sessile sporangium adaxial on laminar sporangiophore. The latter condition was met in the recently discovered pollen organ of the Triassic plant *Dinophyton* (Krassilov & Ash 1987) in which sporangium or occasionally a bunch of three sporangia arose adaxially on a membranous blade (Fig. 5A-B). In *Ixostrobus*, the putative pollen organ of the Czekanowskiales, lateral androclade branches bore adaxial four-lobed synangia above a reflexed sterile tip (Krassilov 1972). The *Astrobaileya*-type stamen with adaxial synangia and apically produced connective could conceivably arise from each of these two Mesozoic pollen structures with a minimum number of imaginary transitional steps.

The paracladia of *Meeusella* are interesting not only as a possible prototype of a branched stamen but also because they show initial steps of

reduction to the typical stamen and staminode. These steps are from the fully developed paracladium with a subterminal pair of stalked sporangial heads to the subsessile and sessile adpressed heads looking much alike thecae of an angiosperm anther. They provide some factual ground to the opinion that the typical anther is a much more complex organ than the traditional interpretation of it, that is, not merely a synangium but a condensed pair of stalked synangia lateral on the axis which formed filament and connective. A further though imaginary step would be a shortening of the main axis, transforming *Meeusella* in to a primordial knob on which a fascicle or paracladia – now stamens – would arise.

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