A NEW GENUS AND SPECIES OF GRASS, EOGRAMINIS BALTICUS (POACEAE: ARUNDINOIDEAE), IN BALTIC AMBER

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Premise of research. This investigation was undertaken to describe a multi-floral grass spikelet enclosed in Baltic amber. The fossil, described in the new genus Eograminis, represents the first definite grass to be described from Baltic amber as well as the first fossil member of the subfamily Arundinoideae. The discovery adds a new plant group to the extensive flora previously described from Baltic amber and provides insights into the ecology of the forest habitat. It also supplies morphological and developmental features that existed in early Cenozoic grasses and establishes a calibration point for future phylogenetic studies regarding the origin and splitting of genera in the subtribe Moliniinae.

Methodology. The piece of amber containing the fossil was reshaped with a diamond blade lapidary trim saw, a belt sander, and a bench polisher until it was possible to view the grass spikelet from all angles. Because of the excellent preservation of the spikelet, observations of the glumes, paleae, and lemmas could be made under direct light with a stereoscopic and compound microscope.

Pivotal results. After the features of the spikelet are characterized, it is described as Eograminis balticus gen. et sp. nov. (Poaceae: Arundinoideae). The new genus is characterized by the presence of stomata with well-developed dome-shaped subsidiary cells, parallel guard cells, and rows of crenulated and non-crenulated epidermal cells with long and short cells and silica bodies.

Conclusions. The spikelet has some features of members of the extant genus Molinia Schrank in the tribe Molinieae, subtribe Moliniinae, a wetland genus with extant species concentrated around the Baltic Sea. However, the sparse scabrosity over the lemma veins, minute or absent keel hooks on the paleae, and bicellular or absent microhairs of Molinia spp. separate it from the fossil. The presence of an immature orthopteran and an “Alternaria-like fungal spore” associated with the fossil grass provides data on the microhabitat of the fossil grass.

Keywords: grass macrofossil, multiple floras, herbivore damage, Eocene.

Introduction

Historically, Baltic amber is the most famous of all amber deposits in the world. Studies on this gem began with Pliny the Elder (Gaius Plinius Secundus) in the first century AD. Pliny explains how Baltic amber, named succinite in his treatise Natural History (book 37, chaps. 11–13), was originally desired for carvings, beads, and a wide assortment of jewelry before its scientific value was realized.

It is still possible today to find pieces of Baltic amber washed up on the beach along the North Sea or beside the shoreline of the Baltic Sea. This is especially common after storms, when wave action loosens pieces of amber from the exposed “blue earth” layer located some 15–20 ft below sea level. Presently, mining operations located along the Baltic Sea coast, especially in the vicinity of the Samland Peninsula and at the Yantarny Amber Quarry near Kaliningrad, provide most fossiliferous Baltic amber.

The type of forest in which the Baltic amber grass spikelet grew is a controversial subject. Some have proposed that fossiliferous amber from the Baltic region was formed in tropical and subtropical forests that covered a large part of northern Europe (Bachofen-Echt 1949; Larsson 1978). Others, such as Sadowski et al. (2017), differ and have transferred paleoecological information from other fossil floras of the Paleogene of Europe to the Baltic amber forest. These authors concluded that the original Baltic amber forest was a diverse, humid, warm-temperate forest with marsh habitats. The presence of the grass described below, as well as of stellate “oak” hairs, flowers from male catkins of...
Fagaceae, and conifer remains in Baltic amber, suggests that for at least part of its existence, the habitat was warm temperate, as in today’s mixed deciduous and conifer forests.

There is also disagreement regarding the true age of Baltic amber. Original age estimates range from 35 to 55 Myr (Larsson 1978; Weitschat and Wichard 2002), from 45 to 55 Myr (Wolfe et al. 2016), or from 23 to 48 Myr (Kosmowska-Ceranowicz et al. 1997; Standke 1998, 2008; Kasinski and Kramarska 2008), or it is simply estimated to be from the late Eocene or early Cenozoic (approximately 34–38 Myr; Sadowski et al. 2017). Most believe that it existed at some period during the Eocene.

While a wide diversity of angiosperms (five families of monocots and 38 families of dicots) have been described from Baltic amber, there are no previous accounts of confirmed fossil grasses in these extensive deposits (Bachofen-Echt 1949; Czeczott 1961; Larsson 1978; Weitschat and Wichard 2002; Sadowski et al. 2017). The purpose of the present study is to describe a new genus and species of grass in Baltic amber that shows morphological features of the Arundinoideae, a subfamily of the Poaceae that includes some 40 species and 16 genera in two tribes (Soreng et al. 2017). The most distinctive species in the tribe Arundineae is the giant reed (*Arundo donax* L.), which occurs in wetland areas throughout warm areas of the globe and can reach over 10 ft in height. The second tribe in the subfamily is the Molinieae, which contains two subtribes. Species in the subtribe Crinipinae occur in Africa, while those in the subtribe Moliniinae occur in Eurasia. The latter subtribe includes the genus *Molinia* Schrank, a Eurasian genus that will be discussed further in relation to extant grass genera with features similar to those of the fossil described below.

**Material and Methods**

The Baltic amber specimen originated from the Samland Peninsula in the Kalinin District of the Russian Federation. It was purchased from a German amber dealer at a gem, rock, and mineral show in Reno, Nevada, in 1993. It will be deposited in the California Academy of Sciences geology type collection in San Francisco, California.

Observations and photographs were made with a Nikon SMZ-10 R stereo microscope and Nikon Optiphot compound microscope with magnifications up to ×1000. Helicon Focus Pro X64 was used to stack photos for better clarity and depth of field. In some figures, portions of the background were removed with Adobe Photoshop for better views of the selected features.

Syninclusia include an immature orthopteran (Insecta: Orthoptera) adjacent to the grass specimen, an *Alternaria*-like fungal spore on a lemma, and numerous oak hairs throughout the amber matrix. Basic features of epidermal patterning and silica bodies are based on Rudall et al. (2014) and Cliford and Watson (1977).

**Results**

**Taxonomic Placement and Description**

The spikelet is well preserved and includes a series of florets. The amber matrix contains numerous bubbles and other debris, and at least two of the lemmas show evidence of insect damage.

**Order**—Poales

**Family**—Poaceae

**Subfamily**—Arundinoideae Kunth ex Beilschm., 1833

**Eograminis** Poinar et Soreng gen. nov.

*Diagnosis.* Spikelet with glumes and several visible florets, all awnless. Epidermal cells of lemmas with long-short cell alternations and longitudinally crenate rondel and irregularly shaped silica bodies. Stomata with parallel guard cells and well-developed dome-shaped subsidiary cells. Strongly crenulate long cell walls. Multicellular microhairs rare.

*Type species.* *Eograminis balticus* Poinar et Soreng sp. nov.

**Fig. 1** Side one view of *Eograminis balticus* gen. et sp. nov. in Baltic amber. The arrow indicates callus hairs. Scale bar = 1.0 mm. The inset shows details of the callus hairs (arrowhead). Scale bar = 0.3 mm.
Etymology. The generic name is derived from the Latin *aeon* (age) and the Latin *graminis* (grass), in reference to its late Eocene age.

*Eograminis balticus* Poinar et Soreng sp. nov.

Etymology. The specific epithet indicates the place of origin of the fossil.

Species diagnosis. Same as for the genus.

Description. Spikelet (figs. 1–3) with lower and upper glumes and several tightly clustered florets. Length of spikelet 6.8 mm; glumes smooth, with faint keel nerve, similar in shape and texture; length of first glume 5.0 mm; length of second glume 4.8 mm; lemmas lanceolate, keel indistinct, smooth to sparsely scabrous, firm, with narrow scarious margin (fig. 7C), outer edges smooth, awnless, apex narrowly acute, with surface similar to that of glumes; length of lemma 5.5 mm; width of lemma 1.0 mm; callus hairs present (fig. 1, inset); length of callus hairs 2.0 mm; longitudinal epidermal cells in apical portion of lemma with rondel, rectangular and longitudinally crenate-shaped silica bodies; length of silica bodies 4–6 μm (fig. 4); longitudinal epidermal cells in midportion of lemma with crenulate long cells alternating with a mixture of tuboid crenulated and noncrenulated short cells (figs. 5, 6), length longitudinal, crenulate epidermal cells of lemma 80 μm; width of longitudinal crenulate epidermal cells of lemma 29 μm; length of cuboid noncrenulate short cells of lemma 14 μm; stomata with dome-shaped subsidiary cells and parallel guard cells (figs. 5, 6); length of stomata in lemma epidermal cells 45 μm; lemma epidermis with multicellular microhairs; length of multicellular microhairs 10 μm (fig. 5, inset); paleae with scabrous hooks in a single file (fig. 7C); length of paleae 5.5 mm; through a hole in the floret made by an insect herbivore, a single stamen

Fig. 2  *Eograminis balticus* gen. et sp. nov. in Baltic amber. A, View of side two (opposite of side one). Scale bar = 0.4 mm. B, Lateral view showing areas of insect damage (arrowheads). Scale bar = 1.0 mm.
is partially exposed, revealing the anther and a portion of the filament (fig. 7C, inset); estimated length of stamen 0.3 mm.

**Holotype.** Deposited in the California Academy of Sciences geology type collection, San Francisco, California, under catalog number 101120.

**Type locality.** Samland Peninsula of the Baltic Sea in the Kalinin District of the Russian Federation.

**Stratigraphic horizon.** Blue Earth Formation, Eocene (34–55 mya; Wolfe et al. 2016; Sadowski et al. 2017).

**Comments.** The opening in the lemma that reveals a portion of an anther (fig. 7C, inset) could have been made by the immature orthopteran (length, 0.7 mm) located at the tip of a floret (fig. 7A). With the available characters, it is not possible to assign the orthopteran to a present family. A bowling pin–shaped fungal spore resembling those of the extant genus *Alternaria* Nees (Ascomycota: Pleosporaceae; Barnett and Hunter 1987) rests on one of the lemmas (fig. 5, inset). There are no obvious signs of fungal hyphae, although species of *Alternaria* are known to infect extant grasses (Farr et al. 1989).

**Discussion**

Presently, the earliest definite grasses are *Programinis burmitis* and *Programinis laminatus* (Bambusoideae) in Burmese amber from 100 mya (Poinar 2004). The presence of alternating long and short epidermal cells as well as several types of silica bodies confirms the original status of *P. laminatus* as a true grass (Poinar 2011). Additional studies of a grass spikelet infected with an ergot fungus in Burmese amber (Poinar et al. 2015) support the original conclusion that *P. burmitis* is a true grass. Fossil grass spikelets have also been described in Tertiary Dominican amber. These include *Alarista succina* Poinar et Columbus

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**Fig. 3** Tips of the florets (arrowheads) of *Eograminis balticus* gen. et sp. nov. in Baltic amber. Scale bar = 1.0 mm.

**Fig. 4** Detail of silica bodies (arrows) in the tip of a lemma of *Eograminis balticus* gen. et sp. nov. in Baltic amber. Scale bar = 13 μm.
Fig. 5 Longitudinal cells with crenulate borders, short cells (arrows), rondels (arrowheads), and stomata (S) in the midregion of the lemma of *Eograminis balticus* gen. et sp. nov. in Baltic amber. F = fungal spore; M = multicellular microhair. Scale bar = 100 μm. The inset shows details of the multicellular microhair and fungal spore. Scale bar = 50 μm.

Fig. 6 Detail of longitudinal cells with crenulate borders, short cells (arrows), and stomata (S) in the midregion of the lemma of *Eograminis balticus* gen. et sp. nov. in Baltic amber. Scale bar = 40 μm.
Fig. 7  *Eograminis balticus* gen. et sp. nov. in Baltic amber. A, Immature orthopteran at the tip of the florets. The arrow indicates putative fecal pellets. Scale bar = 0.4 mm. B, Detail of a portion of the lemma eaten away by an herbivore, possibly the orthopteran. Scale bar = 0.3 mm. C, Scabrous edge of the palea midrib. Scale bar = 35 μm. The inset shows herbivore damage to the lemma, revealing a partial stamen with an anther (upper arrow) and a partial filament (lower arrow). Scale bar = 0.2 mm.
(Bambusoideae: Bambuseae; Poinar and Columbus 1992, 2012) and *Pharus primuncinatus* Poinar et Judziewicz (Pharoideae: Pharoideae; Poinar and Judziewicz 2005). Crepet and Feldman (1991) documented compression fossils of a grass spikelet and leaves from the Paleocene/Eocene of North America that Soreng and Davis (1998) suggested might represent a member of the genus *Streptogyna* P. Beauv.

Because of the lack of access to leaves, pistils, and complete stamens, it is difficult to align *Eograminis balticus* gen. et sp. nov. with any modern genus. However, the spikelet has features of members of the genus *Molinia* Schrank in the subtribe Moliniinae of tribe Molinieae of the Arundinoideae (Watson and Dallwitz 1994; Soreng et al. 2017). These features of *Molinia* that resemble those of *Eograminis* include spikelets that are one to five flowered, awnless, and 3.2–7.0 mm long and smooth glumes overlapping at the base (fig. 8). The lemmas are three veined (veins flush), lanceolate, indistinctly keeled to rounded on the back, and sparsely scabrous over the veins (fig. 8, inset). They are firmly chartaceous with narrow scarious margins, the edges are with or without a few hooks, and the apex is narrowly acute but firm. There are crenulated long cells on the lemma epidermis (fig. 9), and the callus is blunt, with hairs up to 0.5 mm long concentrated laterally. The paleae are firm, of the same texture as the glumes but smooth, or, if they are scaberulous on the

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**Fig. 8** Spikelets of *Molinia arundinacea* RJS 5868. Note the resemblance to those of the fossil (see fig. 1). Scale bar = 1.4 mm. The inset shows the slightly scabrous lemma surface. Scale bar = 0.5 mm.
keels, then the hooks are not in a single file (Watson and Dallwitz 1994; Soreng et al. 2017).

*Molinia* (moor grass) is a wetland genus with two species mostly confined to Europe, their occurrence concentrated around the Baltic Sea. The genus is also found in coastal to subalpine habitats in sand and in subalpine to sphagnum bogs and fens in forests. Compared with *Molinia arundinacea* Schrank, *Molinia caerulea* (L.) Moench has fewer-flowered spikelets with mostly glabrous calluses, a shorter stature, and narrower panicles, and it is more cold tolerant (Watson and Dallwitz 1994; Soreng et al. 2017).

Microhairs of *Molinia* are bicellular, similar to those of *Eo-graminis*, but are rare on species of *Molinia s.s.* (Watson and Dallwitz 1994), as on *Eo-graminis*. They are common on *Moliniopsis* Hayata of far east Asia (recognized as phylogenetically distinct from *Molinia* by Soreng et al. [2017]); they are of the panicoid type in *Moliniopsis* and are (45–)48–54(–57) μm long and 6.0–8.4 μm wide at the septum. In *Molinia*, the microhair total length-to-width ratio at the septum is 5.7–8.6; microhair apical cells are 24–27 μm long, and the microhair apical cell-to-total length ratio is 0.42–0.57.

The lemmas of *Molinia* have sparse scabrosity over the veins (fig. 8, inset), which is not the case with *E. balticus*. Otherwise, the crenulated long cells on the lemma epidermis of *M. arundinacea* resemble those of the fossil (fig. 5). The palea keel of *Eo-graminis* is coarsely scabrous, with hooks in a single file (fig. 7C), whereas in *Molinia*, the palea keel hooks are minute and diffusely arranged (*M. arundinacea*) or smooth (*M. caerulea*). Paleae in *Eo-graminis* are equal to the lemmas, whereas in *Molinia*, the paleae can be either distinctly shorter than the lemmas (*M. arundinacea*) or equal to the lemmas (*M. caerulea*). Multicellular microhairs are rare in grasses but are known from leaves of *Guaduella* Franch. (subfamily Puelioideae) and members of the Arundinarioideae tribe (subfamily Bambusoideae; Metcalfe 1960). However, the disposition of microhairs has focused on leaf blades rather than on spikelets. Unlike our fossil, Bambusoideae taxa with simple multiple-flowered spikelets tend to have spikelet bracts with more and obvious nervation, often including cross-venation, and more ornamentation on bract edges and surfaces.

Previous supposed graminid remains in Baltic amber include a putative spikelet of *Zeites succineus* Caspar (1872) and putative leaf fragments of *Graminophyllum succineum* Conwentz (1886). However, there is no evidence that either of these species is a true grass (Sadowski et al. 2016). *Eo-graminis* represents the first definite grass described from Baltic amber and the first fossil member of the Arundinoideae and provides a view of the morphological features that existed in early Cenozoic grasses. The fossil can also be used as a calibration point for analyses of the divergence times of certain grass lineages. The fossil with features close to *Molinia* Schrank suggests that the split between *Molinia* and its closest relatives, *Moliniopsis* Hayata, *Hakonechloa* Makino ex Honda, and *Phragmites* Adans., could extend back to between the minimum and maximum age ranges of the Blue Earth Eocene amber deposits (34–55 mya; Wolfe et al. 2016; Sadowski et al. 2017).

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