(SS32) Evolutionary novelties in Land Plants and developmental mechanisms behind

Date: August 24 (oral), 25 (poster)
Place: Room 5336 (oral), Room 6317 (poster)
Organizers: Toshihiro Yamada & Harufumi Nishida
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Purpose: Land Plants innovated their body plan since the invasion of the land. Such innovations include acquisition of elaborated sporophyte, multicellular apical meristem, leaf, integument, carpel, perianth, and so on.
In this symposium, we will discuss how developmental mechanisms responsible for these innovations were evolved in light of palaeobotany. We also welcome perspectives from developmental biology which "predict" future palaeobotanical findings.

Oral Presentation

Aug. 24 [PM3] Room: 5336

Chair: Harufumi Nishida

16:20-16:40 **Insight in land plant evolution from comparative genomics and developmental genetics** SS32-O01 (373)

Tomoaki Nishiyama

16:40-17:00 **Evolution of angiospermy through regulation of cytokinin** SS32-O02 (584)

Toshihiro Yamada, Charles S. Gasser

17:00-17:20 **New insights on the phylogeny of Paleozoic ferns and implication on foliar organ evolution** SS32-O03 (79)

Adèle Corvez, Jean Galtier, Véronique Barriel, Jean-Yves Dubuisson

17:20-17:40 **Merge of EvoDevo and paleobotany to infer the common ancestor of land plants and evolutionary mechanisms of extended diploid generation and branching in land plants** SS32-O04 (171)

Mitsuyasu Hasebe

Poster Presentation

Aug. 25 [PM1] Room: 6317

13:30-14:30 **Evaluating the evolutionary novelties implied by two divergent reconstructions of *Tobleria biscuspis*** SS32-P01 (541)

Isabel Van Waveren, Bodo Schuetze

The epidermal structure of subepidermal swellings of *Lepidopteris* from the Upper Permian of North China SS32-P02 (607)

Yi Zhang, Shao-Lin Zheng, Serge V. Naugolnykh

The relationship between *Fascipteris* and *Symopteris* SS32-P03 (513)

Xiao Tan, Ge Sun, Yi Zhang

SS32-O01 (373)
Insight in land plant evolution from comparative genomics and developmental genetics

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In the last decade, we had a large progress in genomic scale information in basal land plants and angiosperms. Our gametophytic transcriptome data in the moss *Physcomitrella patens* showed that homologs of sporophyte dominant plant *Arabidopsis thaliana* is expressed in the gametophyte, which implied that the sporophyte in land plants evolved by recruiting genes that functioned in the gametophytic generation in the ancestors (Nishiyama *et al*. 2003). We further determined the genome sequences of the moss *Physcomitrella patens* (Rensing *et al*. 2008) and the spikemoss *Selaginella moellendorffii* (Banks *et al*. 2011). These sequences allowed us to assess which genes are present in common and revealed that really high proportion of genes regulating *A. thaliana* development have orthologous group member in *P. patens* and *S. moellendorffii*. Developmental genetics studies revealed that rhizoids in *P. patens* gametophyte and root hair in *A. thaliana* sporophyte are regulated by homologous genes (Menand *et al*. 2007). On the other hand, the class 1 KNOX genes regulate sporophyte development in both *P. patens* and *A. thaliana* and no gametophytic role have been found (Sakakibara *et al*. 2008). Taken together, gametophyte and sporophyte have some common mechanisms for development and apparently sporophyte specific pathways.

Keywords: genome sequencing, gene phylogeny.

SS32-O02 (584)
Evolution of angiospermy through regulation of cytokinin

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Angiosperms are most characterized by the ovules which are enclosed in the carpel and this character is referred to as angiospermy. In other words, evolution of the angiospermy is the most prominent event in angiosperm's history. It is widely accepted that carpel is derived from sporophyll and ovules are formed ectopically on the adaxial side of this sporophyll. This ectopic ovule formation should precede the closure of the sporophyll. Recently, we applied 6- Benzylaminopurine (6-BAP), artificial cytokinin, to wildtype Arabidopsis and found that regulation of cytokinin could play a key role on the evolution of angiospermy. The ovules treated with 6-BAP exhibited various phenotypes, and the most severe and striking phenotypes were obtained when we applied it to ovules with two integuments initiating. In these ovules with severe defects, expansion of two integuments were inhibited and inner integument became carpel-like structure from which ectopic nucelli were formed. Formation of megaspore mother cell is also inhibited in many ovules. These ovule phenotypes are closely similar to those of *bell1* (*bel1*) mutants, suggesting that *BEL1* would be involved in the regulation of cytokinin. Similar phenotypes are also observed in overexpressor of Class I Knotted-like homeobox (KNOX1) genes which could directly activate the cytokinin

synthesis in shoot apex. On the other hands, full-dose of cytokinin is required for proper formation of placenta because over-disintegration of cytokinin inhibits the proliferation of placental cells. This contrary response to cytokinin between ovule and placenta suggests that repression of the cytokinin is required for the ovule formation on the placenta. This kind of regulation would be true for the ancestral unclosed carpel and ectopically-formed ovules. Thus, cytokinin repression in ovules would be a key innovation which would be acquired through the evolution of angiospermy.

Keywords: ovule, carpel, angiospermy, cytokinin, EvoDevo.

SS32-O03 (79)

New insights on the phylogeny of Paleozoic ferns and implication on foliar organ evolution

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The origin and evolution of the foliar organ, especially the megaphyll, is one of the major questions in the field of evolutionary developmental biology of land plants. Because all living euphyllophytes (involving horsetails, ferns and seed plants) display megaphylls (except reversals such as in horsetails), a unique origin seems the *a priori* most parsimonious scenario. Conversely, paleobotanical data strongly support a multiple origin in monilophytes (horsetails and ferns) and lignophytes (fossil progymnosperms and seed plants). Molecular evo-devo analyses are mostly focused on living seed-plants. The Monilophytes and their fossils, often neglected in such studies, are nevertheless pertinent models for investigating the convergent evolutionary scenarii that would have provided the foliar organ in euphyllophytes. In addition, a complete phylogenetic framework is strongly needed as a prerequisite to understand where and when the foliar organ and its potential precursors would have appeared. The evolutionary relationships among living monilophytes are currently well known, but few phylogenetic analyses involving fossil taxa were carried out. Therefore, the aims of this study were: 1) to reconstruct the phylogeny of monilophytes using morphology and anatomy data and selecting fossil and living representatives, more particularly Paleozoic fossil taxa of importance which have not been taken into account in any recent phylogenetic study, and 2) to infer on this phylogeny the evolution of anatomical and morphological traits that could contribute to the acquisition of the megaphyll. New insights into the relationships among basal monilophytes and new interpretations of such morphological and anatomical traits and of the definition of the foliar organ are thus discussed.

Keywords: Monilophytes, megaphyll, cladistic, morphology, anatomy.

SS32-O04 (171)

Merge of EvoDevo and paleobotany to infer the common ancestor of land plants and evolutionary mechanisms of extended diploid generation and branching in land plants

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The life cycle of land plants alternates between a haploid multicellular gametophyte and a diploid multicellular sporophyte. The haploid generation is more prominent in basal land plants, bryophytes, whereas the diploid generation dominates in seed plants. Genes regulating the alteration of generations are mostly unknown. Apogamy is a process that cells of the gametophyte other than the egg cell initiate sporophyte development. We found that deletion of *CURLY LEAF* ortholog in the moss *Physcomitrella patens* caused apogamy. Side branch initial cells, which usually form protonema or gametophore apical cells, formed sporophyte apical cells. The induced apogamous sporophyte continuously grew with an indeterminately grown apical cell. Astonishingly, it formed branches and the morphology was similar to protracheophytes. An induction of exogenous *PpCLF* in the deletion mutant formed sporangium-like organs at the tip of branches. These results suggest that the evolution of regulatory networks of *PpCLF* was related to the extension of diploid generation and the branch formation in land plants.

Keywords: protracheophytes, artificial evolution, branched moss sporophytes, the common ancestor of land plants.

SS32-P01 (541)

Evaluating the evolutionary novelties implied by two divergent reconstructions of *Tobleria biscuspis*

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In the early nineteen hundreds *Tobleria biscuspis* was described as part of the Early Permian Jambi palaeoflora and the probable dispersed seed scale complex of an early conifer. In reviewing this flora, several cones were found in close association to the dispersed seed scale complexes. The systematic analysis of the numerous dispersed and attached organs of *Tobleria biscuspis* demonstrated a continuum within and between the attached and dispersed organ categories that gave rise to two 3-D digital reconstructions. These two reconstructions are presented and each of them is placed in a conifer phylogeny. The evolutionary novelties implied by each reconstruction and its phylogeny are described and analyzed (1)in the light of the most parsimonious pathway to the *Tobleria biscuspis* cone; (2)in comparison with traits typical of the Early Permian Jambi mesic to xeric palaeoflora to which *Tobleria biscuspis* belongs; (3)in the context of the climatic regime of increased seasonality and aridity of the Early Permian.

Keywords: palaeobotany, early conifers, phylogeny, Early Permian, SE Asia.

SS32-P02 (607)

The epidermal structure of subepidermal swellings of *Lepidopteris* from the Upper Permian of North China

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A new species *Lepidopteris baodensis* Zhang et al. belonging to the Peltaspermaceae family and represented by two ultimate pinnae in the collection under study, was recently discovered at the Baijiagou of Baode, Shanxi, North China, from the Upper Permian Sunjiagou Formation (Zhang et al., 2012). The distinguished epidermal structure of subepidermal swellings of *Lepidopteris* is discovered. The upper surface of the ultimate rachis, the midrib and secondary veins are smooth, whereas the lower surface of the ultimate rachis, the midrib and secondary veins are covered with triangular, trapezoid, rounded, or ligulate subepidermal swellings, which show different natures from intercalary pinnules. The subepidermal swelling on the ultimate rachis, more or less paired, attaining a maximum length of at least 3 mm long by 1.5 mm wide, is composed of ordinary epidermis cells with stomatal apparatus, forming longitudinal files and numerous groups. Ordinary epidermis cells and stomatal apparatus in each group set in a concentric pattern. The subepidermal swellings on a midrib, single or paired, generally 300–500 μm long by 300–400 μm wide, are also composed of ordinary epidermis cells and stomatal apparatus, only forming 3–4 groups. Ordinary epidermis cells and stomatal apparatus in each group also set in a concentric pattern. The subepidermal swelling on a secondary vein single, generally 200–300 μm long by 150–200 μm wide, is composed of ordinary epidermis cells and stomatal apparatus, forming a concentric pattern. The new species *Lepidopteris baodensis* and its unique epidermal structure of subepidermal swellings enlarge and supplement our knowledge in taxonomy and anatomy of *Lepidopteris* as well as the Upper Permian stratigraphy of China. It also provides an opportunity to understand the relationship between Euramerican floras and Cathaysian floras in paleoclimatic, paleoenvironmental and paleogeographical context.

Keywords: epidermal structure, subepidermal swellings, *Lepidopteris*, Upper Permian, China.

SS32-P03 (513)
The relationship between *Fascipteris* and *Symopteris*

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Fascipteris Gu et Zhi, as a typical Permian element of Cathaysian flora, is characterized by pinnate frond; linear pinnules, entire to undulate in margin and contracted in base, with strong midrib, secondary veins fascicled in type, neither rachial veins nor interfascicular veins present. Since the genus was named, 11 species have been recorded. In these species, *Fascipteris* is probably ascribed to Marattiaceae because two rows of synangia on a pecopteroid-type pinnule have been found in either the fertile fronds of *F*. (*Ptychocarpus*) *densata* or *F*. (*Ptychocarpus*) *stena*. *Symopteris* (Heer) Hsü, as a typical Middle-Late Triassic element of the floras in the North Hemisphere, is characterized by unipinnate or bipinnate frond; pinnae with strong rachises, ovate, linear to ensiform; pinnules ovate, linear to ensiform, alternate or subopposite, with an entire, undulate, lobed to parted margin; midrib thick and strong; secondary veins fascicled in type; sporangia appearing in several regularly longitudinal rows attached to the lower side of the pinnae. Most of the fossils have originally been referred to the genus *Bernoullia* Heer, a junior synonym of *Bernoullia* Oliver (extant Bombacaceae). So far, eight species have been identified, three from Europe, i.e. *Symopteris helvetica* (Heer) Xu, *S. lunzensis* (Stur ex Krasser) Xu, *S. rumpfii* (Schenk) Kust. et al.; one from

Kazakhstan i.e. *S. aktjubensis* Brik; and four from East Asia, i.e. *S. zeilleri* (P'an) Xu., *S. pecopteroides* (Feng et al.) Kust. et al., *S. densinervis* Xu et Duan; *S. pseudolobifolia* (Yang) Kust. et al. The oldest known representative of the genus probably occurred in the Anisian of the Linjiawaizi of Benxi, Liaoning, NE China. During the Late Triassic its diversity increased in Europe and Asia, while the latest occurrence is in the Rhaetian of Vietnam. *Symopteris* is similar to the *Fascipteris* mophologically in their fronds that are pinnate in form and secondary veins that are fascicled in type; but the latter probably has two rows of synangia on a pecopteroid-type pinnule, occurred in the Permian, while the former has sporangia appearing in several regularly longitudinal rows, occurred in the Middle-Late Triassic.

Keywords: *Fascipteris*, *Symopteris*, synangia, Permian, Triassic.