



乌达煤田早二叠世阿瑟尔期乌海拟齿叶 (*Paratingia wuhaia*)复叶形态的种内变异研究*

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提要 本文基于内蒙古乌达煤田早二叠世阿瑟尔期原位埋藏成煤植物群——“植物庞贝”中的乌海拟齿叶的树冠标本, 全面揭示了该种的复叶形态变化。乌海拟齿叶的羽状复叶由大叶和小叶构成, 对该种鉴定特征的原始描述仅反映了羽状复叶中上部大叶和小叶的特征, 而缺乏其复叶下部的小叶形态特征。近年来积累的代表同一树冠的羽状复叶标本, 不仅清晰地展示了复叶中上部的小叶形态, 也揭示了其羽状复叶下部的小叶形态特征, 其小叶顶端深裂为2或3个裂片或多个细齿, 叶脉二歧分叉, 放射状展开。因此, 当前标本完整地揭示了乌海拟齿叶小羽片的种内形态变异特征; 而原先该地区发现的记录为大同拟齿叶*Paratingia datongensis*的标本, 实际上代表了乌海拟齿叶复叶的中下部。

关键词 拟齿叶属 阿瑟尔期 乌达凝灰岩植物群 形态多样性

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Intraspecific morphological variation of *Paratingia wuhaia* frond from the Asselian (Early Permian) of the Wuda coalfield

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Abstract Tree crown leaves of *Paratingia wuhaia* from the Asselian (early Early Permian) *in situ* preserved peat-forming flora, known as the Wuda Tuff Flora or the “vegetational Pompeii” in the Wuda Coalfield, reveal notable intraspecific

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variation in frond morphology. The once-pinnate compound leaves of *Paratingia wuhaia* consist of large and small pinnules. However, the original diagnosis only described the morphology of those pinnules of the middle to distal portions of the frond, leaving the small pinnules of the basal unknown. Newly collected crown frond specimens preserve both the basal and apical portions of the once-pinnate compound leaves, with both large and small pinnules visible. These specimens show that the small pinnules at the basal part of the frond are fan-shaped with 2–3 deep lobes or multiple slender teeth and with veins that radiate and bifurcate. This demonstrate that previously reported specimens of *Paratingia datongensis* with this type of small pinnule morphology from the same locality actually represents the basal and middle portions of the once-pinnate compound leaves of *Paratingia wuhaia*.

Key words *Paratingia*, Asselian, Wuda Tuff Flora, morphological variability

SYSTEMATIC PALEONTOLOGY

Phylum Tracheophyta Sinnott, 1935 ex Cavalier-Smith, 1998

Class Progymnospermopsida Beck, 1960

Order Noeggerathiales Němejc, 1931 emend. Wang *et al.*, 2021a

Family Tingiostachyaceae Gao *et Thomas*, 1987 emend. Wang *et Spencer*, 2017

Genus *Paratingia* Zhang, 1987

Type species *Paratingia datongensis* Zhang, 1987

Paratingia wuhaia Wang *et al.*, 2021a emend.

(Figs. 2–7)

1999 *Paratingia datongensis* Zhang: Sun *et al.*, p. 1025; pl. 1, figs. 1–3; pl. 2, figs. 1, 2.

2003 *Paratingia datongensis* Zhang: Sun *et Deng*; pl. 1, fig. 9.

2010 *Paratingia datongensis* Zhang: Sun; pl. 3, figs. 6, 8.

2014 *Paratingia* sp.: Wang, Pfefferkorn *et Feng*, p. 2789; figs. 2h–2j.

2021a *Paratingia wuhaia*: Wang *et al.*; figs. 1–3; figs. S2–S23 in SI Appendix.

Holotype PB22126, deposited at the Nanjing Institute of Geology and Paleontology, Chinese Academy of Sciences.

Emended diagnosis The stem is monopodial and unbranched. The once-pinnate compound leaves and pseudo-strobili are directly attached to the upper part of the stem, either together, or with only the compound leaves and stem forming the crown. The pinnules are arranged in four rows, with plagiotropic attachment. Two rows of large pinnules are attached on the lower surface of the rachis, and two rows of small pinnules are

attached on the upper surface. Large pinnules are oval, elliptical, lanceolate, asymmetrically lanceolate or sward-shaped; their basal portions are semi-amplexicaul, and teeth are present on both the lateral margins and the apex. Small pinnules are oval or elliptical with toothed margins. Some small pinnules at the basal part of the frond divide into two or three lobes at the distal margin, with each lobe further dividing into several fine teeth; others split into multiple slender teeth. The leaf venation is radial with several veins extending from the pinnule base and bifurcating one to three times before reaching the teeth on the lateral and distal margins. Pseudo-strobili are cylindrical, heterosporous, and bisporangiate. Sporophylls are whorled, proximally disk-shaped or dissected into segments, distally upturned and dissected. Sporangia are attached adaxially and proximally to sporophyll in single ring. Megasporengia are arranged in a vertical row, each bearing a single functional megaspore. Microspores are of the *Calamospora*-type. Both the rachis and the axes of the pseudo-strobili possess bilaterally symmetrical vascular bundles. The stem exhibits the anatomical characteristics of gymnosperm wood.

Specimens Examined PB205895–PB205900.

Locality Wuda Coalfield, Wuhai City, Inner Mongolia.

Horizon and age Uppermost Taiyuan Formation; Asselian (Early Permian).

1 前言

拟齿叶属(*Paratingia*)仅发现于中国乌拉尔世的地层(张泓, 1987; 孙克勤等, 1999; 孙克勤、邓胜徽, 2003; 孙克勤, 2010; Wang et al., 2009, 2014, 2021a), 是华夏植物群的特色分子之一, 生活于潮湿低地环境中, 是重要的成煤植物(张泓, 1987; 孙克勤, 2010; Pfefferkorn and Wang, 2007; Wang et al., 2014)。

拟齿叶属(*Paratingia*)基于中国山西大同下二叠统山西组的叶部化石标本建立, 模式种为大同拟齿叶(*P. datongensis*), 其属征鉴定为: “羽叶状枝条。轴粗强, 具腹背性; 叶具不等叶性, 互生, 四行排列, 两行在上, 两行在下。大叶位于上面, 与轴呈宽角, 卵形, 椭圆形至披针形, 基部半抱茎状, 侧边和顶端具齿; 小叶位于下面, 与轴呈狭角, 和大叶同形, 但面积小于大叶。叶脉放射状, 二歧分叉”(张泓, 1987)。

该属标本亦被发现于内蒙古乌达煤田苏海图煤矿和五虎山煤矿下二叠统山西组(孙克勤等, 1999; 孙克勤、邓胜徽, 2003; 孙克勤, 2010)。王军等(Wang et al., 2009)报道了乌达拟齿叶(*Paratingia wudensis*), 标本采自内蒙古乌达煤田下二叠统太原组6号煤层和7号煤层之间的火山凝灰岩, 对该属植物的整体形态、复叶和拟孢子囊穗的形态结构, 以及原位大、小孢子形态等有了全面的认识。随后, 王军等(Wang et al., 2021a)基于同一火山凝灰岩层中的化石标本建立了乌海拟齿叶(*P. wuhaia*), 揭示其主干具有裸子植物木材的解剖特征, 并由此确定瓢叶目属于前裸子植物(Wang et al., 2021a)。至此, 从Sternberg (1821)描述捷克波西米亚地区晚石炭世营养叶*Noeggerathia foliosa*以来, 最终把两个世纪悬而未决的瓢叶目系统分类位置问题解决了。

目前, 关于拟齿叶植物化石的产地和层位主要来自如下两个地区: 其一是山西平朔煤田下石盒子组的大同拟齿叶(*Paratingia datongensis*) (张泓, 1987), 采自煤层顶板; 其二是内蒙古乌达煤田太原组和山西组中, 包含乌达拟齿叶(*Paratingia wudensis*)和乌海拟齿叶(*Paratingia wuhaia*) (孙克勤、邓胜徽, 2003; 孙克勤, 2010; Wang et al., 2009, 2021a)。

Pfefferkorn和Wang (2007)在对内蒙古乌海市乌达煤田早二叠世植物群落进行研究时, 自7号煤层底板至6号煤层顶板共识别出4个连续分布的原地和亚原地的印痕—压型植物群落。其中位于6号煤层和7号煤层之间火山凝灰岩层中的第2个植物群落生长在沼泽环境中, 保留有大量保存完好的叶、繁殖器官和茎干化石(Wang et al., 2012, 2013), 与乌达煤田曾记录的*Caulopteris wudaensis*—*Paratingia datongensis*组合及*Lepidodendron posthumii*—*Paratingia datongensis*植物群落进行对比, 在化石埋藏类型、保存状态和植物类群组成上总体一致, 属于同一段地层的植物化石组合(孙克勤、邓胜徽, 2003; 王军, 2006; 孙克勤, 2010; Pfefferkorn and Wang, 2007; Wang et al., 2009)。根据何自新等(2004)对鄂尔多斯盆地地质剖面的研究, 乌达煤田6、7号煤层被划归为早二叠世太原组顶部。据此, Pfefferkorn和Wang (2007)报道的4个连续分布的植物群落的层位被厘定为太原组, 位于乌达煤田山西组之下几米处(Wang, 2010; Wang et al., 2012, 2014; Schmitz et al., 2021)。

根据现有报道, 在内蒙古乌达煤田报道的大同拟齿叶(*Paratingia datongensis*)的标本(孙克勤、邓胜徽, 2003; 孙克勤, 2010)和乌海拟齿叶(*P. wuhaia*)标本(Wang et al., 2014; Wang et al., 2021a)在叶片形态、化石标本的岩性与保存状况上高度相似, 两者为采自同一层位的同一种植物。笔者近年来在乌达煤田对该属标本进行了专门的采集, 针对复叶的形态变异进行探讨, 以便更好地认识这类植物的复叶发育过程。

2 材料和方法

本文研究的化石材料采自内蒙古乌达煤田6号煤层和7号煤层中间的火山凝灰岩层的中部及下部, 其层位属于下二叠统太原组(Pfefferkorn and Wang, 2007; Wang et al., 2012, 2014, 2021b; Schmitz et al., 2021)。文中所展示的标本主要为2021年在乌达煤田北边开展样方调查时采集(图1)。该化石产地已入选第二批国际地科联世界100地质遗产地名录(IUGS, 2024)。

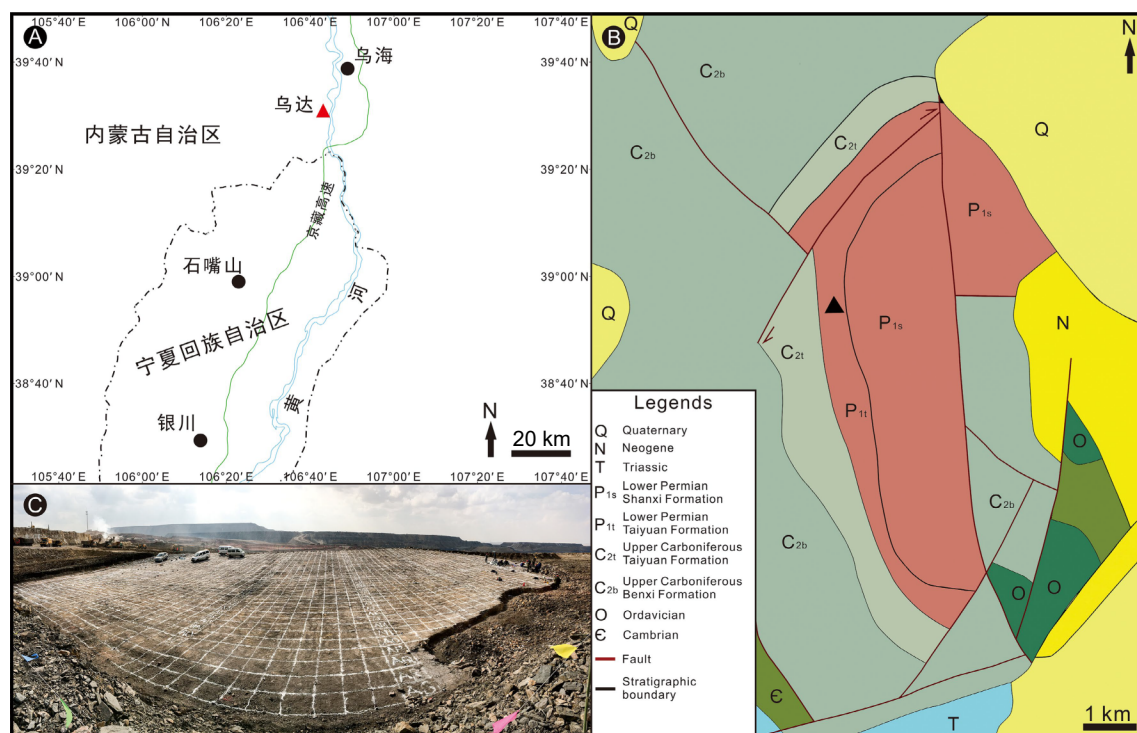


图1 内蒙古乌达煤田的地理位置和地质图

Fig. 1 Map showing geographic location and stratigraphic horizon of the Wuda Coalfield, Inner Mongolia

A. 三角形标志为本文的化石产地。B. 指示乌达煤田的地层分布情况, 三角形图标所在地为本文化石标本的具体产地。C. 指示6号煤层和7号煤层之间的凝灰岩层的层面。A的审图号为GS (2025) 1508号; B修改自何学智等(He *et al.*, 2021)。

A. Red triangle indicates fossil locality. B. Showing stratigraphic distribution of the Wuda Coalfield; black triangle indicates fossil site. C. Showing bedding plane of the tuff bed between coal seams No. 6 and No. 7. The approval number for A is GS (2025) 1508; B is modified after He *et al.* (2021).

化石标本首先采用Farion-Demaret等(1999)的实验方法, 通过气刻笔将标本表面覆盖的岩石移除。然后将部分标本置于无水乙醇中, 并采用尼康D800单反相机对其进行宏观拍照。使用Image J软件对标本进行测量来获取相关数据, 和Photoshop CS 6.0软件进行图版制作。

目前为止, 瓢叶目植物营养叶和繁殖器官描述术语存在多种争论, 缺乏关于该类群描述术语选用标准的专门研究。考虑到瓢叶目营养叶和繁殖器官中轴内具单一的、两侧对称的维管束, 而非裸子植物放射状排列的维管束, 本文标本的描述术语将继续沿用瓢叶目描述术语最新研究中的方案, 即采用“复叶(compound fronds)”代替“叶枝(leafy shoots)”, 采用“小羽片(pinnule)”代替“叶子(leaf)”, 采用“拟孢子囊穗(pseudo-strobili)”来描述繁殖器官(Wang *et al.*, 2021a, 2021b)。另外, 为方便描述及与前人研究进行对比, 本文将继续采用“大叶”来翻译“large pinnules”, 继续采用“小叶”来翻译“small pinnules”。

3 系统古生物学

维管植物门 Phylum Tracheophyta Sinnott, 1935
ex Cavalier-Smith, 1998

前裸子植物纲 Class Progymnospermopsida Beck, 1960

瓢叶目 Order Noeggerathiales Němejic, 1931
emend. Wang *et al.*, 2021a

齿叶穗科 Family Tingiostachyaceae Gao *et*
Thomas, 1987 emend. Wang *et* Spencer, 2017

拟齿叶属 Genus *Paratingia* Zhang, 1987

模式种 *Paratingia datongensis* Zhang, 1987

乌海拟齿叶 *Paratingia wuhaia* Wang *et al.* 2021a
emend.

(图2-7)

1999 *Paratingia datongensis* Zhang: 孙克勤等, 1025页; 图版1, 图1-3; 图版2, 图1, 2。

2003 *Paratingia datongensis* Zhang: 孙克勤, 邓胜徽; 图版1, 图9。

2010 *Paratingia datongensis* Zhang: 孙克勤; 图版3, 图6, 8。

2014 *Paratingia* sp.: Wang, Pfefferkorn *et* Feng, p. 2789; figs.

2h-2j.

2021a *Paratingia wuhaia*: Wang et al.; figs. 1-3; figs. S2-S23 in SI Appendix.

种征(修订) 单轴茎, 茎干不分枝。一次羽状复叶和拟孢子囊穗直接着生在茎干的顶部, 三者一起, 或仅由复叶和茎干一起形成树冠。小羽片呈四行排列, 倾斜着生在叶轴上。叶轴下侧的两行小羽片(大叶)较大, 形状为卵形、椭圆形、披针形、非对称披针形或剑形; 基部呈半抱茎状, 叶缘具齿。叶轴上侧的两行小羽片(小叶)较小, 形状为卵形或椭圆形, 叶缘具齿。部分位于复叶下部的小叶顶端深裂为2或3个裂片, 且这些裂片会继续分裂为数个细齿, 或者小叶顶端深裂为多个细长的齿。叶脉放射状排列; 数条叶脉自小羽片基部延伸出来, 并在延伸至小羽片叶缘的齿中之前二歧分叉1至3次。拟孢子囊穗形状为圆柱形, 具异型孢子和大小孢子囊; 孢子叶轮生, 近轴端盘状或裂成几个裂片, 远轴端向上弯曲且分裂。孢子囊呈单环状着生在孢子叶近轴端的上表面上。大孢子囊中含一个大孢子, 小孢子为*Calamospora*型。叶轴和拟孢子囊穗的中轴均具有两侧对称的维管束。茎干具有裸子植物类型的解剖特征。

材料 本文标本保存在中国科学院南京地质古生物研究所, 化石编号PB205895—PB205900。

产地层位 中国内蒙古乌海市乌达煤田, 二叠系乌拉尔统阿瑟尔阶太原组最上部。

3.1 描述

主要选取三块保存完整程度不同的树冠标本, 展示乌海拟齿叶一次羽状复叶上小叶的形态变化。根据各自的一次羽状复叶的排列状况, 并结合化石保存属于原位埋藏的特征, 这些化石应该属于树冠的一部分。

第一块标本(PB205895)共约20枝羽状复叶保存于该化石表面(图2), 主干在标本的右上部分出露良好, 直径约25 mm, 可清楚地观察到左右两侧一次羽状复叶从主干以宽窄不同的角度伸出的状况; 两侧的复叶几乎垂直于主干着生, 其上下紧邻的个别复叶以狭角着生。其余未观察到与主干有机连生的复叶(主干左下侧2枝、右下侧4—5枝), 依其伸展情况, 推测也着生于同一树冠。左侧的两枝复叶, 下部外侧叶轴比较细的一枝代表了复叶的上部和

近顶部, 其基部未保存; 下部内侧叶轴比较粗壮的复叶可能是基部着生于该树冠的上部, 而复叶的前端部分垂下来的状态。标本右下侧指向右下方的4枝代表了复叶的远端部分, 其基部有可能就是标本右上部出露的5—6枝复叶, 其中间部分被另外两枝复叶压覆; 压覆它们的这两枝复叶顶端向上, 叶轴较细, 基部未被保存, 根据叶轴的伸展方向, 推测是着生于树冠部分主干的下部。所有叶子均为一次羽状复叶, 叶轴不分叉, 基部较粗, 向顶渐狭; 小羽片呈四行斜生于叶轴上, 具背腹性和不等叶性; 数条叶脉自小羽片基部放射状伸出, 于小羽片中下部二歧分叉1至3次, 末梢直达小羽片叶缘的齿内, 每个齿中含一条叶脉。当前标本大叶整体上呈披针形, 小羽片边缘具微齿, 部分大叶顶端略微朝复叶顶端弯曲; 小叶整体上为椭圆形或卵形, 边缘具微齿(图2-D)。在复叶下部区域, 大叶形状呈非对称的披针形; 其下侧缘(靠近复叶基部)平滑似全缘, 较为平直; 上侧缘(远离复叶基部)呈明显的弧形且具细长的齿, 齿长可达4 mm (图2-B)。与此同时, 复叶下部区域的小叶虽整体形态上呈椭圆形或长椭圆形, 但其顶端或分裂为2至3个裂片, 且每个裂片再次分裂为数个纤细的长齿, 或深裂为多个细长的齿; 齿长可达7 mm (图2-C)。

第二块标本(PB205896)中复叶和茎干的叠覆关系及各自的倾向性, 表明两者均来自同一植株的树冠(图3)。主干出露于标本的左侧, 其余区域展示了10余枝从主干上向右下方呈垂落状态的复叶; 复叶的顶部未保存, 仅展示了下部至中部区域的叶形特征。总体上, 位于复叶下部区域的大叶亦呈非对称的披针形、上侧缘呈明显的弧形, 且上侧缘具明显的细齿, 向复叶的上部逐步转变为比较对称的披针形, 叶片的长度也明显增加; 位于复叶基部的小叶顶端深裂为2至3个裂片(图3-B, 3-C), 而在复叶远端区域的小叶, 如标本右侧出露较好的几个小叶, 表明它们已逐步过渡为椭圆形、卵形。特别是着生在叶轴下端的小叶的顶端深裂呈齿状或裂片状(图3-D); 而同一叶轴上端的小叶则呈较为规律的椭圆形或卵形, 叶缘齿不明显, 且相邻的大叶呈披针形。

第三块标本(PB205897)示6枝复叶辐射状地由下向上伸展, 表明它们可能代表了一个主干在标本下方的树冠局部(图4)。可以清晰地观察到复叶下部区域小叶的顶端均深裂为2至3个裂片或多个细

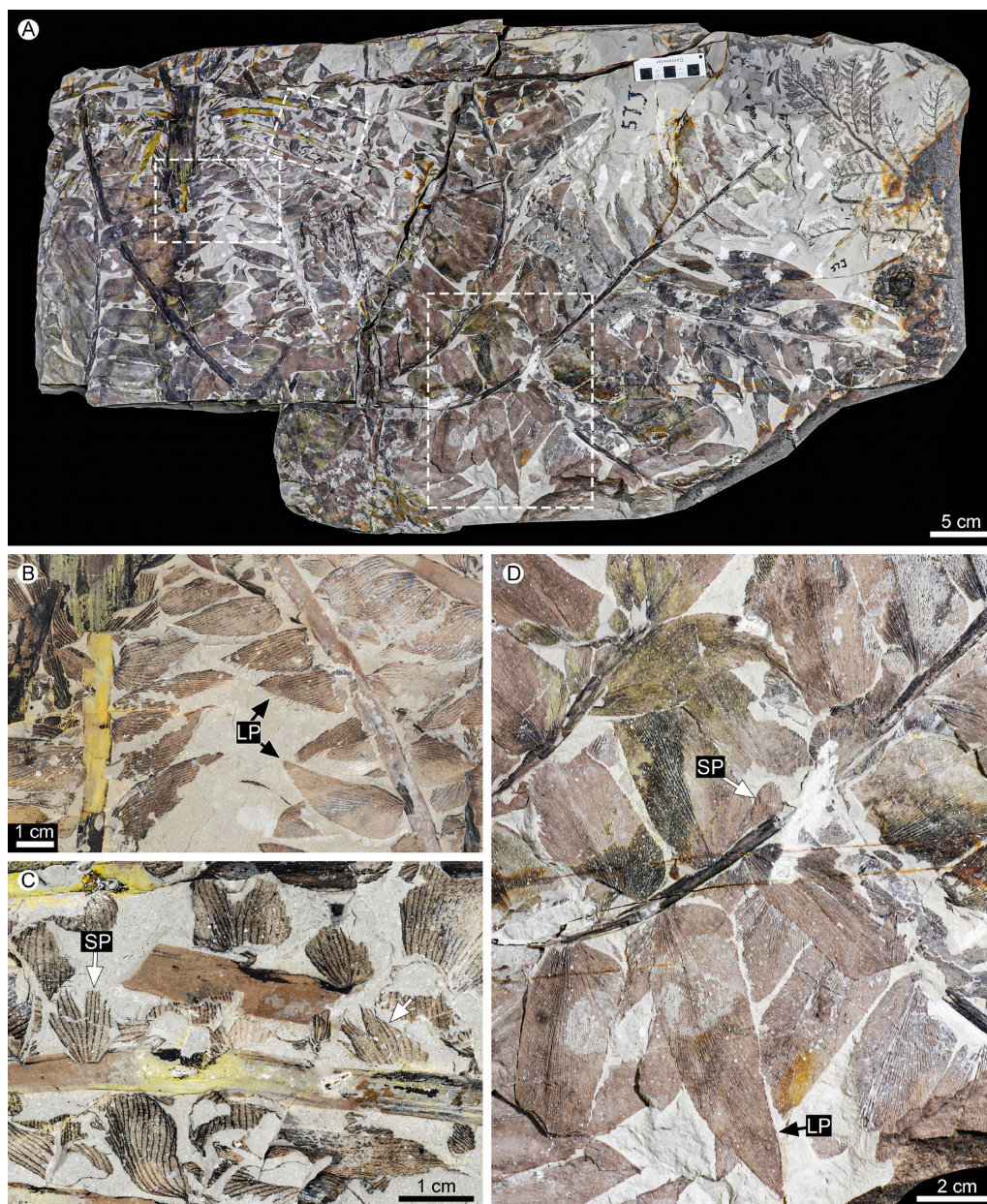


图2 乌海拟齿叶(*Paratingia wuhaia*)的茎干及一次羽状复叶

Fig. 2 Stem and once-pinnate compound leaf of *Paratingia wuhaia*

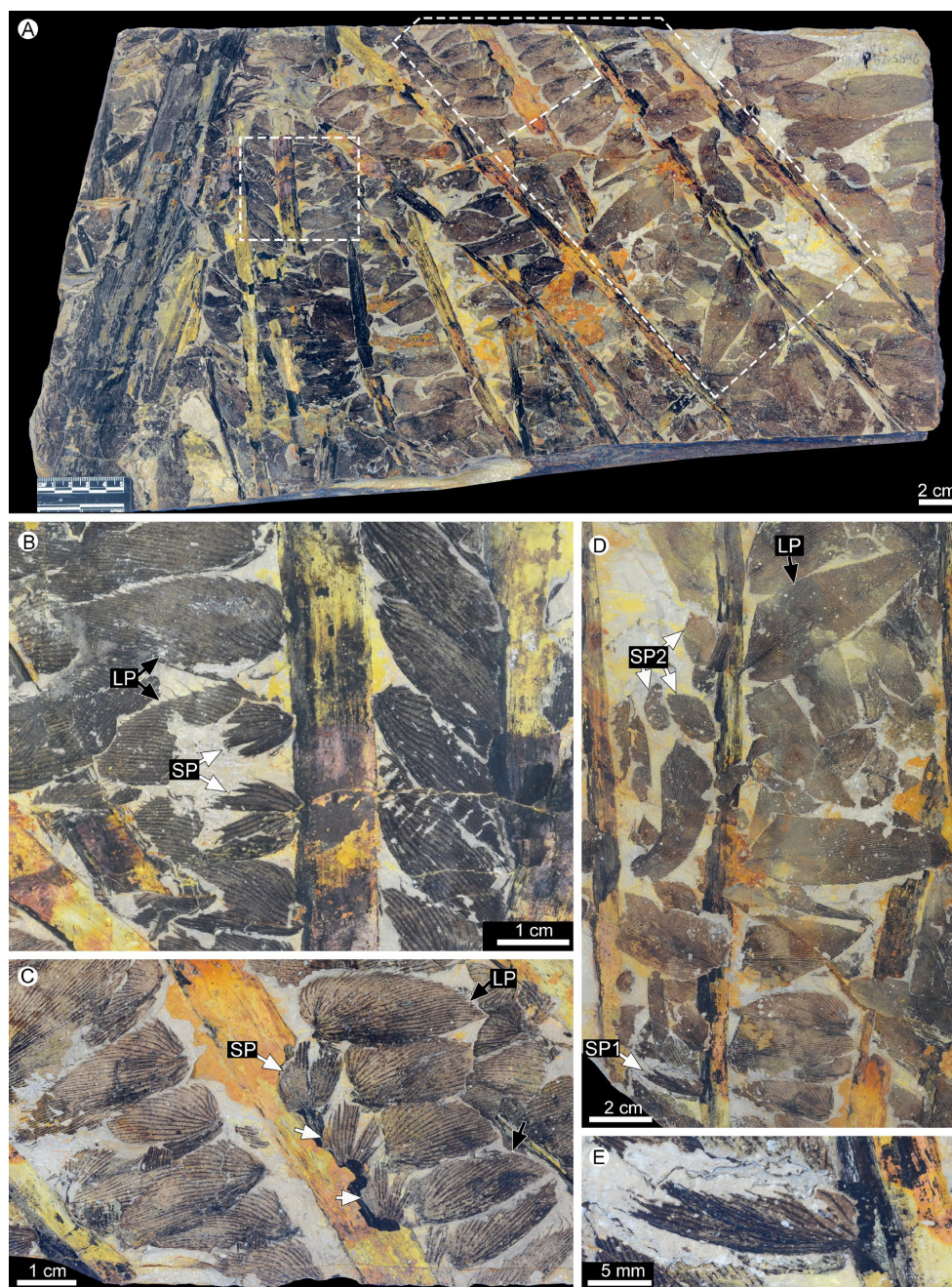
A. 标本概览(标本编号: PB205895), 示复叶着生在茎干上。B. 图2-A中左侧方框区域的放大, 示复叶下部区域非对称披针形的大叶(黑色箭头)。C. 图2-A中间方框区域的放大, 示复叶下部区域顶端深裂的小叶(白色箭头)。D. 图2-A右侧方框区域的放大, 示复叶中部区域披针形的大叶(黑色箭头)和顶端具微弱细齿的小叶(白色箭头)。注: LP = large pinnules (大叶); SP = small pinnules (小叶)。

A. Overview of specimen PB205895, showing compound leaves directly attached to the stem. B. Enlargement of the area (left quadrangle in A) showing asymmetric, lanceolate large pinnules (indicated by black arrows) at the basal part of leaf. C. Enlargement of the area (middle quadrangle in A) showing small pinnules with deeply lobed distal margin (indicated by white arrows) at the basal part of the leaf. D. Enlargement of the area (right quadrangle in A) showing a lanceolate large pinnule (indicated by black arrow) and a small pinnule with weak fine teeth on the distal margin (indicated by white arrow) at the middle part of the leaf. Abbreviations: LP = large pinnules; SP = small pinnules.

长的齿(图4-C, 4-E), 复叶上部的小叶呈椭圆形、卵形等(图4-B); 图4-C和4-D的复叶比较清楚地显示了同一复叶中, 自下而上, 小叶的顶端由深裂过渡到仅具微齿。标本右侧的一枝复叶(图4-B)显示上部

的大叶形态为具尖顶的卵形。

此外, 一些单独保存的复叶, 有时也显示小叶形态从复叶基部的多裂片齿状到复叶中上部椭圆形或卵形且具微弱细齿的变化(图5-A)。大多数情

图3 乌海拟齿叶(*Paratingia wuhaia*)的茎干及一次羽状复叶Fig. 3 Stem and once-pinnate compound leaf of *Paratingia wuhaia*

A. 标本概览(标本编号: PB205896), 示复叶着生在茎干上。B, C. 图3-A左侧和中间方框区域旋转180°的放大, 示复叶下部区域非对称披针形的大叶(黑色箭头)和顶端深裂的小叶(白色箭头)。D. 图3-A右侧方框区域旋转180°的放大, 示同一复叶上不同部位的小叶; 基部的小叶(SP1)其顶端深裂, 而上部的小叶(SP2)其顶端仅具微弱细齿; 以及披针形的大叶(LP)。E. 图3-D中顶端深裂的小叶(SP1)的放大。注: LP = large pinnules (大叶); SP = small pinnules (小叶)。

A. Overview of specimen PB205896 showing compound leaves directly attached to the stem. B, C. Enlargements of the area (left quadrangle in A) and the area (upper middle irregular pentagon in A) after 180° rotation showing asymmetric, lanceolate large pinnules (indicated by black arrows) and small pinnules with deeply lobed distal margin (indicated by white arrows) at the basal part of the compound leaves. D. Enlargement of the area (right irregular hexagon in A) after 180° rotation showing a small pinnule (SP1) with deeply lobed distal margin at the basal part, small pinnules (SP2) with only weak fine teeth on the distal margin at the upper part of the same compound leaf, and a lanceolate large pinnule (LP). E. Close-up of the small pinnule (SP1 in D) with deeply lobed distal margin. Abbreviations: LP = large pinnules; SP = small pinnules.

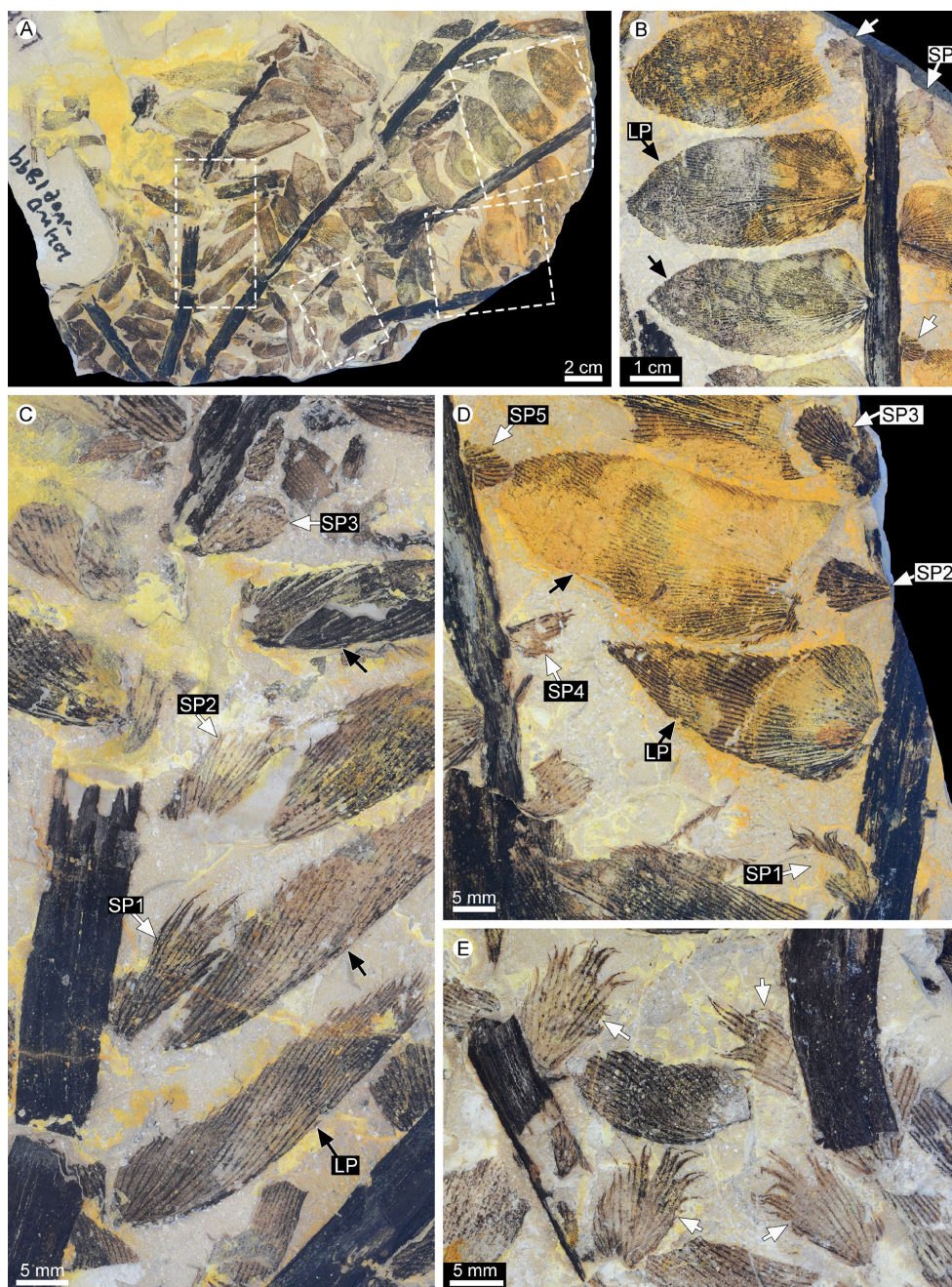
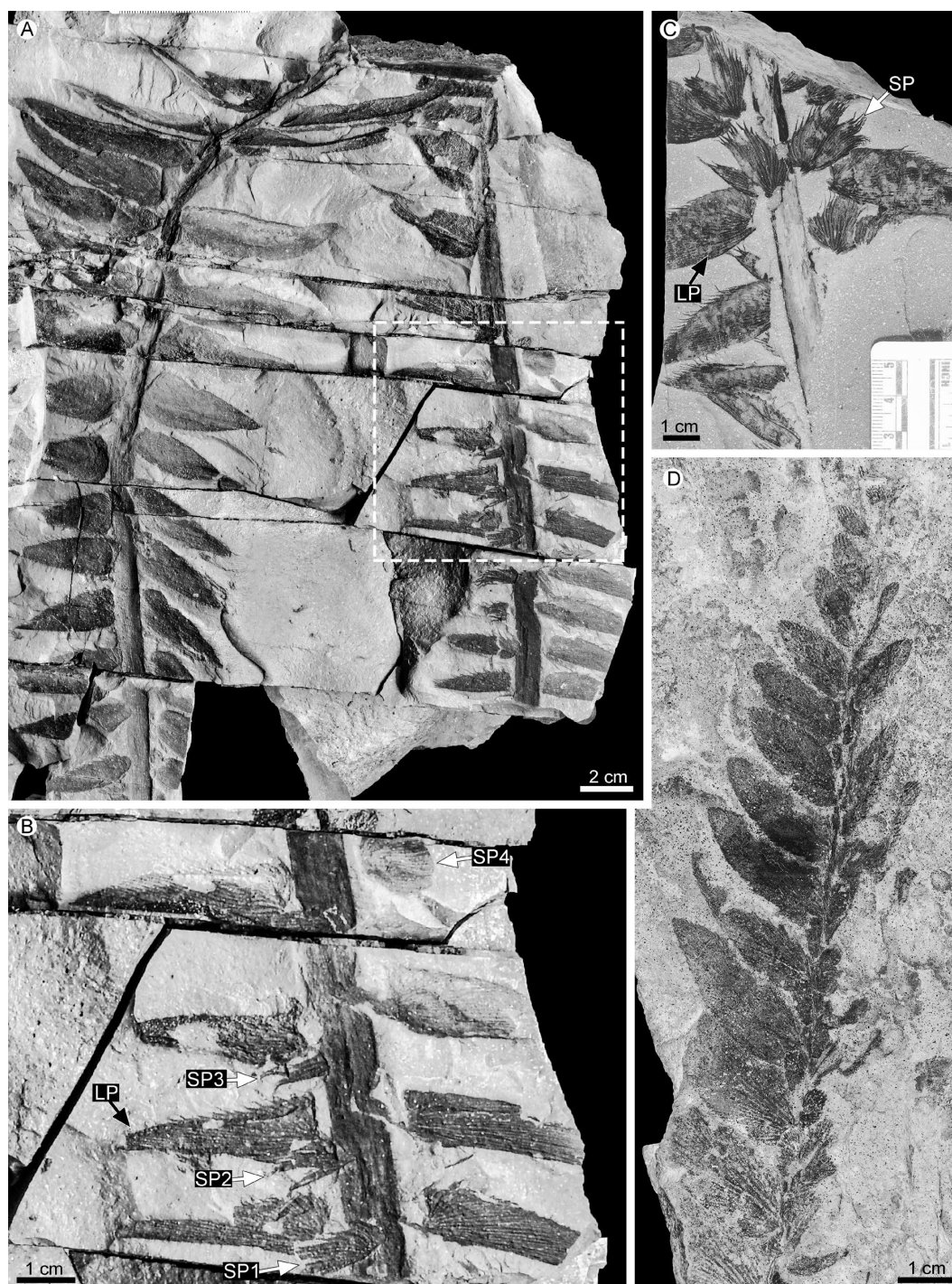


图4 乌海拟齿叶(*Paratingia wuhaia*)的一次羽状复叶, 根据朝向其可能来自一个树冠

Fig. 4 Once-pinnate compound leaves of *Paratingia wuhaia*, probably belong to the same crown based on their orientation

A. 标本概览(标本编号: PB205897), 示复叶的整体形态。B. 图4-A右上方框区域的放大, 示卵形的大叶(黑色箭头)和顶端未深裂的小叶(白色箭头)。C. 图4-A左侧方框区域的放大, 示小叶顶端由深裂(SP1, SP2)向仅具微弱细齿(SP3)的变化。D. 图4-A右下方框区域的放大, 示小叶顶端由深裂(SP1, SP4)向仅具微弱细齿(SP2, SP3, SP5)的变化。E. 图4-A左侧第2个方框区域的放大, 示复叶下部区域顶端深裂的小叶(箭头)。注: LP = large pinnules (大叶); SP = small pinnules (小叶)。

A. Overview of specimen PB205897 showing general morphology of the compound leaves. B. Enlargement of the area (upper-right irregular pentagon in A) showing ovoid large pinnules (indicated by black arrows) and small pinnules with weak fine teeth on the distal margin (indicated by white arrows). C. Enlargement of the area (left quadrangle in A) showing the transition of the small pinnules from deeply lobed (SP1, SP2) to weakly toothed (SP3) distal margin. D. Enlargement of the area (lower right quadrangle in A) showing the transition of the small pinnules from deeply lobed (SP1, SP4) to weakly toothed (SP2, SP3, SP5) distal margin. E. Enlargement of the area (lower middle quadrangle in A) showing small pinnules with deeply lobed distal margin (indicated by arrows). Abbreviations: LP = large pinnules; SP = small pinnules.

图5 乌海拟齿叶(*Paratingia wuhaia*)的复叶Fig. 5 Compound leaves of *Paratingia wuhaia*

A–C. 展示复叶中非对称披针形至披针形的大叶和顶端深裂或仅具微齿的小叶。B. 图5-A方框区域的放大, 示同一复叶中顶端深裂(SP1–SP3)和仅具微弱细齿(SP4)的小叶。D. 展示复叶顶部区域由披针形渐变为卵形、椭圆形或长椭圆形的大叶; 卵形或椭圆形的, 且顶端仅具微弱细齿的小叶。标本编号: A. PB205898; C. PB205899; D. PB205900.

A–C. Showing asymmetric lanceolate to lanceolate large pinnules, small pinnules with deeply lobed or weak fine teeth on the distal margin. B. Enlargement of the area (quadrangle in A) showing small pinnules with deeply lobed (SP1–SP3) and weakly toothed (SP4) distal margin. D. Apical part of a compound leaf showing lanceolate, elliptical, ovoid, and oblong large pinnules, elliptical and ovoid small pinnules with weakly toothed distal margin. Specimen numbers: A, PB205898; C, PB205899; D, PB205900.

况下, 这些单独保存的复叶标本分别显示局部或者中上部的小叶形态(图5-C, 5-D, 6-G)。

上述标本比较充分地展示了乌海拟齿叶大叶和小叶的形态特征在种内具有多变性(图2-5, 图7)。相对于复叶下部区域而言, 复叶顶部区域大、小叶

的形态变化较弱, 复叶中部区域和上部区域的大、小叶的形态特征基本一致。从复叶基部向顶端, 大叶逐步由小变大再变小, 形状由非对称形转变为披针形, 再渐变为卵形、椭圆形或长椭圆形; 小叶由扇形前端深裂齿状, 逐步变化成为卵形或椭圆形,

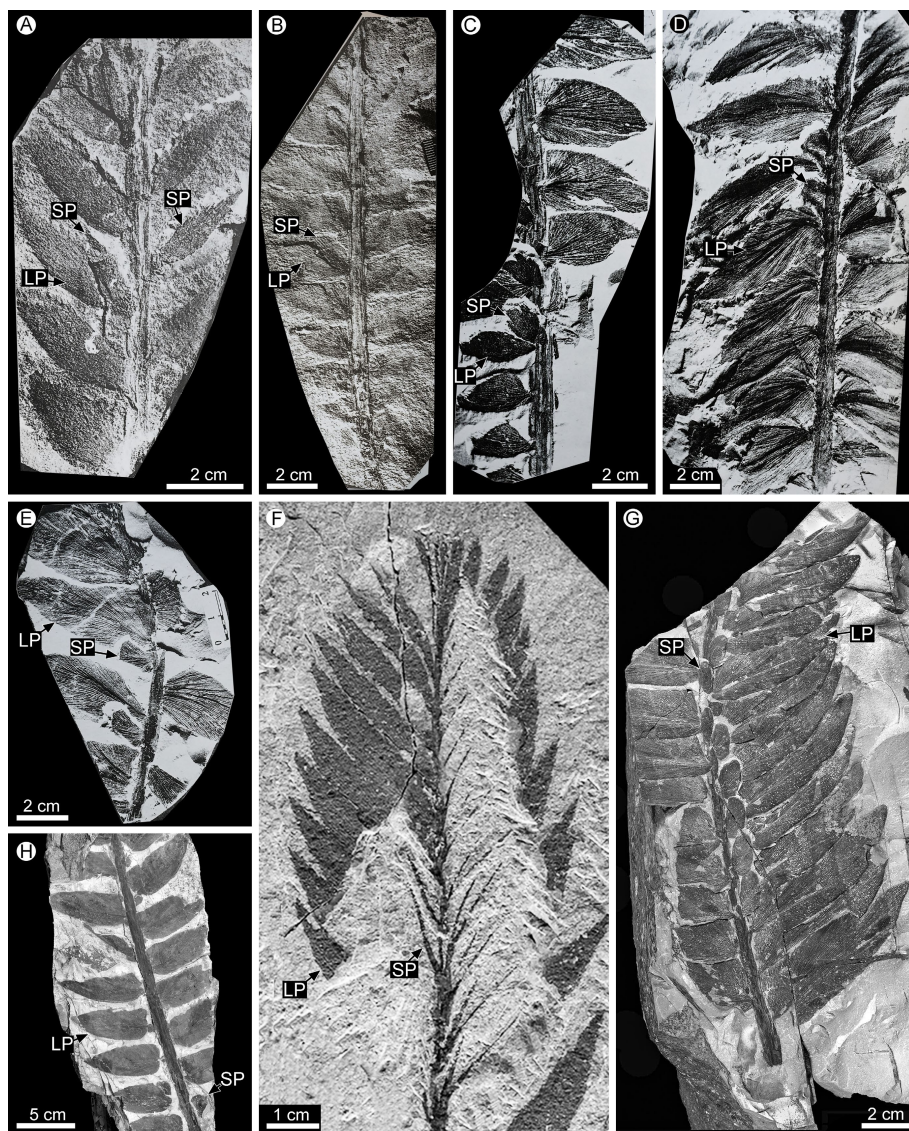


图6 大同拟齿叶(*Paratingia datongensis*)、乌达拟齿叶(*P. wudensis*)和乌海拟齿叶(*P. wuhaia*)

Fig. 6 Specimens of *Paratingia datongensis*, *P. wudensis*, and *P. wuhaia*

A, B. 大同拟齿叶, 来自张泓(1987), 示小叶形状与相邻大叶同形, 小叶面积较小且前端未深裂。C-E. 孙克勤等(1999)记录的大同拟齿叶, 示小叶与相邻大叶形状及面积差异悬殊, 且部分小叶前端深裂。F. 乌达拟齿叶(Wang et al., 2009), 示其具针状的小叶。G-H. 乌海拟齿叶(Wang et al., 2021a), 示小叶与大叶的形状及面积差异悬殊, 小叶前端未深裂。标本编号: A. Mp-84061; B. Mp-84062; F. PB20781; G. PB22136; H. PB22133。注: LP = large pinnules (大叶); SP = small pinnules (小叶)。

A, B. *Paratingia datongensis* (Zhang, 1987) showing small pinnules similar in shape to adjacent large pinnules; small pinnules are relatively smaller and lack deeply lobed distal margin. C-E. *Paratingia datongensis* (Sun et al., 1999) showing significant differences in both shape and size between small pinnules (some with deeply lobed distal margin) and adjacent large pinnules. F. *Paratingia wudensis* (Wang et al., 2009) showing needle-shaped small pinnules. G-H. *Paratingia wuhaia* (Wang et al., 2021a) showing significant differences in both shape and size between small pinnules (distal margin not deeply lobed) and their adjacent large pinnules. Specimen numbers: A, Mp-84061; B, Mp-84062; F, PB20781; G, PB22136; H, PB22133. Abbreviations: LP = large pinnules; SP = small pinnules.

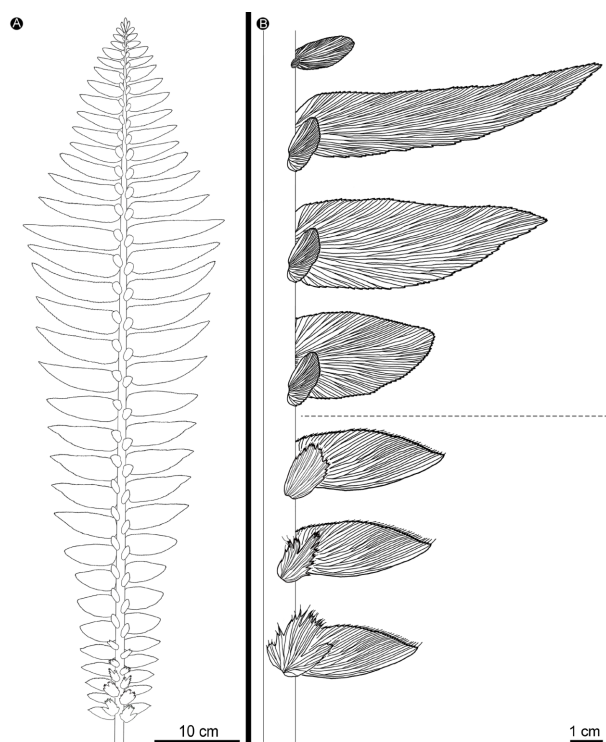


图7 乌海拟齿叶(*Paratingia wuhaia*)种内叶形态变化的示意性复原图
Fig. 7 Schematic diagram showing intraspecific morphological variation of *Paratingia wuhaia* frond

A. 复叶的整体示意性复原图, 示大叶和小叶自基部至顶端的变化趋势。
B. 虚线下方为复叶基部区域, 大叶呈不对称披针形, 小叶常深裂, 大叶和小叶的叶缘具明显的齿; 虚线上方为复叶其余部位, 大叶呈披针形至椭圆形, 小叶为椭圆形至卵形, 大叶和小叶的叶缘仅具微弱的齿。

A. Once-pinnate compound leaf showing variation of large and small pinnules from the base to the apex. B. Basal part of the leaf (below dashed line) with asymmetrically lanceolate large pinnules and often deeply dissected small pinnules; both large and small pinnules possess distinctly toothed margins. Middle and distal portions of the leaf (above dashed line) with lanceolate to elliptical large pinnules and elliptical to ovate small pinnules; both large and small pinnules possess only weakly toothed margins.

边缘具微齿, 总体上逐渐变小。

3.2 比较和讨论

当前标本具一次羽状复叶、背腹性和不等叶性、叶呈四行排列, 以及大叶和小叶均具二歧分叉的放射状脉序等特征, 其与拟齿叶属(*Paratingia*)鉴定特征的定义(张泓, 1987)一致。目前为止, 仅3个种被归入拟齿叶属, 分别为大同拟齿叶(*P. datongensis*) (张泓, 1987; 图6-A, 6-B)、乌达拟齿叶(*P. wudensis*) (Wang et al., 2009; 图6-F)和乌海拟齿叶(*P. wuhaia*) (Wang et al., 2021a; 图6-G, 6-H) (表1)。其中, 大同拟齿叶(*P. datongensis*)的模式标本(张泓, 1987)的小叶缺乏顶端深裂的报道, 且其大叶的长

宽比要小于乌海拟齿叶。乌达拟齿叶(*P. wudensis*)也因其小叶呈针状而明显区别于乌海拟齿叶。相对而言, 当前标本复叶中部至上部区域的大叶呈披针形、小叶呈椭圆形或卵形、大小叶叶缘仅具微弱细齿, 以及大小叶尺寸差异悬殊等特征与王军等(Wang et al., 2021a)命名和描述的乌海拟齿叶(*P. wuhaia*)完全一致, 因此当前标本确证属于乌海拟齿叶(*P. wuhaia*)。同时, 当前标本不仅展示了乌海拟齿叶定义中所述特征(Wang et al., 2021a), 而且全面揭示了其复叶小羽片的形态特征的形态变化, 即: 从基部向顶端, 大叶形状由非对称披针形转变为披针形、卵形、椭圆形或长椭圆形; 小叶由扇形及前端深裂齿状, 过渡为卵形或椭圆形且前端仅具微齿; 尤其是复叶基部扇形且前端深裂齿状的小叶, 在模式标本(Wang et al., 2021a)上是缺失的, 而当前标本提供了有力补充。

本文认为原先报道的乌达煤田的大同拟齿叶(*Paratingia datongensis*) (孙克勤等, 1999; 孙克勤、邓胜徽, 2003; 孙克勤, 2010; 图6-C–6-E)实际上属于乌海拟齿叶(*P. wuhaia*)。一方面, 这些标本形态特征与乌海拟齿叶非常一致: 如孙克勤(2010)和孙克勤等(1999)的标本(当前图6-C–6-E)所示, 图6-C的标本与乌海拟齿叶中下部的形态完全一致, 大叶叶片前缘弧曲强烈而后侧叶缘微弱弧曲, 逐步向上过渡为卵形或披针形, 同时小叶也为扇形且前端具粗齿裂; 图6-D–6-E的标本属于乌海拟齿叶中上部复叶的典型形态, 披针形大叶和卵形小叶等特征与当前标本所展现的乌海拟齿叶的叶形态变化非常吻合。相反, 另一方面, 这些标本与张泓(1987)所定义的大同拟齿叶的形态差别非常显著: 大同拟齿叶的大叶和小叶形态上总体一致, 特别是小叶顶端深裂的特征在大同拟齿叶模式标本上毫无体现。据此, 当前研究认为上述以往报道于乌达煤田中的大同拟齿叶的标本应归于乌海拟齿叶。

叶片形态被视为研究光合作用、蒸腾作用、防御机制、落叶习性、气候和环境条件的一项重要指标(Royer and Wilf, 2006; Adams et al., 2008; Xu et al., 2009; Kidner and Umbreen, 2010; Givnish and Kriebel, 2017)。根据以往研究, 乌达拟齿叶(*Paratingia wudensis*)和联合齿叶(*Tingia unita*)的刺状小叶被推

表 1 本文标本与拟齿叶属(*Paratingia*)各种的对比
Table 1 Comparison of present specimens and other records of *Paratingia*

特征	种名				
	本文标本	<i>Paratingia datongensis</i>	<i>Paratingia wuhaia</i> (= <i>P. datongensis</i>)	<i>Paratingia wudensis</i>	<i>Paratingia wuhaia</i>
叶的排列方式	四行叶	四行叶	四行叶	四行叶	四行叶
叶轴	不分叉; 宽约1—13 mm	不分叉	不分叉; 宽 约5—10 mm	不分叉	不分叉; 宽约2—11 mm
大叶形状	非对称的披针形、 披针形、 卵形或椭圆形; 边缘具齿, 具尖顶	椭圆形、长椭圆形、披针形、 剑形或卵形; 边缘具齿, 具尖顶	剑形至长三角形; 边缘具齿, 具尖顶	椭圆形、菱形; 边缘具齿, 具尖顶	披针形或非对称的披 针形; 边缘具齿
大叶尺寸	长约7—102 mm; 宽约4—25 mm	长约8—42 mm; 宽约7—14 mm	长约28—60 mm; 宽约20—30 mm	长约19—65 mm; 宽约3—13 mm	长约24—90 mm; 宽约 9—31 mm
大叶长宽比	2 : 1—5 : 1	1 : 1—3 : 1	2 : 1—4 : 1	2 : 1—7 : 1	2 : 1—5 : 1
小叶形状	卵形或椭圆形; 边缘具微齿, 顶端深裂或否	与大叶同形	卵形至椭圆形; 全缘或否	针状; 深裂	卵形或 非对称的卵形
小叶尺寸	长约5—25 mm; 宽约4—16 mm	较小于大叶	长约15—18 mm; 宽约7—8 mm	长可达25 mm; 宽约1—2.5 mm	长约12—18 mm; 宽约6—9 mm
小叶长宽比	1 : 1—3 : 1	3 : 1—4 : 1	1 : 1—2 : 1	10 : 1—20 : 1	2 : 1
叶脉	放射状脉序, 二歧分叉	放射状脉序, 二歧分叉	放射状脉序, 二歧分叉	放射状脉序, 二歧分叉	放射状脉序, 二歧分叉
产地	内蒙古乌达煤田	山西大同七峰山	内蒙古乌达煤田	内蒙古乌达煤田	内蒙古乌达煤田
层位	太原组	山西组	山西组	太原组	太原组
引用文献	本文	(张泓, 1987)	(孙克勤等, 1999; 孙克勤、邓胜徽, 2003)	(Wang <i>et al.</i> , 2009)	(Wang <i>et al.</i> , 2021a)

测可能具有保护拟孢子囊穗、防御食草动物的作用(Wang *et al.*, 2009; 2021c)。然而, 与前两者不同, 乌海拟齿叶(*P. wuhaia*)的拟孢子囊穗并未与复叶交错着生于茎干, 而是形成独立的繁殖区域。鉴于此, 当前标本顶端深裂为裂片状或刺状的小叶可能不具有防御作用。相较于无齿的叶片, 具齿的叶片被推测具有更加活跃的光合作用和蒸腾作用, 处于遮阴处或处于同等年均温条件下的湿润生境中的叶片会出现更多的锯齿, 且在弱光条件下异形叶的发育可以实现光能捕获的最大化(Royer and Wilf, 2006; Xu *et al.*, 2009; Kidner and Umbreen, 2010; Givnish and Kriebel, 2017)。同时, 基于其他类群植物的研究, 背腹性和不等叶性特征亦被认为是在光照不足的环境中实现光能捕获最大化的适应性演化(Dengler, 1999; Ali and Kikuzawa, 2005)。因此, 基于乌海拟齿叶复叶及其大、小叶的着生方式和形态特征, 位于复叶下部区域顶端深裂的小叶的存在可能是为了在光照相对遮蔽的环境条件下尽可能减小叶片间的相互遮阴, 进而使植株获取更多的光能来进行光合作用。

4 结 论

化石植物系统分类学研究, 对标本保存状态和质量的依赖性极强。相对于化石标本常碎块化保存的现状, 完整的植物化石能够为相关类群的分类学研究提供更加详细的信息。得益于“植物庞贝”火山灰原位埋藏, 大量化石标本外形完整且内部解剖结构留存, 乌海拟齿叶是基本实现整体重建的物种之一。本文进一步揭示了该种复叶中大、小叶的种内形态变异特征, 特别是发现了其复叶下部大叶呈非对称披针形和小叶顶端深裂的特征, 复叶顶部大叶由披针形逐渐过渡为椭圆形或卵形的特征。并且, 经详细对比, 原先报道于乌达煤田中的大同拟齿叶(*P. datongensis*)的标本实际上属于乌海拟齿叶(*P. wuhaia*)。

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