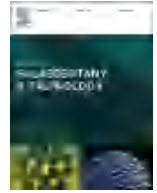




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Middle-Late Jurassic fossils from Northeast China confirm the affiliation of *Umaltolepis* seed-bearing structures and *Pseudotorellia* leaves

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abstract

Umaltolepis seed-bearing structures and *Pseudotorellia* leaves were considered to be produced by the same plant according to their consistent association in the same bed and similarities in cuticular structures. Here we describe new fossils of *Umaltolepis* and *Pseudotorellia* based on well-preserved materials from the Middle-Late Jurassic Daohugou Bed in eastern Inner Mongolia, Northeast China. *Umaltolepis* *zhoui* sp. nov. is an umbrella-like, four-lobed cupule that was borne on a stalk at the tip of a short shoot. The stalk is cylindrical, with a prominent cup-like flange situated at the tip of the stalk and below the cupule. The short shoot bears growth cycles consisting of alternating pseudo-whorled bud scales and abscission scars. The cupule lobes are resinous, having sparse, longitudinally oriented stomata. *Pseudotorellia* *zhoui* sp. nov. is established based on a two-order leafy shoot and isolated leaves. The ultimate short shoot bears terminal clustered strap-shaped leaves, and alternating pseudo-whorled bud scales and abscission scars on surface. Leaves have acute apex, cuneate base; each bearing 4 to 8 longitudinal parallel veins. Abaxial cuticle has sparse, longitudinally to leaf margin oriented stomata which are arranged in 1–3 discontinuous files in the stomatal bands. The co-occurrence of *U. zhoui* and *P. zhoui* in the Daohugou Bed and their similarities in cuticular structures and morphology of attached short shoots further confirm that *Umaltolepis* and *Pseudotorellia* are produced by the same plant. These fossils also provide new evidence for a close relationship between the Mesozoic *Umaltolepis*-*Pseudotorellia* plant and living Ginkgo.

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1. Introduction

The genus *Umaltolepis* Krassilov was established based on compressed reproductive organs from the Late Jurassic of the Bureja River Basin, Russian Far East (Krassilov, 1970, 1972). The type species *U. vachrameevii* was initially interpreted as an unlobed or bilobed bract with a single, inverted seed borne on the abaxial side (Krassilov, 1972). However, a recent study based on the three-dimensionally preserved material from the Early Cretaceous of Mongolia clearly demonstrated that *Umaltolepis* was an umbrella-like, four-lobed cupule with a slender central column that bears four pendulous winged seeds at its tip (Herrera et al., 2017). The interpretation is also supported by re-examination of the original material of *U. vachrameevii* (Herrera et al., 2017), and detailed studies of *Umaltolepis* from the Middle Jurassic to Early Cretaceous of Central China, Uzbekistan, East Siberia, and Mongolia (Dong et al., 2019; Nosova, 2020, 2021; Nosova and Kostina, 2022). Until now, nine species of *Umaltolepis* have been reported from the Early Jurassic to Early Cretaceous of Eurasia (Krassilov, 1972;

Wang, 1984; Chen et al., 1988; Schweitzer and Kirchner, 1995; Herrera et al., 2017; Dong et al., 2019; Nosova, 2020, 2021).

Umaltolepis has been believed to be the seed-bearing organs of the plants that produced leaves of *Pseudotorellia* Florin, a strap-shaped fossil leaves with longitudinal parallel veins that is thought to be a ginkgophyte (e.g., Harris, 1935; Harris et al., 1974; Zhou, 2009; Zhou et al., 2020). Krassilov (1970, 1972) initially proposed the close association of *U. vachrameevii* and *P. angustifolia* Doludenko based on their co-occurrence in the same bed and the similarities in their cuticles. Besides, their similarities also include the form of the scales attached on the basal part of the stalk of *U. vachrameevii* and scales borne on the short shoots that the leaves of *P. angustifolia* are attached to. The affiliation of *Umaltolepis* and *Pseudotorellia* was subsequently been confirmed by material from the Early Jurassic of Iran, Middle Jurassic of Central China, Uzbekistan, and East Siberia, and the Early Cretaceous of Central Mongolia, North China and Russian Far East (Wang, 1984; Chen et al., 1988; Schweitzer and Kirchner, 1995; Herrera et al., 2017; Dong et al., 2019; Nosova, 2020, 2021; Nosova and Kostina, 2022), although seed-bearing structures of *Umaltolepis* and leaves of *Pseudotorellia* were never found organically connected. Nevertheless, the *Umaltolepis*-*Pseudotorellia* plant is thought to be closely related to

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Ginkgoales because of the similarities of the leaves of *Pseudotorellia* to extant and fossil Ginkgo, as well as other taxa of Ginkgoales in leaf venation and cuticular features (Krassilov, 1970, 1972; Zhou, 2009; Herrera et al., 2017; Dong et al., 2019; Zhou et al., 2020).

Here we add to knowledge of the plant of *Umaltolepis*-*Pseudotorellia* based on new, exceptionally well-preserved fossils from the Middle-Late Jurassic Daohugou Bed in eastern Inner Mongolia, Northeast China. The new *Umaltolepis* is described based on a small number of complete seed-bearing structures that are attached to short shoots. Associated *Pseudotorellia* fossil includes a leafy shoot with two-orders of branching with ultimate short shoot bearing a cluster of strap-shaped leaves, leaves in a cluster, and isolated leaves. The new material of two-order leafy shoot with attached leaves is the most completely known fossil record of *Pseudotorellia*. This is also the best-preserved record of the fertile short shoot with attached *Umaltolepis* cupules. The striking similarities of the short shoots bearing *Umaltolepis* and *Pseudotorellia* short shoots and leaves from the Daohugou Bed in overall morphology, forms and size of bud scales as well as abscission scars of leaf bases on surface of the short shoot, and in cuticular structures of the new *Umaltolepis* cupules and *Pseudotorellia* leaves from Daohugou Bed further confirm their association. Besides, the new material from the Daohugou Bed also provide evidence for a close relationship between the *Umaltolepis*-*Pseudotorellia* plant and extant Ginkgo. The evidence includes the similarities in arrangement of leaves borne in clusters on short shoots, and in the morphology and arrangement of persistent bud scales and abscission scars on surface of short shoot, as well as in the cup-like flanges below the seed-bearing organs.

2. Material and methods

2.1. Geological setting and age

The fossil material examined here was collected from the Daohugou Bed in the vicinity of the Daohugou village (41°19'25" N, 119°14'40" E) in Ningcheng County, eastern Inner Mongolia Autonomous Region, Northeast China (Huang, 2016; Dong et al., 2018). The Daohugou Bed belongs to the Haifanggou Formation which comprises a thick sequence of grayish to green, very finely laminated tuffaceous silty claystone alternating with layers of tuff (Huang, 2016). The Haifanggou Formation is overlain by volcanic rocks of the Tiaojishan Formation and unconformably overlies the Archean genesis (Huang et al., 2015). The fossiliferous beds occur in the Daohugou village are mostly located in the middle to upper parts of the Haifanggou Formation (Huang et al., 2015). The Daohugou Biota is well-known for yielding diverse, exceptionally well-preserved vertebrate (e.g., Ji et al., 2006; Meng et al., 2006; Luo et al., 2007; Zhang et al., 2008; Zhou et al., 2013; Xu et al., 2016), invertebrate (e.g., Ren et al., 2009; Wang et al., 2010; Huang et al., 2012, 2013; Cai et al., 2014; Huang, 2016), and plant fossils (e.g., Zhou et al., 2007; Wang et al., 2010a, 2010b; Pott et al., 2012; Dong et al., 2020). Radiometric dating of the volcanic rocks overlying the fossil beds indicates the minimum age of the Daohugou Biota to be approximately ~165–158 Ma, corresponding to the late Middle–early Late Jurassic (Chen et al., 2004; Liu et al., 2004; Yang and Li, 2008; Xu et al., 2016; Huang, 2019). A late Middle–early Late Jurassic age for the Daohugou fossiliferous Bed is also supported by evidence from the palynology (Na et al., 2015), the fossil plants assemblage (Pott and Jiang, 2017), as well as the analyses from the invertebrate and vertebrate assemblage (Huang et al., 2015; Xu et al., 2016). The fossil plant assemblage from the Daohugou Bed is very diverse, and consists of algae, lichens, bryophytes, lycopods, horsetails, ferns, seed ferns, bennettites, ginkgophytes, czekanowskiales, conifers, as well as some reproductive organs and seeds of uncertain affinities (e.g., Zheng et al., 2003; Li et al., 2004; Zhou et al., 2007; Wang et al., 2010a, 2010b; Zhang et al., 2011; Pott et al., 2012; Heinrichs et al., 2014; Sun et al., 2015; Han et al., 2016; Liu and Wang, 2017; Na et al., 2017, 2021; Pott and Jiang, 2017; Dong et al., 2018, 2020; Shi et al., 2021).

2.2. Fossil preparation and photography

Fossil specimens were photographed using a Sony α 6000 digital camera equipped with a Sony SEL30M35 microlens. Details of the seed-bearing structures, leafy shoots and leaves were observed and photographed using a Zeiss Axio Zoom.V16 stereomicroscope equipped with a Zeiss AxioCam 512 color digital camera system at the Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences (NIGPAS). Line drawings of the figured fossil specimens were drawn with CorelDraw 2021 to highlight their morphological features. Then the line drawings were printed out and colored with pencils by the first author.

Carbonaceous membranes from leaves and seed-bearing structures were cleaned with dilute hydrochloric acid (HCl) for 5 to 6 h, followed by 50% hydrofluoric acid (HF) for 24 h, then thoroughly washed in distilled water. Pieces of cleaned fossil cuticles were macerated in Schulze's solution (35% HNO₃ with a few crystals of KClO₃) for approximately 6 to 10 h. The macerated cuticle fragments were then washed thoroughly in distilled water and then followed by dilute ammonia. Isolated cuticles were washed again in distilled water and finally mounted on preparation slides with glycerin jelly. The cuticle slides were examined and photographed with differential interference contrast illumination using an Olympus BX53 microscope equipped with an Olympus DP73 camera at NIGPAS. Cuticles for scanning electron microscope (SEM) examination were dehydrated in a series of alcohol, mounted on stubs with conductive tape, dried in air, coated with platinum, and then observed and photographed using a TESCAN MAIA 3 GMU at NIGPAS.

Two-order leafy shoot, short shoot, and stalked seed of extant Ginkgo biloba L. used for comparison are collected from living trees at the NIGPAS. Photos of extant specimens were also photographed using a Sony α 6000 digital camera equipped with a Sony SEL30M35 microlens.

The studied fossil specimens, cuticle slides and SEM stubs, are deposited in the Palaeobotanical Collection of the NIGPAS with the catalog numbers PB23880–PB23887. The terminology for describing the seed-bearing structures of *Umaltolepis* follows Herrera et al. (2017). Terminology for descriptions of stomata and epidermal cells of *Pseudotorellia* leaves follows Shi et al. (2018).

3. Results

3.1. Systematic paleobotany of seed-bearing structures

Order: GINKGOALES sensu lato.

Family: UMALTOLEPIDACEAE Zhou.

Genus: *Umaltolepis* (Krassilov) Herrera, Shi, Ichinnorov, Takahashi, Bugdaeva, Herendeen, et Crane.

Species: *Umaltolepis* zhoui Dong, Shi, Zhang, Wang, et Wang, sp. nov. (Plate I, 1–4, Plate II, 1–4, Plate III, 1–10).

Etymology: The specific epithet is in honor of Zhiyan Zhou for his landmark contributions to understanding evolution and diversity of Mesozoic ginkgophytes.

Locality: Daohugou village (41°19'25" N, 119°14'40" E), Ningcheng County, Inner Mongolia Autonomous Region, Northeast China.

Stratigraphic horizon and age: Haifanggou Formation, late Middle–early Late Jurassic (~165–158 Ma).

Holotype: PB23880 (Plate I, 1, Plate II, 1, 2).

Other studied material: PB23881 (Plate I, 2, Plate II, 3), PB23882 (Plate I, 3), PB23883 (Plate I, 4, Plate II, 4).

Repository: Palaeobotanical Collections, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Diagnosis: Short shoots with alternating pseudo-whorls of persistent bud scales and abscission scars. Each pseudo-whorl consisting of 6 to 8 bud scales and 6 to 8 abscission scars. Persistent bud scale triangular, with an acute apex; abscission scar rhomboidal. Short shoot bearing seed-bearing structure at the apex. Seed-bearing structure consisting

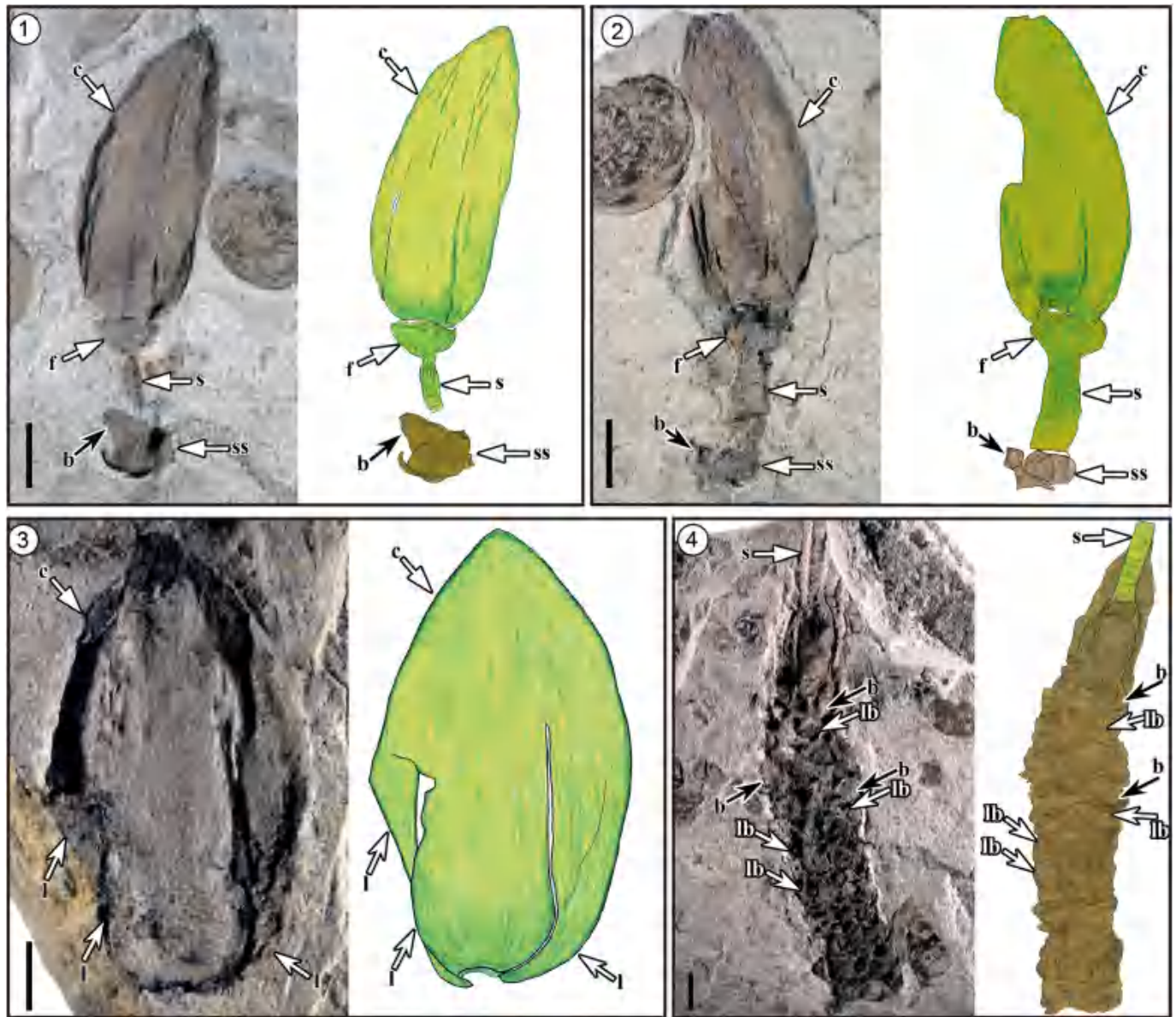


Plate I. *Umultolepis zhoui* sp. nov. 1–2. Seed-bearing structures and reconstructive drawings showing closed cupules, stalks extend into a cup-like flange at the tip, and fragmentary short shoots bearing a small number of bud scales. 1. Holotype, PB23880. 2. PB23881. 3. Seed-bearing structure and reconstructive drawing showing an isolated cupule with three lobes visible. PB23882. 4. Fertile short shoot with proximal portion of a stalk attached at the distal portion. Note the outer surface of the short shoot covering with pseudo-whorls of bud scales and abscission scars left by leaf bases. Abbreviation: c, cupule; f, flange; s, stalk; ss, short shoot; b, bud scale; l, lobe; lb, leaf base. PB23883. Scale bars = 2 mm.

of cylindrical stalk bearing an umbrella-like, four-lobed cupule with a slender central column at the tip. The stalk having a prominent cup-like flange surrounding the base of cupule. Cupule ovate to elliptical in outline, with an acute apex, dehiscent below into four ovate lobes. Lobes commonly with a semicircular distal notch. Cuticle of lobes thick, with sparse and scattered, longitudinally oriented stomata, and epidermal cells arranged in short, discontinuous longitudinal rows. Stoma with 2 sunken guard cells surrounded by 3–4 specialized lateral subsidiary cells and 2 unspecialized polar cells. Epidermal cells elongated, with straight anticlinal walls and more or less oblique end walls. Elongated or small fusiform-shaped resin bodies present in cupule lobes.

Description: The studied material is represented by two completely preserved seed-bearing structures (Plate I, 1, 2) attached to fertile short shoots, one isolated cupule (Plate I, 3), and a short shoot with proximal portion of the stalk of a seed-bearing structure in which the cupule is not preserved (Plate I, 4).

The stalked seed-bearing structure is borne on the apex of fragment of a short shoot (Plate I, 1, 2). The observed short shoot fragments with seed-bearing structures are ca. 2.0–2.1 mm wide and ca. 1.0 mm long, bearing persistent bud scales (Plate I, 1, 2). Persistent bud scales are triangular, ca. 0.91–1.20 mm long and ca. 0.75–1.14 mm wide at the base, with an acute apex (Plate II, 2). Each seed-bearing structure consists of a short stalk with a distinct cup-like flange and a four-lobed cupule (Plate I, 1, 2). The stalk is robust, slightly curved near the base, ca. 3.0–3.8 mm long and 0.6–1.1 mm wide, bearing numerous irregular horizontal wrinkles on their outer surface (Plate I, 1, 2, Plate II, 3). The flange at the tip of the stalk is prominent and cup-like, ca. 1.1–1.6 mm long and ca. 1.9–2.2 mm wide at widest portion (Plate I, 1, 2, Plate II, 1). Cupules are immediately disposed above the flange, radially symmetrical, ca. 8.5–13.2 mm long, ca. 3.6–7.6 mm wide at the widest part, typically ovate to elliptical in lateral outline, with an acute to slightly rounded apex (Plate I, 1, 3). The cupules are more or less dehiscent with splitting mostly occurring from the base for one half to two-thirds

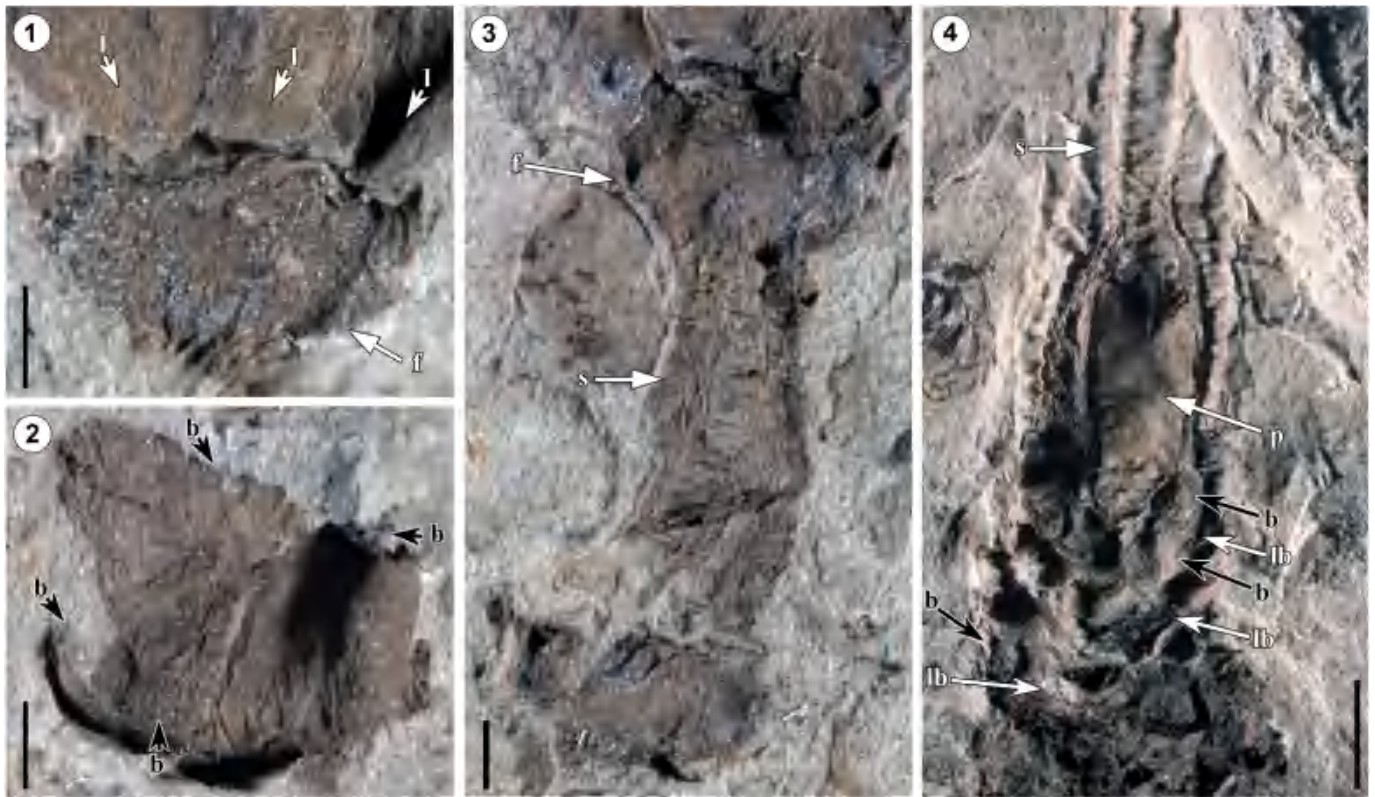


Plate II. *Umultelepis zhoui* sp. nov. 1. Magnification of the middle part of seed-bearing structure exhibited in Plate I, 1 showing bases of three cupule lobes and details of cup-like flange. PB23880. 2. Magnification of the lower part of fossil shown in Plate I, 1 displaying persistent bud scales on short shoot. PB23880. 3. Magnification of the stalk of seed-bearing structure exhibited in Plate I, 2 showing cup-like flange situated at the tip of stalk. Note numerous irregular horizontal wrinkles on outer surface of stalk. PB23881. 4. Magnification of the upper part of fossil exhibited in Plate I, 4 showing stalk inserted at the distal portion of short shoot which covered with alternating pseudo-whorls composing of triangular bud scales and rhomboidal scars left by leaf bases. Note the pith of short shoot visible at the upper part where cortex is destroyed. PB23883. Abbreviation: l, lobe of cupule; f, flange; b, bud scale; s, stalk; lb, leaf base; p, pith. Scale bars: 1, 2 = 0.5 mm; 3, 4 = 1 mm.

length of the cupule (Plate I, 1, 2, 3). The four lobes of the cupule are similar in shape and size, ovate in outline, each having a semicircular notch at the base (Plate I, 3, Plate II, 3). The lobe is ca. 2.0–4.2 mm wide, and ca. 4.1–7.5 mm long, usually with fine longitudinal striations on the outer surface (Plate I, 1, 2, 3). The central column borne on the flange of the stalk was completely covered by the cupule, but their outline is indicated by the dark colored adpression in the center of the cupule (Plate I, 1, 2). The column is slightly curved, ca. 0.5 mm wide, and ca. 7.1–7.6 mm long (Plate I, 2).

Only one of the three studied cupules has fragmentary carbon membranes preserved (Plate I, 3). Cupule lobes are resinous, possessing thick outer cuticle, ca. 2–4.5 μm in thickness (Plate III, 4), with sparse and scattered stomata (Plate III, 1, 2, 4). Epidermal cells usually arranged in short, discontinuous longitudinal files, commonly quadrangular to irregular in outline, slightly elongated along the long axis of the lobe, often with oblique end walls; ca. 48–130 μm long and ca. 21–130 μm wide, with a length/width ratio of 1.9–4.9 (Plate III, 1–4). Anticlinal walls of cells are straight and well-developed, 2.8–3.5 μm in thickness (Plate III, 4). Periclinal walls of epidermal cells are lacking cuticular thickenings or papillae, commonly densely distributed with small holes in the internal view (Plate III, 4). Stomata are sparsely distributed on the lobes, longitudinally oriented (Plate III, 1, 2, 4). Stomatal complexes are ca. 48–130 μm long and ca. 48–130 μm wide, composed of 2 sunken guard cells surrounded by 3–4 specialized lateral subsidiary cells and 2 unspecialized polar cells (Plate III, 5, 6). Ledges of guard cells are sunken, kidney-shaped, ca. 73–80 μm long and ca. 19–26 μm wide; their cuticular anticlinal walls attached to the lateral subsidiary cells are strongly developed and butterfly-like (Plate III, 5, 6). These developed anticlinal walls are almost at the same plane with guard cells (Plate III, 5, 6) probably because of the squeezing during the fossil

preservation. Lateral subsidiary cells are a little narrower than ordinary epidermal cells, ca. 45–74 μm long and ca. 18–27 μm wide, elongated along the stomatal pit (Plate III, 5, 6). The inner periclinal surface of the lateral subsidiary cells have distinct hollows (Plate III, 5, 6) possibly indicating that the lateral subsidiary cells develop cuticular papillae or ridges on their external view. Polar cells are similar to ordinary epidermal cells in shape, but usually shorter, ca. 17–37 μm long and ca. 20–32 μm wide. Resin bodies are present in the cupule lobes (Plate III, 7–10). They are elongated, fusiform, about 240 μm in diameter (Plate III, 7–9); some bodies are small, ca. 95–101 μm long and ca. 45–47 μm wide at the widest part (Plate III, 10).

A completely preserved short shoot bears only the proximal portion of the stalk of seed-bearing structure (Plate I, 4). The short shoot is 2.0 cm long, 0.5 cm wide, with alternating pseudo-whorls of persistent bud scales and abscission scars left by leaf bases which reflect rhythmic growth (Plate I, 4). There are about 12 rhythmic growth cycles visible on the short shoot. Each cycle consists of about 3 to 4 bud scales and 3 to 4 abscission scars on one side of surface (Plate I, 4), which indicates each cycle has 6 to 8 bud scales and 6 to 8 abscission scars. The seam-like zone often can be identified between adjacent two growth cycles. The persistent bud scale is triangular in outline, usually with an acute apex, ca. 1.20–1.65 mm long at the base and ca. 0.73–1.05 mm wide at the widest part (Plate I, 4). Abscission scars of leaf bases on the short shoot are more or less rhomboidal in outline, ca. 1.20–1.74 mm long at the longest part and ca. 0.31–0.42 mm wide at the widest part. The presumed stalk at the terminal position of short shoot is bare, straight, cylindrical in outline, 4.1 mm long and 1.2 mm wide, bearing numerous irregular horizontal wrinkles on the outer surface (Plate II, 4). The pith of the short shoot is visible at the upper part where the outer layer of cortex and enclosing bud scales have been decayed or

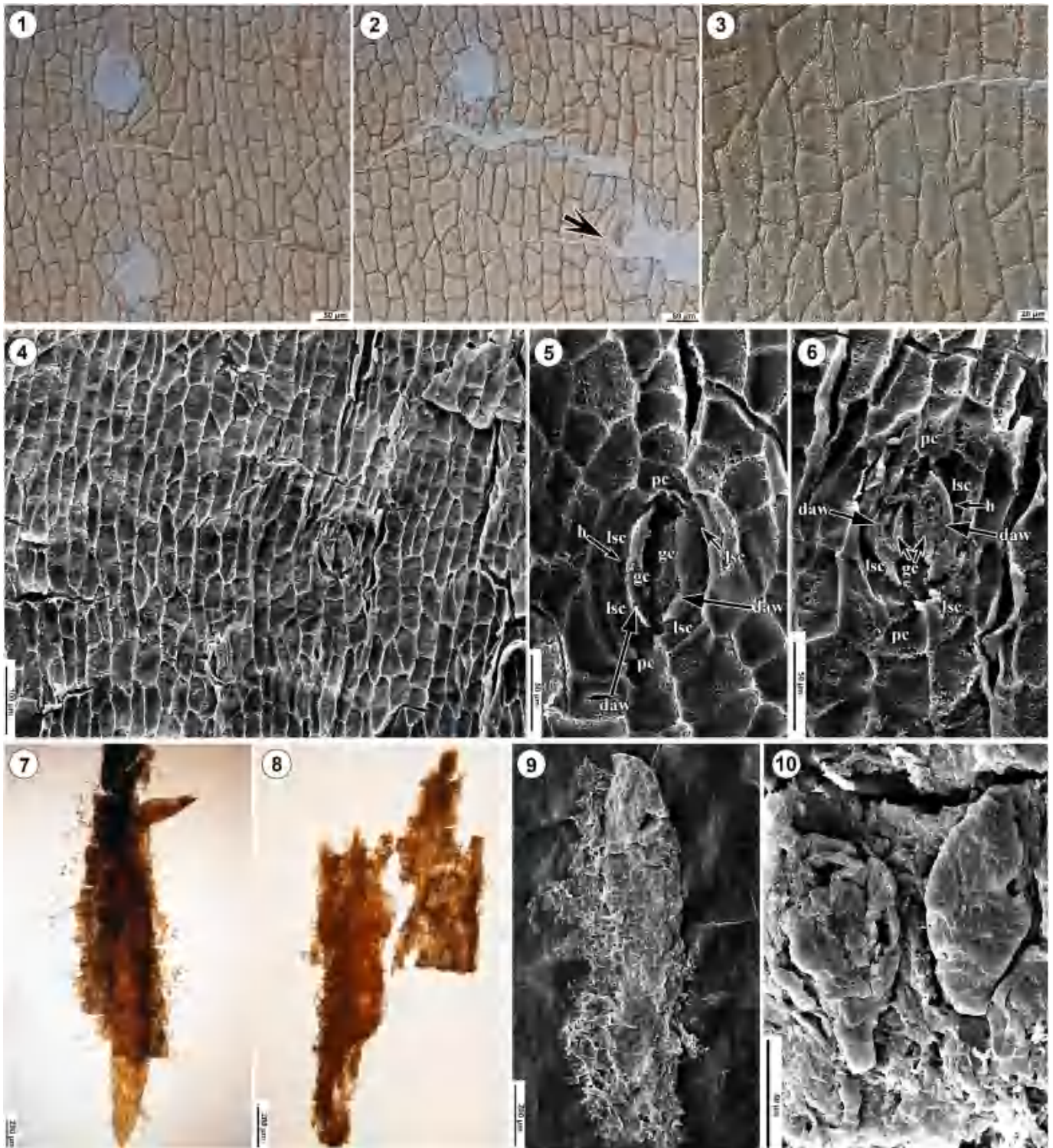


Plate III. *Umlalopsis zhoui* sp. nov., light micrographs and scanning electron micrographs of cuticle and resin bodies obtained from cupule lobes. PB23882. 1. Cuticle showing epidermal cells. 2. Cuticle showing epidermal cells and probable one broken stomatal complex (arrow). 3. Details of epidermal cells showing quadrangular cell outlines with straight anticlinal walls and oblique end walls. 4. Inner surface of cuticle showing short, discontinuous longitudinal files of epidermal cells and two scattered, longitudinally oriented stomatal complexes. 5. An individual stoma showing 2 sunken guard cells with strongly developed cuticular anticlinal walls, surrounded by 4 lateral subsidiary cells and 2 polar cells. Note the guard cell's strongly developed anticlinal walls touching to lateral subsidiary cells look like at the same plane with guard cells, and the hollows developed on periclinal walls of lateral subsidiary cells. 6. An individual stoma with 2 sunken guard cells surrounding by 3 lateral subsidiary cells and 2 polar cells. Note outward strongly developed anticlinal walls of guard cells butterfly-like, and the hollows developed on periclinal walls of lateral subsidiary cells. 7–10. Resin bodies obtained from the cuticle of cupule lobes. 7. An elongated and fusiform resin body. 8. Two small, elongated resin bodies. 9. An elongated and fusiform resin body. 10. Two small fusiform resin bodies. Abbreviation: gc, guard cell; lsc, lateral subsidiary cell; pc, polar cell; daw, developed anticlinal walls; h, hollow. Scale bars: 1, 2, 5, 6, 10 = 50 μm ; 3 = 20 μm ; 4 = 100 μm ; 7, 8, 9 = 200 μm .

displaced during transport and burial (Plate II, 4). The pith is about 2.1 mm wide and covered by the outer cortex of ca. 0.75–1.1 mm thick (Plate II, 4).

Remarks: The complete short shoot with only proximal part of the stalk of seed-bearing structure preserved is assigned to the same species as the stalked cupules of *Umaltolepis zhoui* sp. nov. based mainly on two reasons: i) the stalk of the cupule is very similar to the broken stalk attached to the completely preserved short shoot in having irregular horizontal wrinkles on the surface, and also in similar width of the stalk (ca. 0.6–1.1 mm wide in seed-bearing structures and ca. 1.2 mm wide in short shoot); ii) bud scales on the completely preserved short shoot are similar to those persistent bud scales attached below the stalk of seed-bearing structures in triangular shape and acute apex, as well as in their similar size, 0.91–1.20 mm long and 0.75–1.14 mm wide in the former, and 1.20–1.74 mm long and 0.73–1.05 mm wide in the latter.

3.2. Systematic paleobotany of associated leafy shoots and leaves

Order: GINKGOALES sensu lato.

Family: PSEUDOTORELLIACEAE Krassilov.

Genus: *Pseudotorellia* Florin.

Species: *Pseudotorellia zhoui* Dong, Shi, Zhang, Wang, et Wang, sp. nov. (Plate IV, 1–4, Plate V, 1–14, Plate VI, 1–9, Plate VII, 1–8, Plate VIII, 1–7).

Etymology: The specific epithet is in honor of Zhiyan Zhou for his landmark contributions to understanding evolution and diversity of Mesozoic ginkgophytes.

Locality: Daohugou village (41°19'25" N, 119°14'40" E), Ningcheng County, Inner Mongolia Autonomous Region, Northeast China.

Holotype: PB23884 (Plate IV, 1).

Other studied material: PB23885 (Plate IV, 3), PB23886 (Plate IV, 4), PB23887 (Plate IV, 2).

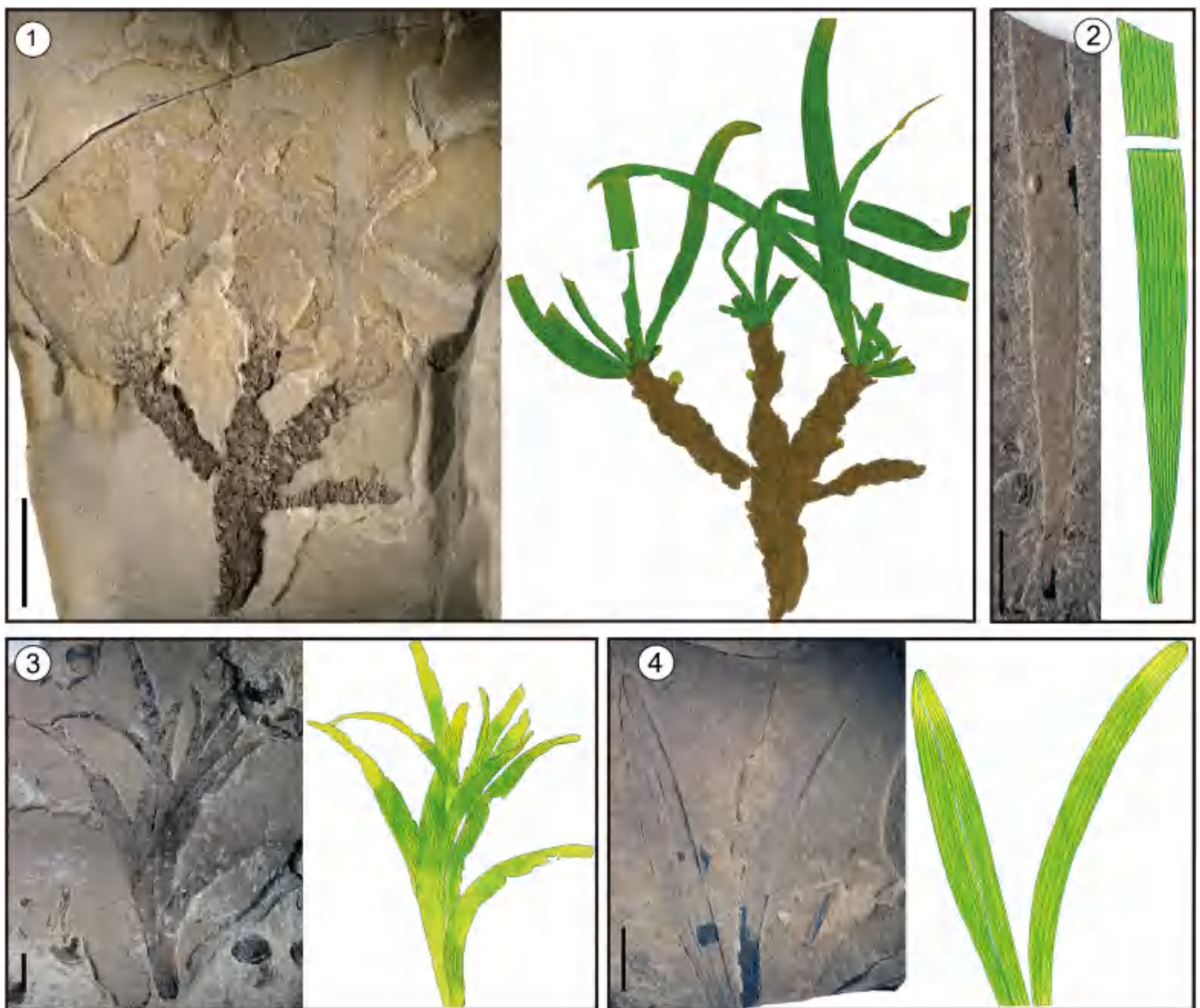
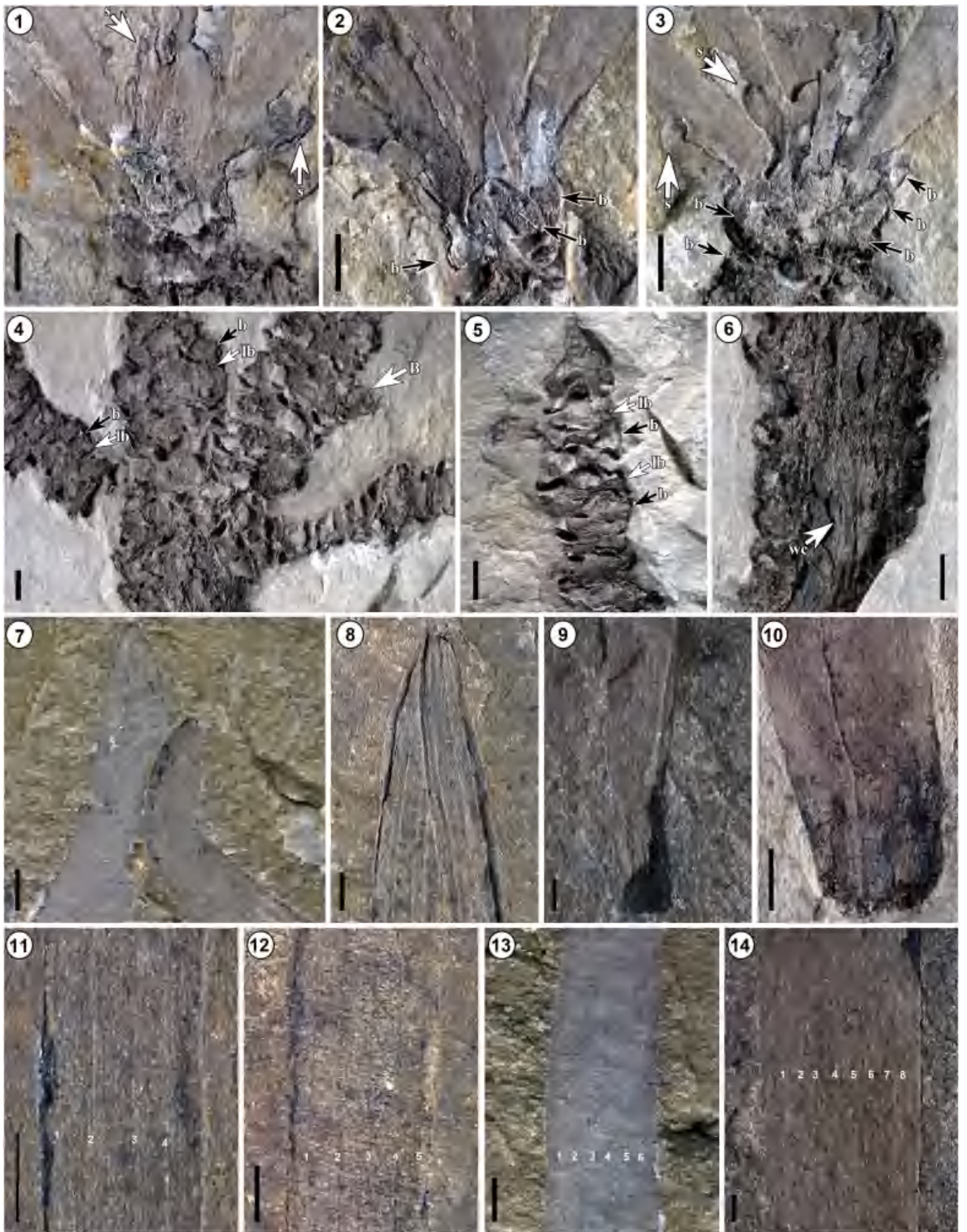


Plate IV. *Pseudotorellia zhoui* sp. nov., light micrographs and reconstructive drawings of a two-order leafy short shoot, isolated leaf blades and clustered leaves. 1. Leafy shoot consisting of penultimate shoot with four ultimate short shoots borne in a whorl at its tip, three with clusters of leaves. Holotype, PB23884. 2. Isolated leaf blade showing two veins enter the base of the leaf and dichotomizes two times to produce eight longitudinal veins in the blade. PB23887. 3. A cluster of ten strap-shaped leaves, each leaf blade with seven to eight parallel veins in the middle of leaf blade. PB23885. 4. Three separate leaf blades presumed belonging to the same cluster. Note basal portion of leaves lacking and each leaf blade having four to six parallel veins. PB23886. Scale bars: 1, 2 = 10 mm; 3 = 2 mm; 4 = 5 mm.



Repository: Palaeobotanical Collections, Nanjing Institute of Geology and Palaeontology, Chinese Academy of Sciences.

Stratigraphic horizon and age: Haifanggou Formation, late Middle-early Late Jurassic (~165–158 Ma).

Diagnosis: Penultimate shoot woody, covered with a thick layer of persistent bud scales, near terminal end bearing spirally arranged ultimate short shoots. Ultimate short shoots with alternating pseudo-whorls of persistent bud scales and abscission scars left by leaves or stalks of reproductive organs. Leaves borne on apex of ultimate short shoots in a cluster of 6 to 10. Leaf blade sessile, strap-shaped to narrowly oblanceolate. Leaves with slightly acute apex, cuneate base, and entire margins. Veins dichotomously branched, each leaf blade with 4 to 8 longitudinal parallel veins that extending to the leaf apex. Leaf cuticle thick, hypostomatic. Adaxial cuticle with distinct narrow costal zones alternating with wide intercostal zones; abaxial cuticle with distinct non-stomatal bands alternating with stomatal bands. Epidermal cells on both cuticle arranged in longitudinal files, more or less elongated, rectangular in outline, with straight anticlinal walls, and often with oblique end walls, each bearing a median longitudinal cuticular ridge on the periclinal walls in external view. Epidermal cells over costal zones of adaxial cuticle usually strongly elongated. Stomata longitudinally oriented to leaf margin, sparse, commonly arranged in 1–3 short, discontinuous stomatal files forming stomatal band. Each stoma with 2 guard cells, surrounded by 2–4 specialized lateral subsidiary cells and 2 unspecialized polar cells. Ledges of guard cells sunken, with well-developed, butterfly-shaped cuticular flanges. Lateral subsidiary cells strongly cuticularized, forming two lateral bow-shaped cuticular ridges flanking elliptical stomatal pit.

Description: The studied material includes impressions of a two-order short shoot consisting of a penultimate shoot bearing four ultimate short shoots, three of them bear clusters of leaves (Plate IV, 1), one detached leafy cluster (Plate IV, 3, 4), three incomplete leaf blades presumed belonging to one cluster, and a compression of isolated, incomplete leaf blade (Plate IV, 2).

The penultimate shoot is up to 3.9 mm wide, and ca. 12.3 mm long preserved, with a prominent woody core covered by a thick layer of bark bearing bud scales (Plate IV, 1, Plate V, 6). Ultimate short shoots are borne in a whorl near the apex of the penultimate shoot, up to ca. 11.0–14.5 mm long and ca. 2.8–3.4 mm wide (Plate IV, 1). The ultimate shoots are cylindrical, with alternating pseudo-whorls of persistent bud scales and abscission scars left by leaves or stalks of reproductive structures (Plate V, 4, 5), which reflect rhythmic growth. Each ultimate short shoot bears ca. 14–20 identifiable rhythmic growth cycles (Plate V, 4, 5). Each cycle consists of 6 to 8 bud scales and 6 to 8 abscission scars (Plate V, 4). The bud scales are triangular in outline, ca. 1.37–1.57 mm long and ca. 1.03–1.07 mm wide at the widest part, with an acute apex (Plate V, 4, 5). The abscission scar is more or less rhomboidal in outline, ca. 1.27–1.63 mm long at the longest part and ca. 0.40–0.63 mm wide at the widest part (Plate V, 4, 5). The short shoot sometimes bears small buds, which are spherical in outline, ca. 0.95–1.50 mm in long and ca. 0.78–0.95 mm in width (Plate IV, 1, Plate V, 4). Presumed stalks of reproductive structures borne at the apex of ultimate short shoots (Plate V, 1, 3). They are clustered together with strap-shaped leaves, but are easily distinguishable from the leaves by their gross

morphology. The presumed stalks are cylindrical in outline, ca. 1.8–2.3 mm long and ca. 0.62–0.78 mm wide, with round apices and more or less rough outer surface (Plate V, 1, 3).

Leaves are borne in a cluster at the apex of ultimate short shoots (Plate IV, 1). Three of four ultimate short shoots in the holotype bear clusters of leaves. Each cluster includes ca. 6–10 leaves (Plate IV, 3, Plate V, 1, 2, 3). Leaves are sessile, strap-shaped to narrowly oblanceolate in outline, obviously curved or falcate (Plate IV, 1). Clustered leaves are mostly incompletely preserved, commonly ca. 2.6–3.5 cm long and ca. 1.6–2.4 mm wide at widest point which is usually around the middle or closer to the leaf apex. The detached leaf blade in our collection is relatively larger than leaves in clusters, up to 6.8 cm in length of preservation and about 6.0 mm wide at the widest portion (Plate IV, 2). Leaves are generally narrowing near the base and being only ca. 0.5–0.8 mm wide at the base (Plate V, 9). Leaf bases are cuneate and taper gradually to form a basal angle of 25–30° (Plate V, 1, 2, 3, 9, 10). Leaf apices are abruptly contracted or acute (Plate V, 7, 8). The leaf margin is entire. Leaves commonly have 4 to 8 parallel veins (Plate V, 11–14). The longitudinal veins are generally equal in width in the middle region of the leaf, conspicuous and slight raised (Plate V, 11–14). A few well-preserved leaves show that two veins extend from the leaf base and dichotomize once or twice very close to the base of the leaf producing all longitudinal veins (Plate IV, 2). These longitudinal veins of one leaf blade run towards the apex through the whole blade without further branching but slightly close to each other before extending to the apex (Plate V, 7, 8).

Leaves are hypostomatic, both adaxial and abaxial cuticles are thick. The adaxial cuticle consists of alternate zones of narrow costal zones and wider intercostal zones (Plates VI, 1, VIII, 1). The costal zones are ca. 38–88 µm in width; each contains 2–3 discontinuous longitudinal rows of narrow epidermal cells (Plates VI, 1, VIII, 1). These epidermal cells are elongated, rectangular in outline, commonly with oblique end walls (Plates VI, 1, VIII, 3). These cells are ca. 85–275 µm long and ca. 15–27 µm wide, with a length/width ratio of ca. 4.5–12.4 (Plates VI, 1, VIII, 1, 3). The intercostal areas are wider, ca. 580–780 µm in width, and composed of more or less rectangular epidermal cells which arranged in longitudinal files (Plates VI, 1, VIII, 1, 2). The cells are slightly elongated, commonly with oblique end walls, ca. 65–176 µm long and ca. 38–78 µm wide, with a length/width ratio of ca. 0.8–4.7 (Plates VI, 2, VIII, 3). Anticlinal walls of epidermal cells both on and intercostal zones are straight, ca. 3.0–4.0 µm in thickness, strongly and unevenly cutinized, with thick, well-developed longitudinal cuticular flanges (Plates VI, 1, 2, VIII, 2, 4). Each cell bears a median longitudinal cuticular ridge that runs from one end wall to the other on the outer surface (Plates VI, 2, VIII, 2, 4). The cuticular ridge is solid, about one-sixth to one-third as wide as the epidermal cell (Plate VI, 2).

The abaxial cuticle consists of alternating stomatal bands between veins, and non-stomatal zones beneath the veins (Plates VI, 3, VII, 1, 2). Generally, stomatal bands are ca. 250–410 µm wide, running from the leaf base to the apex. Each band consists of 11–14 epidermal cells that are ca. 47–224 µm long and ca. 22–32 µm wide, with a length/width ratio of ca. 1.6–10.4 (Plates VI, 3, VII, 1, 2). Non-stomatal zones are ca. 320–450 µm in width, and each consists of 11–14 rows of epidermal cells which are ca. 139–305 µm long and ca. 23–41 µm wide, with a

Plate V. *Pseudotorellia zhoui* sp. nov., light micrographs of clustered leaves, surface of short shoot, and leaves. 1. Details of clustered leaves borne at the apex of short shoot showing cuneate leaf bases and two probable stalks of seed-bearing structures. PB23884. 2. Details of clustered leaves borne at the apex of short shoot showing cuneate leaf bases and persistent triangular bud scales below leaves. PB23884. 3. Details of cluster of leaves borne at the apex of short shoot showing cuneate leaf bases and two presumed stalks of seed-bearing structures. Note persistent bud scales below the leaves are triangular with acute apex. PB23884. 4. Surface of short shoots showing pseudo-whorls of bud scales, abscission scars left by leaf bases, and a small bud. PB23884. 5. Details of an ultimate short shoot showing terminal end, bud scales, and abscission scars left by leaf bases. PB23884. 6. Details of penultimate shoot showing woody core of the shoot covered by a layer of bark composed of bud scales. PB23884. 7. Distal parts of two leaf blades in Plate IV, 1 showing slightly acute apices. PB23884. 8. Distal parts of two leaves in Plate IV, 4 showing acute apices. Note veins extending to the apex. PB23886. 9. Basal part of leaf blade in Plate IV, 2 showing two veins enter the base of leaf. PB23887. 10. Basal part of a cluster in Plate IV, 3 showing two cuneate leaf bases. PB23885. 11. Middle part of leaf blade in Plate IV, 4 showing four prominent longitudinal veins. PB23886. 12. Middle part of leaf blade in Plate IV, 4 showing five prominent longitudinal veins. PB23886. 13. Middle part of leaf blade in Plate IV, 1 showing six prominent longitudinal veins. PB23884. 14. Middle part of leaf blade in Plate IV, 2 showing eight longitudinal veins. PB23887. Abbreviation: s, stalk; b, bud scale; lb, scar left by leaf base; B, bud; wc, woody core. Scale bars = 1 mm.

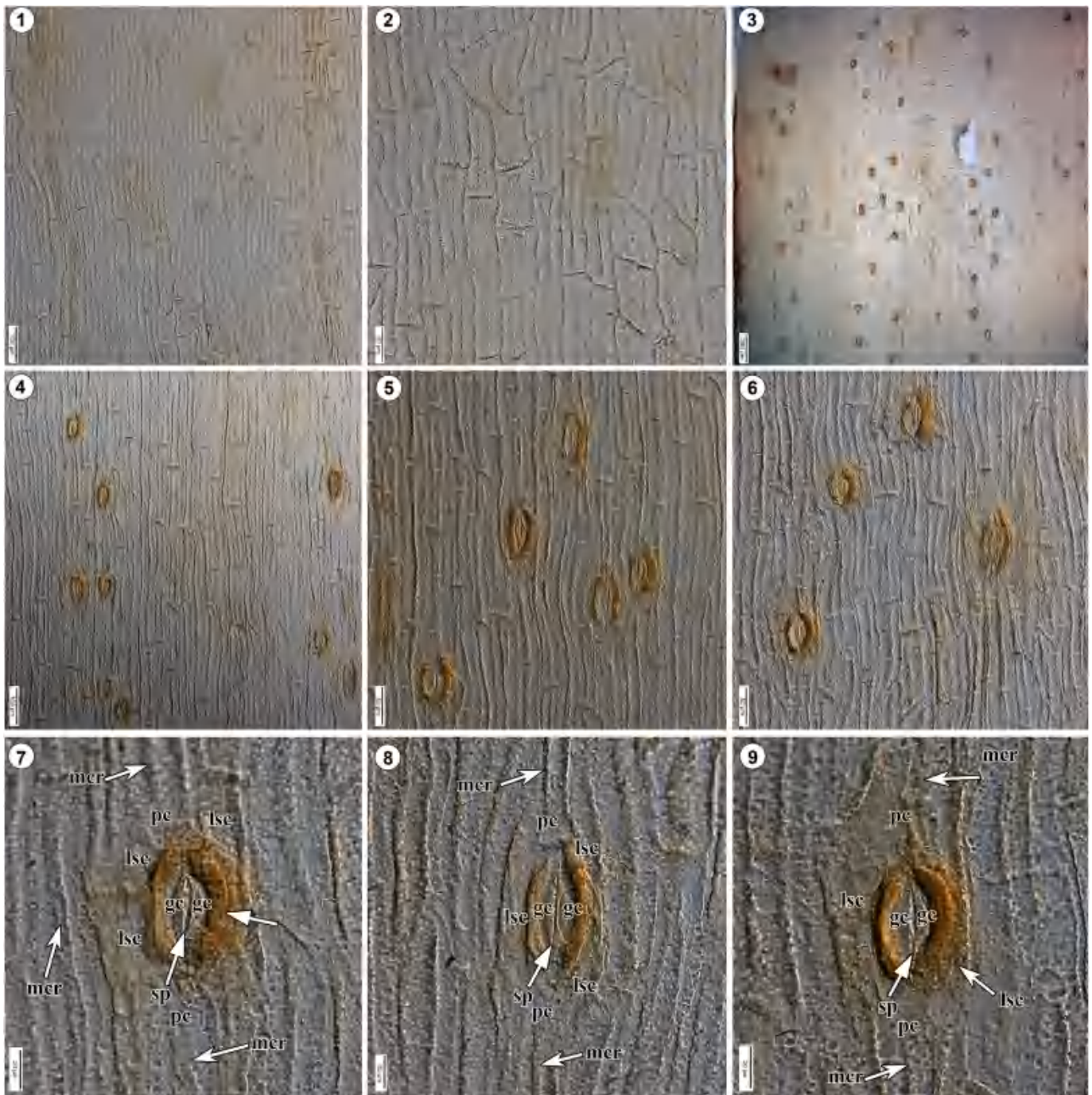


Plate VI. *Pseudotorellia zhoui* sp. nov., light micrographs of leaf cuticle and stomata. All cuticle obtained from the specimen of PB23887. 1, 2. Adaxial cuticle showing elongate rectangular epidermal cells arranged in longitudinal files. Note prominent longitudinal cuticular ridges on periclinal walls of epidermal cells. 3. Abaxial cuticle showing distinct non-stomatal zones composed of narrow elongated epidermal cells, alternating with stomatal bands having sparse, longitudinally oriented stomata. 4. Abaxial cuticle showing alternate stomatal bands and non-stomatal bands. Note epidermal cells on both stomatal and non-stomatal bands arranged in longitudinal files, elongated, rectangular, with prominent longitudinal cuticular ridges on periclinal walls. 5, 6. Details of stomatal band on abaxial cuticle, showing sparse, longitudinally oriented stomata. Note prominent longitudinal cuticular ridges on periclinal walls of epidermal cells. 7–9. Individual stoma showing 2 sunken guard cells surrounded by 2–4 lateral subsidiary cells and 2 polar cells. Note two bow-shaped cuticular ridges flanking the stomatal pit, and polar cells similar to ordinary epidermal cells in form and in having prominent longitudinal median cuticular ridges on periclinal walls. Abbreviation: gc, guard cells; lsc, lateral subsidiary cells; pr, polar cells; mcr, median cuticular ridges on periclinal walls; sp, stomatal pit. Scale bars: 1, 4 = 100 μm ; 2, 5, 6 = 200 μm ; 3 = 200 μm ; 7, 8, 9 = 20 μm .

length/width ratio of ca. 3.4–13.2 (Plates VI, 4, VII, 1). In addition to the differences in size, epidermal cells over stomatal bands and non-stomatal bands are similar in arrangement and outlines, and are usually obviously elongated, more or less rectangular in outline, often with oblique end (Plates VI, 4, VIII, 5, 6). They are generally arranged in longitudinal files, with straight anticlinal walls and well-developed thick cuticular flanges (Plate VIII, 5, 6). Periclinal walls of these epidermal

cells on external view bear a prominent longitudinal median cuticular ridge which runs from one end to the other and are usually occupying one-third width of the epidermal cells (Plate VI, 4, Plates VII, 2, VIII, 7). The ridges on neighboring cells in a longitudinal row are generally joined together leading to those ridges are longitudinally continuous over several cells (Plates VI, 4, 5, 6, VIII, 7). Inner cuticular surface of periclinal walls of abaxial epidermal cells usually has an ill-defined

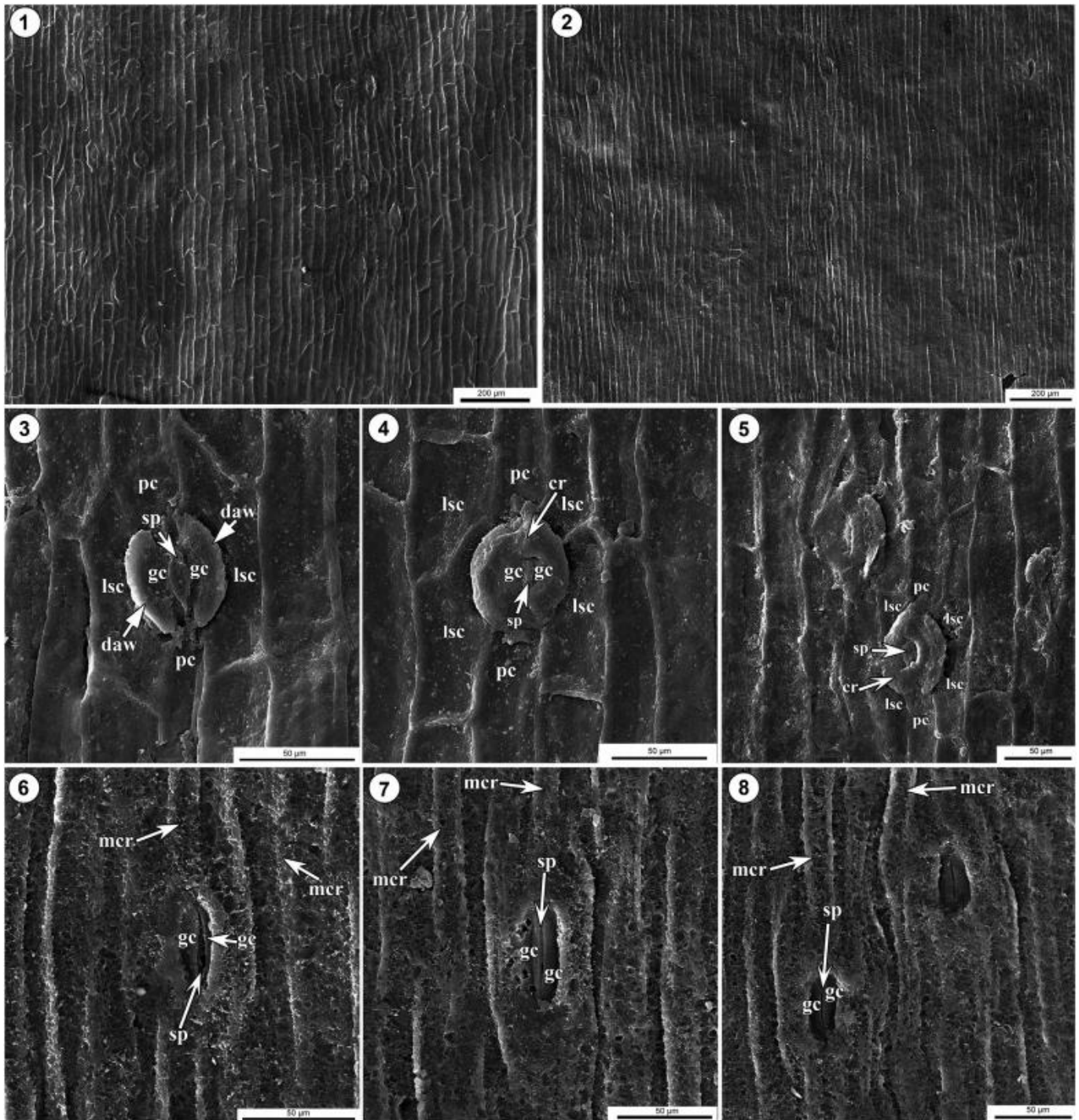


Plate VII. *Pseudotorellia zhoui* sp. nov., scanning electron micrographs of abaxial cuticle and stomata. All cuticle obtained from the specimen of PB23887. 1. Inner surface showing stomatal bands with sparse, longitudinally oriented stomata, alternating with non-stomatal bands bearing elongated rectangular epidermal cells. 2. Outer surface showing alternating stomatal bands and non-stomatal bands. Note strongly developed median cuticular ridges on periclinal walls of cells. 3. Inner surface showing a stoma with 2 lateral subsidiary cells and 2 polar cells. Note the well-developed butterfly-like flanges between guard cells and lateral subsidiary cells. 4. Inner surface showing a stoma with 4 lateral subsidiary cells and 2 polar cells. Note the strongly cutinized inner periclinal walls of guard cells, and the similar form of polar cells and ordinary epidermal cells. 5. Inner surface showing two stomata, one of which bearing 4 lateral subsidiary cells and 2 polar cells. Note the strongly cutinized inner periclinal walls of guard cells. 6–8. Outer surface showing details of stoma with sunken guard cells and bow-shaped ridges. Note strongly developed cuticular ridges on epidermal cells. Abbreviation: gc, guard cells; lsc, lateral subsidiary cells; pc, polar cells; mcr, median cuticular ridges on periclinal walls; sp, stomatal pit. Scale bars: 1, 2 = 200 μ m; 3–8 = 50 μ m.

median groove (Plate VIII, 5, 6) which corresponds to the cuticular ridges on outer surface.

Stomata are longitudinally oriented to leaf margin, sparse, arranged in 1–3 short, discontinuous longitudinal files in each stomatal band (Plate VI, 3, 4, 5, Plate VII, 1). Ledges of guard cells are sunken (Plate

VII, 6–8), commonly surrounded by 2–4 specialized lateral subsidiary cells and 2 unspecialized polar cells (Plate VI, 7–9, Plate VII, 3–5). Stomatal pits are elliptical in outline, ca. 32–60 μ m long and ca. 14–16 μ m wide at the widest portion (Plate VI, 7–9, Plate VII, 6–8). Stomatal aperture is slit-like or closed (Plate VI, 3–5). The cuticular anticlinal

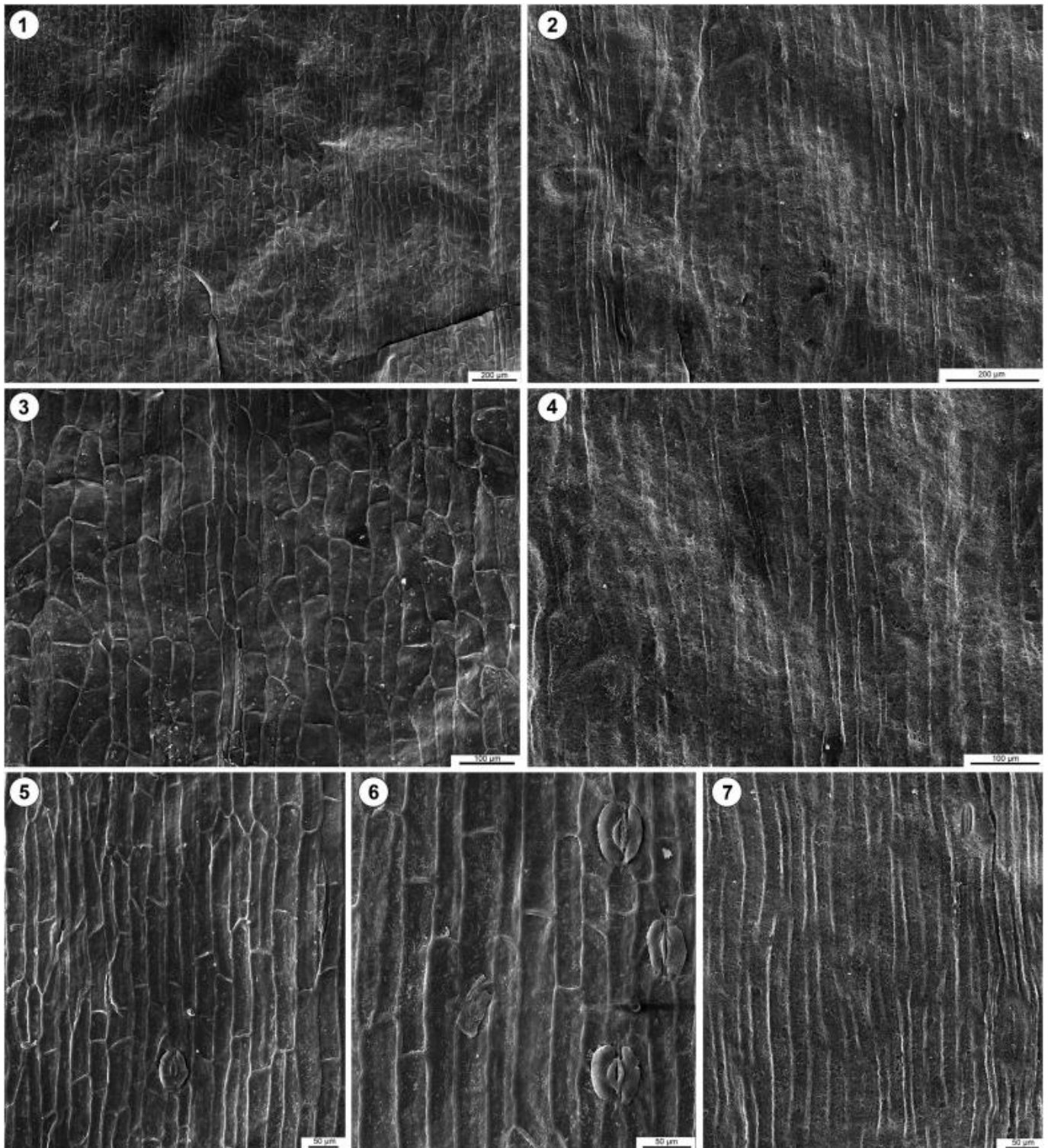


Plate VIII. *Pseudotorellia zhoui* sp. nov., scanning electron micrographs of adaxial (1–4) and abaxial (5–7) cuticle. All cuticle obtained from the specimen of PB23887. 1. Inner surface of adaxial cuticle showing narrow costal zones and wide intercostal zones. 2. Outer surface of adaxial cuticle showing narrow costal zones and wide intercostal zones. Note strongly developed longitudinal cuticular ridges on epidermal cells on costal zones. 3. Details of inner surface of adaxial cuticle showing epidermal cells on both costal and intercostal zones. Note cells on intercostal rectangular with straight walls and oblique end walls, and cells on narrow costal zones narrowly elongated, rectangular with straight walls. 4. Details of outer surface of adaxial cuticle showing strongly developed cuticular ridges. 5, 6. Epidermal cells on stomatal bands of abaxial cuticle showing elongated rectangular cell outlines and longitudinal arrangement. 7. Details of outer surface of stomatal bands on abaxial cuticle showing developed longitudinal cuticular ridges on epidermal cells. Scale bars: 1, 2 = 100 μm ; 3–7 = 50 μm .

walls between guard cells and lateral subsidiary cells are strongly developed, butterfly-like in outline, ca. 17–23 μm wide (Plate VII, 3). A cuticular ring probably formed by strong cutinization of the lateral and inner walls of both guard cells sometimes covers the butterfly-like structures

in internal view (Plate VII, 4, 5). Polar cells are similar to ordinary epidermal cells in form and size, as well as in bearing longitudinal cuticular ridges (Plate VII, 3, 4, 5). Lateral subsidiary cells are also more or less similar to ordinary epidermal cells in form, size, and anticlinal walls (Plate

VI, 8, Plate VII, 4), but in some case they are elongated pentagonal in outline (Plate VI, 8, Plate VII, 3). On the external view the periclinal walls of the lateral subsidiary cells are thickened and form two distinct, lateral, bow-shaped cuticular ridges flanking the stomatal pits (Plate VII, 6, 7, 8). On the internal view the periclinal walls of the lateral subsidiary cells are nearly smooth (Plate VII, 3, 4, 5) indicating cuticular ridges are solid.

4. Comparison and discussion

4.1. Assignment of *Umaltolepis zhoui* sp. nov. and comparison with other described species

In gross morphology, the seed-bearing structures described here strongly recall those referred to the type species, *Umaltolepis vachrameevii* Krassilov from the Late Jurassic of the Bureya River Basin, Siberia (Krassilov, 1972; Herrera et al., 2017). They both have a seed-bearing structure consisting of a stalked cupule borne on the apex of a short shoot with umbrella-like cupule formed by a central column bearing thick, resinous four-lobed outer covering (Herrera et al., 2017).

Umaltolepis is an extinct genus of seed-bearing structures which have been thought to be a ginkgophyte occurring during the Jurassic and the Early Cretaceous in Eurasia (Herrera et al., 2017; Nosova, 2021). Including the type species, nine species of *Umaltolepis* have been described mainly based on fossil cupules and their cuticular structure (Krassilov, 1972; Wang, 1984; Chen et al., 1988; Schweitzer and Kirchner, 1995; Herrera et al., 2017; Dong et al., 2019; Nosova, 2020, 2021). Among these fossil taxa, only in three species the stalk of the cupule is preserved: the type species *U. vachrameevii* (Krassilov, 1972; Herrera et al., 2017), *U. mongoliensis* Herrera et al. from the Early Cretaceous of Tevshiiin Govi, Central Mongolia (Herrera et al., 2017), and *U. yimaensis* from the Middle Jurassic of Central China (Dong et al., 2019). *Umaltolepis yimaensis* clearly differs from the new species in having an obviously curved stalk of the cupule (Dong et al., 2019). *Umaltolepis mongoliensis* resembles *U. zhoui* in forms of cupules and stalks, and also in the cuticular structures but differs in having larger cupules and stalks (Herrera et al., 2017). In *U. mongoliensis*, cupules are 9–19 mm long and 5.6–9 mm wide, and stalks are 5.4–7.1 mm long and 1.6–2.2 mm in diameter (Herrera et al., 2017); while cupules in *U. zhoui* are 8.5–13.2 mm long and 3.6–7.6 mm wide, and stalks are 3.0–3.8 mm long and 0.6–1.1 mm in diameter. Moreover, the stalk of *U. zhoui* extends into a prominent raised, cup-like flange at the tip, which is 1.9–2.2 mm in diameter and much wider than the stalk (0.6–1.1 mm in diameter); however, in *U. mongoliensis* the flange at the tip of cupule stalk is similar or only slightly wide than the stalk (1.5–2.2 mm in diameter) (Herrera et al., 2017). The seed-bearing structures of *U. vachrameevii* are distinguishable from those of *U. zhoui* by only relatively minor feature: the epidermal cells of cupule lobes with slightly curved, strongly cuticularized anticlinal walls (Krassilov, 1972).

Other six species of *Umaltolepis* are described only based on isolated cupules. Among these species, *U. coleoptera* Schweitzer & Kirchner from the Early Jurassic of northern Iran lacks cuticular features (Schweitzer and Kirchner, 1995), which makes a detailed comparison with *U. zhoui* impossible. Cupules of *U. hebeiensis* Wang from the Early Cretaceous of North China (Wang, 1984; Chen et al., 1988; Zhou et al., 2020) and *U. rarinervis* Krassilov from the Early Cretaceous of Russian Far East (Krassilov, 1972) differ from *U. zhoui* in having larger cupules: 15–20 mm long and ~ 5 mm wide in *U. hebeiensis*, and 17–18 mm long and 11–12 mm wide in *U. rarinervis*. Cupules of *U. sogdianica* Nosova from the Middle Jurassic of Uzbekistan are smaller: 6–9 mm long and 3.3–4.7 mm wide (Nosova, 2020). *Umaltolepis involuta* Nosova from the Middle Jurassic of Uzbekistan differs from all other species of the genus by possessing inward-bending lobe edges (Nosova, 2020). In *U. irkutensis* Nosova from the Middle Jurassic of Eastern Siberia, the papillae are sometimes present on periclinal walls of epidermal cells on

cupule cuticle (Nosova, 2021), which are different from the smooth periclinal walls in cupule cuticles of *U. zhoui*.

4.2. Assignment of *Pseudotorellia zhoui* sp. nov. and comparison with other described species

The leafy shoot, clustered leaves, and detached leaf blade are considered to belong to the same plant species based on similarities in leaf form, size, and detailed venation. These fossils are readily accommodated in the genus *Pseudotorellia* Florin based on size, form, and details of cuticular structure of their leaves. Among Mesozoic fossil plants, *Agathis* Salisb., *Eretmophyllum* Thomas, *Heidiphyllum* Retallack, *Phoenicopsis* Heer, *Pelourdea* Seward, *Desmiophyllum* (Solms-Laubach) Lesquereux, and *Podozamites* Braun also have strap-shaped leaves and longitudinal parallel veins as in the fossil leaves of *Pseudotorellia zhoui* sp. nov. (Retallack, 1980; Ash, 1987; Stockey and Atkinson, 1993; Anderson and Anderson, 2003; Huang et al., 2016; Shi et al., 2018; Nosova et al., 2020). However, the leaves of *Agathis*, *Eretmophyllum*, and *Heidiphyllum* clearly differ from the Daohugou *Pseudotorellia* leaves in irregularly oriented stomata on abaxial leaf cuticle (Harris et al., 1974; Stockey and Atkinson, 1993; Anderson and Anderson, 2003). Leaves of *Phoenicopsis* are distinguished from leaves studied here in absence of longitudinal median ridges on periclinal walls of epidermal cells (Huang et al., 2016; Nosova et al., 2020). *Pelourdea* has leaves inserted in helix (Ash, 1987), which is clearly different from the clustered leaves of *P. zhoui*. Leaf blade of *Desmiophyllum* differs from the Daohugou leaves in having a rounded apex and a broad petiolate base (Retallack, 1980), and leaves of *Podozamites* are easily distinguished from leaves studied here in helically inserted leaves and transversely oriented stomata on leaf cuticle (Shi et al., 2018).

The genus *Pseudotorellia* was established by Florin (1936) based on compression fossil leaves, initially described as *Feildenia* Heer by Nathorst (1897), from the Lower Cretaceous of Advent Bay, Spitsbergen. Fossil leaves assigned to the *Pseudotorellia* are common in Late Triassic to Early Cretaceous floras of the northern hemisphere, with more than 43 species have been described (Lundblad, 1968; Bugdaeva, 1999; Kiritchkova and Nosova, 2009; Nosova and Golovneva, 2018; Shi et al., 2018; Dong et al., 2019; Nosova, 2021). Excepting the Daohugou fossil, *P. krassilovii* Bugdaeva which was described from the Lower Cretaceous of Southern Primorye, Russia Far East is the only previously known taxa exhibiting a two-order leafy shoot (Bugdaeva and Markevich, 2009). However, unlike *P. zhoui*, in *P. krassilovii* the short shoots bearing clustered leaves are alternately arranged on a long shoot.

Among the published species of *Pseudotorellia*, *P. zhoui* is more or less comparable to *P. angustifolia* Doludenko (Krassilov, 1972), *P. retusa* Bose & Manum (Bose and Manum, 1990), *P. vachrameevii* Gomolitzky (Gomolitzky, 1965), *P. gobiense* Kostina & Herman (Kostina et al., 2015), *P. resinosa* Shi et al. (Shi et al., 2018), *P. palustris* Shi et al. (Shi et al., 2018), *P. henanensis* Zhou (Zhou, 1983), *P. yimaensis* Dong et al. (Dong et al., 2019), and *P. irkutensis* Nosova (Nosova, 2021) in integrated features of leaf morphology, epidermal cells, and stomatal complexes. Among these species, leaves of *P. retusa* are shorter (10–19 mm long) than those of *P. zhoui* (Bose and Manum, 1990). *Pseudotorellia angustifolia*, *P. yimaensis*, and *P. resinosa* differ from *P. zhoui* in having resin bodies in leaves, and in sometimes or commonly lacking papillae or cuticular thickenings on periclinal walls of epidermal cells (Krassilov, 1972; Dong et al., 2019). *Pseudotorellia irkutensis* is different in having fewer parallel veins (3–5) per leaf, as well as in their epidermal cells lacking cuticular ridges on periclinal walls (Nosova, 2021). Each leaf blade of *P. palustris* possesses 8–14 parallel veins (Shi et al., 2018); stomata of *P. vachrameevii* and *P. gobiense* bear prominent papillae surrounding stomatal pit on outer surface (Gomolitzky, 1965; Kostina et al., 2015); epidermal cells of *P. hunanensis* sometimes have large papillae (Zhou, 1983), which can distinguish these species from the Daohugou fossil leaves.



Plate IX. *Ginkgo biloba* L., light micrographs of a leafy shoot, a fragmentary short shoot, and a stalked seed for comparison. 1. A three-order short shoot in which each ultimate short shoot bears a cluster of leaves at the apex. 2. A fragment of short shoot showing the rhythmic growth cycle consisting of the pseudo-whorled triangular bud scales and rhombus abscission scars left by leaf petioles. 3. A stalked seed. Note the cup-like collar at the tip of peduncle and below the seed. Abbreviation: b, bud scale; lb, scar left by leaf petiole base; c, collar; p, peduncle. Scale bars: 1 = 2 cm; 2, 3 = 1 cm.

4.3. Attribution of seed-bearing structures of *Umaltolepis zhoui* sp. nov. and leafy shoot and leaves of *Pseudotorellia zhoui* sp. nov. to the same plant

The seed-bearing structures of *Umaltolepis* and *Pseudotorellia* leaves have been considered to be produced by the same plant based on their co-occurrence in field and their similarities in cuticular features of cupule lobes and leaves (Krassilov, 1972; Herrera et al., 2017; Dong et al., 2019; Nosova, 2021). The affiliation of *Umaltolepis* and *Pseudotorellia* is now further confirmed by discovery of stalked seed-bearing structures of *U. zhoui* sp. nov. and leaves and leafy shoots of *P. zhoui* sp. nov. from the Daohugou Bed. Moreover, cupule lobes of *U. zhoui* and leaves of *P. zhoui* have similar cuticular features including thick cuticle, longitudinally oriented epidermal cells with rectangular outline, strongly developed straight anticlinal walls and oblique end walls, as well as longitudinally oriented stomatal complexes in which two guard cells are sunken and have butterfly-like cuticular anticlinal walls at their junction with the lateral subsidiary cells (Plate III, 5, 6, Plate VII, 4).

Pseudotorellia zhoui described here is mainly based on a two-order leafy shoots with clustered leaves and presumed cupule stalks borne on the apex of ultimate short shoot (Plate IV, 1); this represents the

best-known species of the genus. *Umaltolepis zhoui* is described based on completely preserved seed-bearing structures attached to fragmentary short shoots (Plate I, 1, 2), as well as a short shoot bearing a broken stalk similar to the stalk of seed-bearing structure (Plate I, 4). These exceptionally well-preserved specimens provide further evidence to enable us to attribute the separately preserved seed-bearing structures of *Umaltolepis* and leaves and leafy shoots of *Pseudotorellia* into the same plant species.

First, stalks in seed-bearing structures of *Umaltolepis zhoui* (Plate I, 1, 2) are comparable to those stalks attached at the apex of short shoots of *Pseudotorellia zhoui* (Plate V, 1, 3) in cylindrical shape and similar width (0.6–1.1 mm in *U. zhoui*, 0.6–0.8 mm in *P. zhoui*). The stalks attached at the apex of short shoots in *P. zhoui* are shorter (1.8–2.3 mm long) compared to those stalks in the seed-bearing structures of *U. zhoui* (3.0–3.8 mm long), probably due to the incomplete preservation of the broken stalk attached to short shoots. Second, the short shoot with stalk of *U. zhoui* bears rhythmic growth cycles consisting of alternating pseudo-whorls of 6–8 persistent bud scales and 6–8 abscission scars left by leaves or stalks (Plate I, 4), a feature that also occurs in ultimate short shoots of *P. zhoui* (Plate V, 4, 5). Their bud scales and abscission scars are also similar in forms and size. In addition, persistent bud scales

attached below the seed-bearing structures of *U. zhoui* is also triangular, with acute apices, 1.20–1.65 mm long and 0.7–1.1 mm wide, all of which are comparable to persistent bud scales attached at the uppermost part of short shoots in *P. zhoui*.

4.4. Affinity between *Umaltolepis*-*Pseudotorellia* plant and *Ginkgo*

The *Umaltolepis*-*Pseudotorellia* plant is thought to be closely related to *Ginkgoales* mainly based on the resemblance of *Pseudotorellia* leaves and those of living *Ginkgo biloba* in the following aspects: two veins entering the leaf base, dichotomous branching of veins, parallel longitudinal veins in the middle region of leaf blade, resin bodies in mesophyll, and the similar leaf cuticular structures, especially the features that cuticle are hypostomatic and stomata are sparsely scattered (Krassilov, 1972; Herrera et al., 2017; Dong et al., 2019; Zhou et al., 2020). The well-preserved two-order leafy shoot with terminal clustered leaves, the stalked complete seed-bearing structures and fertile short shoot of *U. zhoui* reveal more morphological features for interpreting this extinct plant. These well-preserved materials provide more additional evidence including similar cup-like flange below the seed-bearing organs, clustered leaves, and unique morphology and arrangement of bud scales and abscission scars left by leaf bases on outer surface of short shoots for further confirming the affinity between the *Umaltolepis*-*Pseudotorellia* plant and *Ginkgo*.

In *Umaltolepis zhoui*, the stalk of seed-bearing structures extends into a cup-like flange at the apex of the stalk (Plate I, 1, 2, Plate II, 1, 3), a morphological feature which is similar to the cup-like collar at the apex of the stalk in ovulate organs of modern *Ginkgo biloba* (Plate IX, 3) and *Ginkgo* fossil species from Mesozoic and Cenozoic age (e.g., Zhou and Zhang, 1989; Zhou and Zheng, 2003; Zhou et al., 2012). Besides, leaves of *P. zhoui* were borne in a cluster at the apex of the ultimate short shoots (Plate IV, 1, Plate V, 1–3), which is also similar to leaves produced in a cluster at the apex of short shoots in *G. biloba* (Plate IX, 1; Fu et al., 1999). In addition, short shoots of *Umaltolepis*-*Pseudotorellia* fossil plant and *G. biloba* both have alternating pseudo-whorls of persistent bud-scales and abscission scars left by leaves or stalks of reproductive organs (Plate I, 4, Plate V, 4, 5, Plate IX, 2; Little et al., 2013). Moreover, bud scales of *G. biloba* are triangular in outline (Plate IX, 2), with an acute apex, and abscission scars left by leaf petiole are rhomboidal in outline, which both are consistent with forms of bud scales and abscission scars of *Umaltolepis*-*Pseudotorellia* plant found in the Daohugou Bed (Plate I, 4, Plate V, 4, 5).

Many morphological features of the Daohugou material, including resin bodies present in cupules of seed-bearing structures, cup-like flanges situated at the upper part of stalks, leaves borne in a cluster at the apex of short shoots, and alternating pseudo-whorls of persistent triangular bud-scales and rhombus abscission scars on short shoots, are similar to those of *Ginkgo*. These morphological similarities of *Umaltolepis* seed-bearing structures to seeds of *G. biloba*, and other previous confirmed morphological and cuticular similarities between leaves of *Pseudotorellia* and *G. biloba*, together further suggest a very close systematic affinity between *Umaltolepis*-*Pseudotorellia* plant and *Ginkgo*. Thus, here we assigned both *Umaltolepis* and *Pseudotorellia* to *Ginkgoales* sensu lato. A recent study based on material from the Early Cretaceous of Mongolia on the *Umaltolepis*-*Pseudotorellia* plant showed that its leaves are similar to those of *Ginkgo*, its seed-bearing structures however are comparable to extinct *Peltaspermales* and *Umkomasiales* (Herrera et al., 2017). It is interesting that the umbrella-like, four lobed cupules covering at the apex of seed-bearing structures of *U. zhoui* from the Daohugou Bed is also supporting such conclusion. Such indications recall the Meyen's concept of the *Ginkgoopsida*, a large and very inclusive clade, included not only *Ginkgoales*, but also some other Mesozoic extinct seed ferns (Meyen, 1984; Herrera et al., 2017).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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