AURITIFOLIA GEN. NOV., PROBABLE SEED PLANT FOLIAGE WITH COMIOID AFFINITIES FROM THE EARLY PERMIAN OF TEXAS, U.S.A.

Dan S. Chaney,[1,]* Sergius H. Mamay,[2] William A. DiMichele,* and Hans Kerp†

*Department of Paleobiology MRC-121, P.O. Box 37012, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, U.S.A.; and †Forschungsstelle für Paläobotanik, Westfälische Wilhelms-Universität Münster, Hindenburgplatz 57, 48143 Germany

Auritifolia waggoneri gen. et sp. nov. has compound leaves and is possibly a peltasperm, with venation similar to *Comia* Zalessky. The frond is once pinnate, >40 cm in length, with a short petiole, subopposite pinnae, increasing in size distally, terminating in two elongate pinnae. The petiole base is swollen. Fronds probably abscised upon senescence. Venation is three ordered, each higher order of progressively smaller diameter. Pinna midveins arise from the main rachis and give rise to secondary veins. Two types of tertiary veins are present. One type arises from the secondaries and forms fascicles; the other type is interfascicular and arises directly from pinna midveins. All tertiaries are of the same diameter. Tertiary veins dichotomize, anastomose, and may terminate in blind endings, so not all extend to the laminar margin. Laminae are amphistomatic. Monocyclic stoma are surrounded by five to six subsidiary cells. Epidermis and palisade parenchyma are uniseriate. *Auritifolia* is most similar to *Comia* in which the tertiaries lack anastomoses and blind endings and terminate at the laminar margin. The leaf architecture of *Auritifolia* differs significantly from that of *Comia*. (Russian and Chinese translations of this abstract are available in the online edition of *International Journal of Plant Sciences*.)

Keywords: peltasperm, Permian, Texas, *Comia*.

Online enhancements: Chinese and Russian abstracts.

Introduction

We describe herein a new genus of Early Permian plant with probable seed plant affinities, possibly a peltasperm. Specimens come from the redbeds of north-central Texas and carbonate rock from boreholes in west Texas. Both are facies of the Lower Permian Clear Fork Group (figs. 1, 2). The Clear Fork (Nelson et al. 2001) is a stratigraphic unit that has been the source of many new taxa of Permian plants (Mamay 1960, 1967, 1973, 1975, 1976, 1986, 1988, 1989; Read and Mamay 1964; Mamay et al. 1988; Chaney and DiMichele 2007) and vertebrates (Romer 1935, 1958; Olson 1948, 1951, 1952, 1954a, 1954b, 1954c, 1955, 1956a, 1956b, 1956c, 1958, 1979; Hotton 1952; Johnson 1981).

Among contemporary late Paleozoic plants, the new genus shares some notable features, particularly venation, with *Comia* Zalessky, which was described first from the Upper Permian of Angaraland (Zalessky 1934). In this type of venation, pinna midveins give rise to secondary veins from which multiple tertiary veins arise, forming a fascicle; one or more tertiary veins also arise directly from the primary vein, between fascicles. This venation pattern, in conjunction with a simple pinnate frond, circumscribes those forms that we refer to as "comioid,"

which describes all species of the genera *Auritifolia* and *Comia* (Mamay et al. 2009). Detailed examination shows, however, that the venation of *Auritifolia* is subtly and consistently distinct from that of *Comia*. Furthermore, the two genera have distinctly different leaf architectures. *Auritifolia* probably grew as a woody tree or shrub along lake and stream margins, in periodically wet substrates in otherwise strongly seasonal climates (DiMichele et al. 2006).

Geographic and Geologic Setting

Auritifolia is known from North America only in rocks of Leonardian (Artinskian, Early Permian) age. It has been collected from surface exposures in the counties of Baylor, Foard, and Taylor, north-central Texas (figs. 1, 2) and from the subsurface in boreholes in Gaines County, in west Texas, where it was previously reported as *Comia* (DiMichele et al. 2000) and later as a comioid of uncertain affinity (Chaney and DiMichele 2007). In north-central Texas, it is restricted to strata of the lower and middle beds of the undifferentiated Clear Fork Group (Hentz and Brown 1987; Hentz 1988; fig. 2). There it occurs in a coastal plain setting in channel-fill sediments, ranging from accretion-bedded sandstones, in which plants were deposited during active flow, to finely laminated claystones deposited in abandoned oxbow channels. In Gaines County, west Texas, *Auritifolia* sp. was found at various depths in three 15.24-cm cores from the Early Permian Clear Fork Group (DiMichele et al. 2000). These rocks are part of a carbonate-
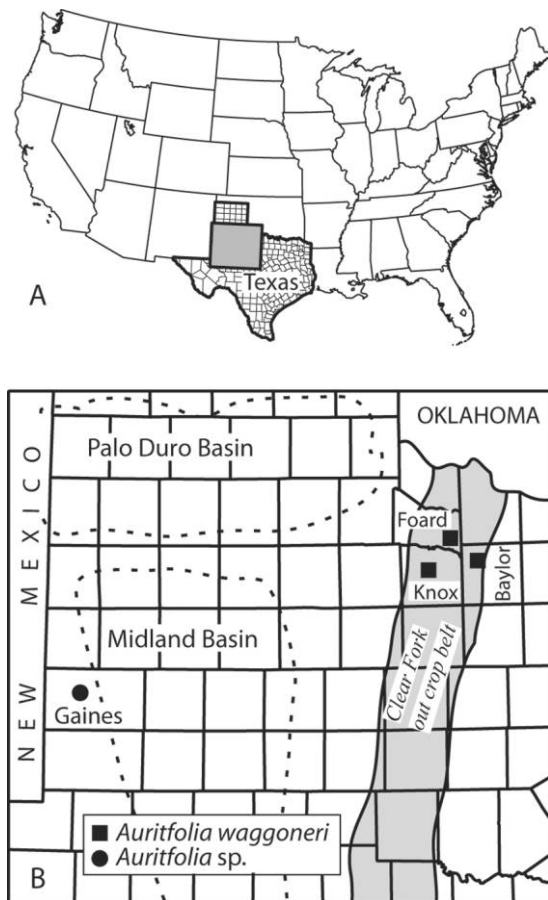
Fig. 1 Index map of north-central Texas. *A*, Continental United States with county boundaries shown for the state of Texas. *B*, North-central Texas, county boundaries indicated by solid lines. Named counties are those from which plants discussed herein were recovered. Permian basins outlined by dashed lines. The outcrop belt of the Clear Fork Group is highlighted in gray for reference.

remove the thick layer of carbonaceous material within the cuticular envelope. Cuticles were embedded in permanent glycerine gelatine slides. Photographs were made with a Leitz Diaplan microscope using Nomarski interference contrast and with an Olympus Vanox T AH-2 microscope, both equipped with a Nikon DS-5M digital camera. Other specimens were examined with SEM. Specimens were air-dried, sputter-coated with gold, and studied with a JEOL JSM-840 SEM. Microphotographs are the only record of cuticular specimens analyzed with SEM because of subsequent cuticular degradation. The two SEM stubs were assigned USNM specimen numbers 530986 and 530987. Multiple images were taken of each stub; for identification, an alphanumeric designation was given to each image, relating it to other images of the same stub. A master set of microphotographs are stored with other plants covered in this report.

Systematics

Terminology

The new genus has fasciculate venation herein described according to the terminology discussed in Mamay et al. (2009).
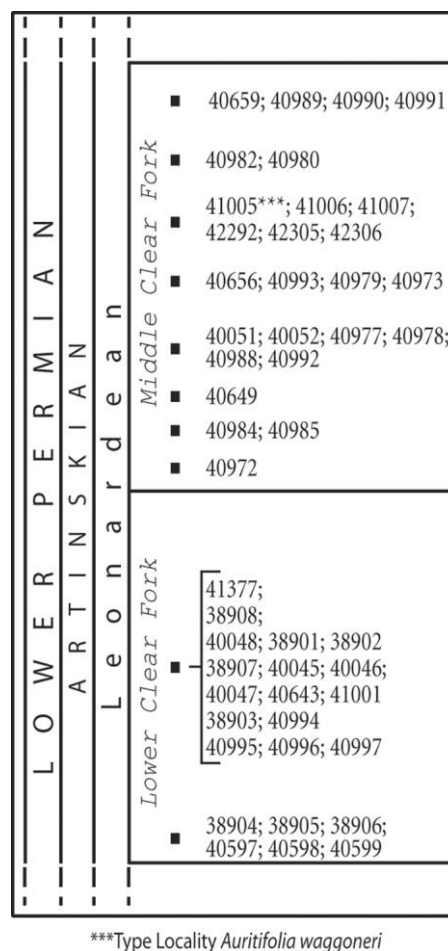
Fig. 2 Stratigraphic occurrence of *Auritifolia waggoneri*. Numbers are USNM collection numbers. One locality may have more than one collection number.

dominated section, interpreted as a complex of reefs and lagoons deposited in a coastal margin setting (Pregger and Dixon 1998).

Berthelin (2002) and Berthelin et al. (2003) report similar specimens under the name *Comia* sp. from the Late Permian of Oman. Although the Oman plants have leaf architecture similar to that of *Auritifolia*, the venation is not preserved in sufficient detail for common affinity to be ascertained with confidence.

Material and Methods

All type and illustrated specimens are stored in the Paleobotanical Collection of the National Museum of Natural History, Smithsonian Institution.
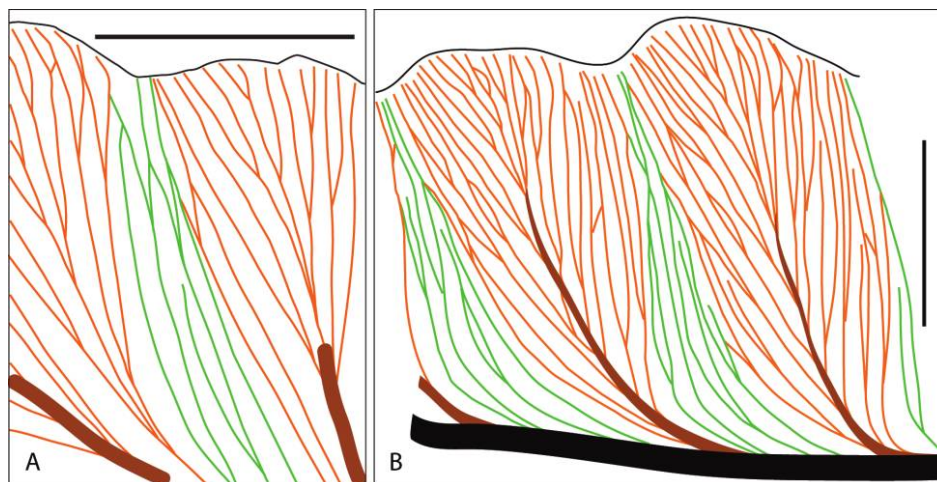
Cuticle was removed from USNM 530985 (locality 41044) from a depth of 2088.5 m (6852 feet) in core from the North Robertson Unit well 3533 Gaines County, Texas. The plants were prepared according to the methods described by Krings and Kerp (1997) and Kerp and Krings (1999). Some specimens were treated with Schulze's reagent for several weeks to

Fig. 3 *Auritifolia waggoneri*, line drawings of portions of paratype USNM 528207, from USNM locality 41005, showing venation patterns, based on fig. 5. Vein colors reflect vein order: black = first-order vein (midrib); brown = second order; reddish brown = third-order fascicular veins; green = third-order interfascicular veins; scale bars = 1 cm. *A*, Line drawing of an enlargement of the margin indicated as *3A* in fig. 5*A*. Detail of the dichotomies, anastomoses, and blind terminations. *B*, Line drawing of fig. 5*B*, showing the comioid fascicular–interfascicular venation complex.

In this terminology, the primary vein refers to the midvein of a pinna. Two kinds of veins arise directly from the primary. Secondary veins arise directly from the primary (fig. 3) and give rise to yet another tertiary order of venation that forms fascicles. Other tertiary veins arise between fascicles, directly from the primary vein and give rise to no additional orders of venation; these are herein referred to as "interfascicular tertiary veins." Vein diameter decreases with each order of venation, though the decrease between primary/midvein and secondary veins is much greater than that between secondary and tertiary veins. Interfascicular tertiary veins are of the same diameter class as the tertiary veins that arise from the secondaries and may dichotomize and anastomose with the tertiary veins of the fascicles between their point of insertion and the margin of the lamina.

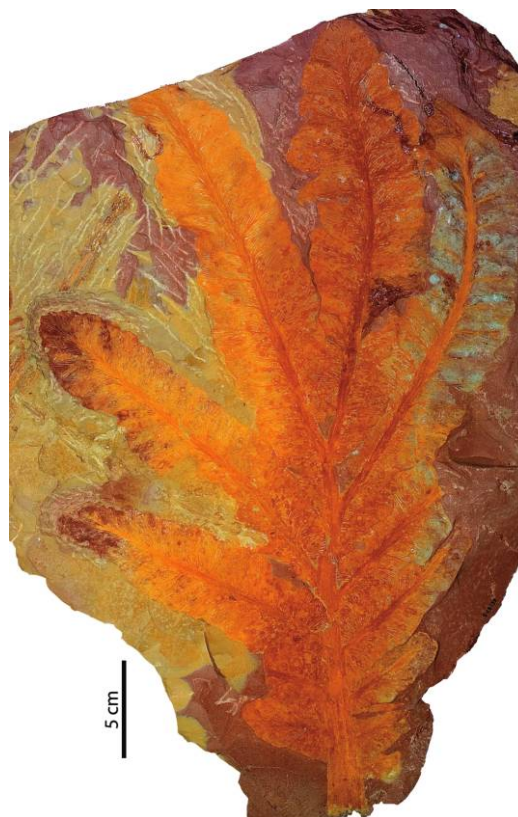Division—*Tracheophyta*

Class—*Spermatopsida*

Order—*Peltaspermales*

Family—*Incertae sedis*

Genus—Auritifolia *Chaney, Mamay, DiMichele & Kerp. gen. nov. (Figs. 3–24)*

Type Species—Auritifolia waggoneri *Chaney, Mamay, DiMichele & Kerp. sp. nov.*

Generic diagnosis. Frond once pinnate. Petiole short. Base of petiole indicates leaf abscission. Overall outline shape spatuloid. Pinnae enlarge in length and width from base to tip of leaf. Terminal pair of subopposite pinnae greatly elongated, apically directed, inserted at acute angle relative to rachis midline. Pinnae vary in number with frond size, subopposite paired insertion at right angle to low angle to main rachis of leaf, linear-lingulate in outline with bluntly rounded apices, entire or irregularly undulate to strongly incised margins. Three orders of coarse venation in pinnae, vein diameter decreasing

with each order. Primary vein straight, located on midline of pinna lamina. Secondary veins inserted directly in primary vein at acute angle. Tertiary veins with two kinds of insertion. One type arises from secondary vein to form a fascicle.

Fig. 4 *Auritifolia waggoneri*, holotype USNM 508135, from USNM locality 41005; scale bar = 5 cm. Typical leaf morphology. Variation in color and preservation from left to right across the specimen is a preservational effect reflecting progressive burial of the leaf by mud.
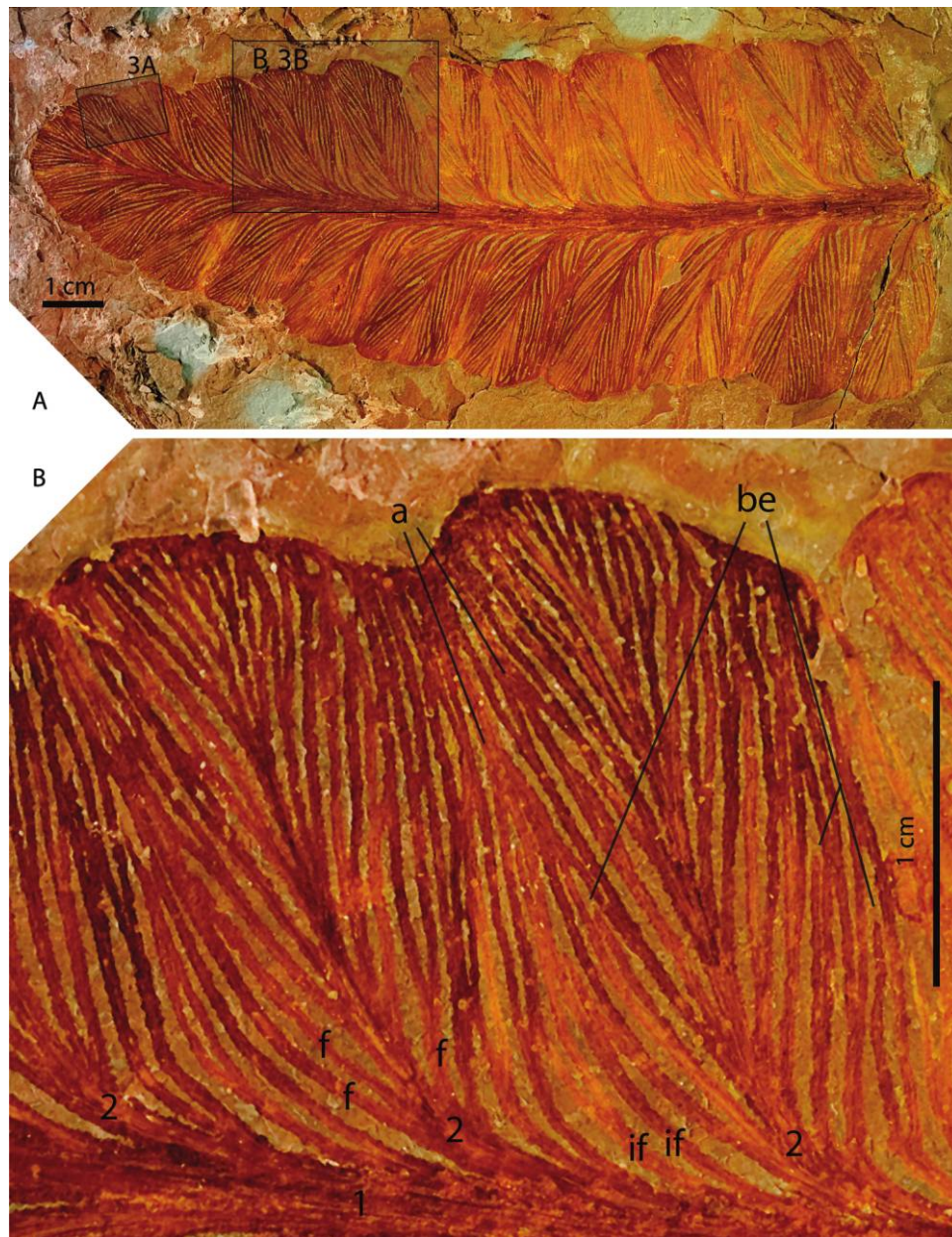
Fig. 5 *Auritifolia waggoneri*, venation paratype USNM 528207, USNM locality 41005; scale bars = 1 cm. *A*, Fascicular bundles end at margin in cusps; interfascicular veins end in sinuses. Area of enlargement indicated by shaded box. *B*, Enlargement of portion of *A*. *1* = first-order vein; *2* = second-order veins; *f* = third-order fascicular veins (representative sample), arising from secondary vein; *if* = third-order interfascicular (representative sample), arising from first-order vein; *a* = anastomoses between *if* veins and between *if* and *f* veins; *be* = blind endings present on both fascicular and interfascicular tertiary veins. See fig. 3 for line drawing of inset 3A.

The other type arises directly from primary vein between fascicles. Most tertiary veins dichotomize, may anastomose, and less frequently terminate in blind endings, and thus not all extend to pinna margin.

Type species. *Auritifolia waggoneri* Chaney, Mamay, DiMichele & Kerp.

Etymology. *Auritus* is Latin for an animal with long ears, a hare, and *folia* is Latin for leaf. The combination is in reference to the morphology of the frond in which the terminal pair of pinnae resembles a pair of rabbit ears.

Known geographic distribution. North-central and west Texas, possibly Oman.

Auritifolia waggoneri *Chaney, Mamay, DiMichele & Kerp. sp. nov. (Figs. 3–19)*

Specific diagnosis. Frond architecture highly variable, length 10–60+ cm, width 5–50 cm, bearing 3 to 18 or more pinnae, each with a slight acroscopic basal constriction, otherwise broadly attached basiscopically, slightly to highly decurrent but
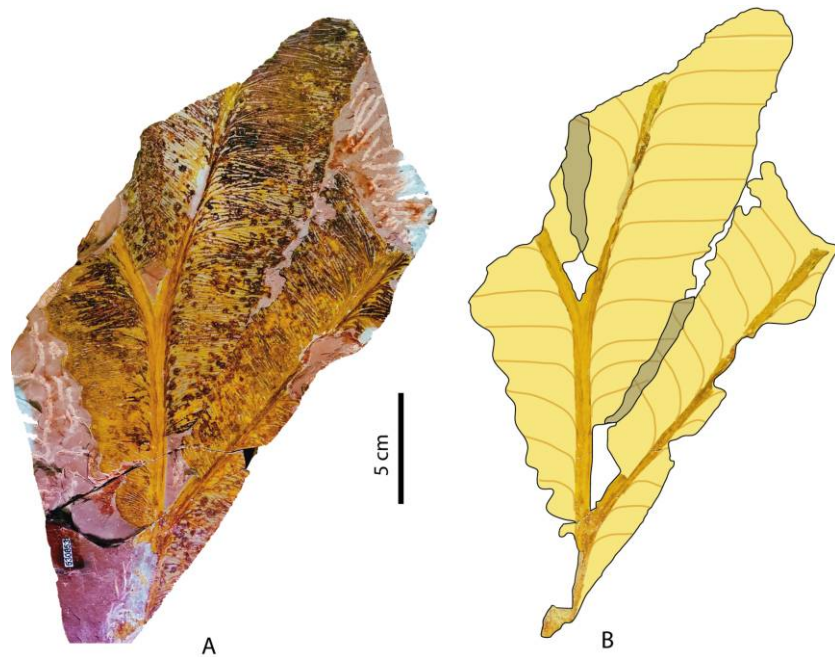
Fig. 6 *Auritifolia waggoneri*, paratype USNM 530853, from USNM locality 41005; scale bar = 5 cm. *A*, Dark circles on the lamina surface are preservational, possibly microorganic in origin. *B*, Line tracing of *A* gray areas indicate regions of overlap between adjacent pinnae. Note attachment of pinnule lamina to primary vein and rachis.

not confluent. Basal pinna pair relatively short, up to 3.0 cm long, each subsequent pinna pair longer, terminal pair longest, 25+ cm long, with maximum observed width 11 cm. Rachis stout, basally to 2.0 cm wide, somewhat flared, di-

minishing acropetally to terminal width of ~0.03 cm. Venation of pinna laminae relatively coarse and three ordered. Secondary veins inserted in primary vein at regular intervals of 1.5–2.5 cm, departing at acute angles of 40°–50°, each
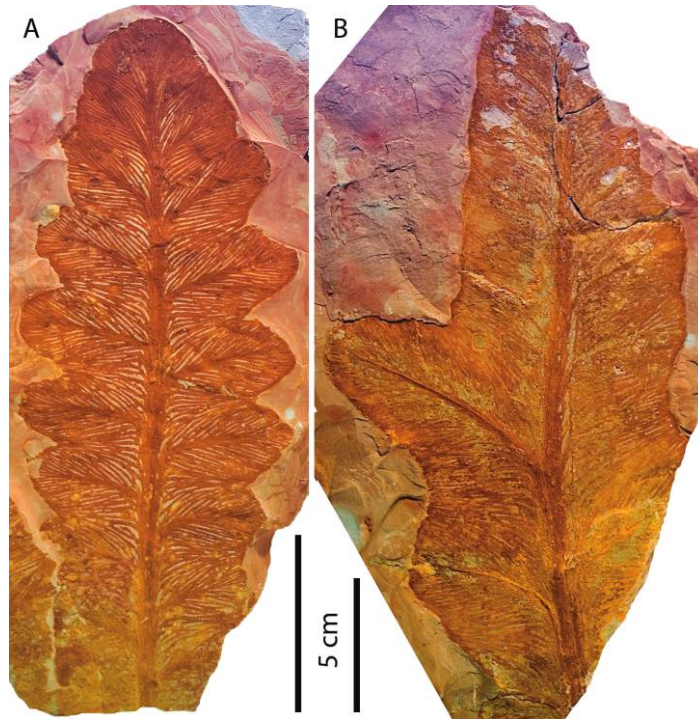
Fig. 7 *Auritifolia waggoneri*, variability in the form of the pinna margin; scale bars = 5 cm. *A*, Paratype USNM 528670, from USNM locality 42292 with highly lobed margin. *B*, Paratype USNM 528669, from USNM locality 42292 with highly developed pinna lobe.
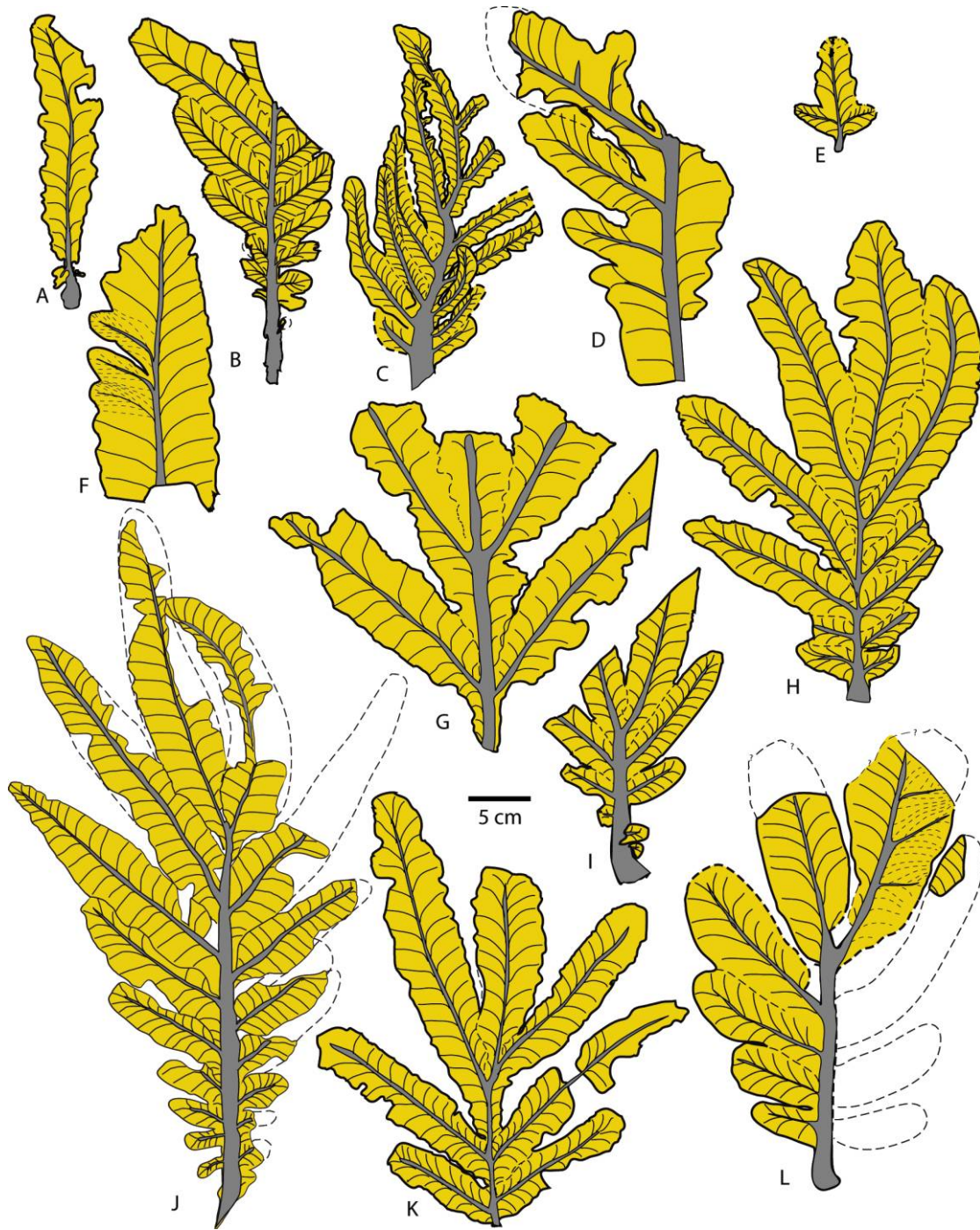
Fig. 8 *Auritifolia waggoneri*, variability of leaf architecture, line drawings; scale bar = 5 cm. *A*, USNM 508136, from USNM locality 41006. Entire leaf, including petiole. *B*, USNM 528605, from USNM locality 41005. Leaf with base, pinnae arranged alternately on rachis. *C*, USNM 528602, from USNM locality 40973. Petiole missing, very thick rachis, terminal dichotomy irregular. *D*, USNM 528607, from USNM locality 40993. Incomplete specimen with asymmetrical development of lamina. *E*, USNM 528608, from USNM locality 41005. Entire leaf, including petiole, very small. *F*, USNM 528603, from USNM locality 41005. Incomplete specimen; cannot be determined whether this represents most of a single leaf or a deeply incised pinnule of very large size. *G*, USNM 528600, from USNM locality 40979. Very large incomplete specimen with what appears to be a tripartite ultimate division. *H*, USNM 508135 holotype of *A. waggoneri*, from USNM locality 41005. Nearly complete frond missing only small part of petiole and tips of a few pinnae. *I*, USNM 528606, from USNM locality 41005. Nearly complete frond with petiole missing tips of three pinnules. This specimen has an unusually large rachis with respect to the number of pinnules and overall size of the leaf. *J*, USNM 530988, from USNM locality 42306. A very large frond with at least 17 pinnae. The base is incomplete. The specimen was too weathered to collect and is recorded only in photographs. *K*, USNM 528601, from USNM locality 40979. Missing petiole, longest pinnule occurs below the ultimate division. *L*, USNM 528604, from USNM locality 40988. Ultimate pinnules approaching additional order of pinnation.
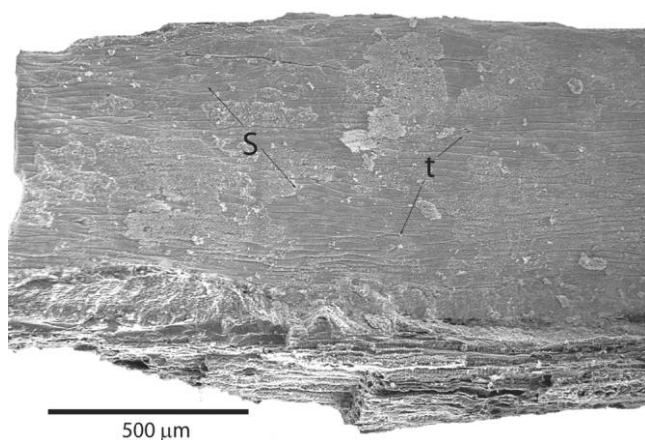
Fig. 9 Epidermis of midvein of *Auritifolia waggoneri*, USNM 528612, from locality 41005; scale bar = 500 μm. SEM image, epidermal surface with stomata in upper four-fifths of image, vascular tissue of the stem in the lower one-fifth of image; tracheid cells of the vein appear as long cylinders. *S* = stomata, only two indicated. *t* = trichome bases.

forming a fascicle by emission of several (5–10) tertiary veins, most dichotomize, a few anastomose, resulting in 10–20 fascicular tertiary veins/fascicle reaching the laminar margin. Two to 10 interfascicular tertiary veins arise from primary vein between fascicles, most anastomose with other interfascicular veins or with fascicular tertiary veins, additionally rare interfascicular tertiary veins terminate, repeatedly in relation to their position in the fascicle–interfascicular couplet, as blind endings; thus only two or three interfascicular veins/cluster reach the pinna margin. Most anastomosis occur in the outer third of the lamina, with blind endings found in the inner half of the lamina. Approximately 10–15 ultimate veins/cm terminate at the pinna margin. Pinnae amphistomatic, stomatal complexes present in the intercostal areas only, monocyclic, guard cells with prominent winglike extensions. Epidermal cells cuboidal on lamina surfaces, axially elongate on rachis, hair bases scattered on upper and lower lamina surfaces irregularly and sparsely.

Holotype. USNM specimen 508135 (fig. 4).

Type locality. USNM locality 41005; Knox County, Texas.

Paratypes. USNM specimens 508136, 528670, 528207, 528607, 528608, 530853, 530856, and 530923.

Referred plants. USNM specimens 531270, 536418.

Additional localities. Lower Clear Fork Formation: The specimens from the lower Clear Fork Formation are largely fragmentary and thus most identifications are tentative. Two unfigured specimens, USNM 531270 and 536418, have typical *Auritifolia* venation and frond architecture and unquestionably document the presence of the genus in the lower Clear Fork. Additional specimens occur at the following lower Clear Fork localities: 40048, 38908, 38903, 40045, 40046, 40047, 40643, 41001, 40994, 38904, 38905, 38906, 40597, 40598, 40599, 40995, 40996, 40997, 41377.

Middle Clear Fork Formation: 40977, 40987, 40988, 40992, 40972, 40649, 40985, 40984, 40980, 40982, 40656, 40993, 40979, 40973, 40659, 40989, 40990, 40991.

Geographic occurrences. Baylor, Foard, and Knox counties, Texas (fig. 1).

Stratigraphic occurrences. Lower and middle Clear Fork Formation, lower Leonardian Series, Artinskian, Cisuralian, Lower Permian (fig. 2). Exact locality information is on file at the National Museum of Natural History but is not published here at the request of the property owners from whose holdings the plants were collected.

Etymology. The epithet *waggoneri* recognizes the generosity of the W. T. Waggoner Estate for its long interest in and support of paleontology and the assistance provided to Smithsonian field crews over many years.

Description

The general morphology of the *A. waggoneri* plant is not known. That these were once pinnate fronds is shown by five specimens that clearly show a flared base indicative of abscission. The spatulate shape of the frond, its termination in a pair of elongate pinnules reminiscent of "rabbit ears," and the fasciculate venation of the pinnae, particularly the anastomoses in combination with blind end terminations of some tertiary veins (figs. 3, 5), are distinctive for this species.

The proximal pinna laminae normally are slightly constricted at the base. In the more distal parts of the frond, the basiscopic sides become decurrent but are not confluent with subjacent pinnae (fig. 6). Specimens may exhibit apparent, but not actual, confluence of successive pinna laminae, a condition that results from overlapping of adjacent pinnae rather than a physical connection. This suggests that in life the pinna were angled or louvered with respect to the overall plane of the frond.

The pinnae are mostly linear–undulate in outline with obtuse apices. Their margination is nondistinctive; the margins are either entire (fig. 5), occasionally shallowly and irregularly sinuous or crenate (fig. 7), or strongly incised. If the margin is incised, the fascicles terminate in the lobes and the sinuses are associated with the interfascicular tertiary terminations (fig. 7).

The great numbers of specimens, albeit mostly fragmentary, provide cumulative features that lead one to a reasonably credible interpretation of the gross physical constitution of the sterile foliage of this species. The most complete specimen, here designated the holotype (USNM 508135; fig. 4), is a nearly complete once-pinnate frond, with 12 pinnae. The overall length of the specimen is 40 cm, and its greatest width is ~25 cm; another larger, but incomplete, specimen (USNM 530851) suggests a width of ~50 cm. The largest nearly complete frond (USNM 530988; this specimen was not collected because of weathering and exists in photographs only; fig. 8*J*) is at least 62 cm in length and 31 cm in width and has 17 or 18 pinnae. The longest of these pinnae was 26 cm, though only 5.7 cm in width. In overall outline shape, the frond of the type specimen is obovate, reaching its greatest width in the distal half.

Frond petioles are short, usually <5.0 cm from the flared base (fig. 4; fig. 8*A*, 8*L*) to the point of attachment of the most basal pinnae. At its base, the petiole may be 3.0 cm wide, but shortly above the base, the stout rachis assumes width of ~1.0 cm, which decreases little toward the frond terminus. The petiole and rachis are usually longitudinally
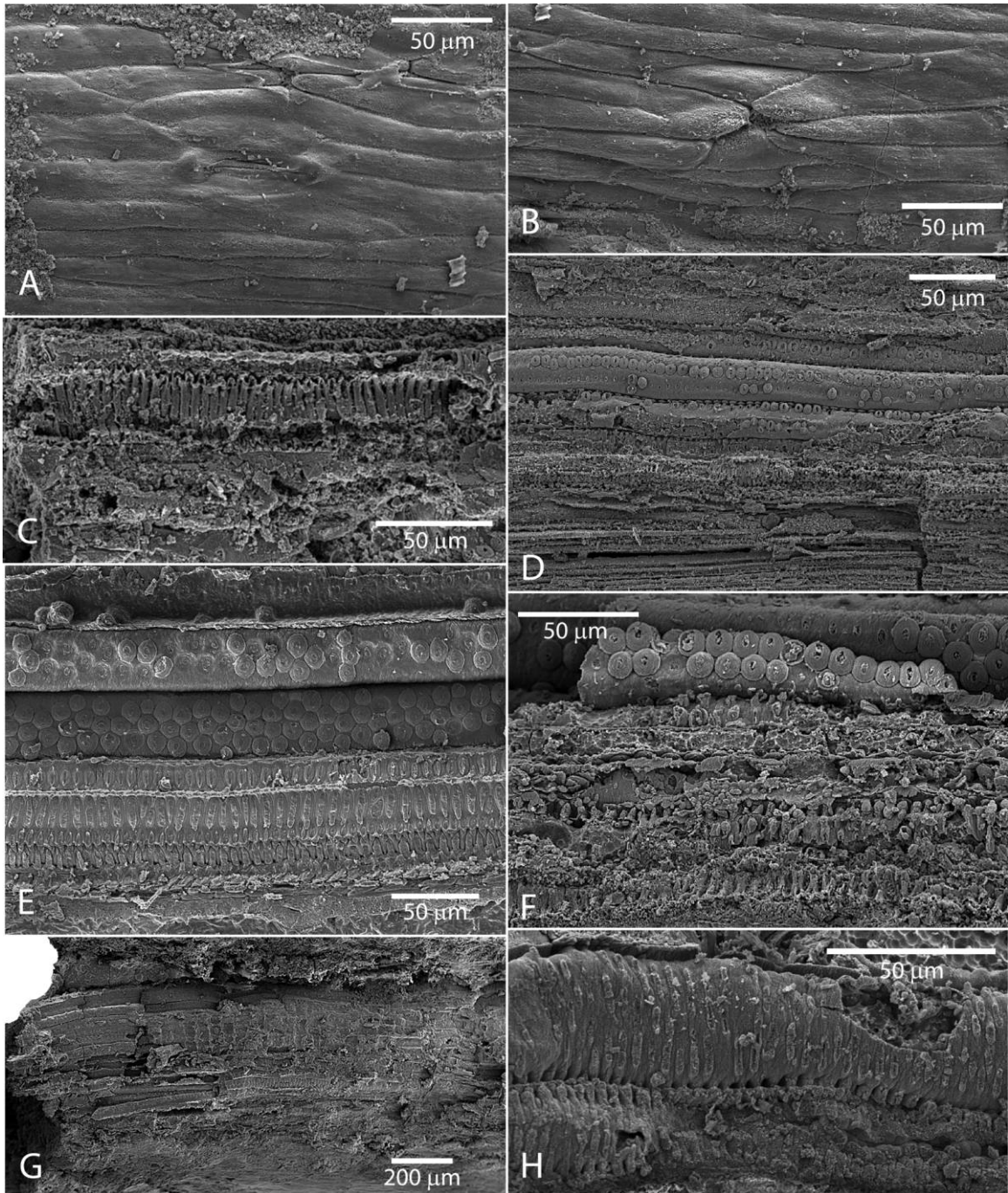
Fig. 10 SEMs of the cellular structure of the midvein of *Auritifolia waggoneri* new gen. et sp. *A–D, F, H,* USNM 528612, from USNM locality 41005. *E, G,* USNM 530923, from USNM locality 41005. *A–F, H,* scale bar = 50 μm; *G,* scale bar = 200 μm. *A,* Single closed epidermal stoma and trichome base (two trichome bases are in the upper right just below the bar scale). The stoma is very simple, consisting of two guard cells with no additional subsidiary cells. *B,* Trichome base. *C,* Helical thickening in a vascular bundle. *D,* Cast of tracheid with circular bordered pits. The "donuts" are casts of the pit chambers between tracheids. A zone of helical thickening is present in the lower one-third of the image. *E,* Tracheids of large size with several rows in an alternating arrangement. Scalariform pitting is seen in the lower half of the image. *F,* Cast of overlapping tracheids with alternating circular bordered pits. Lower half of image shows grooved helical thickenings. *G,* Tracheids aligned left to right with a ray of 20+ cells, indicating that the midvein of *Auritifolia* was woody at least near its base. *H,* Cast of tracheid with alternate scalariform pits.
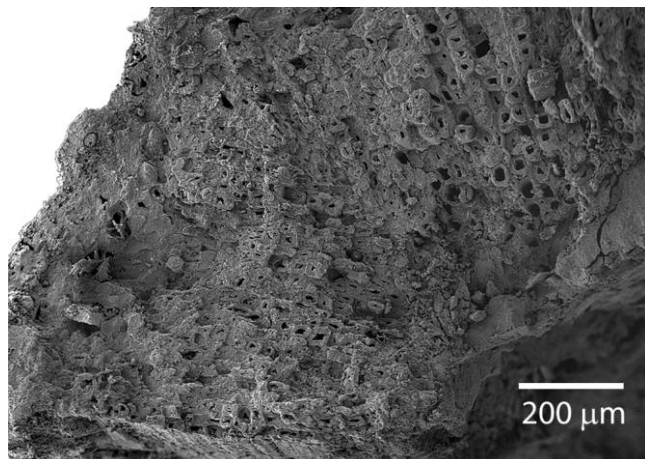
Fig. 11 *Auritifolia waggoneri*, SEM image of cross section in proximal part of the midvein. USNM 530923, from USNM locality 41005; scale bar = 200 μm. Note the radial arrangement of the tracheids, supporting the interpretation that at least the base of the leaf was woody.

wrinkled but show no significant additional features. However, the squarely truncate base suggests a clean abscission of the foliage.

In its proximal half, the rachis is monopodial, but that symmetry becomes modified beyond the approximate middle of the frond, where a series of overtopped, pseudodichotomous frond divisions become apparent (fig. 4; fig. 8H, 8J–8L). This frond architecture is clearly seen in the form and distribution of the pinnae. The basal two or three pairs of oppositely arranged pinnae are borne a short distance above the petiolar base and are relatively short, some <3.0 cm in length (fig. 4; fig. 8A, 8B, 8E, 8H, 8I, 8L). Successive pinnae, however, increase greatly in length, so that the median ones are more than twice the length of the basal ones. Further-
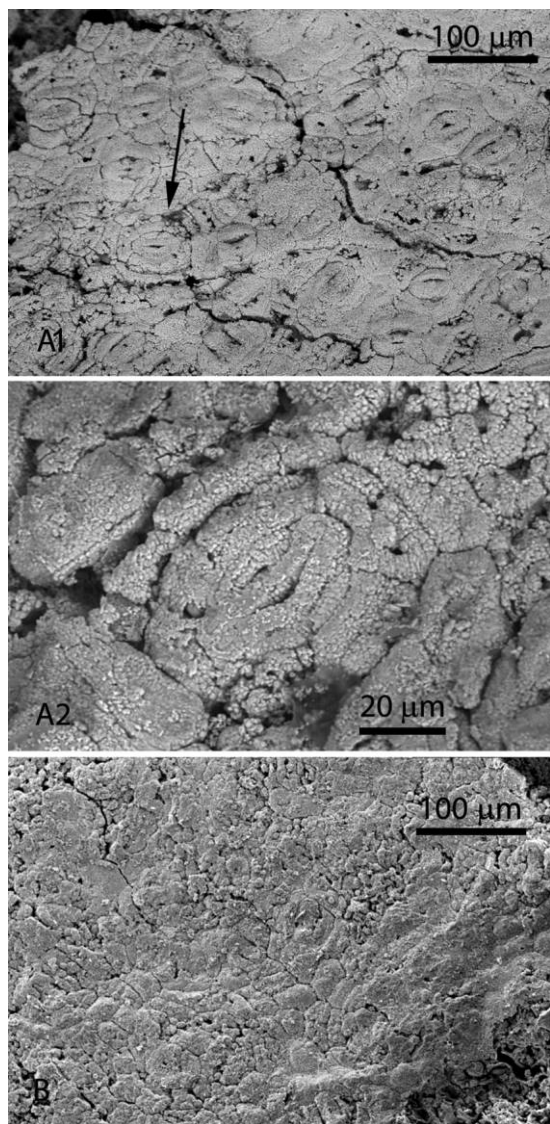
more, the opposite distribution of pinnae becomes altered distally by the pseudodichotomous or overtopping division of the rachis, with one pinna resultantly longer than its counterpart (figs. 4, 8H). Thus, the most distal pinnae are much longer and broader than the most basal ones and the general frond form seems discordant with the more usual lanceolate to ovate frond architecture exhibited in *Comia* (Mamay et al. 2009). None of the several nearly complete specimens in our collections evidence diminution in size of terminal pinnae. Consequently, we assume that the leaf form shown by the holotype (fig. 4) is the normal configuration for foliage of this species. Where observed in attachment to a frond, distal pinnae attain ~20 cm in length and 4.0–6.0 cm in width. They create a narrow angle (~30°–45°) with each other as the result of their overtopping division, whereas the basal pinnae are nearly perpendicular to the rachis (fig. 4). A much greater pinna size is indicated by several unattached, incomplete fragments, two of which are each 11 cm wide and ~25 cm long (USNM 530855 and 530856). By projection of the margins beyond the broken ends, one may reasonably assume that these pinnae were 40 cm or more in length and were parts of huge compound leaves.

The venation stands out in sharp contrast to the surrounding lamina (fig. 5). The midvein is stout, usually 0.3–0.4 cm wide, but attains as much as 0.8 cm in thickness in the larger specimens (fig. 8C, 8H).

Secondary veins arise oppositely or suboppositely at regular intervals of 1.5–2.5 cm in the largest specimens (figs. 5, 7). These veins depart at a narrow angle to the midvein, and a short distance from it bend gently outward and emit a close series of tertiary veins (5–10), most of which dichotomize once with a few anastomosing before they reach the laminar margin; on rare occasions, some end in blind terminations (fig. 5). Thus, 10–20 ultimate veins terminate at the laminar margin per fascicle. The fascicle as a whole assumes an almost straight or slightly bowed course to the margin at an angle of ~60°. Two to 10 interfascicular tertiary veins arise
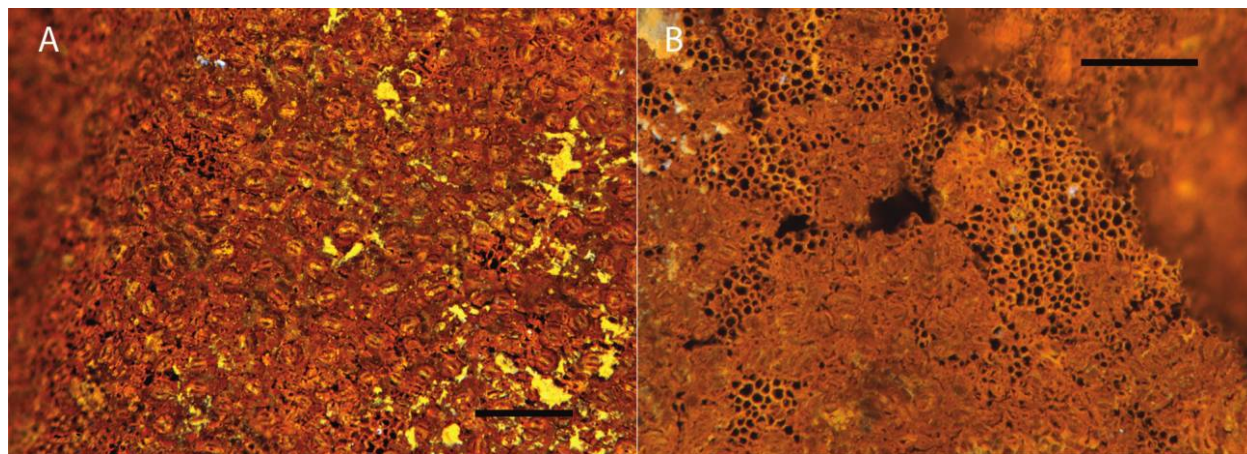
Fig. 12 *Auritifolia waggoneri*, epidermis, permineralized adaxial intercostal lamina. USNM 528671, from USNM locality 41005; scale bars = 250 μm. *A*, LM image of stomatal pattern on adaxial surface near rachis; preservation has resulted in damage to the adaxial surface of the guard cells, resulting in parallel holes lateral to the randomly oriented stoma. *B*, LM image of epidermis and the palisade parenchyma from approximately midpoint of pinnule lamina. Stomata are randomly oriented. Portions of the epidermis are allowing comparison of the distribution of stomata and the underlying palisade parenchyma.

Fig. 13 *Auritifolia waggoneri*, SEM images of epidermis from laminar regions of the leaf, USNM 528671, from USNM locality 41005. *A1*, Intercostal adaxial epidermis, arrow indicates stoma illustrated in *A2*. *A2*, Adaxial intercostal stoma with two guard cells and what appear to be subsidiary cells. *B*, Abaxial intercostal epidermis.
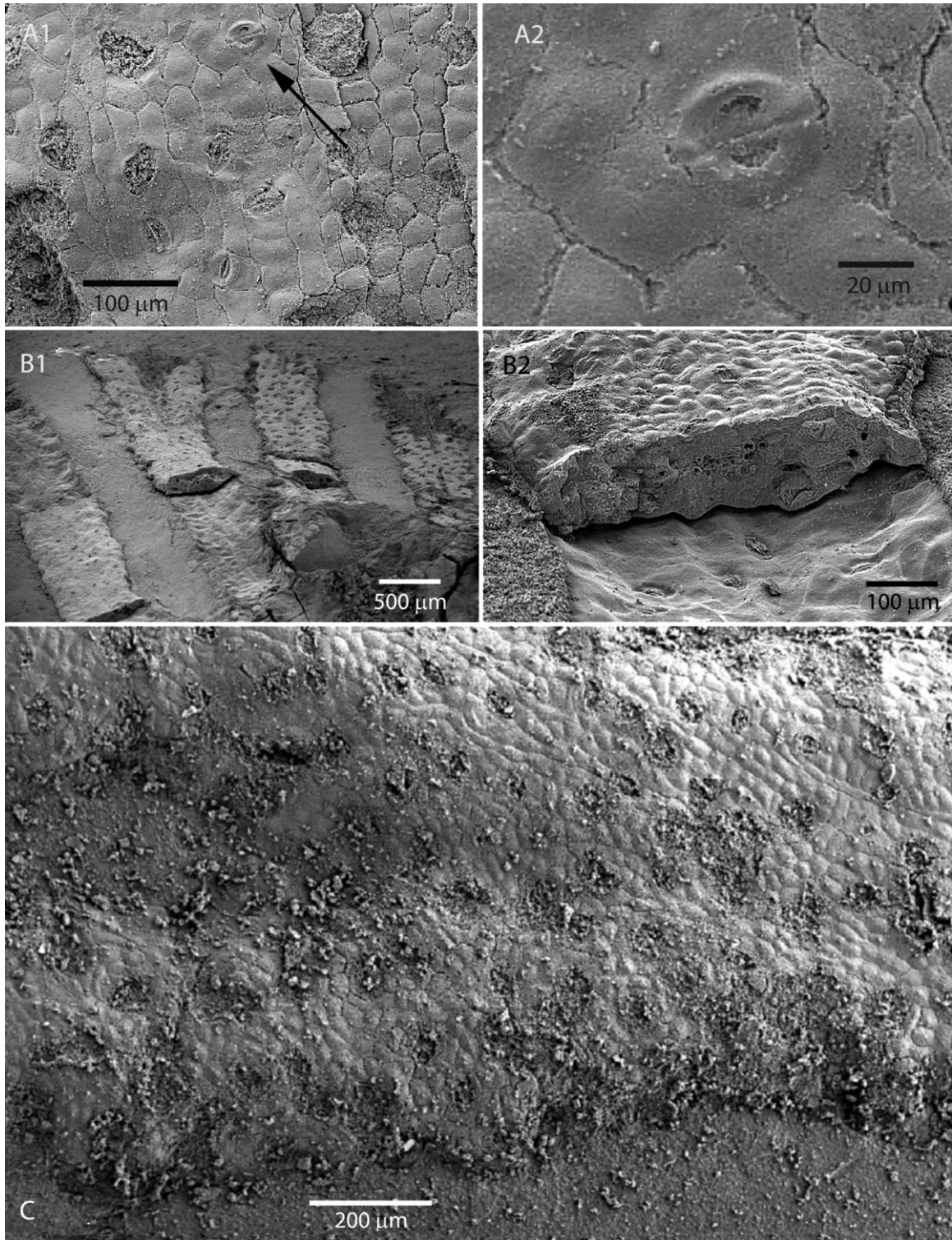
long. Stomatal complexes are scattered and rare in proportion to normal epidermal cells (fig. 9). The stomatal complexes and associated guard cells are oval, ~30 μm wide and 75 μm long, without preferential orientation. The stomatal apparatus is monocyclic. There are sparse but distinctive, features formed by the convergence of four or more epidermal cells to form a fenestra (fig. 9; fig. 10A, 10B). Though no structure is preserved, these are most likely trichome bases perhaps of a glandular nature.

Internally, the veins have tracheids with secondary wall thickenings that range from grooved annular rings, to densely packed scalariform, to alternating circular bordered pits (fig. 10C–10F, 10H). Pit apertures conform to the outline shape of the pit border and are either elongate or circular. On the basis of the distance between apertures, the pits are spaced 5.7 μm apart on average. The peculiar spherical appearance of these features results from their preservation as casts (fig. 10D). Near the base of the main rachis, distal to the petiole, rays (fig. 10G) and radially arranged tracheids (fig. 11) indicate the presence of secondary vascular or "woody" tissue. The rays range from 3 to more than 20 cells in height. On the basis of the preservational factors, the nature of the crossfield pitting is difficult to characterize, but there appear to be four pits per intersection (crossfield); however, it is possible to find areas in which there appear to be a greater or lesser number per field.

The adaxial and abaxial epidermal cells are somewhat irregular in shape, but most are isodiametric and approximately the same size (figs. 12, 13). Cells of the costal and intercostal regions differ slightly in shape and arrangement; the costal cells are squarer and slightly less irregular in shape and are not arranged in rows (figs. 13, 14).

Leaves are amphistomatic (figs. 13, 14). In laminar portions of the pinnae, stomatal complexes are dense and randomly oriented (figs. 12–14). Stomata are present in both the costal and intercostal areas of the lamina. The stomatal complex is generally monocyclic in morphology with two pairs of cells flanking the guard cells lateral to the long axis of the stoma. Another pair of polar cells marks the ends of the guard cells. It is possible that in some instances a third ring of cells surrounds these proximate subsidiary cells. Subsidiary cells average ~50 μm in diameter (on the basis of the measurement of 182 such complexes in fig. 12). Although the epidermal surfaces of the intercostal areas are poorly preserved (fig. 13), exquisite preservation was found in one specimen, USNM 530923 (fig. 14), in which the stomata are monocyclic and randomly oriented and distributed. The costal epidermal cells in the area midway to the leaf margin are of uniform size ($\div$50 μm) and shape (rhomboidal). No trichome bases were observed on any of the lamina fragments examined.

Internally, the laminae consist of a uniseriate adaxial epidermis, uniseriate palisade parenchyma immediately below the epidermis, spongy parenchyma beneath the palisade layer (cells distorted during preservation), and a uniseriate abaxial epidermis (figs. 15, 16). The total thickness of the leaf is ~0.4 cm (fig. 15C). The thickest observed palisade parenchyma is ~17.5 μm, thinning toward the pinnule margin (fig. 15D). Irregularly, cells up to 122 μm across, with circular bordered pitting on all walls, may occur in the spongy

from the midvein (figs. 3, 5). Of the interfascicular veins, some dichotomize and then anastomose. Anastomoses of tertiary veins may occur between interfascicular veins, between fascicular veins, or between interfascicular and fascicular veins. Other tertiary veins terminate blindly in the medial half of the lamina (figs. 3, 5). This results in only two or three of the interfascicular veins reaching the laminar margin.

Microfeatures. Several specimens are, in part, petrifactions, or casts, in which intricate surficial and internal cellular detail are preserved, extremely unusual for a deposit that primarily produces a compression flora. These features have been examined with LM and SEM.

The epidermis of the rachis is composed of elongate cells (fig. 9; fig. 10A, 10B), ~20 μm wide and from 54 μm to >450 μm

Fig. 14 *Auritifolia waggoneri*, SEM images of tertiary veins and costal epidermis. USNM 530923, from USNM locality 42292. Axial orientation cannot be determined because of the lack of preserved palisade cells. *A1*, Costal epidermis, arrow indicates stoma in *A2*. *A2*, Costal stoma with two guard cells and no subsidiary cells. *B1*, Oblique view of four veins, proximal end toward viewer. Note dichotomy in second vein from left. Also notice that the intercostal lamina of the leaf is not preserved. *B2*, Close-up of vein second to left in *B1*. Stomata are visible on the upper surface of costal epidermis. Impressions of stomata are also visible in the underlying clay showing that this leaf is amphistomatic. *C*, Epidermal surface, stomata are apparent but poorly preserved. Epidermal cells are not elongate, in contrast to those on the midvein of rachis.
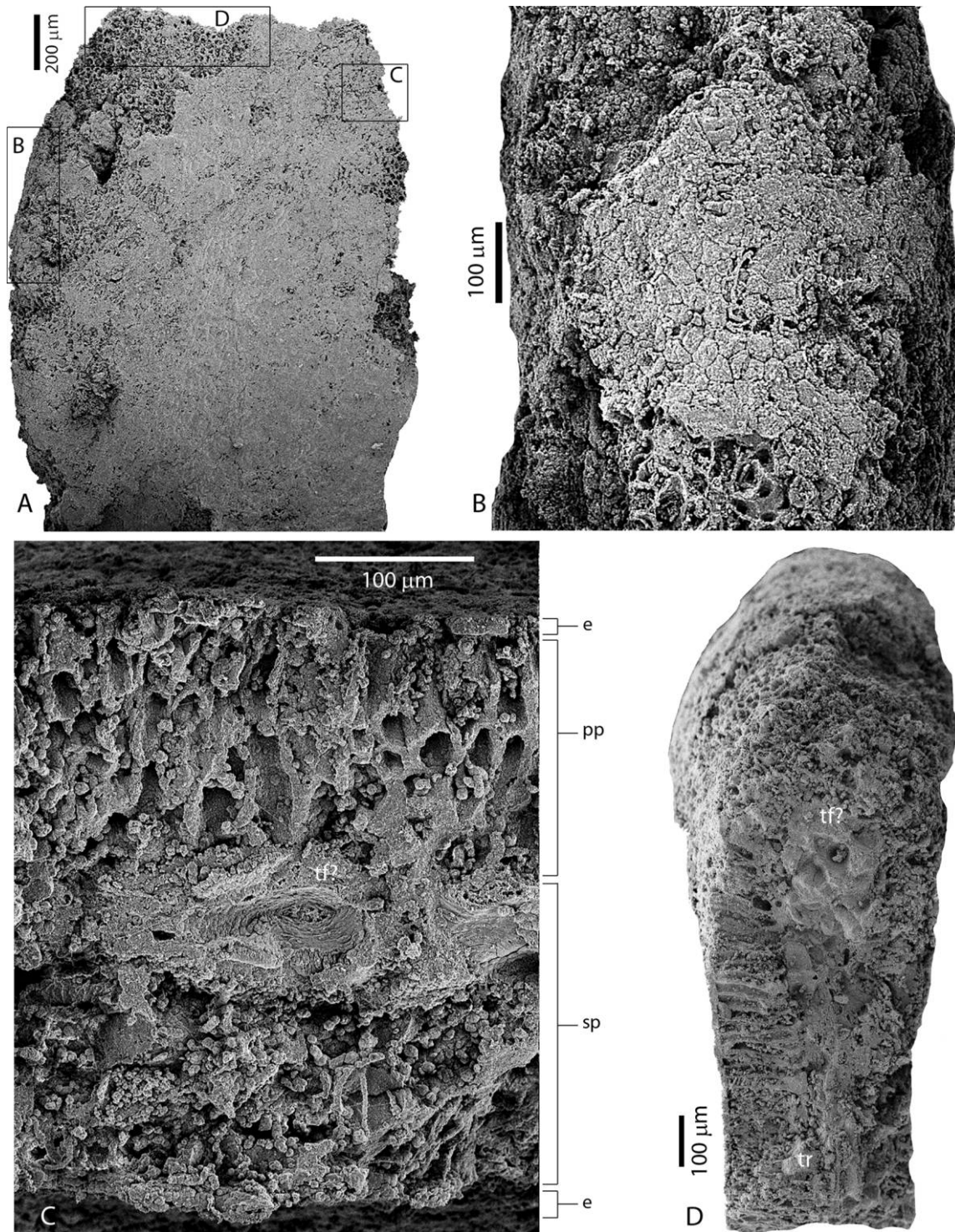
Fig. 15 *Auritifolia waggoneri*, SEM images of pinnule edge. USNM 528671, from USNM locality 41005. *A*, Scale bar = 200 μm; *B–D*, scale bars = 100 μm. *A*, Pinna adaxial surface, distal end at top of image. Palisade parenchyma beneath epidermis partly exposed. Boxes indicate locations of the other three elements of this figure. *B*, Enlargement of *A* rotated on vertical axis 90° to view edge of pinnule. Note lack of stomata. *C*, Enlargement of *A* rotated on vertical axis 90° then 90° on a horizontal axis to allow cross-sectional view. Cross section of pinnule, adaxial surface at top; *e* = epidermis; *pp* = palisade parenchyma; *sp* = spongy parenchyma; *tf?* = possible transfusion tissue, the surfaces of which are covered with pits. *D*, Rotation of *A* to edge-on view showing actual edge of pinnule. Cross section of pinnule edge with adaxial surface to left, edge to top. Single layer of palisade parenchyma thins and terminates toward the leaf edge. Effect somewhat exaggerated because of damage at upper left where epidermis and upper ends of palisade cells are missing. At edge, epidermis appears to overlie spongy parenchyma directly. Several large transfusion cells (*tf?*) have large number of pits between adjoining cells. Elongate tracheal elements (*tr*) of a vascular bundle are seen in the lower part of the image.
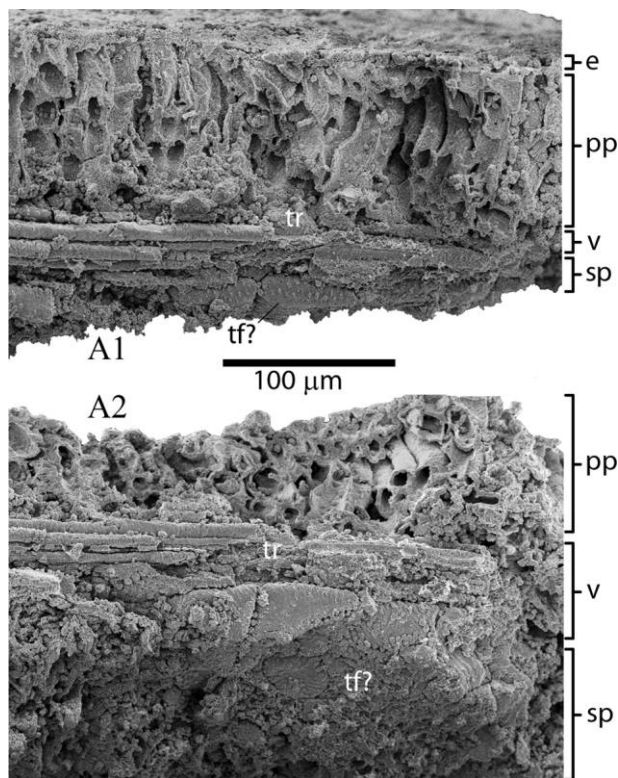
Fig. 16 *Auritifolia waggoneri*, SEM images of the vascular cells in the lamina. USNM 528671, from USNM locality 41005; scale bar = 100 μm; *e* = epidermis; *pp* = palisade parenchyma; *v* = vascular tissue; *sp* = spongy parenchyma; *tr* = tracheal elements; *tf?* = transfusion tissue. *A1*, Cross section of pinna, palisade cells viewed obliquely. Vein composed of several tracheids in lower part of image. Note relationship of transfusion tissues to tracheal elements of the vascular bundle. *A2*, View of same area of pinna as in *A1*, rotated to view from the bottom into the lower ends of the palisade cells showing ?transfusion cells.

parenchyma at the margins of the lamina, where they may be densely packed together (figs. 15–17).

Species Indet *Auritifolia sp.* (Figs. 20–24)

Geographic occurrences. North Robertson Unit (oil field), Gaines County, Texas.

Stratigraphic occurrences. Numerous levels between depths of 1780 and 2255 m below the surface within the Clear Fork Group (DiMichele et al. 2000).

Originally published as *Comia* sp., DiMichele et al. (2000, p. 527) describe this plant as follows: "Leaves are pinnately compound … There are three orders of venation in each pinna, organized in distinct fascicles … Secondaries arise from a main vein. At regular intervals some secondaries give rise to nonanastomosing, open dichotomous, strongly up-swept tertiaries that form a fascicle. Between fascicles are one or more individual secondaries that do not divide further. This distinct venation, though clearly related to callipterid venation, is often difficult to differentiate from the latter when preservation is poor or fragmentary."

Reexamination of compression plants and cuticle preparations indicates that vein anastomoses are present, although

the existence of veins with blind ending has yet to be demonstrated. In addition, because specimens of this plant are known only from drill core, the architecture of the frond is not known sufficiently to characterize it confidently. Thus, despite excellent cuticular preservation, the characters of venation as presently understood, particularly the unbranched interfascicular tertiaries and lack of blind ending tertiary veins, and the lack of clearly understood gross architecture of the leaf, preclude the identification of this plant as *A. waggoneri*. *Auritifolia* sp. may represent a distinct species. Assignment to *Auritifolia* is based on both venation and gross morphological features and epidermal similarity seen between petrifactions of *A. waggoneri* and cuticle preparations of *Auritifolia* sp. The venation of *Auritifolia* sp. is comioid (fig. 20*B*) with tertiary-vein anastomoses reminiscent of those seen in *A. waggoneri* specimen USNM 528207 (fig. 5). Leaf gross morphology also hints at *Auritifolia* form, for example, USNM 508171 (fig. 20*A*), in which there is an unequal division of what appears to be the terminal portion of the rachis, implying overtopping similar to that seen in *A. waggoneri* specimen USNM 508135 (fig. 4).

Occurrence. *Auritifolia* sp. is preserved in carbon-rich CaCO$_3$ muds of the Central Basin Platform of the Permian Basin. It is inferred that these plants grew on intermittently emergent islands in a shoreline setting (DiMichele et al. 2000).

Description

Compressions of this form occur in 15.24-cm drill core and are known only from subsurface samples. Thus, it is not possible to obtain a complete or even nearly complete specimen. On the basis of on multiple partial specimens, pinnule attachment and arrangement appear to be like *A. waggoneri*. The veins are three ordered and grouped in the comioid fascicular and interfascicular configuration. There is a clear constriction of the interfascicular veins at the margin and anastomoses are observable in some specimens. Thickness of the cuticle in these specimens obscures the finer details of the underlying vein patterns. Because of this and the limited size
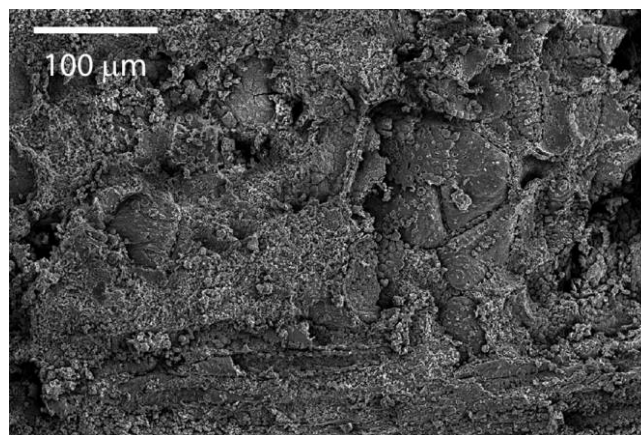
Fig. 17 *Auritifolia waggoneri*, SEM images. USNM 530923, from USNM locality 42292 of the ?transfusion cells showing their relationship to each other as well as to the surrounding spongy parenchyma and a vascular bundle; scale bar = 100 μm.
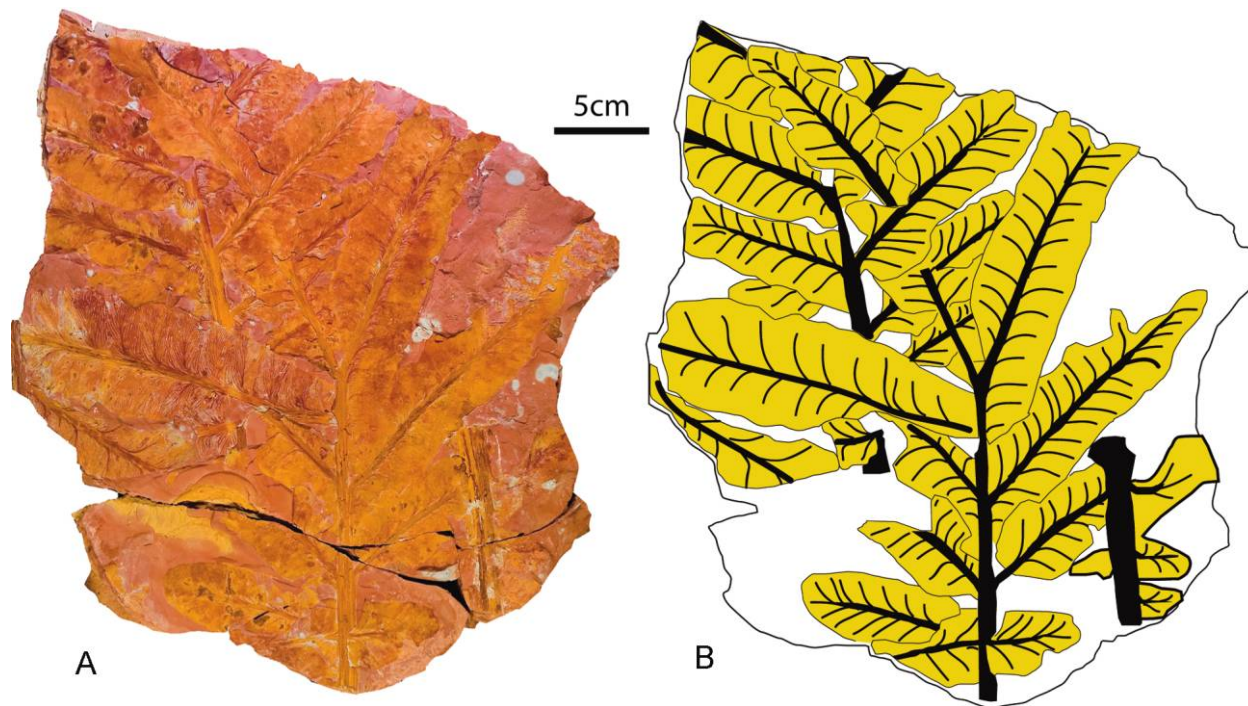
Fig. 18 *Auritifolia waggoneri*, leaf mat. USNM 530854, from USNM locality 41005; scale bar = 5 cm. *A*, Actual specimen. *B*, Line drawing of *A*. Portions of six individual fronds based on orientation, size, and superposition of elements.

and number of available specimens, the blind endings, which are so diagnostic of *A. waggoneri*, have not been observed.

Leaves of *Auritifolia* sp. are amphistomatic (fig. 21). Cuticles are very thick with very thick anticlinal walls. The epidermal cells of the adaxial surface are larger than those of the abaxial surface. The epidermis of the adaxial surface shows a differentiation into costal and intercostal fields, the latter being characterized by more rectangular, often somewhat elongated cells. The epidermis of the abaxial surface does

not show such a clear differentiation and consists entirely of isodiametric cells.

Stomatal complexes consist of two guard cells with very prominent cuticular half-circular flanges/flaps (fig. 22*B*, 22*C*) over their entire length, reaching up to ~10–15 μm deep. Although the adaxial surface is differentiated in costal and intercostal fields (figs. 23*D*, 24*A*), stomata occur in intercostal fields only. Guard cells sometimes show a delicate pattern of more or less parallel fine striae, so-called wood lamellae (fig.
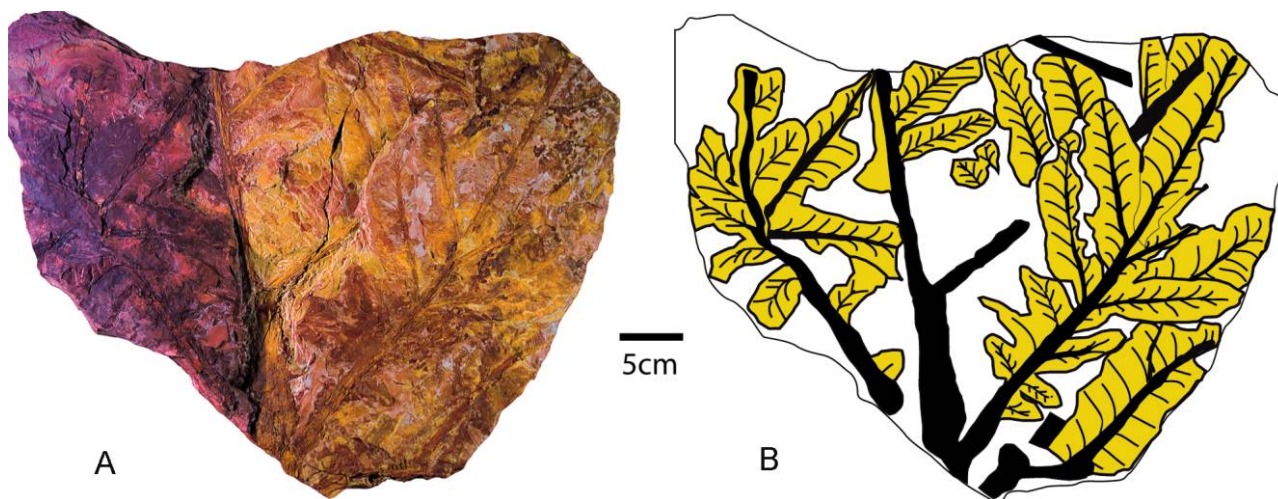
Fig. 19 *Auritifolia waggoneri*, leaves attached to branch or main trunk. USNM 530962, from USNM locality 41005; scale bar = 5 cm. *A*, Actual specimen. *B*, Line drawing of *A*.
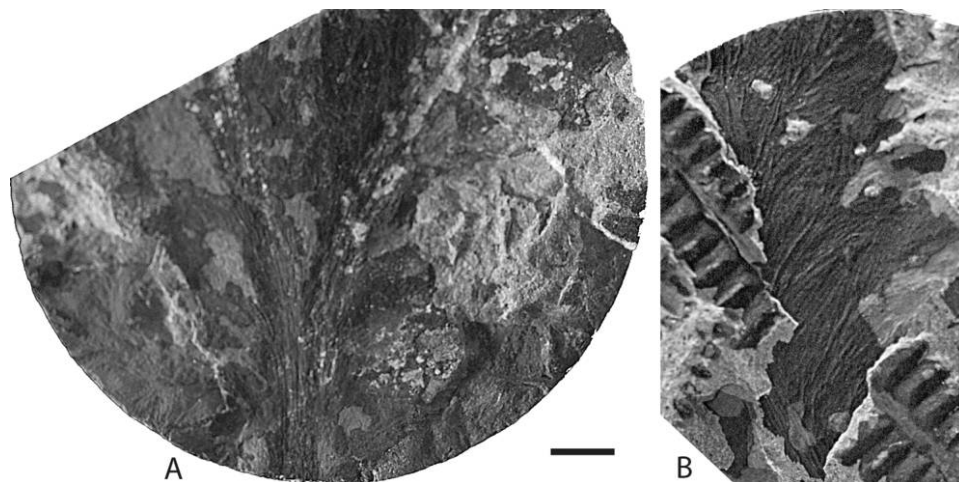
Fig. 20 *Auritifolia* sp. Two specimens from Gaines County, Texas; scale bar = 1 cm. *A*, USNM 508172, from USNM locality 41052. The ultimate bifurcation of the overtopping. *B*, USNM 508178, from USNM locality 41047. *Auritifolia* sp. is overlain by a fragment of the gigantopterid leaf *Delnortea abbottiae.*

24C). The anticlinal walls are very thick, 3.5–16 μm (average 8.5 μm) wide and cells often show additional thickenings or inward-projecting pegs at the cell corners. Costal fields consist of up to 10, usually 5–6 rows of more or less rectangular, often slightly elongate cells. Cells of the intercostal fields are 13.5–63 μm long (average 38 μm) and 7–21 μm wide (average 14 μm). Cells of the intercostal fields are isodiametric, 18–41 μm in diameter (average 28 μm). Stomata are monocyclic, rarely incomplete dicyclic, with four to six subsidiary cells, randomly distributed in the intercostal fields and deeply sunken. Occasionally, stomata are locally concentrated into denser clusters; in such cases, cell wall cutinization is often strong and adjacent stomata sometimes share one or two subsidiary cells. Stomata are irregularly orientated; the stomatal pore is 14–25.5 μm long (average 14.5 μm). Each subsidiary cell usually bears a centrally positioned solid papilla (fig. 24*B*); papillae often cover the stomatal pore.
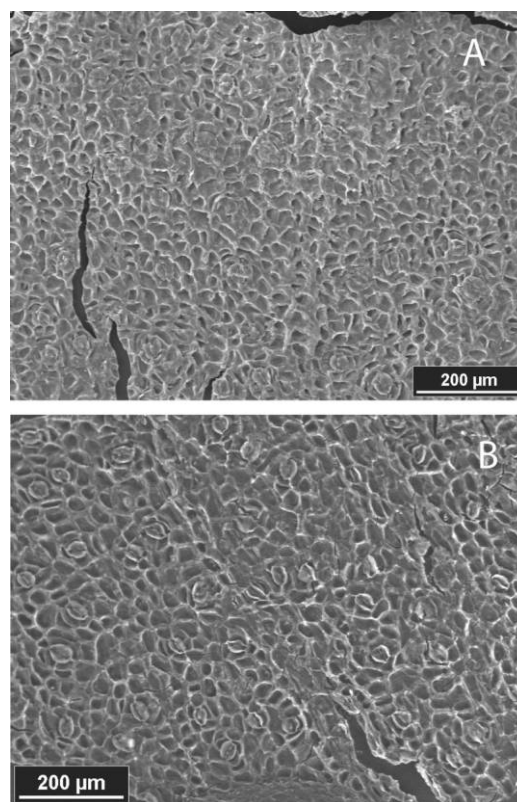
The cuticle of the abaxial surface (figs. 21*A*, 23*C*) is not differentiated into costal and intercostal fields and consists entirely of isodiametric cells, being 16–36.5 μm (average 25 μm) in diameter; anticlinal walls are 2.5–9.5 μm (average 5.5 μm) wide. Stomata are more or less regularly distributed but not orientated in a specific direction. Stomata are similar in shape to those of the adaxial surface but slightly smaller; stomatal pores are 16–20.5 μm (average 13 μm) long.

The cuticles of the upper and lower epidermis are clearly differentiated as in many pteridosperms. It can be assumed that the costal fields are overlying the veins. However, although larger pieces of cuticle ($\geq$1.5 cm) have been recovered, it is not possible to recognize a clear venation pattern on the cuticles. The lower surface is very uniform. The cuticle is very thick as are the anticlinal walls. Noteworthy are the small pegs of cuticular material at the cell corners.

Discussion

The two forms of *Auritifolia* described in this article differ subtly in morphology. They also differ in their inferred

habitats of growth. These different growth environments may have had a major effect on the morphology of the plants, such that the differences observed may reflect phenotypic plasticity. However, the environments of growth are sufficiently different

Fig. 21 *Auritifolia* sp., SEM images of the cuticle from USNM locality 41044; scale bars = 200 μm. *A*, Cuticle of the abaxial surface pb-1–3 USNM 530986a. *B*, Cuticle of the adaxial surface pb-2–9 USNM 530987a.
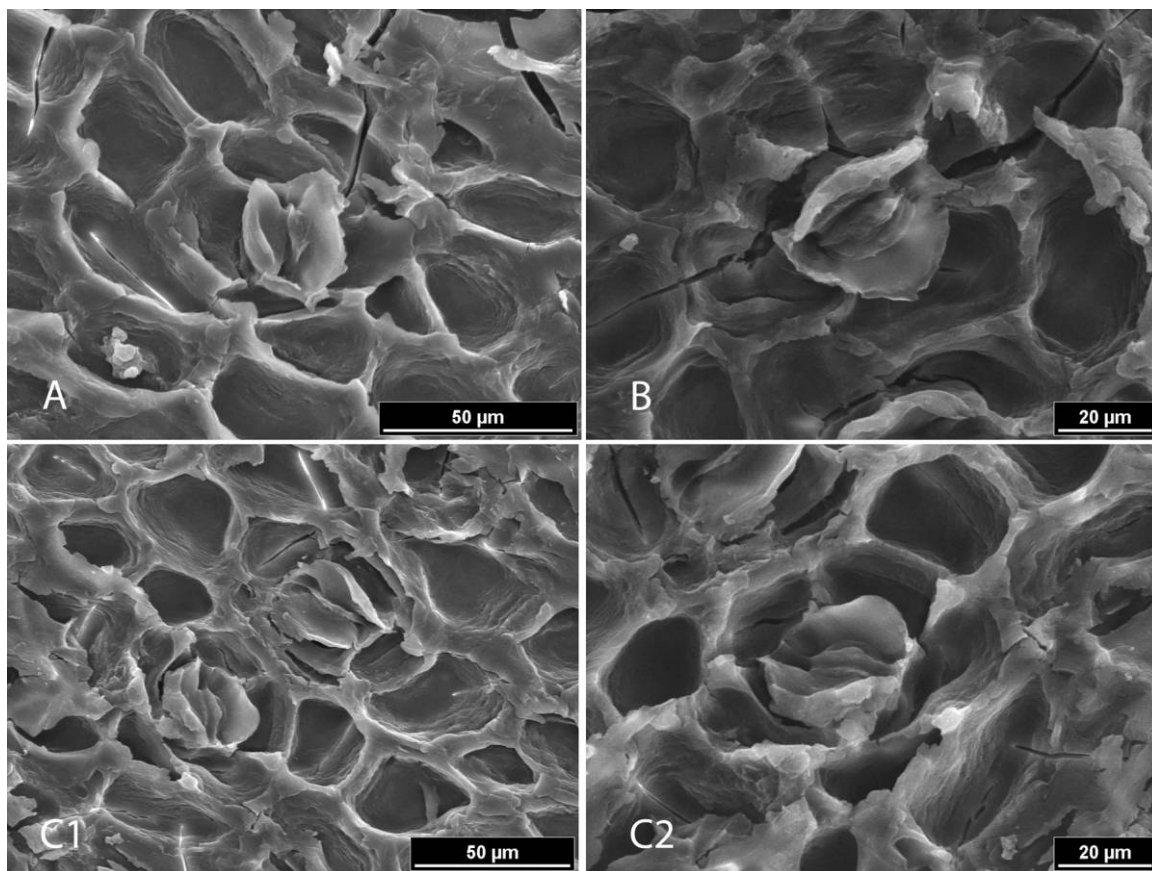
Fig. 22 *Auritifolia* sp., SEM images of internal views of stomatal complexes, from USNM locality 41044. *A*, *C1*, Scale bars = 50 μm. *B*, *C2*, Scale bars = 20 μm. Note the cuticular flanges on the guard cells. *A*, Abaxial stoma pb-2–8 USNM 530987d. *B*, Adaxial stoma pb-2–2 USNM 530987b. *C1*, Adaxial surface; overview with two adjacent stomata pb-2–3 USNM 530987c1. *C2*, Adaxial surface close-up of stoma in lower left corner of C1 pb-2–7 USNM 530987c2.

in terms of the physical conditions they represent that it is reasonable to expect them to be occupied by different species.

Auritifolia waggoneri is widespread in rocks of the Early Permian middle Clear Fork Formation. Specimens occur in channel-fill sediments of various kinds, ranging from siltstone to fine sandstone bars deposited in active channels, to laminated claystones deposited in abandoned channels. In the latter deposits, inferred to be ponds, leaves are found both in isolation and in dense mats (fig. 18). In some of the pond deposits, conditions existed to allow the petrifaction of the cellular material by the iron mineral, goethite. This goethite may preserve the cell walls (fig. 12*B*) or may create casts of original cellular morphology (fig. 10*D*–10*F*). At most sites, the specimens collected are preserved as compressions without anatomy. Remnant organic plants have been replaced by iron oxides of varying hydration states thus giving the specimens a range of colors from yellow to red to blue green.

In north-central Texas, *A. waggoneri* overlaps with *Comia* through much of the section. However, in the upper part of its range, *A. waggoneri* is very common and *Comia* is extremely rare, whereas in the lower part of the ranges of these taxa, *Comia* is abundant and *Auritifolia* rare. Paleosol evidence (Tabor and Montañez 2004) indicates a general drying trend

through Clear Fork time. The rocks of the upper Clear Fork Formation, from which plant fossils are not known, are a complex of evaporites and weakly developed paleosols, probably deposited or developed in a coastal-plain setting. This general climatic shift corresponds to a shift in the sedimentology of the strata and thus suggests that there may be a change in the stream and pond-side environments that favors *Comia* in the lower beds and *A. waggoneri* in the middle beds.

The extreme variability in frond architecture of *Auritifolia* (fig. 8) falls within the range of morphological parameters for the frond shape and size of *A. waggoneri* as diagnosed. The aspects of leaf architecture that define *Auritifolia* include the overtopping development and the increase in size of pinnae from basalmost to most distal. The diagnostic venation, aside from its general comioid character, includes the constriction of the interfascicular zone at the laminar margin. The specific diagnostic features, in addition to those for the genus, are quantitative characteristics and the qualitative feature of the anastomoses and blind endings of the tertiary veins.

A few apparently "aberrant" specimens have been noted (fig. 7; fig. 8*A*, 8*D*–8*G*). The morphological variation that these specimens document could have been caused by a number of factors, such as developmental stages in plant growth,
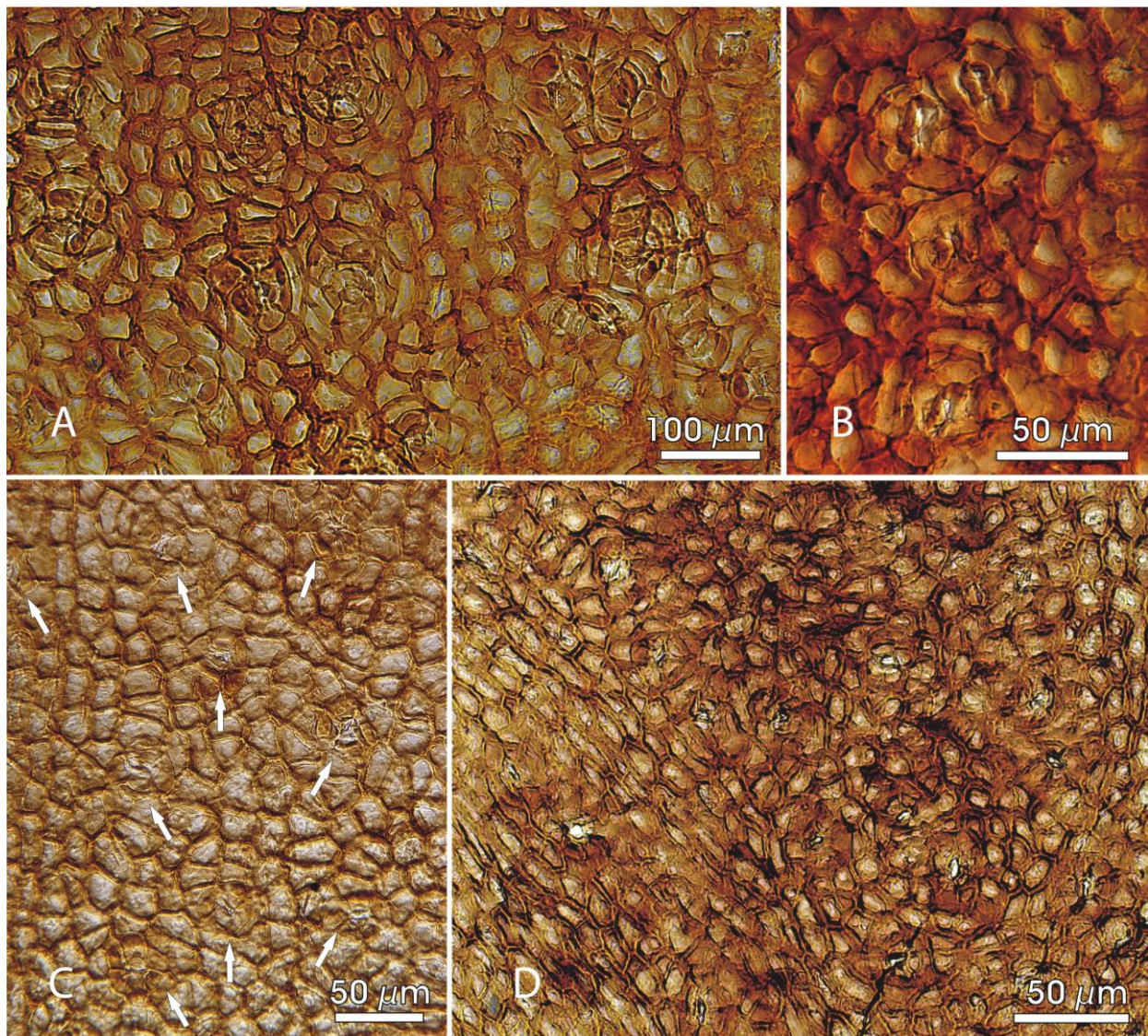
Fig. 23 *Auritifolia* sp., LM images of cuticles. *A*, Scale bar = 100 μm; *B*, *C*, scale bars = 50 μm. *A*, Cuticle of the adaxial surface with several stomata USNM 530959, from USNM locality 41044. *B*, Cuticle of the adaxial surface with three stomata USNM 530955, from USNM locality 41044. *C*, Cuticle of the abaxial surface with several, regularly distributed stomata (arrows) USNM 530944, from USNM locality 41044. *D*, Cuticle of the adaxial surface with a costal field (left) with more or less rectangular cells and an intercostal, stomatiferous field (right) with isodiametric cells USNM 530953, from USNM locality 41044.

position in the crown, or local conditions such as dry versus wet years.

An interesting feature seen on the holotype of *A. waggoneri* as well as a few other specimens, but by no means a majority of them, appears in the presence of many randomly positioned, oval or circular lesions, some as large as 0.03 cm in greatest dimension (figs. 4, 6). These are delimited by a dense, dark outline, within which there are no observable contents. Their origin is unknown, but their irregular distribution suggests that these objects are not indigenous to the plant but are likely due to fungal infestation or insect damage.

The woody nature of the petiole and lower part of the rachis demonstrated by the radially arranged tracheids with rays indicates the presence of secondary xylem (figs. 10*G*,

11) and may indicate that the leaf remained attached to the main stem of the plant for more than one growing season. In one instance, parts of several leaves have been found in what appears to be physical connection to a larger axis (fig. 19). Unfortunately, the specimen is not complete enough to really shed light on the overall architecture of the *Auritifolia* plant. However, a woody petiole base does suggest attachment to a woody stem of some sort, indicating that *Auritifolia* was not an herbaceous plant and probably was at least a shrub or small tree, if not something considerably larger.

Auritifolia waggoneri is the most abundant comioid plant in the USNM collections from the Clear Fork Formation in north-central Texas. Leaves are found both in isolation and in dense mats (fig. 18).
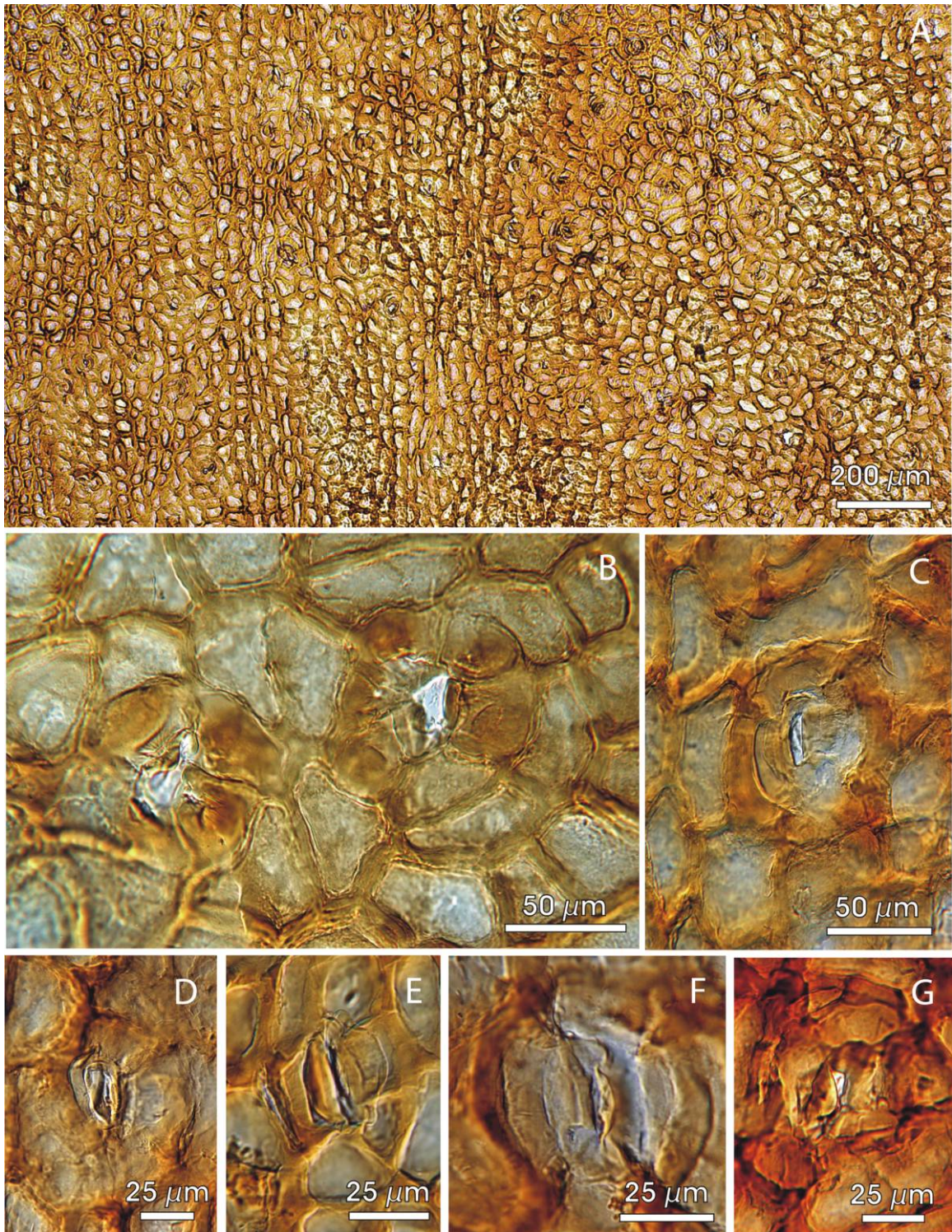
Fig. 24 *Auritifolia* sp., LM images of cuticles. *A*, Scale bar = 200 μm; *B, C*, scale bars = 50 μm; *D–G*, scale bars = 25 μm. *A*, Cuticle of the adaxial surface with intercostal field with stomata and costal fields without stomata USNM 530947, from USNM locality 41044. *B*, External view of two stomata showing subsidiary cells with solid papillae USNM 530944, from USNM locality 41044. *C*, Internal view of a stomatal complex showing the finely striated wood lamellae (right guard cell) USNM 530953, from USNM locality 41044. *D*, Internal view of stoma with cuticular flanges on the guard cells, USNM 530953, from USNM locality 41044. *E*, Internal view of stoma with cuticular flanges on the guard cells, USNM 530948, from USNM locality 41044. *F*, Internal view of stoma with cuticular flanges on the guard cells, USNM 530953, from USNM locality 41044. *G*, Internal view of stoma with cuticular flanges on the guard cells, USNM 530955, from USNM locality 41044.

Auritifolia compares most closely with *Comia* among contemporary, late Paleozoic plants. The venation is coarse, in comparison to that of *Comia*, but exhibits comioid morphology with fascicles and interfascicular zones. There is a marked spatial constriction between fascicles at the laminar margin, not seen in species of *Comia* (Mamay et al. 2009). Both *Auritifolia* and *Comia* are closely associated with peltaspermous reproductive organs of the *Sandrewia/Autunia* type, including in deposits where these taxa occur independently and with few or no other plants of possible peltaspermous affinity. Thus, one may suspect affinity at some level in the phylogenetic hierarchy with the Peltaspermales, but exactly how these plants are related awaits a fuller analysis of phylogenetic relationships with the peltasperms.

Auritifolia sp. from west Texas grew in a coastal environment, probably on small, intermittently emergent islands, under a seasonally wet climate and subject to salt-spray effects. Morphologically, the plant has many features typical of a xerophyte, possibly even one with succulent habit. The very strong cutinization and the deeply sunken stomata with solid papillae overarching the stomatal pores are typical xeromorphic features. Such xeromorphic features are seen in plants growing under arid conditions or other habitats where they experienced water stress, i.e., in soils with high concentrations of specific ions, such as peat mires and coastal, brackish habitats. On the basis of the cuticle alone, it is not possible to differentiate among the possible causes of xeromorphic morphology; for a detailed discussion on this topic, see Krings et al. (2005). However, the thick layer of carbonaceous material inside the leaves, representing the mesophyll, and the xeromorphic characters mentioned above suggest that *Auritifolia* sp. was a succulent plant.

Detailed studies of cuticles have been carried out for very few plants from the Lower Permian of North America. Differences such as those described above between the cuticles of the adaxial and abaxial surfaces of *Auritifolia* sp. have frequently been observed in Late Paleozoic pteridosperms, e.g., in *Glenopteris splendens*, a probable peltasperm from the Lower Permian of east-central Kansas (Krings et al. 2005). *Glenopteris splendens* has robust pinnate to apically pinnatifid compound leaves with amphistomatic pinnules (Krings et al. 2005). Even though the foliage of this latter taxon is thick enough to be classified as xeromorphic, the cuticles of *Auritifolia* sp. described here are much thicker than those of *Glenopteris*. This latter taxon also differs from *Auritifolia* sp. in having small warts on the anticlinal walls in the shape of

the stomata and in the occurrence of stomata in the intercostal fields of the adaxial cuticle.

The evolutionary relationship of the comioids must remain indeterminate until evidence of their reproductive biology can be adduced. Occasional co-occurrence of *A. waggoneri* with *Sandrewia/Autunia* type fructifications, typical of peltasperms (Kerp 1988), leads us to suggest peltaspermalean affinity (DiMichele et al. 2005). However, this must be considered only as an informed inference, given our present state of knowledge. If peltaspermalean, these new taxa contribute to a growing awareness of the importance of peltasperms in both tropical and north-temperate ecosystems during the Permian (Naugolnykh and Kerp 1996; Naugolnykh 1999; Kerp 2000), a time when this group may have been undergoing a rapid and morphologically wide-ranging evolutionary radiation.

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