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THREE NEW SPECIES OF *PALMOXYLON* FROM THE EOCENE GREEN RIVER FORMATION, WYOMING

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Abstract.— Silicified, upright axes of *Palmoxylon* are abundant in the Green River Formation in Eden Valley, Wyoming. Three new species of *Palmoxylon*, as well as the previously described *Palmoxylon macginitiei* Tidwell et al., were collected. These new species are *P. edenense*, *P. contortum*, and *P. colei*. They are compared to *P. macginitiei* and other anatomically similar *Palmoxylon* species. *Palmoxylon edenense* appears to be the most abundant species at this locality.

Silicified remains of palm axes are very abundant in the Green River Formation in Eden Valley, Wyoming, near the collection site of *Palmoxylon macginitiei* (Tidwell et al., 1971). For the most part, these remains consist of axes in growth position surrounded by tough, silicified *Chlorellopsis* algae. However, one axis (*P. colei*) was collected lying down, as though it had fallen prior to fossilization. Weathered fragments eroded from these axes are found on the ground surface throughout the area.

The upright specimens occur in groups of threes and are arranged in either a triangular or linear alignment. Although the investigated specimens in these groupings were of the same species (either *P. macginitiei* or *P. edenense*), no rhizomous or soboliferous connections were uncovered between them.

With the exception of *Palmoxylon contortum*, the specimens vary from 6 to 12 inches in diameter and are generally 2 to 3 feet high. The incomplete horizontal stem of *P. colei* is nearly four feet in length. The preservation of the specimens is essentially the same as that discussed for *P. macginitiei* (Tidwell et al., 1971).

Palmoxylon edenense Tidwell, n. sp.

Figures 1, 2, 5A, 9

Stem

Central Zone: This zone is characterized by the usual random arrangement of its vascular bundles. The bundles vary in size from 700 to 900 μ high by 500 to 600 μ wide. There are approximately 85 bundles per cm^2. The f/v ratio of these bundles is 3:1, although

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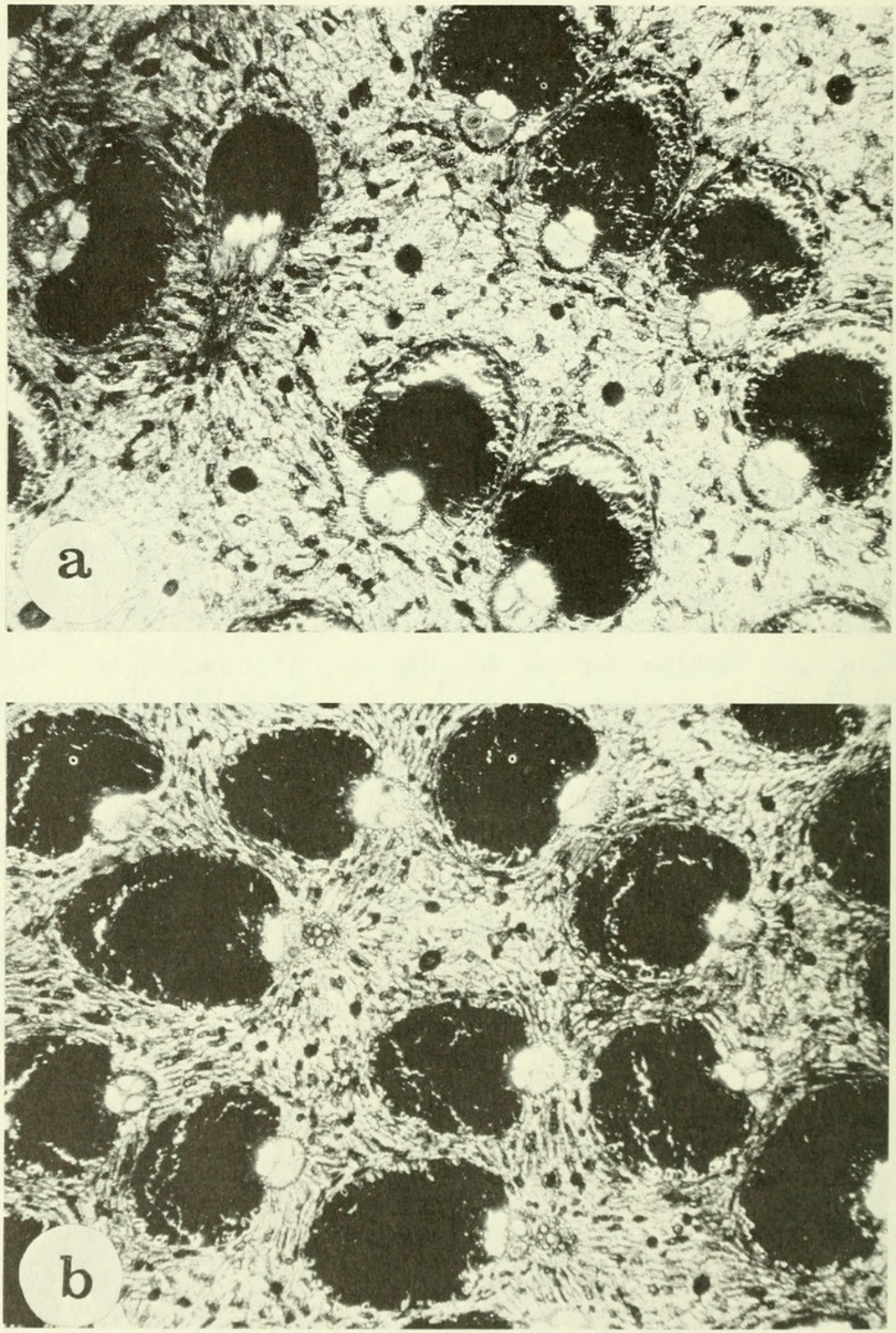

Fig. 1. *Palmoxylon edenense*. Cross-sections illustrating bundles of the (A) subdermal and (B) dermal zones (30X each).

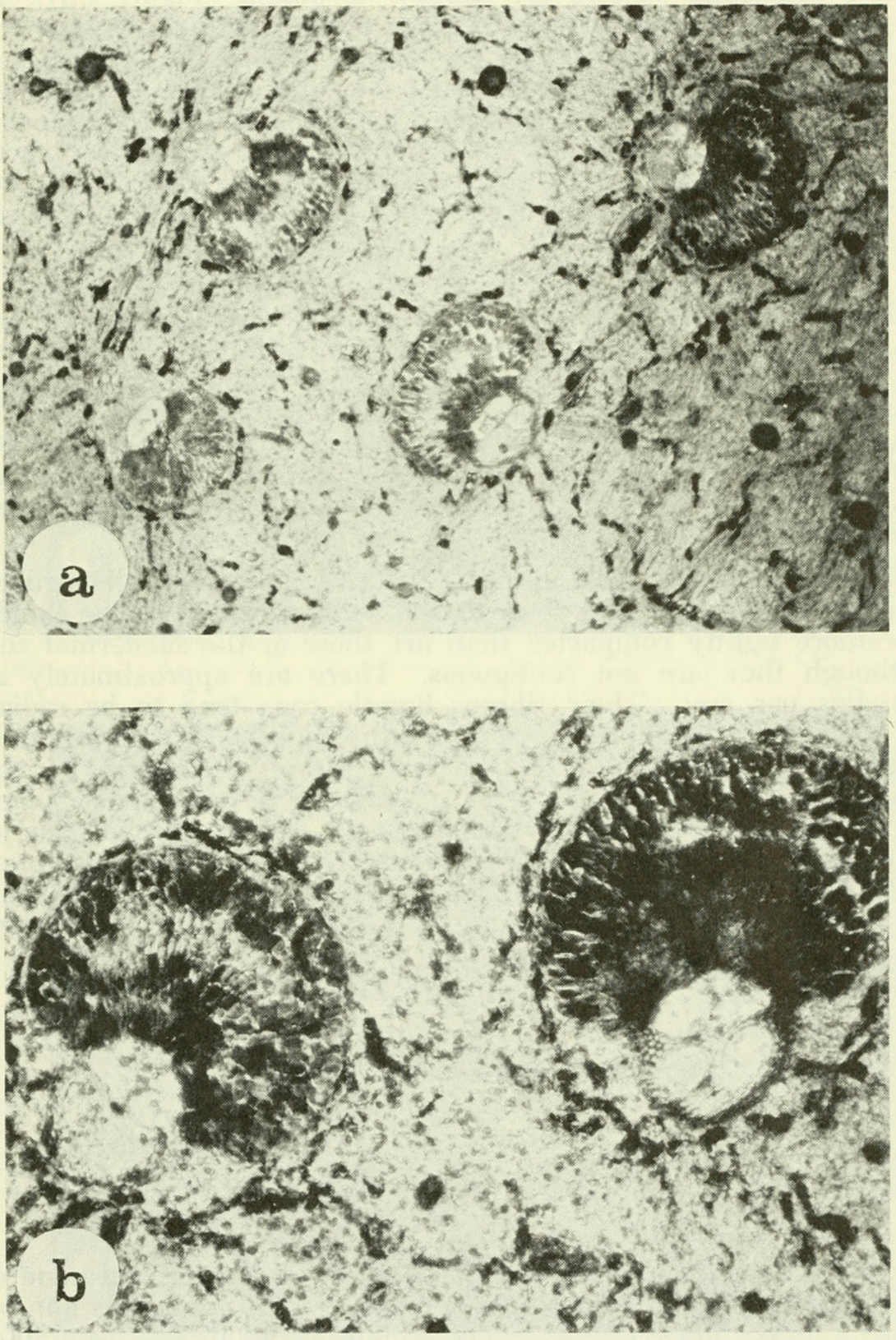

Fig. 2. *Palmoxylon edenense*. A. Cross-section of the central zone (30X). B. Enlarged bundles of the central zone (60X).

this may vary slightly (3.5:1.0). The fibrous bundle cap is oval to flabellate, having a shallow median sinus with rounded auricular lobes. Auricular sinuses are shallow to absent (Figure 2B). The cap is encased by one or two layers of tabular parenchyma, whereas radial parenchyma surrounds the vascular tissue. The bundles are typically bivascular, with metaxylem elements 78 to 91 μ in diameter and protoxylem elements varying from 25 to 35 μ. The phloem is not structurally preserved. The ground tissue is tightly compacted, consisting of elongated parenchyma cells. Numerous fibrous bundles, 350 per cm^2, varying in diameter from 52 to 104 μ are present but lack stegmata.

Subdermal Zone: Bundles of this zone tend to be irregularly oriented near the central zone and more or less regularly aligned close to the dermal zone. These bundles are similar in overall shape to those of the central zone, although their bundle caps are larger. The f/v ratio of the bundles is 5:1. There are approximately 100 bundles per cm^2 ranging in size from 600 to 700 μ high to 400 to 500 μ wide. The reniform bundle cap is usually as high as it is wide. The bundles are bivascular, and the size and shape of their vessel elements is similar to those of the central zone.

Cortical and Dermal Zone: The bundles are all regularly oriented with their caps towards the stem periphery. The bundles are more tightly compacted than are those of the subdermal zone, although they are not contiguous. There are approximately 205 bundles per cm^2. Their fibrous bundle caps tend to be radially elongated. The bundle f/v ratio of this zone is 7:1. The bundles, which are 600 to 800 μ high by 280 to 470 μ wide, are smaller than those in the other zones. As in the other zones, the fibrous cap is surrounded by tabular parenchyma, and radial parenchyma ensheaths the vascular tissue. The xylem contains two metaxylem elements that average about 50 μ in diameter. The radial and tabular parenchyma composing the ground tissue is compact. Numerous fibrous bundles and leaf traces appear throughout his zone.

Repository.— Brigham Young University, 916 (Holotype)
Locality.— Eden Valley, Wyoming
Horizon.— Green River Formation
Age.— Eocene

Palmoxylon colei, Tidwell, n. sp.
Figures 3, 4, 5B

Stem

Central Zone: The vascular bundles of the central zone are irregularly oriented and loosely compacted. This zone has approximately 115 bundles per cm^2. The bundles range in size from 500 to 600 μ in both height and width. Their f/v ratios vary from 2.5:1 to 3:1. The bundle cap fits Stenzel's *Reniformia* group (Stenzel, 1904) by having rounded auricular lobes with shallow auricular sinuses. The median sinus is only slightly indented, giving the

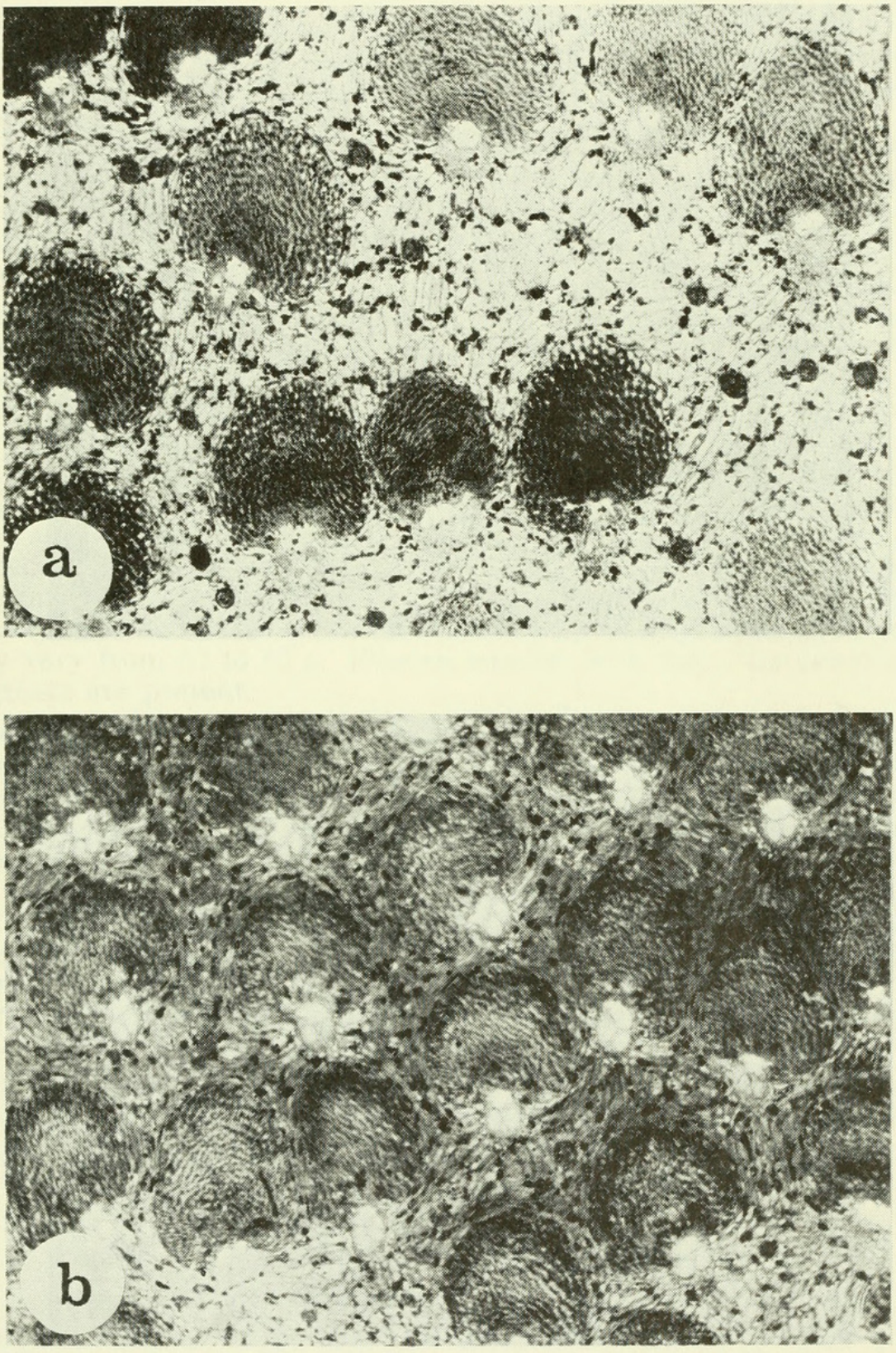

Fig. 3. *Palmoxylon colei*. Cross-sections of the (A) subdermal and (B) dermal zones (30X).

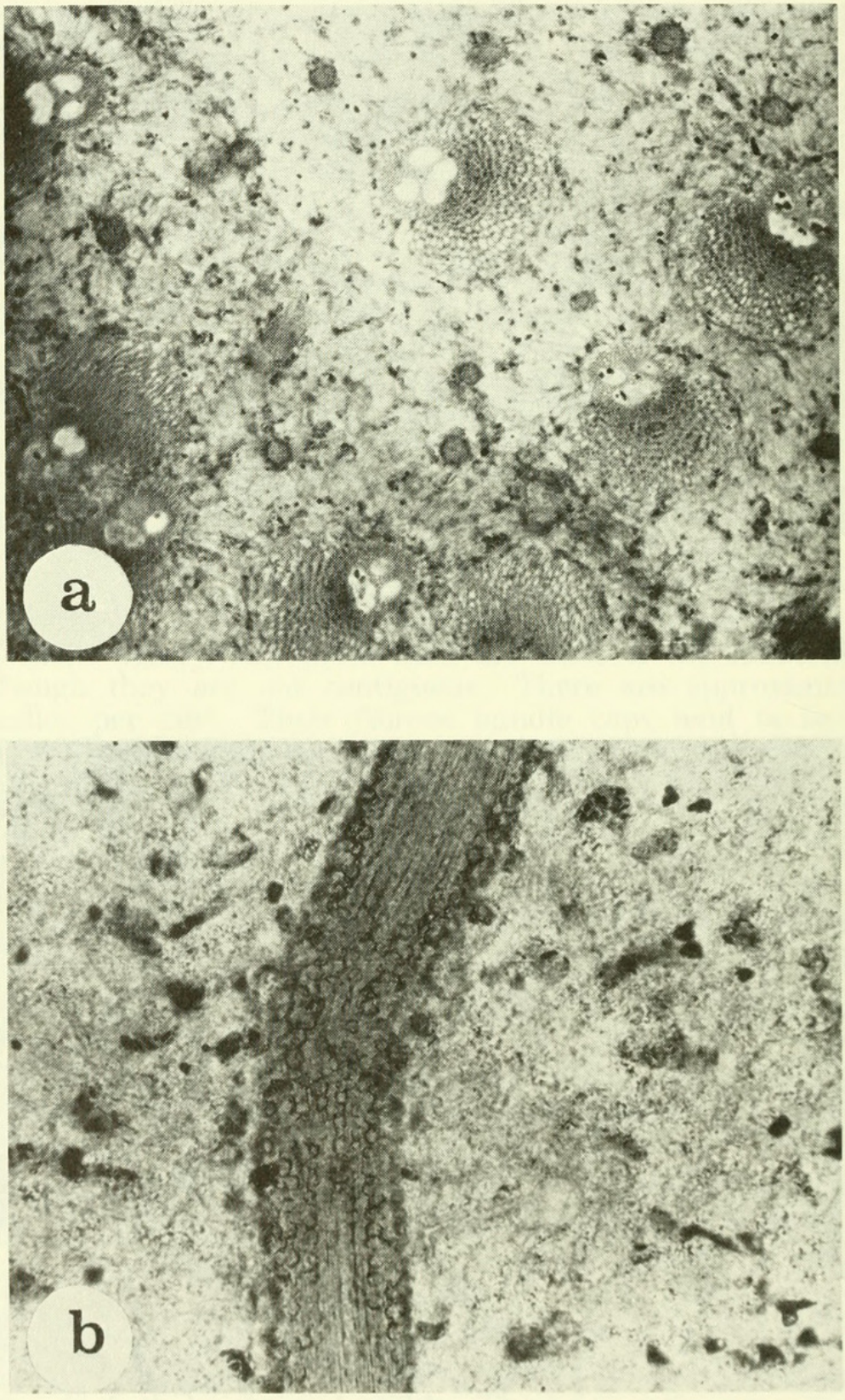

Fig. 4. *Palmoxylon colei*. A. Cross-section of the central zone (30X). B. Longitudinal section of a fibrous bundle demonstrating the stegmata along its surface (240X).

bundle cap its characteristic kidney shape (Figure 4A). The fibrous caps are encased by one or two layers of tabular parenchyma, but the vascular portion is encircled by radial parenchyma. The bundles are typically bivascular and the metaxylem elements are 65 to 85 μ at their widest diameters. The protoxylem, when present, varies from 30 to 40 μ in diameter. The phloem is not structurally preserved.

The ground tissue consists of thin-walled, tightly compacted, tabular and radial parenchyma, and has approximately 290 fiber bundles per cm^2. These bundles exhibit characteristic stegmata, and their diameters vary from 78 to 120 μ (Figure 5B).

Subdermal Zone: The bundles of this zone are irregularly aligned near the central zone and regularly aligned near the dermal zone. There are approximately 160 bundles per cm^2 in this region. The bundles are slightly larger than those of the central zone, being approximately 600 to 750 μ high and 500 to 650 μ wide. They have an f/v ratio of about 6:1, although this may vary slightly from bundle to bundle. The bundles are basically the same shape as those of the central zone, although the fibrous cap may approach a sagitate form in some. The presence of departing leaf traces that are attached to the vascular portion of several of the bundles is also notable. The bundles are commonly bivascular but may be trivascular. The metaxylem vessels are generally about 75 μ in diameter, although they vary from 65 to 85 μ. Fibrous bundles with their characteristic stegmata are present.

Cortical and Dermal Zone: The bundles of the cortical and dermal zone are tightly compacted, with approximately 230 bundles per cm^2. They are regularly aligned and have an f/v ratio of about 8:1. The bundle caps are reniform in shape but are elongated radially. The caps have rounded lobes and the auricular sinuses of the cap are shallow to nearly absent. The bundles are approximately 650 μ high and 400 μ wide. There are commonly two, occasionally three, metaxylem elements per bundle. Each element has an average diameter of 52 μ.

This specimen was named for its collector, Mr. Walter N. Cole, of Provo, Utah.

Repository.— Brigham Young University, 917 (Holotype)

Locality.— Eden Valley, Wyoming

Horizon.— Green River, Formation

Age.— Eocene

Palmoxylon contortum Tidwell, n. sp.

Figures 6, 7

Stem

The vascular bundles of all the zones are essentially the same size and shape, with the only observable difference being the degree of compaction. The number of bundles per cm^2 varies from 350 in the central zone to 500 in the dermal zone. They are tightly ap-

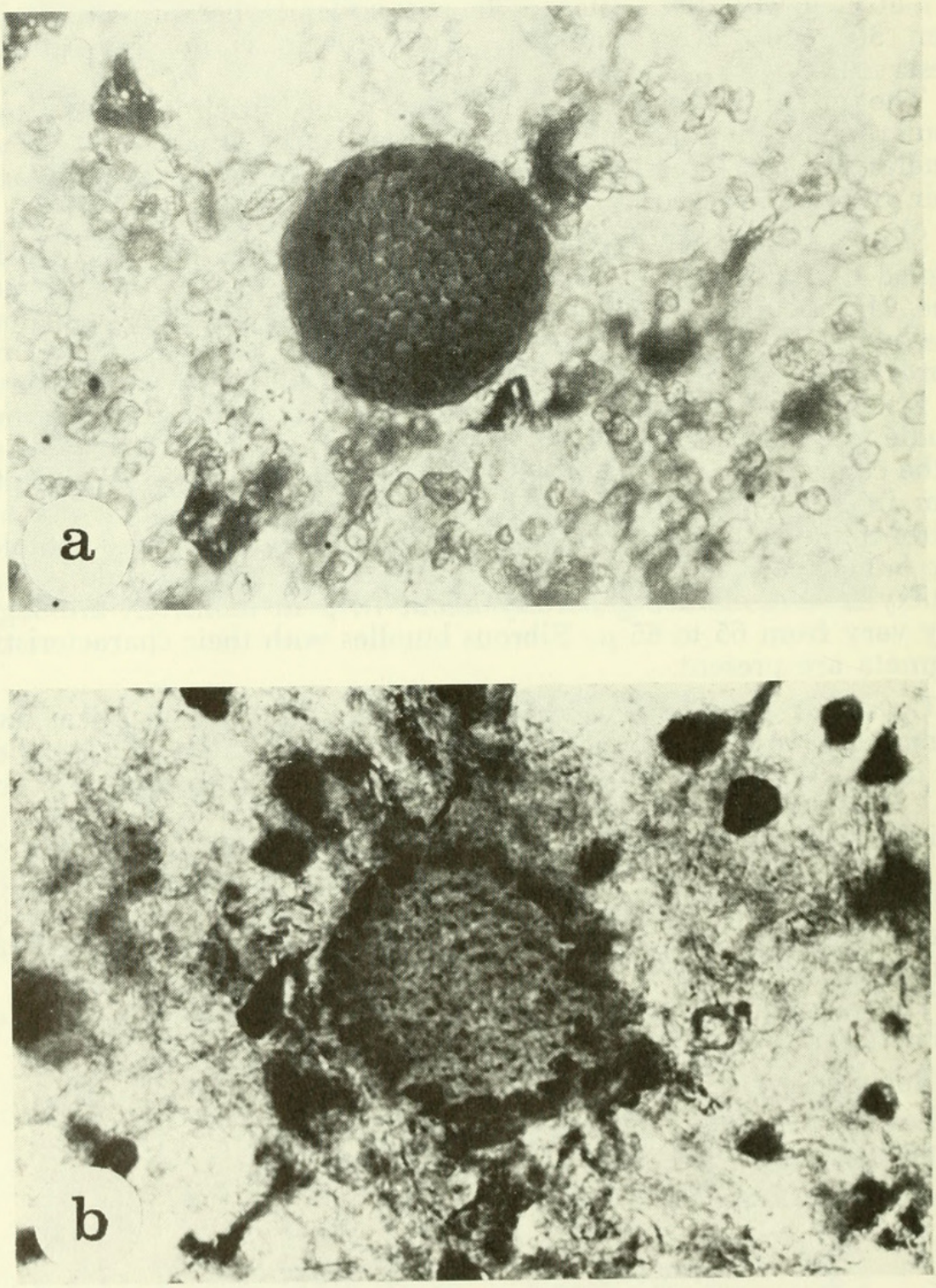

Fig. 5. A. Cross-section of a fibrous bundle of *Palmoxylon edenense*. B. A fibrous bundle of *P. colei* illustrating the stegmata surrounding the fibers. Both are 160X.

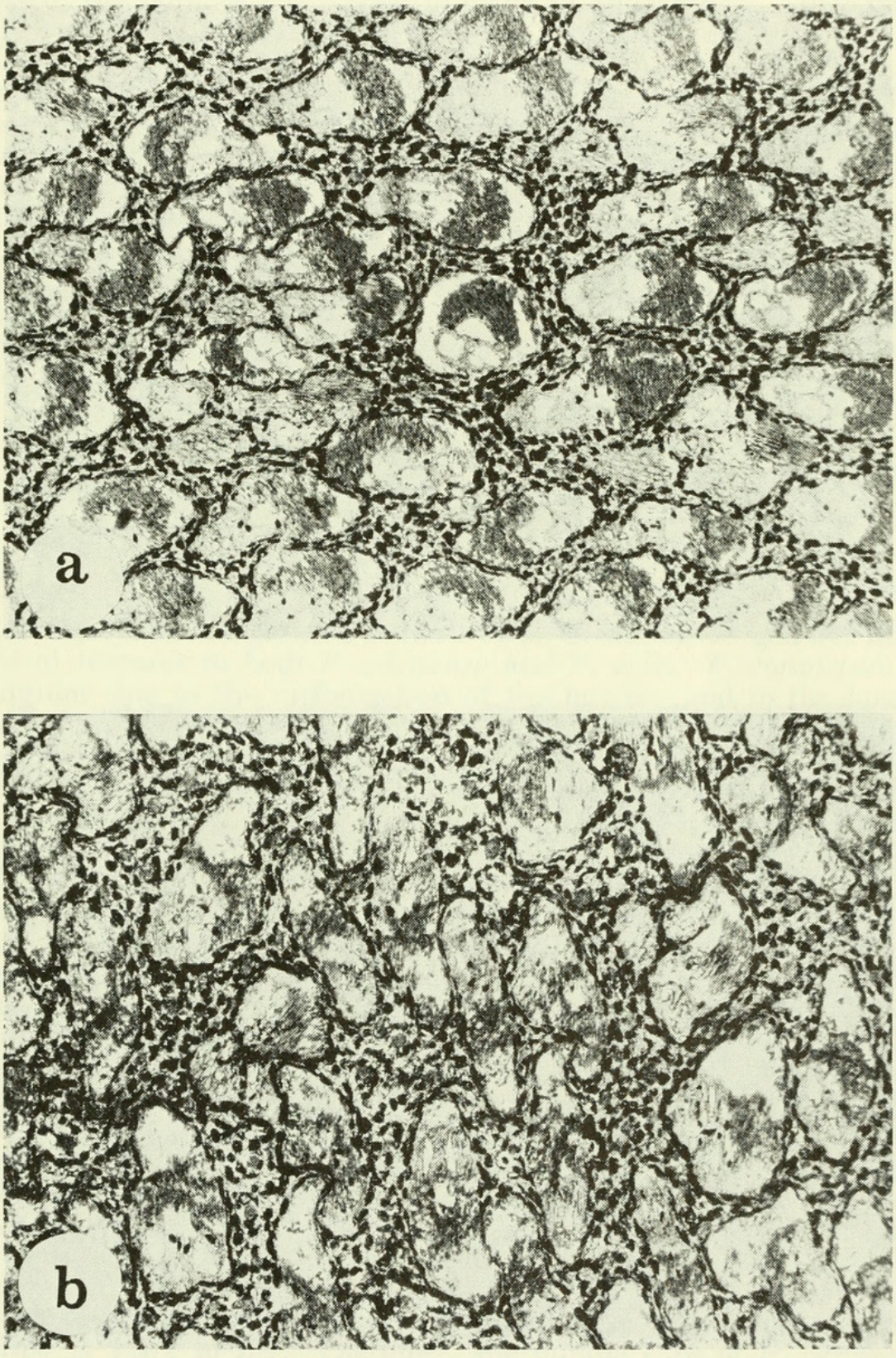

Fig. 6. *Palmoxylon contortum*. Cross-sections of the (A) dermal and (B) central zones showing the extreme closeness of the bundles causing their distortion (30X).

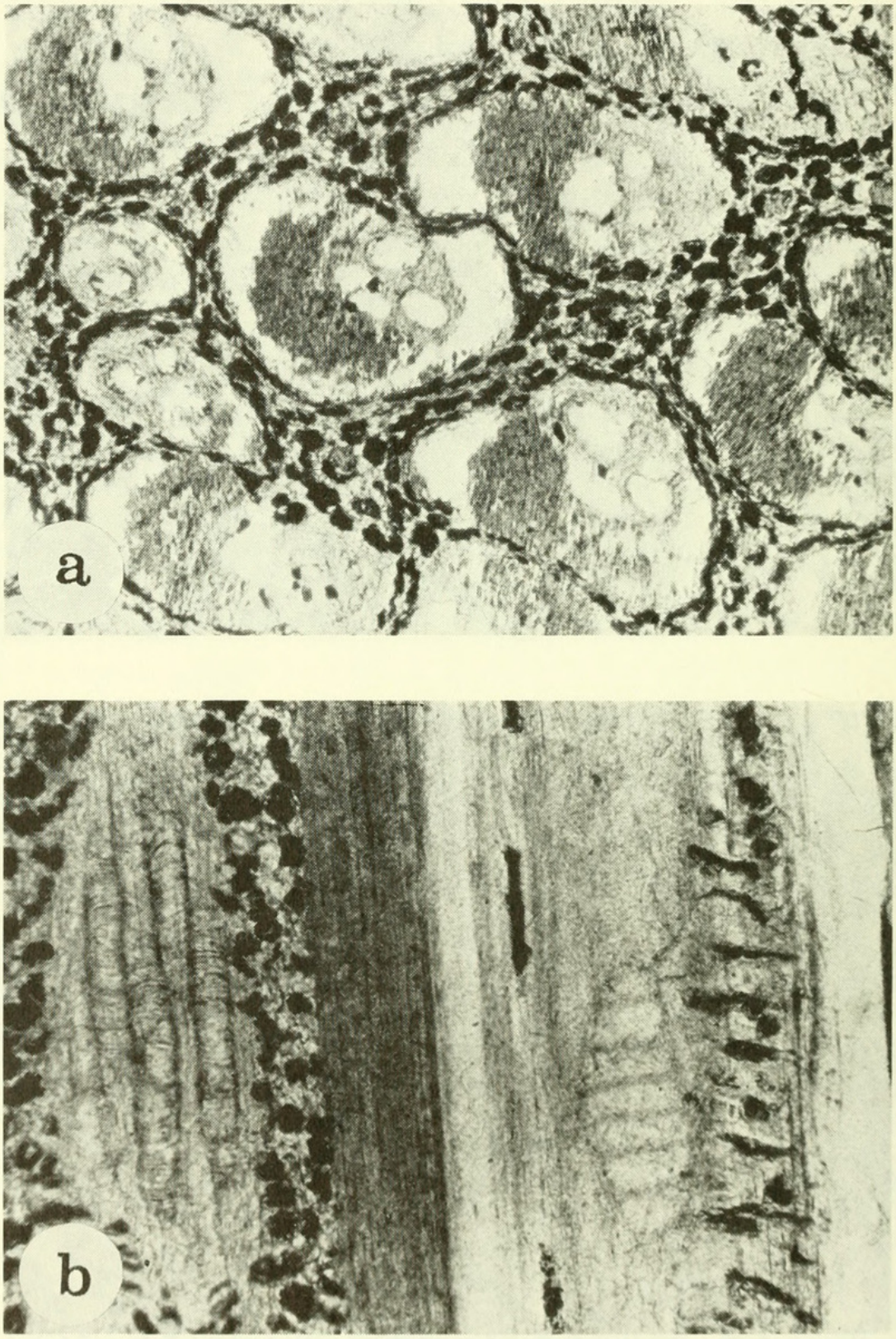

Fig. 7. *Palmoxylon contortum*. A. Cross-section of the dermal zone (30X). B. Longitudinal section of scalariform thickenings on some protoxylem vessels (240X).

pressed in all three zones but are distorted in the subdermal and dermal zones due to extreme bundle compaction. Where not compressed, the bundles are blocky to ovate in appearance. They typically lack auricular lobes and sinuses but have definite median sinuses. These bundles commonly contain more vascular than fibrous tissue, with an f/v ratio between 1:1 and 1:1.5. Both the vascular and fibrous cells are surrounded by tabular parenchyma. Bundle size varies from 320 to 400 μ high and 300 to 500 μ wide. The bundles are characteristically bivascular, with the large metaxylem elements averaging about 55 μ in diameter. The ground tissue is tightly compact, consisting mostly of thin-walled columnar parenchyma. Numerous sclerotic bundles ranging from 40 to 50 μ in diameter, without stegmata, are present. Specimens of this species were donated by Mrs. Marian Whitehead of Salt Lake City, Utah. They were approximately two inches in diameter.

REPOSITORY.— Brigham Young University, 918 (Holotype)
LOCALITY.— Eden Valley, Wyoming
HORIZON.— Green River Formation
AGE.— Eocene

COMPARISONS

Palmoxylon macginitiei Tidwell et al. is similar in general anatomical features to both *P. edenense* and *P. colei*. *P. contortum* is dissimilar due to the disfiguration of the bundles and to the larger number of the vascular bundles per cm^2 and its overall size. All of these species have scalariform perforation plates on their metaxylem elements.

In order to delineate the above species, to give additional information, and to correct an error in the previous description of *Palmoxylon macginitiei*, a brief description of that species is included. *P. macginitiei* is characterized by the shape and size of its fibrovascular bundles (Figure 8A). They are oval, rarely rounded, and have a reniform bundle cap. The vascular portion of the bundle is blocky in appearance and is typically bivascular *with tyloses common* in the metaxylem elements (Figure 8B). The metaxylem vessels have scalariform perforation plates. The bundle size varies from 600 to 700 μ high by 450 to 500 μ wide in the central zone to approximately 420 μ high by 600 μ wide in the cortical and dermal zone. The number of bundles per cm^2 ranges from 104 in the central portion to 212 in the outer dermal zone.

Palmoxylon edenense, although similar to *P. macginitiei*, should be considered a separate species because of the difference in degree of bundle compaction and bundle shape. *P. edenense* has an fV ratio of 3:1 to 3.5:1 in the central zone, whereas the ratio for *P. macginitiei* is 1.5:1 to 2:1. Therefore, the bundle caps of *P. edenense* are larger than those for *P. macginitiei*. Hence, more definite auricular lobes and sinuses are present than in *P. macginitiei*, and the overall outline of the vascular portion is more rounded and not as blocky in appearance. The fibrovascular bundles of *P. edenense* are

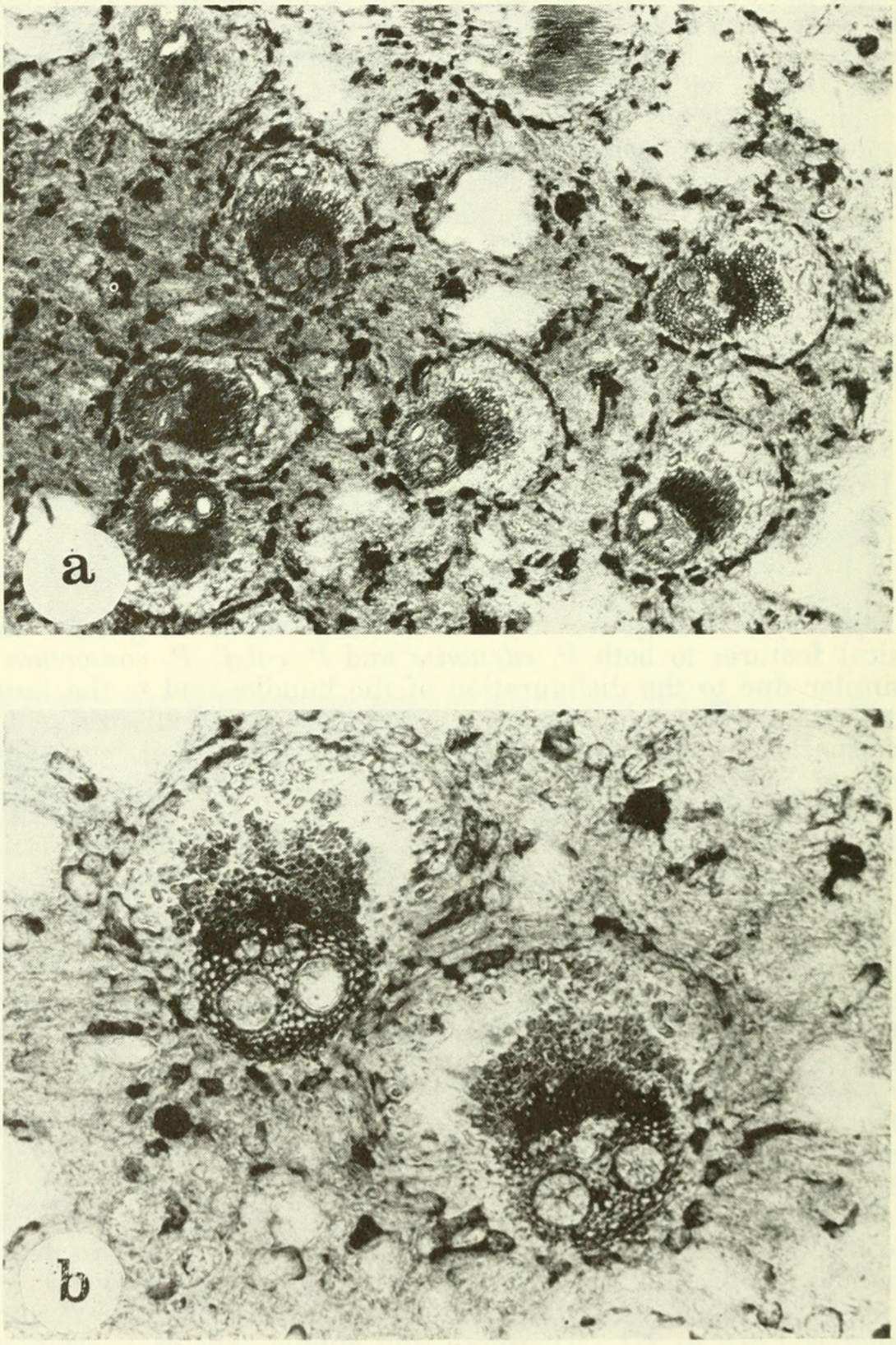

Fig. 8. *Palmoxylon macginitiei.* A. Cross-section of the central zone (30X). B. Enlarged cross-section of bundles showing tyloses in the vessels (60X).

less compacted, with 85 bundles per cm^2 in the central zone to 205 bundles per cm^2 in the cortical and dermal zone.

Palmoxylon colei is unique in that it possesses stegmata, an anatomical structure which sets it apart from *P. macginitiei*. It also differs from the latter in bundle shape, with less vascular tissue in the central zone. Also both *P. colei* and *P. edenense* characteristically lack tyloses in the metaxylem elements.

Palmoxylon edenense is similar to *P. macginitiei*. Therefore, the comparisons between *P. macginitiei* and other previously described *Palmoxylon* species (Tidwell et al., 1971) would also be valid for *P. edenense*. Although further study has shown that *P. crassipes* Unger is similar, it differs in that it has a complanate bundle cap and less vascular tissue in the central zone. The bundle cap of *P. edenense* tends to be less rounded and more flabellate with a deeper median sinus. *P. hungaricum* Greguss (Greguss, 1959) shows a close affinity to *P. edenense* but has larger and more widely spaced fibrovascular bundles.

The presence of stegmata (stegmata is an anatomical feature found only in fossil palms [Stenzel, 1904]) in *Palmoxylon colei* restricts the number of similar species for comparison. Stenzel (1904) described three species exhibiting stegmata: *P. densum*, *P. confertum*, and *P. astrocaryoides*. These all differ from *P. colei* in their characteristic bundle shape, with *P. densum* also having distinctly smaller bundles. Sahni (1964) described *P. pondicherriense*, a palm with stegmata from India. This species is dissimilar from *P. colei* in that the bundles in the latter are less numerous and that they have a reniform bundle cap instead of the lunarian form of *P. pondicherriense*.

Palmoxylon contortum is a unique fine-bundled palm, and only a few species of *Palmoxylon* are even similar. *P. liebigianum* Shenk, which Sahni regards as synonymous with *P. kvishna*, also exhibits compact bundles, 150 per cm^2 in the central zone to 250 per cm^2 in the dermal zone, although the fibrovascular bundles of *P. liebigianum* are not appressed and disfigured, and its vascular bundles have lunarian-shaped bundle caps rather than reniform. *P. ceylanicum* Unger was considered by Stenzel (1904) as a variety of *P. liebigianum*. However, Sahni (1964) concluded that *P. ceylanicum* should be maintained as a separate species. He based this on the vascular bundles of *P. ceylanicum* being thinner and more crowded than in *P. liebigianum*. *P. contortum* differs from the above by its distinctive bundle shape, its degree of compaction, and its characteristic bundle distortion.

Palmoxylon colei varies from *P. simperi* Tidwell, *P. pristina* Tidwell, and *P. gustavsoni* Tidwell et al. by having stegmata which the latter species lack; and *P. contortum* varies from them by its smaller size and by having more compressed, distorted bundles.

Discussion

In comparing *Palmoxylon edenense* and *P. macginitiei* with *P. simperi* Tidwell and *P. gustavsoni* Tidwell et al., it is a case of com-

paring species representing the basal portion of palm stems, or the so-called "stemless" varieties, from the Green River Formation with the distal portions of *P. simperi* and *P. gustavsoni*. Tomlinson and Zimmermann (1967) illustrated the different vessel types they had mascerated from a species of *Sabal*. The base of the stem had rather long vessels with scalariform perforation plates similar to the Eden Valley taxa; whereas those near the middle and top of the same axis had short vessels with simple pores like *P. simperi* and *P. gustavsoni*. *P. simperi* and *P. gustavsoni*, whose stem bases have not been observed, are from the same geographical area in central Utah (Tidwell et al., 1972). Scott et al. (1972) implied that all specimens from this area are of the same species; however, they most probably represent the middle to upper portions of *P. simperi* and *P. gustavsoni*. Thus, in comparing these latter two species to each other at about the same stem elevation and from the same zone (central), they are quite distinct and probably portray more than a delineation between form species.

As further discussed by Tomlinson and Zimmerman (1967), the apical portion of a palm stem is always softer than the basal part. Consequently, when dead, they generally rot from the apex to base. The anatomy of the upper portions of the stem of living palms is easily sectioned and thus studied, whereas the basal portions are most often fossilized. Therefore, the matching of the anatomy of fossil and living forms becomes a dubious procedure, and comparisons between the different parts of the stem may result in rather inaccurate conclusions. Therefore, comparisons between species representing the basal portion of the palm stems with those of the upper part would not be conclusive.

The specimens of *Palmoxylon macginitiei* and *P. edenense* appear to be complete palm axes. They do not indicate any truncation of the stems as would be anticipated if the stem had been originally taller (Figure 9). The bases of these specimens are surrounded with roots, whereas the middle and upper portions of these same axes have numerous attached petiole bases. The apices of these specimens consist of overlapping petiole bases. In progressing up the stem, each successive base becomes smaller and closer to the center of the axis.

These stems may represent either very young stems or the so-called "stemless" palms similar to *Nipa*, some species of *Acanthococos* and *Serenoa*. Several forms of Palmae do not have any trunks above ground and thus are similar to the specimens from Eden Valley. In *Serenoa repens*, leaves appear to come right out of the ground, whereas *Attalea cohune* grows for many years before its trunk shows and has been mistaken as trunkless (McCurrah, 1960). Living *Nipa* palms balance enormous stemless rosettes on the treacherous semiliquid mud of estuaries by means of a stout horizontal trunk (Corner, 1966). These spread by means of branching rootstocks. In the Philippine Islands, a *Nipa* marsh has been reported covering approximately 20,000 acres (McCurrah, 1960).

The particularly numerous upright specimens from Eden Valley

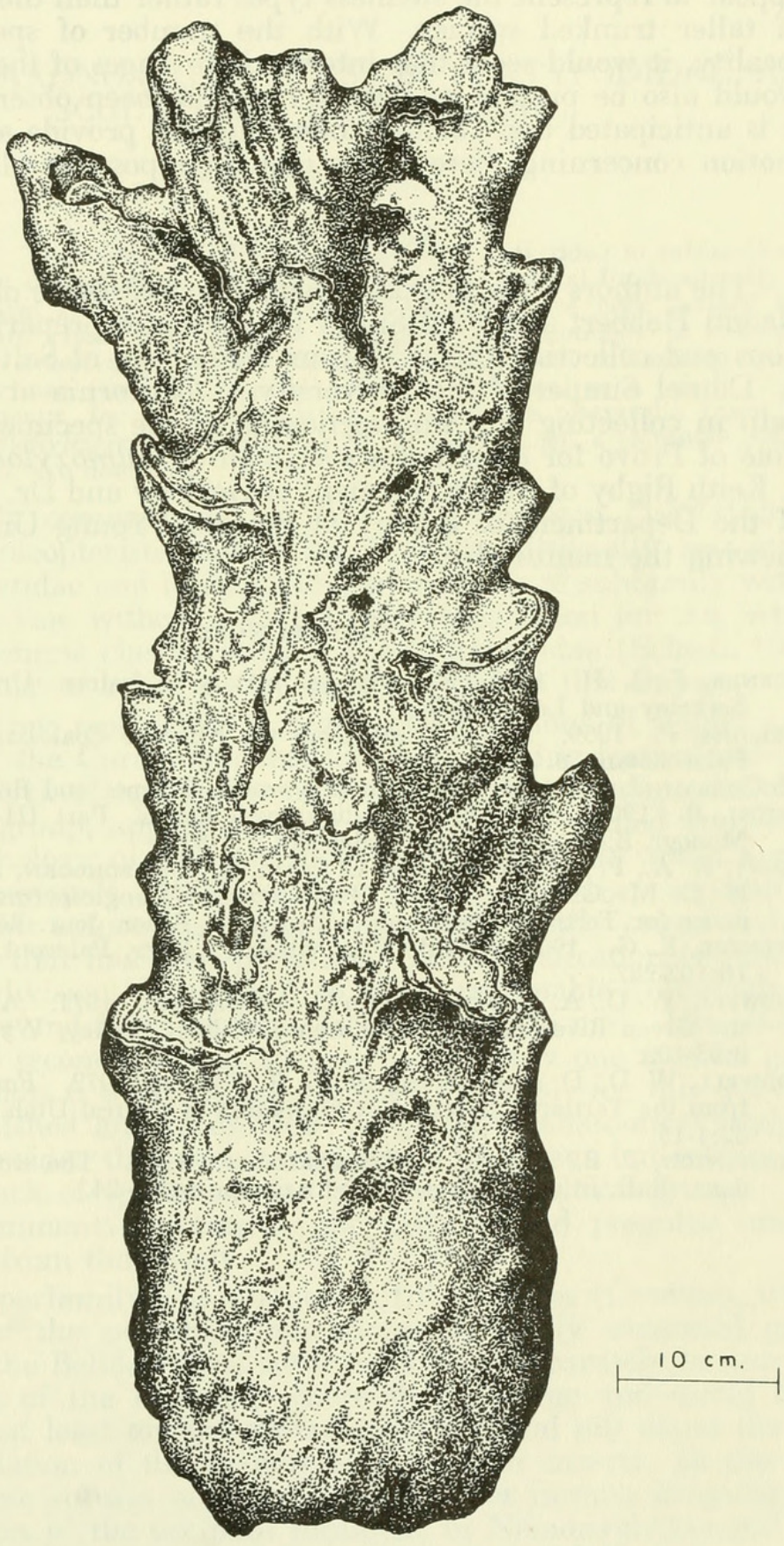

Fig. 9. A specimen of *Palmoxylon edenense* drawn after collecting. Note the attached petioles. Roots are present in the lower portion of the specimen.

appear to represent the stemless types rather than the younger forms of taller trunked species. With the number of specimens at this locality, it would seem that intermediate stages of the trunked forms would also be present and these have not been observed. However, it is anticipated that further collecting will provide additional information concerning these forms and their possible placement.

Acknowledgments

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References

Corner, E. J. H. 1966. The natural history of palms. Univer. Calif. Press, Berkeley and Los Angeles.

Greguss, P. 1959. A palmtrunk from the Miocene Coal Basin of Salgotarjan. Palaeobotany 8:19-21.

McCurrah, J. C. 1960. Palms of the world. Harper and Brothers, New York.

Sahni, B. 1964. Revisions of Indian fossil plants. Part III—Monocotyledons. Monogr. Birbal. Sahni Inst. Palaeobot. 1:1-89.

Scott, R. A., P. L. Williams, L. C. Craig, E. S. Barghoorn, L. J. Hickey, and H. D. MacGinitie. 1972. "Pre-Cretaceous" angiosperms from Utah: Evidence for Tertiary age of the palm woods. Amer. Jour. Bot. 59:886-896.

Stenzel, K. G. 1904. Fossile Palmenholzer. Beitr. Palaeont. Geol. Ost.—Ung. 16:107-287.

Tidwell, W. D., A. D. Simper, and D. A. Medlyn. 1971. A *Palmoxylon* from the Green River Formation (Eocene) of Eden Valley, Wyoming. Botanique 2:93-102.

Tidwell, W. D., D. A. Medlyn, and G. F. Thayn. 1972. Fossil palm materials from the Tertiary Dipping Vat Formation of Central Utah. Great Basin Nat. 32:1-15.

Tomlinson, P. B., and M. H. Zimmermann. 1967. The wood of monocotyledons. Bull. Internat. Assoc. Wood Anatomists 2:4-24.