Palmlike Plants from the Dolores Formation (Triassic) Southwestern Colorado

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By ROLAND W. BROWN

A SHORTER CONTRIBUTION TO GENERAL GEOLOGY

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CONTENTS

ILLUSTRATIONS

A SHORTER CONTRIBUTION TO GENERAL GEOLOGY

PALMLIKE PLANTS FROM THE DOLORES FORMATION (TRIASSIC) IN SOUTHWESTERN COLORADO

By Roland W. Brown

ABSTRACT

Plant remains from the Dolores formation in southwestern Colorado include a few small twigs of the conifer *Brachyphyllum* and large, many-ribbed leaves described as those of an angiosperm, tentatively regarded as a primitive palm and named *Sanmiguelia lewisi*. This is the earliest known angiospermous flowering plant. Its occurrence in the Middle to Late Triassic, however, indicates that evidence for the origin of the angiosperms should be looked for in the earlier Triassic or late Paleozoic.

GEOLOGIC OCCURRENCE OF THE PLANTS

In September 1953, G. Edward Lewis, of the U. S. Geological Survey, searching for fossil remains in the upper part of the San Miguel River valley in southwestern Colorado, found a palmlike leaf impression in the red Dolores formation near Placerville. This specimen, 38 cm long and 20 cm wide, was fragmentary, lacking the apex and base. Therefore, further search was made at the same locality early in 1954, but Lewis found only a few more fragments, none of which gave a clue to the nature of the basal or petiolar portion of the leaves. However, in September 1954, Lewis and the writer, at an outcrop one-half mile north of the original site, succeeded in finding fairly good specimens that illustrate the salient features of these leaves, some of which were still attached to part of a structureless cast of a stem. Further exploration of the fossil-bearing bed along its outcrop for 10 miles on both sides of the San Miguel River yielded equally good material to the writer in June, 1955.

The principal locality is in SE¼ sec. 12, T. 43 N., R. 11 W., in a low cliff of reddish calcareous sandstone, on the hillside of the right bank, 420 feet above the San Miguel River and 145 feet above the base of the Dolores formation, near the old Fall Creek post office, about 2¼ miles southeast of Placerville. Exposed there is the following pertinent sequence of strata, omitting the overlying 1000 feet of the Jurassic Wanakah and Morrison formations, and 250 feet of the Cretaceous Dakota sandstone:

Partial section at old Fall Creek post office, Colorado

Jurassic
- Entrada sandstone. 50 ft. Whitish massive sandstones with few dark, shaly or limy thin-bedded strata.

Triassic
- Dolores formation. 485 ft. Bright red, calcareous, massive and thin-bedded cliff-forming sandstones, few shales, and some conglomerates. It yields remains of metoposaurs, phytosaurs, and plants. The lowermost whitish conglomeratic sandstone rests on an erosion surface of the Cutler formation.

Permian
- Cutler formation. 275 ft. Dark red shales and sandstones, with fragmentary plants.

The Dolores formation, named and described by Whitman Cross (1899) from exposures in the valley of Dolores River in southwestern Colorado, at first included the red beds that are now known as the Cutler formation. However, the discovery in 1904 near Ouray of an angular unconformity below the fossiliferous horizon in the Dolores caused Cross and his associates (Cross, Howe, Ransome, 1905; Cross, Ransome, 1905; Cross, Howe, Irving, 1907) to restrict the name Dolores to the Triassic strata and to name the more reddish underlying beds the Cutler formation, provisionally of Permian age. Cross reported that R. C. Hills in 1880 and 1882 had announced the discovery of fossils in the Dolores, including reptilian teeth, ganoid fishes, mollusks, and plants. Before these could be described, however, they were lost. Cross said that in the course of his survey of the area more reptilian teeth and a plant, identified by David White as *Pachyphyllum* [an error for *Brachyphyllum*] *münsteri*, were found. All of these fossils reputedly indicated the Triassic age of the Dolores. At the Fall Creek post office locality in the Dolores the writer and Lewis in 1954 found phytosaurian teeth and the plant impressions described in the following pages, including the object of unknown identity (pl. 33, fig. 4).

The nonmarine sediments of the Triassic in the "four corners" area of the southwestern States are believed

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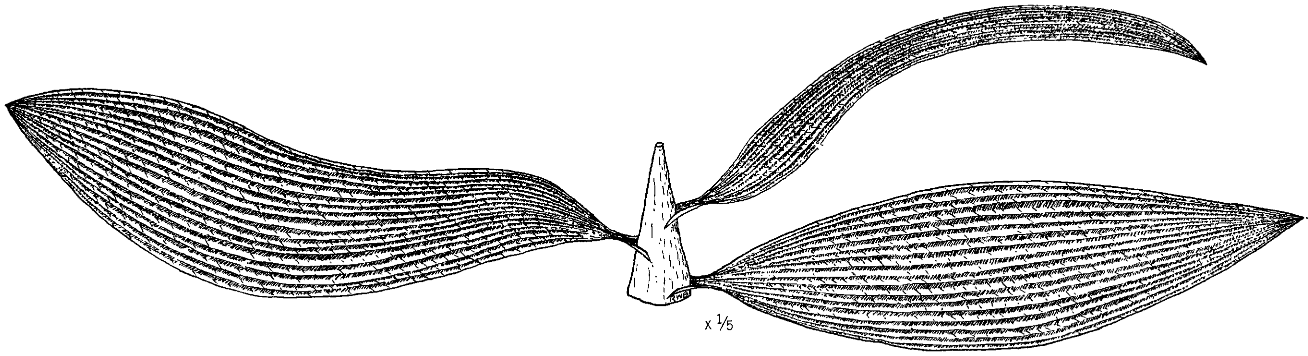


FIGURE 29. Tentative reconstruction of *Sanmiguelia lewisi* Brown. In life the leaves were probably somewhat stiff, like the lower right hand leaf, rather than undulant. No sheaths or crests are shown because discernible evidence for them is lacking. × 1/5

to have accumulated on floodplains and in scattered pools and lakes at not many hundreds of feet above sea level. Such plants, therefore, as were entombed in the sediments, most likely originated in the lowlands of the basin of deposition, whereas remains of more distant upland plants did not get into the fossil record. Whatever the reason, whether land vegetation was sparse on account of climatic conditions, or whether the circumstances attending the accumulation of the sediments were unfavorable, plant remains in the Dolores apparently are relatively scarce.

DESCRIPTION OF THE SPECIMENS

CONIFERS

Brachyphyllum münsteri Schenk

Plate 33, figures 1, 3

Brachyphyllum münsteri Schenk, 1867, Die fossile flora der Grenzschichten des Keupers und Lias Frankens, p. 187, pl. 43, figs. 1–12.

The coniferous twigs from the Dolores formation, here figured, resemble closely those shown by Schenk from the Rhaetic formation at Bamberg, Germany. Neither these nor Schenk's specimens, however, quite match the usual conception of the features of the genus *Brachyphyllum* with its closely appressed foliage. They can be compared with the twigs of some species of *Palissya*, *Sequoia*, *Sphenolepidium*, *Araucarites*, and others found in the Triassic and later formations. Without cones or other distinguishing features, the identification of remains of this kind is fraught with much uncertainty. Probably the specimen collected by Cross (1899) in the Telluride quadrangle and identified by David White as *Pachyphyllum münsteri*, was a representative of this species—the *Pachyphyllum* being an error for *Brachyphyllum*. Apparently, that specimen is now lost.

Numerous species of conifers have been described from the Triassic of the United States, and particularly from the southwestern States, notably in and around the Petrified Forest National Monument near Holbrook, Arizona. There is, therefore, nothing especially unusual about the presence of such remains in the Triassic of southwestern Colorado.

MONOCOTYLEDONS

SANMIGUELIA Brown, n. gen.

Plants with alternate, simple, large, elliptic, strongly pleated, monocotyledonous, palmlike leaves. Stem rounded, tapering rapidly toward the apex, but other features unknown.

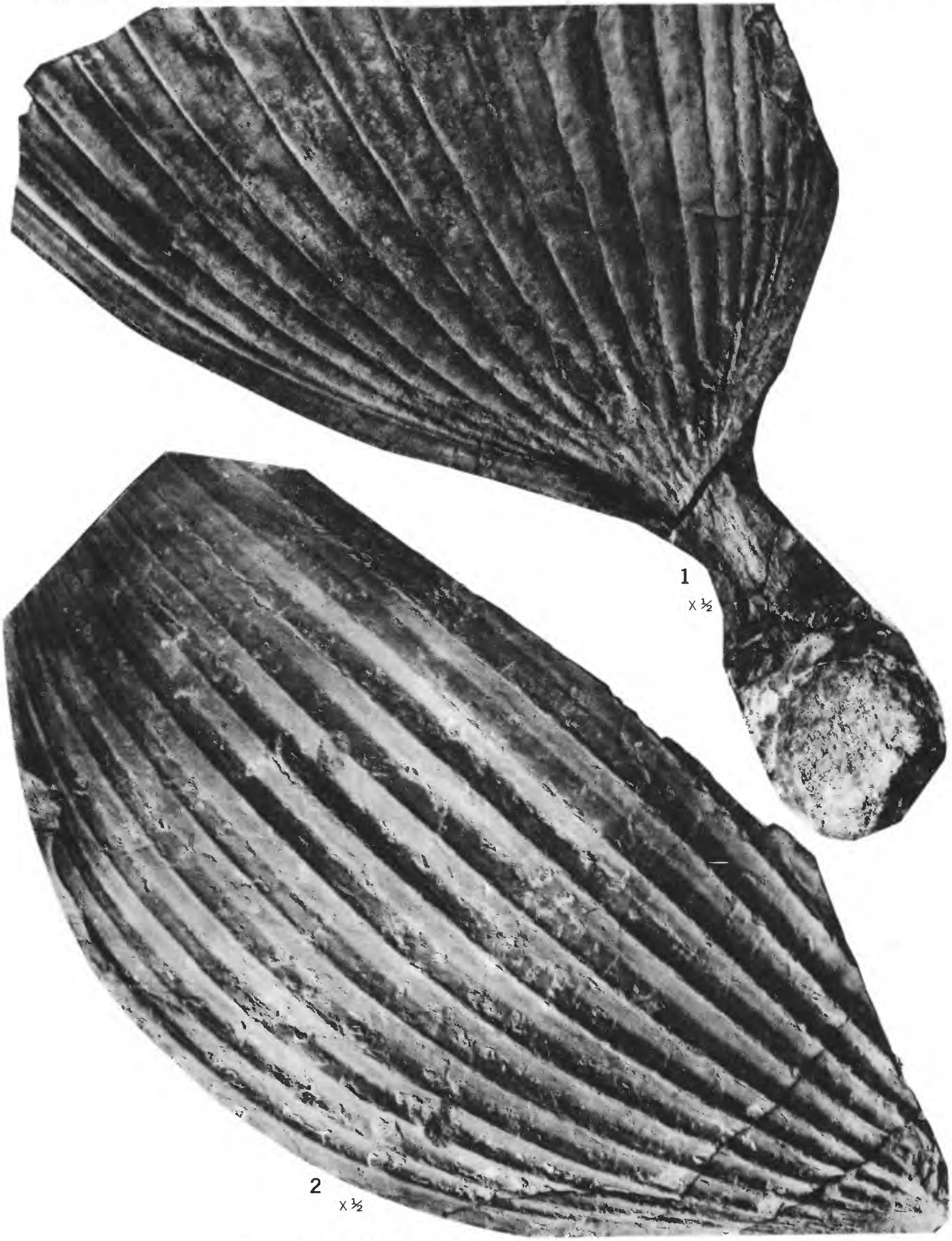
Sanmiguelia lewisi Brown, n. sp.

Plate 32, figures 1, 2; plate 33, figure 2

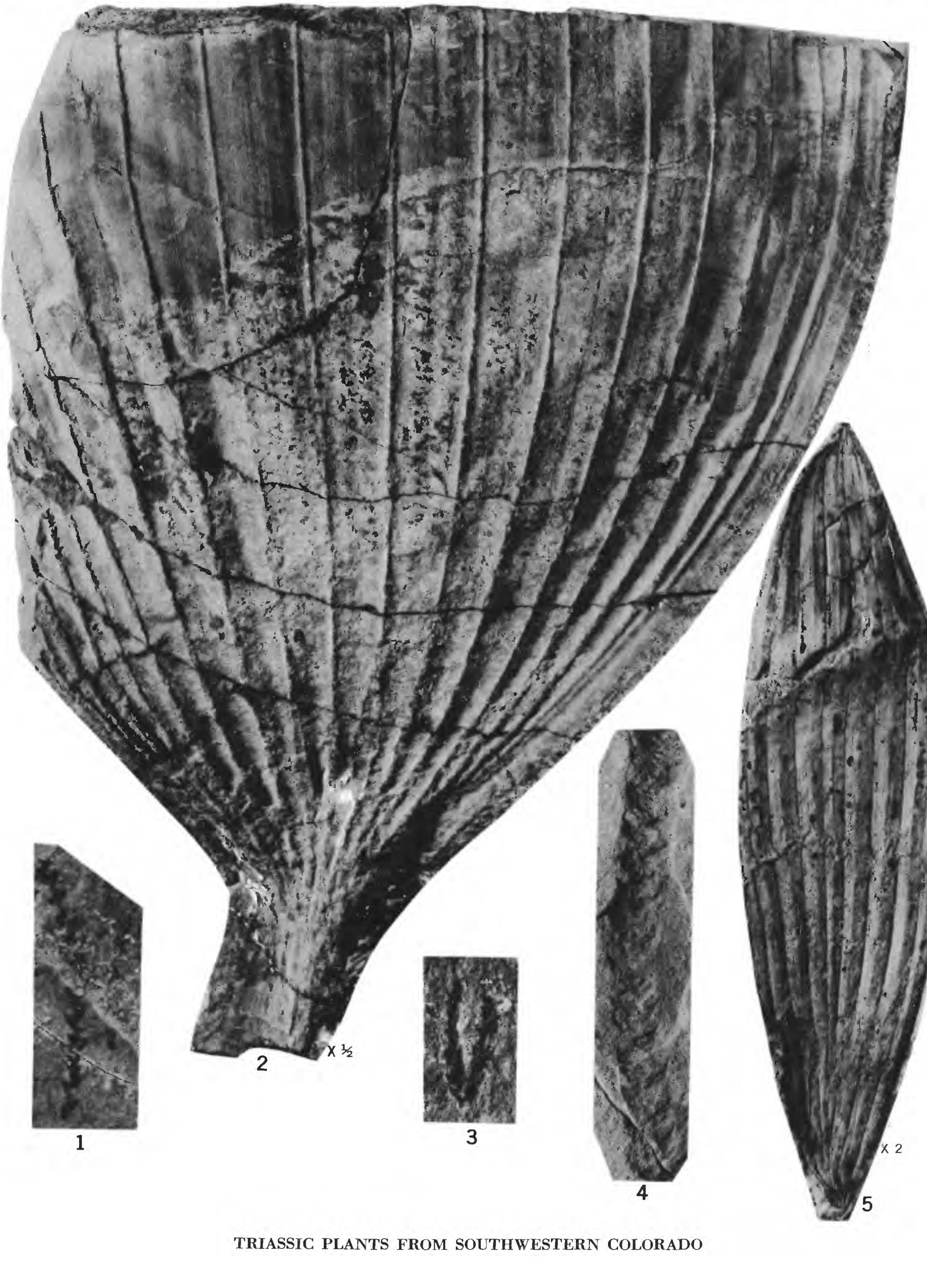
Elliptic to ovate entire, firm-textured leaves, attaining a length of 40 cm and width of 25 cm, conspicuously pleated, the strong ribs or veins converging toward the apex and the base. Midrib not differentiated. Between the 16 to 20 ribs are closely spaced parallel veinlets, as in all palms. The leaves are attached to the stem alternately by broad, thin, clasping, or probably sheathing petioles at vertical intervals of 4 cm, as shown by three leaves preserved in one block of sandstone. These permit a tentative reconstruction of the plant (fig. 29). However, neither sheaths nor crests (hastulas, ligules) are discernible, either because none existed or because the preservation around the stem is poor. The stem, now only a calcitic cast without cell structure, is rounded and in a vertical distance of 10 cm narrows rapidly from a diameter of 4 cm to a blunt point, thus suggesting that it is the apical portion of a low, but mature plant.

PLATE 32

FIGURES 1, 2. *Sanmiguelia lewisi* Brown. Fig. 1 shows the broad base of the petiole clasping the grayish, granular, rounded stem. The latter is a calcitic cast without cellular structure. × ½



TRIASSIC PLANTS FROM SOUTHWESTERN COLORADO



TRIASSIC PLANTS FROM SOUTHWESTERN COLORADO

The generic term *Sanmiguelia* is feminine and is from the name of the river at the type locality. The species is named for G. Edward Lewis, vertebrate paleontologist of the U. S. Geological Survey and discoverer of the first specimens.

RELATIONSHIPS OF SANMIGUELIA

Sanmiguelia lewisi is regarded tentatively but credibly as a primitive palm. Superficially its leaves resemble those of species of other monocotyledonous genera, such as *Carludovica*, *Curculigo*, *Cypripedium*, *Joinvillea*, *Lilium*, *Potamogeton*, *Setaria*, *Smilacina*, *Veratrum*, and others. In some of these the plicate or accordion-pleated feature of the foliage is almost as strongly and comparably developed, and there may be no distinct midrib. Consequently, it is regrettable that no flowers, fruits, or stems with cell structure, have been found with *Sanmiguelia* to eliminate the foregoing genera completely and to establish its identity as a palm conclusively.

Besides the suggestive morphologic appearance of its leaves, further reason for believing that *Sanmiguelia* represents a palm is derived from consideration of the probable ancestral features of primitive palms. The late Robert T. Jackson, from observations of the juvenile leaves of palm seedlings and with numerous lucid illustrations, discussed this phase of the subject in part, as follows (Jackson, 1899, p. 124, pl. 23):

> Amongst palms many species present interesting features of localized stages in development. I have studied the development of seedling palms of thirty-seven species and from published figures of von Martius and others know something of the early characters of forty-five species distributed through twenty-eight genera. Seedlings of all species have simple, early seed-leaves, and these are always one of two types. The first and most primitive type of seed-leaf is elongate, lanceolate, or oval, terminating more or less acutely, and with a longer or shorter rachis, usually long. This type is seen in *Latania* (pl. 23, fig. 94), *Corypha* (pl. 23, fig. 104), *Cocos* (pl. 23, fig. 102), *Phoenix* (pl. 23, figs. 100, 103, 103a), and many other genera. The second type of nepionic or seed-leaf is similar to the first, except that it is distally cleft. It is characteristic of *Chrysalidocarpus* (pl. 23, fig. 95), *Kentia* (pl. 23, fig. 96), *Caryota* (pl. 23, fig. 98), and many other genera. Very young specimens of genera which have distally cleft leaves or exceptional individuals show a transient distal fusion of the apices of the leaf, as in *Kentia* (pl. 23, fig. 96), demonstrating that the cleft type is only a modification of the first or entire type. In some types as *Stevensonia grandifolia* J. Dunc. (*Phoenicophorum sechellarum* H. Wendl.), which have distally cleft leaves, the first leaves are entire, the cleft character appearing later (third leaf of the specimen in hand). This is a further demonstration of the primitive nature of the entire type * * *. In *Latania commersoni* J. F. Gmel. (*L. borbonica* Lam.), the seed-leaf is ovate, lanceolate (pl. 23, fig. 94); during growth the later leaves become relatively broader, until, by distal tension, splits take place (pl. 23, fig. 93), and in the adult the leaf is a quite broad, fan-leaf type * * *. In the growth of a pinnate-leaved palm, when a new leaf first appears, the pinnae cling together laterally on their outer margin and to the distal leaflet, in such a way that the whole leaf simulates the entire type and demonstrates the simple dynamic genesis of this type of compound leaf from an ovate leaf like that of the young * * *. Also the distal tip of pinnate leaves repeats the form of nepionic leaves * * *. Some palms sucker from the base, and in such suckers we might expect to find localized stages in development, as is the case. In *Raphis flabelliformis* L'Herit., a fan-leaf palm, suckers from the base have simple leaves like pl. 23, fig. 94, and only in later growth are the typical fan-leaves of the species acquired * * *. Suckers of *Chrysalidocarpus lutescens* repeat the form of the seedling so closely that they are practically identical in leaf characters * * *.

To Jackson's discussion of juvenile leaf forms should now be added Eames' recent interesting observations on the development of leaves in the mature stages of palms (1953). In general, the simple seedling leaves are succeeded, according to the kind of palm, by pinnate or palmate leaves. Study of histological preparations of leaf primordia indicates that the palmate is derived from the pinnate form, the central pinna of the palmate being the distal pinna of the pinnate leaf, and the rachis of the palmate leaf being shortened or telescoped. The rein or marginal flange that is present on erupting leaves of mature plants is seldom seen on the leaves of juvenile plants.

Ancestral or reminiscent features have not been as definitely recognized in the lineage of the palms as they have in such genera as *Ginkgo* (Brown, 1939, p. 246; 1943, p. 862, figs. 1a–1c) and *Cercidiphyllum* (Brown, 1939). Until now the fossil record of the palms has dated from the Jurassic Lias. Lignier (1895, 1908), from collections in Normandy, described and illustrated as *Propalmophyllum liasinum*, fragmentary portions of fan-shaped leaves showing chiefly the apexes of the petioles and bases of the fans, with a few ribs. Of these Seward (1931, p. 366) said—

> Some French fossils described by Prof. Lignier as *Propalmophyllum* bear a striking resemblance to pieces of a palm leaf, though they cannot be accepted as proof of the existence of palms in a Jurassic flora.

Nevertheless, in a table on page 414 of the same book, Seward indicates Palmae as dating from the Jurassic. I, myself, see no reason for doubting Lignier's identi-

PLATE 33

FIGURES 1, 3. Coniferous twigs of *Brachyphyllum münsteri* Schenk. × 1
2. *Sanmiguelia lewisi* Brown, showing the numerous parallel veinlets between the prominent ribs. × ½
4. Unknown object, probably an animal trail. × 1
5. *Paloreodoxites plicatus* (Lesquereux) Knowlton, from the Paleocene Dawson arkose near Ramah, Colo. × 2

fication of his leaves as palms. True, some fragmentary Jurassic and later fossils, superficially somewhat resembling the fragments figured by Lignier, have been mistaken for remains of palms; but these are the egg capsules of chimaeroid fishes (Brown, 1946).

The first authentic remains of palms found in the United States are from the early Upper Cretaceous. From then on, both fan and feather palms are not uncommon. The fossil wood of palms, known as *Palmoxylon*, is fairly abundant at some localities. When thoroughly silicified it is attractive and durable; and in Aboriginal American days it was sometimes used for making arrow-points and other artifacts. Fossil trunks, or portions thereof, that are sometimes misidentified as *Palmoxylon*, are the Mesozoic ferns known as *Tempskya*. The fossil fruits of palms, particularly of *Nipa*, are known. Others, sometimes called *Palmocarpon*, are somewhat indefinite and doubtful.

More particularly pertinent to the discussion of the relationships of *Sanmiguelia lewisi* are leaves of *Paloreodoxites plicatus* (Lesquereux) Knowlton (pl. 2, fig. 5) from Paleocene strata in the Denver basin, Colorado—the Denver formation at Golden; and the Dawson arkose at Ramah. The small fragment from the Raton formation at Tercio, described by Knowlton (1917, p. 287, pl. 63, fig. 1), must be regarded as doubtfully identified. These elliptic to ovate leaves (approximately 20 cm in length and 7 cm in width, with 12 ribs) were called *Oreodoxites plicatus* by Lesquereux (1883, p. 122, pl. 18, figs. 1–4). Knowlton (1930, p. 41, pl. 11, figs. 1–4) changed the generic name of this species to *Paloreodoxites* because the genus *Oreodoxites* was founded by Göppert on an indefinite Permian seed, and because Lesquereux may not have known of Göppert's genus but thought he was creating the name anew on the basis of similarities he saw between his leaves and those of the living *Oreodoxa*. Actually, as there appears to be no close relationship between *Paloreodoxites* and *Oreodoxa*, Knowlton's name is not too happy a substitute.

The prime question now is, Are the leaves of *Paloreodoxites plicatus* leaflets of a large compound leaf, as Lesquereux seems to have conjectured; simple, mature leaves; or simple, seedling leaves? Because none of these leaves has been found attached to a rachis or stem, their exact nature is open to speculation. The leaves could be simple seedling leaves of fan or of feather palms, both kinds having been present in the Denver basin and adjoining areas during Paleocene time. The leaves could be mature leaflets of a pinnate palm, or they could be mature leaves of a primitive kind of palm, a leftover from early Mesozoic time.

Whatever the answer to the foregoing question, the leaves of *Sanmiguelia* resemble somewhat those of *Paloreodoxites* and some from the Stonesfield slates in the Jurassic Oolite at Eyeford, England, called *Lilia* [an error for *Lilium*] *lanceolata* Buckman (in Murchison, 1845, p. 93, pl. 2, fig. 3). This is Buckman's description—

> Leaf ovato-lanceolate, with a slight acuminated point—leaf-stalk short. An elegant parallel veined endogenous leaf, having much the appearance of leaves of the liliaceous tribe of plants.

On the same plate Buckman figured two somewhat similar but more fragmentary leaves as *Naiadea acuminata* and *Stricklandia acuminata*, both of which he described as endogenous leaves. Seward (1904, p. 121, 122) synonymized "*Lilia*" and *Naiadea* with *Podozamites stonesfieldensis* and *Stricklandia* with *Baiera phillipsi*. As I have not seen these specimens I can form an independent opinion of them only from Buckman's descriptions and illustrations. Consideration of these almost persuades me that perhaps Seward's disposition of the specimens was not altogether appropriate. Particularly, I am doubtful about Buckman's pl. 2, fig. 3 of "*Lilia*". How Buckman, whose other illustrations seem to be fairly accurate, could have drawn a coarsely ribbed leaf from a specimen that, if Seward is correct, should have no ribs but only numerous closely spaced parallel veins, as in typical *Podozamites*, I do not comprehend. His illustration looks too much like those of small leaves of *Paloreodoxites*, *Sanmiguelia*, or seedling leaves of living palms, to be dismissed too lightly as *Podozamites*. Moreover, Seward (1904, p. 152, pl. 11, figs. 5, 6) described and figured as *Phyllites* a poplarlike leaf from the same beds. This leaf has the appearance of an authentic dicotyledonous leaf, and if it is such, it strongly supports the opinion that primitive palms, or at least monocotyledons, also could have existed simultaneously somewhere and perhaps in the same flora.[1] Furthermore, the fan palms (*Propalmophyllum*) of Lignier were already in existence in Lias time in Normandy. The doubtful nature of "*Lilia*," and the impossibility of demonstrating any but a superficial resemblance among "*Lilia*," *Paloreodoxites*, and the specimens here being reported, necessitate a new name for the Colorado monocotyledon.

Possibly *Sanmiguelia lewisi* represents some plant other than a palm or similar monocotyledon with parallel-veined leaves. For example, *Cordaites* has strap-shaped leaves whose veins are closely spaced but the leaves are not plicate or strongly ribbed. Perhaps the yuccalike leaves sometimes reported from Triassic

[1] Under the name *Sassendorfites benkerti*, Oskar Kuhn, in a report just received from Germany, describes and illustrates another dicotyledonous leaf, this from lower Jurassic strata at Sassendorf, near Bamberg. (Orion, Jahrg. 10, no. 19–20, Oct. 1955.)

localities under the name *Yuccites* are cordaitean foliage. Some cycads have leaves comparable in size to those of *Sanmiguelia* but the veins are not ribbed as in palms, and, if closely parallel, may fork or anastomose to make a notably reticulate pattern. So far as I am aware, no other extinct or living plants, except palms and species of the monocotyledons already mentioned, have leaves that match or closely resemble those of *Sanmiguelia lewisi*. This species, if not a primitive palm, is a palmlike monocotyledon, whose simple leaves without midribs are fully developed, not seedling leaves, of a mature plant. If this be true, these specimens are the oldest known megascopic remains of the angiospermous flowering plants.

Botanists and paleobotanists have long been looking for evidence concerning the time, place, and manner of origin of the angiospermous plants. Adequate summaries of the speculations on this matter may be found in Arnold (1947, p. 333–365) and Axelrod (1952), with pertinent bibliographies. *Sanmiguelia lewisi* does not seem to provide answers to some of the fundamental questions involved in this speculation: Did the monocotyledons come from the dicotyledons or the dicotyledons from the monocotyledons or did both descend from a common ancestor? Did woody monocotyledons derive from herbaceous ancestors? Did the angiosperms originate in upland areas, according to Axelrod's thesis? As representatives of the angiosperms existed in the early Jurassic it is not altogether surprising now to find their ancestors in the Triassic. Perhaps their ultimate origin must be sought in the Paleozoic.

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