Acta Palaeobotanica 66(1), 113–124, 2026
https://doi.org/10.35535/acpa-2026-0007

e-ISSN 2082-0259
ISSN 0001-6594

Vegetative and reproductive morphology of *Kohlsia parachutensis* gen. et sp. nov., an herbaceous angiosperm from the Eocene Green River Formation of western Colorado, USA

STEVEN R. MANCHESTER[1*], WALTER JUDD†[1,2] and BRUCE H. TIFFNEY[3]

[1]Florida Museum of Natural History, Dickinson Hall, 1659 Museum Road, Gainesville, FL 32611-7800, USA; e-mail: steven@flmnh.ufl.edu, ORCID: 0000-0003-0238-7977

[2]University of Minnesota Herbarium, Bell Museum, 2088 Larpenteur Ave. West, University of Minnesota, St. Paul, MN 55113, USA

[3]Department of Earth Science and College of Creative Studies, University of California, Santa Barbara, Santa Barbara, CA 93106, USA

Received 6 Faebruary 2026; accepted for publication 3 June 2026

ABSTRACT. A new angiosperm genus is recognized based on complete plants preserving roots, stems, linear leaves, inflorescences and infructescences from the late part of the early Eocene of western Colorado, USA. The plants of *Kohlsia parachutensis* gen. et sp. nov. measure 5–8 cm in height, and are characterized by an apparent basal rosette of alternate leaves and a short main axis terminated by a racemose inflorescence with lateral racemose inflorescences arising alternately. Based on the short stature, heterophyllous leaves, and depositional context we infer that it was potentially a rooted semiaquatic. The fused hypogynous perianth of five tepals and single-seeded fruits lead us to consider it likely to be a superasterid, but its ordinal and familial affinities remain obscure. *Kohlsia* is a rare example of an herbaceous angiosperm from the Green River flora.

KEYWORDS: Pentapetalae, impression fossils, extinct Eudicot, infructescence

INTRODUCTION

The Eocene Green River shales of the central Rocky Mountains were deposited in a series of large lakes on the eastern margin of the Laramide orogeny (Lawton, 2008) and are rich in fossil plants. Several localities from former Lake Uinta, an Eocene great lake of eastern Utah and western Colorado, have previously received attention, including sites near Bonanza, Utah and Douglas Pass, Colorado (Brown, 1934; MacGinitie, 1969; Johnson and Plumb, 1995). However, the flora preserved in sites on the southeastern margin of Lake Uinta, exposed in the Piceance Creek Basin of Colorado, has received less attention in the literature although an overview of the co-occurring insect and spider fauna was presented by Dayvault et al. (1995) and a scorpion was discovered in the same strata (Perry, 1995; Santiago-Blay et al., 2004).

Museum collections of paleobotanical material from the Piceance Creek basin include some species shared with other sites of the Parachute Creek Member of the Green River Formation (MacGinitie, 1969), but also include some unique elements. Here we describe a new angiosperm genus based on unusually complete specimens extending from roots to the leaves and inflorescences. Using the available

* Corresponding author

morphological characters, we attempt to infer the phylogenetic relationships of these fossils to extant plants.

MATERIALS AND METHODS

Specimens were collected from thinly laminated shales which also yield abundant insect remains (Dayvault et al., 1995; Barna et al., 2023) from sites near Anvil Points in Garfield County, Colorado and along Piceance Creek in Rio Blanco County, Colorado (Table 1). These sites are in the southeastern part of the Piceance Creek Basin of northwestern Colorado and occur in the upper portion of the Parachute Creek Member of the Green River Formation (O'Sullivan, 1986; Hail and Smith, 1997; Anderson and Smith, 2017). According to Dayvault et al. (1995), these sites, which they referred to as sites A and B, are 45 to 55 m below the key stratigraphic marker known as the Mahogany oil shale bed, whereas Douglas Pass (site C of Dayvault et al., 1995; frequently collected and well represented in museum collections), apparently lacking *Kohlsia*, is about 45 m above the Mahogany bed. A lower bracket on the age of the fossiliferous horizon is provided by a $^{40}Ar/^{39}Ar$ sanidine date of 51.24 ± 0.52 Ma (Smith, 2007; Smith et al., 2008) on the Yellow Tuff marker bed a few meters above the base of the Parachute Creek Member and about 300 m below the Mahogany zone as mapped by Pipiringos and Johnson (1975), thus ~250 m below the beds yielding the investigated fossils. Conversely, an upper bracket on the age is provided by the $^{40}Ar/^{39}Ar$ biotite date of 48.37 ± 0.23 Ma (Smith, 2007; Smith et al., 2008) for the Wavy Tuff of Remy (1992) situated ~30 meters above Mahogany zone. We thus estimate an early Eocene age of ~49 Ma for the beds yielding these fossils.

Abundant evaporite minerals, including halite and nahcolite, and the occurrence of stromatolites and mud cracks, provides evidence of shallow water conditions and periodic drying, and has led to the interpretation that the Parachute Creek Member in the Piceance basin was deposited under saline conditions of a playa lake (Roehler, 1974; Lundell and Surdam, 1975; Young, 1995; Jagniecki and Lowenstein, 2015).

We studied specimens in the collections of the Smithsonian Natural History Museum, Washington, D.C. (USNM), the Denver Museum of Nature and Science (DMNH), the Museum of Natural History at the University of Colorado, Boulder (UCM), and the Florida Museum of Natural History at the University of Florida, Gainesville (UF).

Initial imaging was carried out with a Canon Rebel Xsi SLR camera either with an EF-S 60 mm macro lens or mounted on a Wild Photomicroscope 400. Additional imagery was obtained with a Keyence VHX-7000 N digital microscope using the shadow effect mode for improved surface topographic detail.

RESULTS

SYSTEMATIC PALEOBOTANY

Order: Indet.

Family: Indet.

Genus: ***Kohlsia***
Manchester, Judd et Tiffney **gen. nov.**

Generic diagnosis. Small plants with an apparent basal rosette of elongate leaves and a short main axis with a terminal inflorescence and three or more lateral inflorescences arising alternately. Leaves simple, alternate, slightly sheathing, narrowly obovate to linear, sometimes strongly lobed (trilobed or pinnatifid). Venation longitudinally reticulodromous. Inflorescence a raceme-like cyme, the axis apparently indeterminate with acropetal maturation; axillary branches determinate, underlain by a bract giving rise to 1–3 peduncles bearing pistillate flowers. Staminate flowers not known. Pistillate flowers actinomorphic, hypogynous with an erect perianth of five fused tepals closely enveloping the gynoecium.

Table 1. Locality data for *Kohlsia parachutensis*

Museum locality number	Name	Latitude	Longitude	Specimens cited
UF 579	Piceance Creek	39.7292944°N	107.9780861°W	UF69437, 60120, 62273, 69437, 71189, 84703
DMNH 304	"Ron Meyer site"	Coordinates withheld, DMNH	Coordinates withheld, DMNH*	DMNH 25648, 53459
DMNH 1290	Anvil Points	39.535°N	107.95166667°W	DMNH 38726, 23394
UCM 2024185	Anvil Points	39.60113°N	108.6744°W	UCM 50003
UCM 2005025 = USNM 41142	Anvil Points	39.5353501°N	107.9502141°W	UCM 50005, 50010, USNM PAL 575439
UCM 2005026	Anvil Points	39.535569058°N	107.949397211°W	UCM 50011a
USNM 41140 & 77288	Anvil Points	39.5343389°N	107.9510806°W	USNM PAL 582037, 580502, 582126, 580380
UCM 2007238	Denson site	39.5083504°N	108.0256871°W	UCM 50005b

* General locality data presented by Perry (1995)

Tepals apically rounded, each with a midvein and a pair of intramarginal veins; the perianth persistent into fruiting condition. Fruits globose to ellipsoidal or reniform, lacking evidence of style(s); indehiscent, endocarp thick (well coalified in the fossils).

Etymology. The generic name recognizes David Kohls whose diligent collecting efforts resulted in many new paleobotanical and paleoentomological specimens deposited at USNM and UCM.

Plant Fossil Names Registry. PFN003493

Type: ***Kohlsia parachutensis* sp. nov.**

Species: ***Kohlsia parachutensis***
Manchester, Judd et Tiffney **sp. nov.**

Figs 1–7

Species diagnosis. As for genus.

Etymology. The specific epithet parachutensis, refers to Parachute Creek, Colorado, namesake of the Parachute Creek Member of the Green River Formation, from which these specimens were collected.

Plant Fossil Names Registry. PFN003494.

Holotype. UF 579-69437 (Figs 1D, 2E, F, 5F, G, 7E–G).

Paratypes. DMNH 38726 (Figs 1A, 2D), UF 579-71189 (Fig. 6A–C) and 579-84703 (Fig. 7C, D), USNM PAL 580380 (Figs 1E, 4B, C).

Additional specimens examined. DMNH 23394, UCM 50005b, UCM50010 [this is the counterpart of USNM 575439], UCM 50011a, UF 579-60120, 62273, 69437, USNM PAL 582037, 580380 (localities in Table 1).

Type locality. Piceance Creek, Colorado (UF loc. 579), coordinates in Table 1. Early Eocene Parachute Creek Member, Green River Formation.

Description. The plants are short, with the aerial portion 2.5–6.3 cm long and the root/rhizome extending up to 3.2 cm in length. The main axes appear to arise from a corm-like structure (Fig. 1A, B, D), bearing several elongate, lax leaves arranged in an apparent basal rosette. The corm-like thickening below the basal rosette of leaves lies at the junction with a root or rhizome, and is seen at multiple levels in some specimens suggestive of iterative growth (Fig. 1B, D).

The erect axis terminates in an inflorescence/infructescence bearing leaves that usually appear to be alternate, possibly spiral (Fig. 1F, G). The leaves are simple, and likely sheathing; the laminae elongate, narrowly obovate to linear, sessile without obvious petioles. They bear longitudinally-trending reticulate venation with the midvein somewhat stronger than the parallel veins on either side of it (Figs 1D, 2D–F). Occasionally the leaves are deeply incised into three lobes (Fig. 2A–C). The central axis and lateral axes are curved to somewhat sinuous (Figs 1A–G, 3A, D, 6A).

The inflorescence axes bear small and tightly-packed underdeveloped fruits near the apex, grading basally to fully-developed fruits that are more widely separated in the upper two-thirds of the stalk, to widely-separated, shed fruits in lower one third (Figs 1F, 3B, 7A, C).

The perianth consists of five basally fused, elongate, radially symmetrical elements in one whorl (Fig. 5A–D) that persists in fruit, underlying the gynoecium and protruding apically. It is not clear whether these are sepals or petals. No stamens or staminal scars have been observed. The superior ovary gives rise to a globose to ellipsoidal fruit that exhibits a black, reflective surface that is well coalified (Figs 1B, F, 2D, 4B–C, G, 5E, 6C, 7A). There is no indication of smaller subunits within these structures to suggest the presence of more than one seed per fruit. The absence of a stigma or style also precludes an estimate of carpel number. There is no evidence of dehiscence, so the fruits are not capsular but could be drupes or achenes. After the fruits are shed, the pedicel and remnants of the perianth remain attached to the infructescence (Figs 4D–G, 5A–D). Keyence shadow effect imagery occasionally suggests a hint of curvature within the fruit, raising the possibility that the embryo was reniform or curved (Fig. 7F, G).

Interpretations. Several features of the fossil are suggestive but not definitive of the original morphology. The lack of observed stamens or staminal scars leads us to speculate that this was a unisexual plant bearing only carpellate flowers and fruits. It may have been dioecious, but the generally poor preservation of the floral structure cautions that it might have been monecious, and the staminate flowers may have been unobvious, indistinct, or shed.

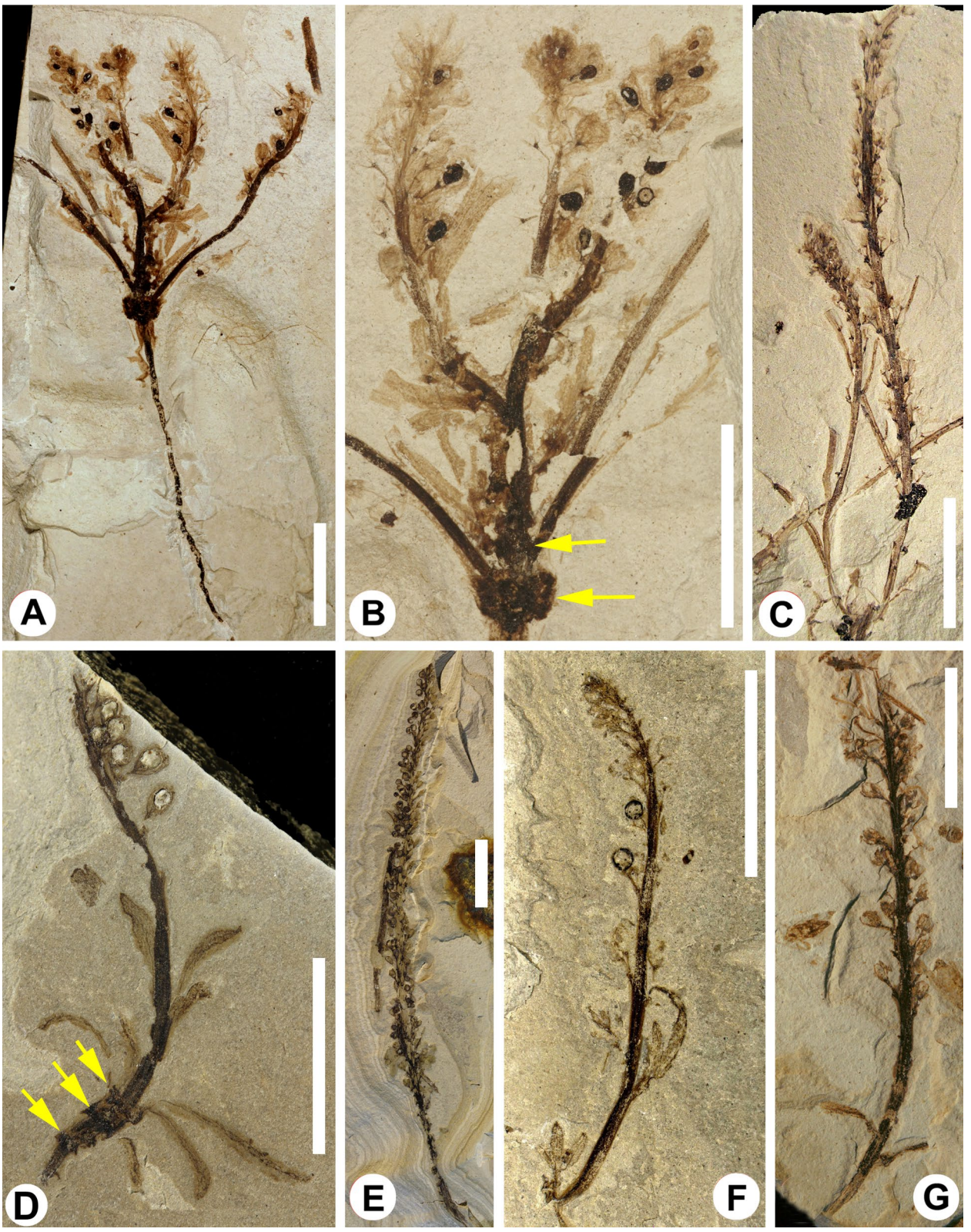

Figure 1. *Kohlsia parachutensis* gen. et sp. nov. **A**. Complete plant showing apparent tap root and terminal infructescences, DMNH 38726; **B**. Enlargement of the counterpart (opposite side) showing corm-like thickenings (arrows) of main axis and infructescences with smaller fruits situated distally; **C**. Portion of plant with two infructescences, USNM PAL 580502; **D**. Plant showing intact leaves and corm-like thickenings (arrows) and terminal infructescence. Holotype, UF 579-69437; **E**. Elongate infructescence, USNM PAL 580380; **F**. Plant with lobed leaves and terminal inflorescence; note diminution and increasingly tight packing of reproductive units towards apex, with sheathing leaves near base, USNM PAL 582037; **G**. Axis with a single inflorescence and two alternate leaves, USNM PAL 582126. Scale bars = 1 cm

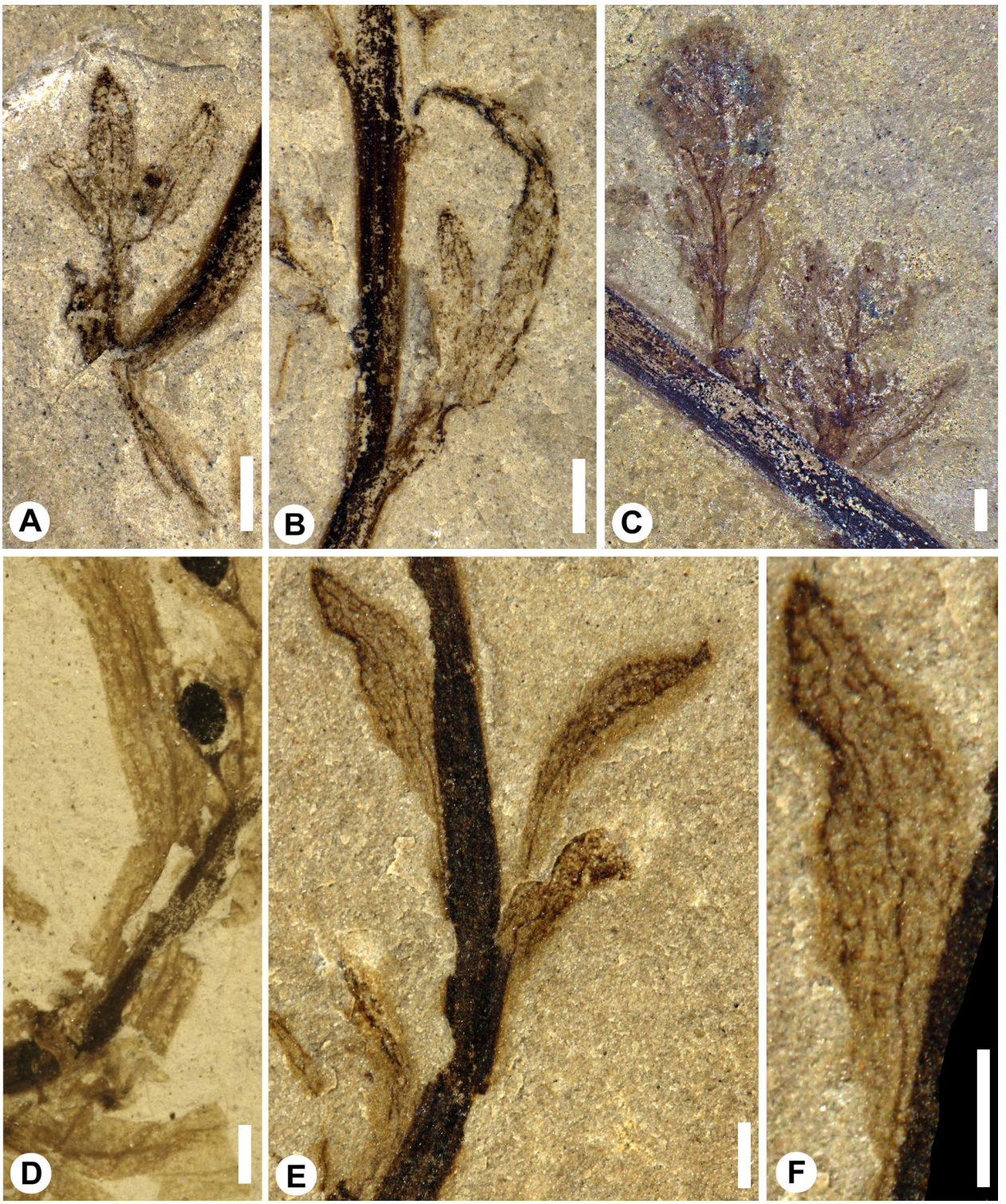

Figure 2. *Kohlsia parachutensis* leaves. **A**. Detail of lobed leaves from Fig. 1F, with prominent midveins and veins converging terminally into possible glands, USNM PAL 582037; **B**. Detail of leaf from Fig. 1F illustrating possible sheathing base, USNM PAL 582037; **C**. Enlargement of irregularly lobed leaves from specimen in Fig. 6A, UF 579-71189; **D**. Enlargement of leaf from Fig. 1A, showing parallel venation, DMNH 38726; **E**, **F**. Enlargement of leaves from specimen in Fig. 1D, showing parallel trending reticulate venation. Holotype, UF 579-69437. Scale bars = 1 mm

The repeated thickenings at the junction of the aerial and rooting portions of the plant (Fig. 1B, D) suggest the possibility of regrowth from the basal portions and thus that these may have been perennial plants. We have interpreted these as rosettes, but we also considered that some of the fossil material might reflect broken-off parts, suggesting possible dispersal by fragmentation in the aquatic environment. Thickenings on some axes (arrows, Fig. 3D) might indicate points of past breakage, generating disseminated branches. If correct, then

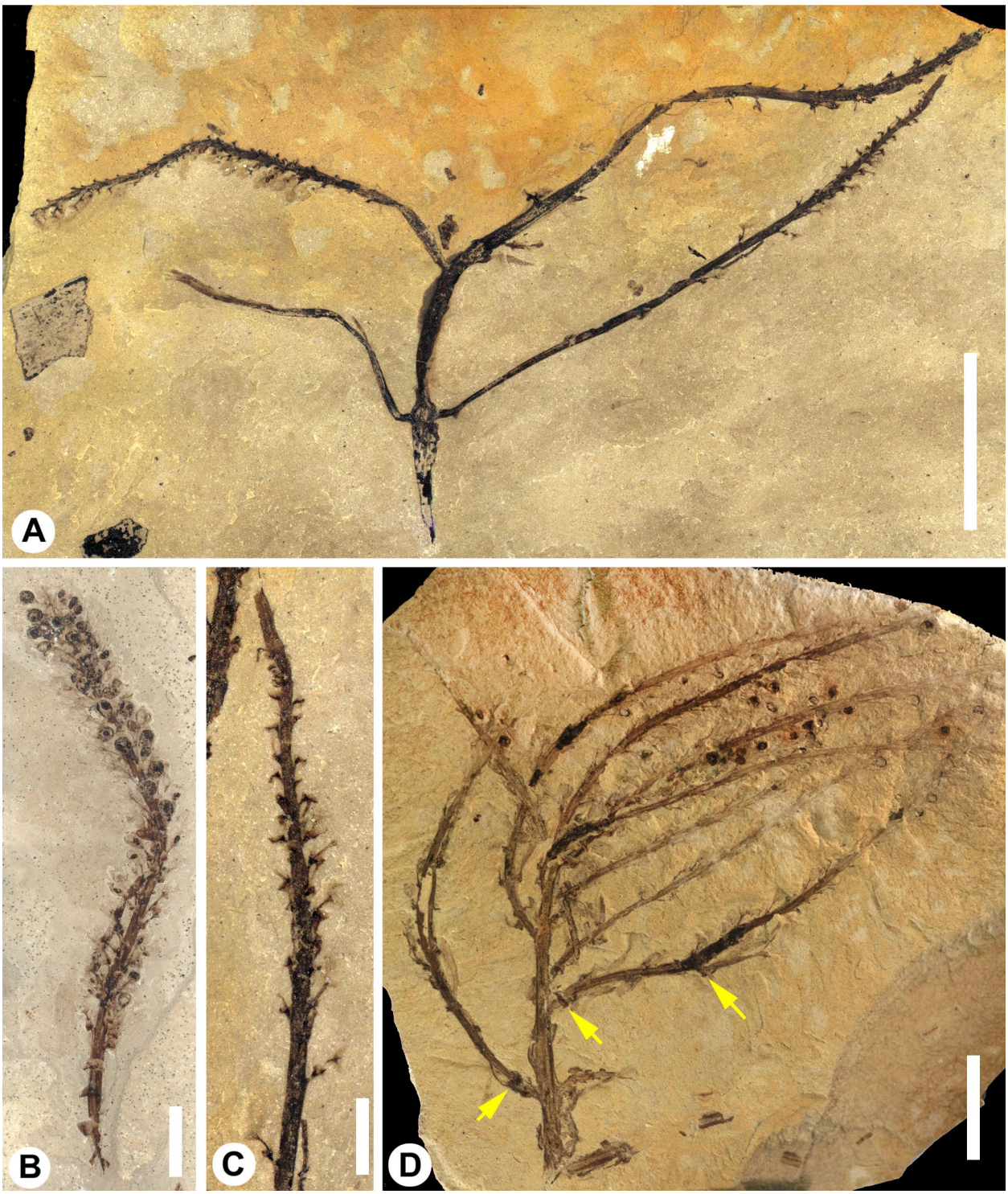

Figure 3. *Kohlsia parachutensis* plant and infructescences. **A**. Plant showing straight main axis and lateral infructescences, UF 579-62273; **B**. Infructescence, UCM 50010 [this is the counterpart of USNM 575439]; **C**. Detail of lower right infructescence from Fig. 3A; **D**. Plant showing thickenings at nodes (arrows) and at least nine infructescences/inflorescences, UCM 50003. Scale bars = 1 cm in A, D, 5 mm in B, 2 mm in C

these were the site of subsequent regrowth in this particular example. However, the strength of the structure interpreted as a tap root in Fig. 1A suggests that, in life, even if dispersed via fragments, the plant was capable of in-situ rooting. The curved to sinuous axes suggest a flexible rather than rigid stance.

At first glance the inflorescence appears to be raceme-like. The diminution of reproductive units towards the tip of the central axis in several specimens (Figs 1F, 3C, 7C) suggests that the main axes were indeterminate. On closer inspection, however, it is seen to be an elongated cyme with axillary branches developing

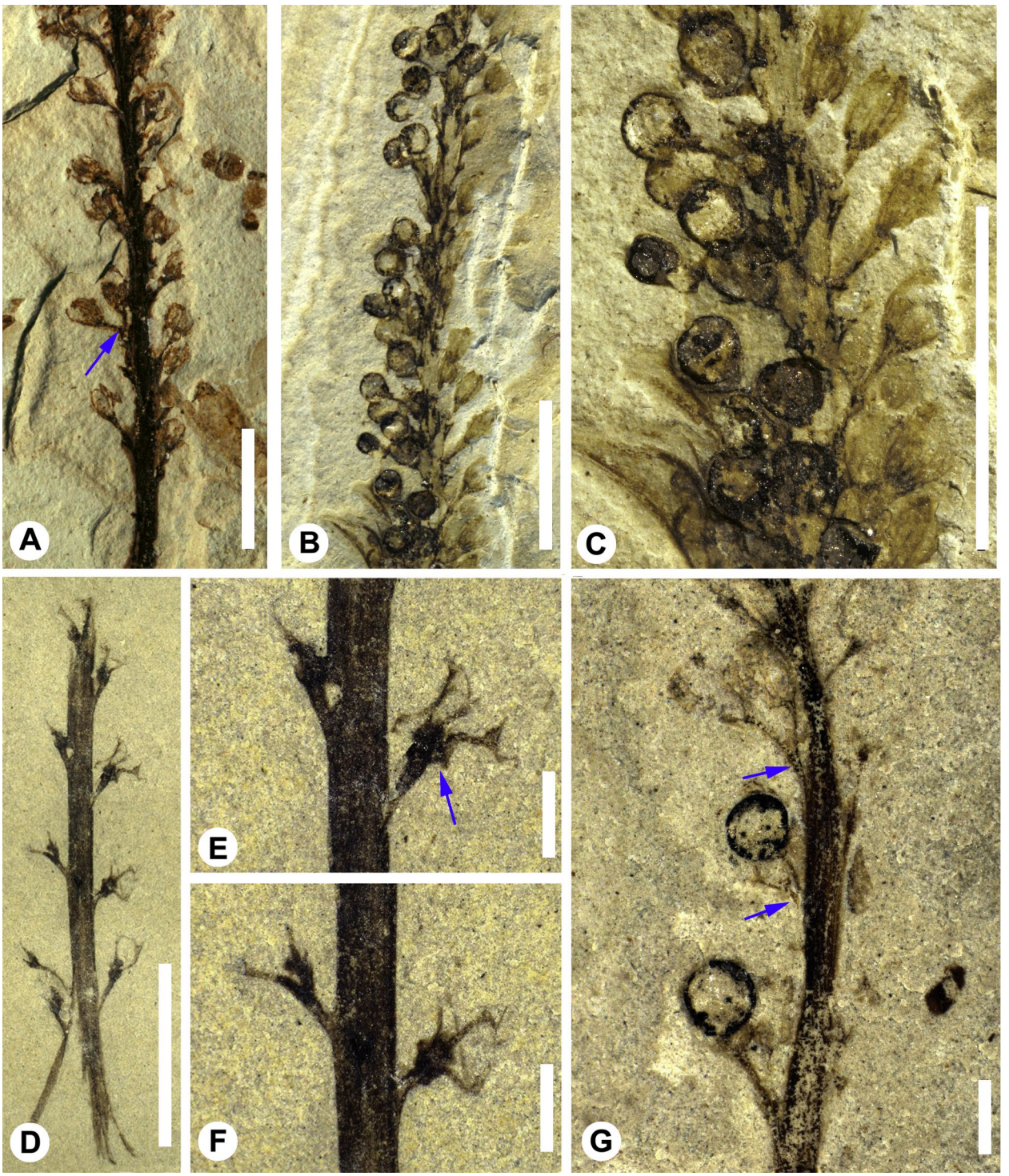

Figure 4. *Kohlsia parachutensis*. **A**. Inflorescence with arrow indicating a node with two flowers, USNM PAL 582126; **B**. Enlargement of inflorescence in Fig. 1E, with flowers showing perianth on the right, and mature fruits with globose endocarps on the left, USNM PAL 580380; **C**. Same, highly enlarged; **D–F**. Infructescence from which the fruits have shed, UF 579-60120. Arrow in E indicates node with pedicels of three fruits; **G**. Enlargement of infructescence from specimen in Fig. 1F with arrows indicating nodes bearing at least two flowers. Note globose endocarps, USNM PAL 582037. Scale bars = 5 mm in A–D, 1 mm in E–G

additional determinate inflorescences (Figs 1A, B, 3A, D). The lateral units arise spirally and exhibit one to three pedicels arising from the same node which represent cymes of two or three flowers/fruits (e.g. Figs 4A, E–G, 6B). Each node is underlain by an obscure bract (Figs 6B, 7E).

The short stalk-like structure between the coalified portion of the fruit body and the perianth seen in several instances (Fig. 5E, F, 7D–F) could be interpreted to indicate that the fruits were stipitate. An alternative interpretation is that the “halo” around the fruit

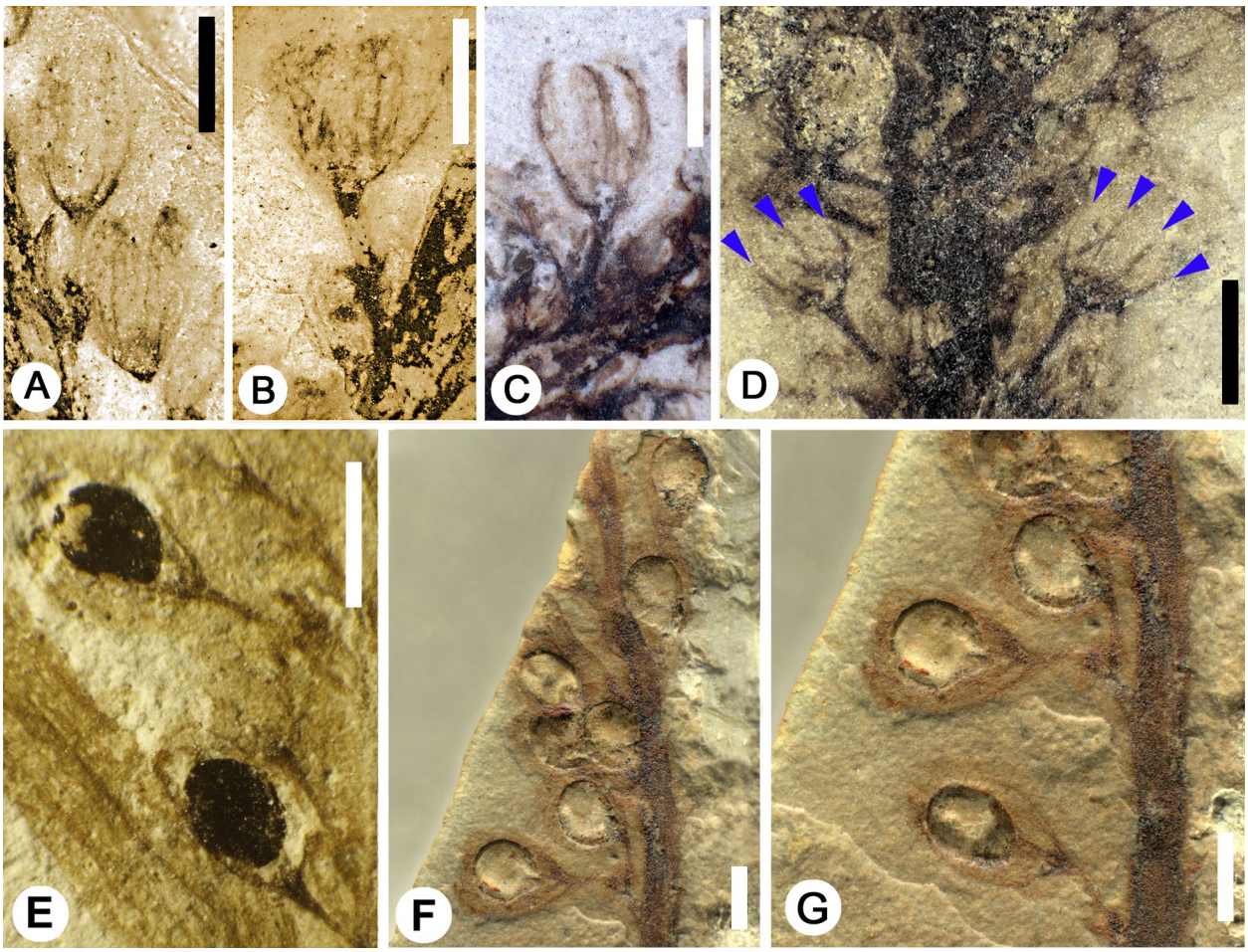

Figure 5. *Kohlsia parachutensis* flowers to show perianth and fruit morphology. **A**, **B**. Enlargements from lower portion of the specimen in Fig. 1E, USNM PAL 580380; **C**. Showing three lobes of what can be inferred to have been 5-lobed perianth, UCM 50005b; **D**. Showing midveins of perianth lobes (arrows), with symmetry leading to inferrence of five tepals, UF 579-71189; **E**. Enlargement from Fig. 1A showing ovoid fruits and underlying perianth, DMNH 38726; **F**, **G**. Enlargement of infructescence from Fig. 1D showing ellipsoid to subglobose endocarps, possibly stipitate, and enclosed by perianth. Holotype, UF 579-69437. Scale bars = 1 mm

(Figs 5F, G, 7E) represents the remains of a fleshy fruit, while the stalk-like structure represents the resistant vascular trace passing through the fruit wall to the endocarp or seed within. Similarly, the very dense charcoalified appearance of the fruits (e.g. Figs 4B, C, 5E) suggests that they possessed a well-lignified and resistant wall. This could be interpreted to indicate a drupaceous fruit with a hard endocarp, or alternatively an achene.

Systematic position. Despite the presence of many useful characters, others are missing or unknown. Consequently, we cannot assign this fossil to an extant family, but we can narrow its systematic affinities to an appreciable degree. *Kohlsia* can be considered an angiosperm on the basis of its flowers and fruits. The lobation in some of the leaves and the presence of five, rather than three, perianth parts rules out monocots, including those with apparently similar habit, e.g. Potamogetonaceae and Alismataceae. The fusion of perianth parts in whorls and their fixed number rules out Magnoliids, so we consider this plant to be a Eudicot. Among the higher eudicots, both Superrosids and Superasterids come into consideration. It is less likely to be a rosid because they tend to have separate floral parts whereas the tepals of *Kohlsia* are basally fused. This basal connation of tepals suggests Sympetalae and thus the Superasterids. Among Superasterids the growth habit of a possible basal rosette led to consideration of the Plantaginaceae, but they typically possess bisexual flowers.

Some Superasterid families can be ruled out on the basis of their epigynous perianth, e.g. Araliaceae, Cornaceae, Rubiaceae. Among Superasterid families with a hypogynous perianth, we considered members of the Caryophyllales, where herbs are common and

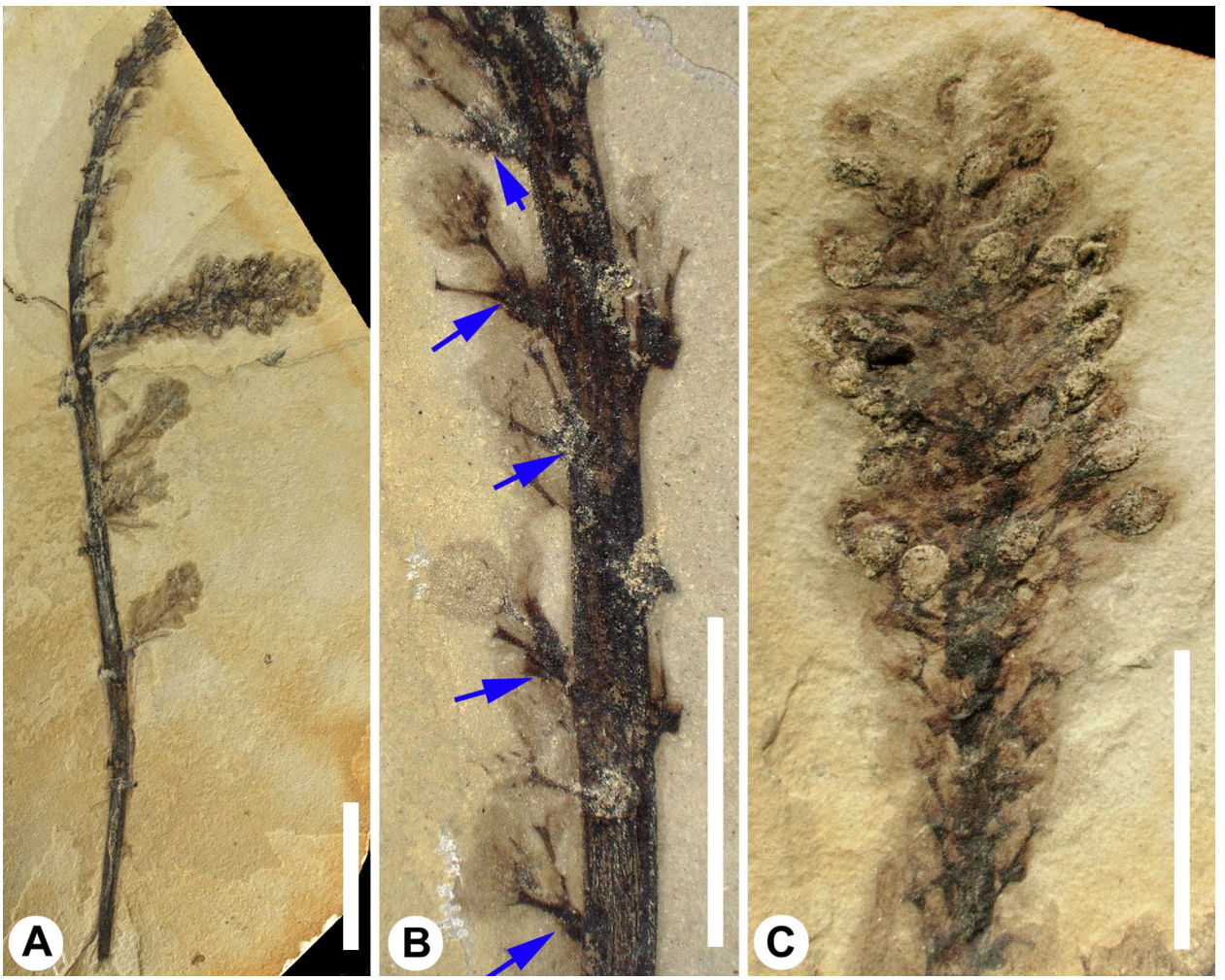

Figure 6. *Kohlsia parachutensis* plant and infructescences. **A**. Slightly sinuous main axis with terminal and lateral inflorescences, UF 579-71189; **B**. Enlargement of terminal inflorescence from counterpart impression of Fig. 6A, arrows indicate bracts subtending nodes with two flowers visible; **C**. Enlargement of upper lateral crowded inflorescence from Fig. 6A, with ovoid fruits protruding. Scale bars = 1 cm in A; 5 mm in B, C

reduced flowers (with tepals, some with single basal ovule) occur in mixed inflorescences and many possess reduced leaf venation, e.g. Phytolaccaceae and Amaranthaceae (incl. Chenopodiaceae). The Amaranthaceae is of particular interest given the possibility that *Kohlsia* might have occurred at least occasionally in saline settings. Additionally, Amaranthaceae bear single-seeded achenes, associated with a persistent perianth, and seeds with a curved embryo. In a similar vein, we also considered families in which aquatic or semi-aquatic plants are common. However, in each case we were unable to locate a genus or indeed a suite of related genera that approximated the characters of the fossil.

Habitat. The small stature of this plant, along with the fact that two examples appear to be preserved as nearly complete plants with both vegetative and reproductive parts intact (Fig. 1A, D), lead us to postulate that *Kohlsia* may have been a marsh plant or semiaquatic plant, growing near the site of preservation. Given that the Green River Formation in the Piceance Basin shows evidence of occasional drying, including mudcracks and salt crystals (Lundell and Surdam, 1975), it is also possible that it was a salt-tolerant plant. This scenario would fit with the variation in foliar characters, as semi-submerged aquatics in particular tend to exhibit heterophylly (Li et al., 2019), and halophytes tend to exhibit reduced leaves relative to their terrestrial relatives. Many aquatic plants reproduce by regenerating asexually via fragmentation (Thomaz, 2025). This leads to the possibility that the morphology is misleading – that the structure that we have identified as a basal rosette with a tap root night in fact be a fragment that was in the process of re-establishing from a node of a broken branch.

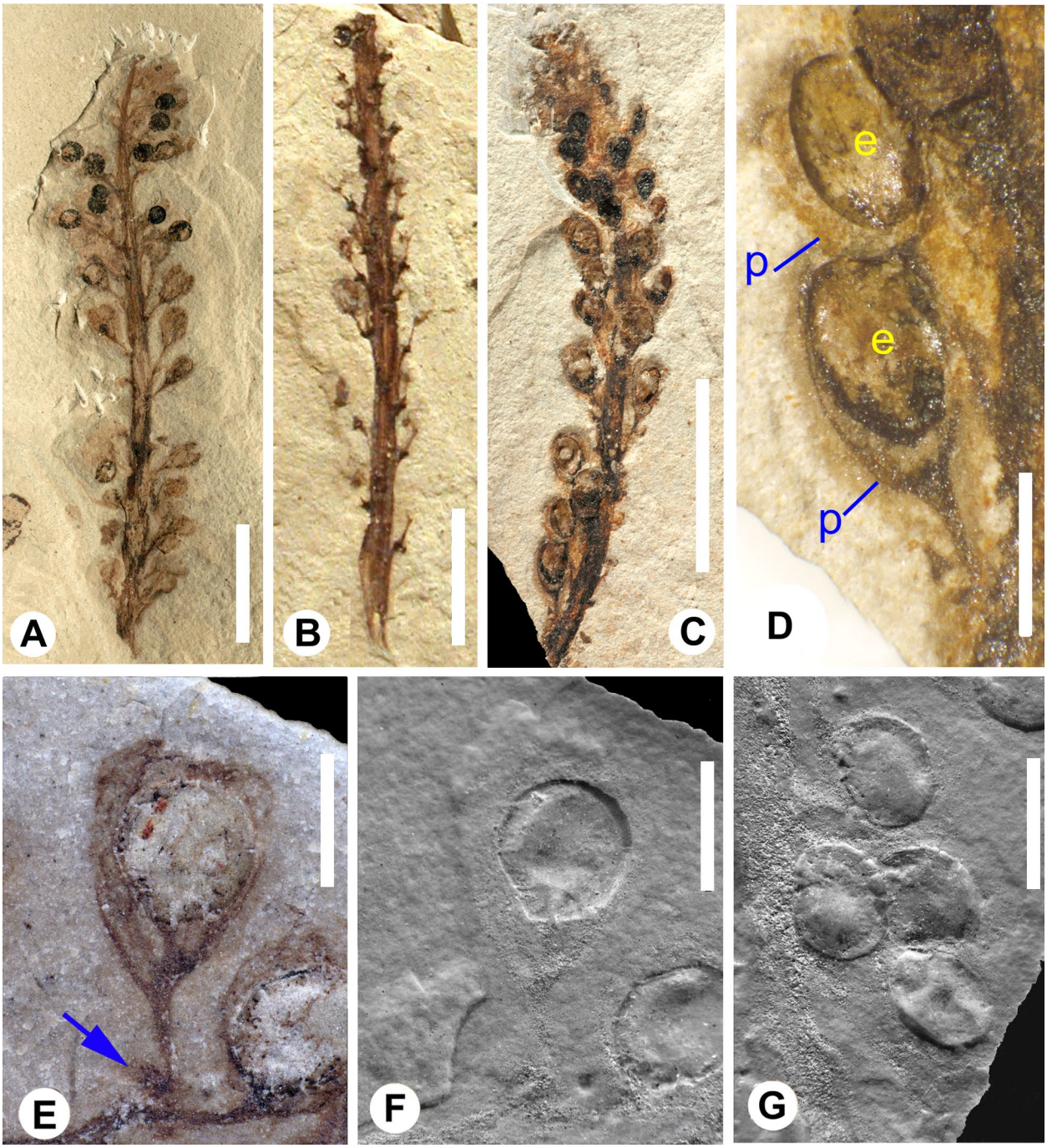

Figure 7. *Kohlsia parachutensis*. **A**. Infructescence with globose coalified fruits in apical one-third, perianth persisting on lower fruits that have apparently dispersed, UCM 50011a; **B**. Axis with most of the fruits shed, DMNH 23394; **C**. Infructescence with smaller, immature fruits toward apex, UF 579-84703; **D**. Enlargement of Fig. 7C showing smooth elliptical outline of endocarps (e) positioned loosely within surrounding perianth (p); **E**, **F**. Enlargement of individual fruit of Holotype, UF 579-69437, with arrow indicating subtending bract, by standard reflected light (E) and shadow effect illumination showing the reniform outline of the lignified portion (F); **G**. Additional fruits from the infructescence in Fig. 7C by shadow effect illumination. Scale bars = 5 mm in A–C, 1 mm in D–G

DISCUSSION

Kohlsia is known only from the shales of the Piceance Creek basin in western Colorado. We have not confirmed its occurrence at other prolific Green River flora sites in Colorado, Utah or Wyoming. The preservation of the whole, or nearly whole, plant in the shale is unusual and informative, proving that the leaves, stem, flowers and fruits all belonged to a single species. However, many aspects of morphology and anatomy remain undetermined. Consequently, we cannot assign it beyond the level of a superasterid angiosperm.

It is noteworthy, however, that *Kohlsia* clearly represents an herbaceous eudicot from the early Eocene, a time frame in which the fossil record is dominated by woody taxa. The only other example of a well-documented herbaceous angiosperm in the Green River shales, to our knowledge, is *Gilisenium hueberi* Lott, Manchester et Dilcher (Polemoniaceae), based on a single specimen with attached stem, root, leaves and fruits from the shales of Bonanza, Utah (Lott et al., 1998). A fuller understanding of the flora represented in the Piceance Creek basin and its similarities and differences to the flora of the western part of the former lake Uinta (Brown, 1934; MacGinitie, 1969; Johnson and Plumb, 1995) and the adjacent Gosiute and Fossil lakes in Wyoming (Wilf, 2000; Grande, 2013) requires further study. However, it seems that *Kohlsia* is a distinctive element of the flora of the southeastern part of lake Uinta.

ACKNOWLEDGEMENTS

Specimens crucial for this study were collected and donated by David Kohls, Jim Barkley, Jalena Dayvault, Sonny Fernandez and Dena Smith. We thank Conrad Labandeira, Scott Wing, Jonathan Wingerath and Jessica Nankano for access to specimens at USNM, Nicole Neu-Yagle for loan of specimens from DMNH and Talia Karim for access to specimens at UCM. Hongshan Wang catalogued and curated the UF specimens. Terry Lott assisted with formatting and proof-reading the text. Helpful comments for improvement of the manuscript were provided by Fabiany Herrera and an anonymous reviewer. Finally, we are greatly saddened to report the death of our friend, collaborator and coauthor, Walter S. Judd (1951–2026), whose contributions to this article, and to the field of systematic botany in general, were substantial.

ADDITIONAL INFORMATION

CONFLICT OF INTEREST. The authors have declared that no competing interests exist.

ETHICAL STATEMENT. No ethical statement was reported.

FUNDING. None.

REFERENCES

Anderson, E.P., Smith, D.M., 2017. The same picture through different lenses: quantifying the effects of two preservation pathways on Green River Formation insects. Paleobiology 43(2), 224–247. https://doi.org/10.1017/pab.2016.29

Barna, P., Zelagin, D., Šmídová, L., 2023. A new Eocene cockroach species from the Green River Formation of Colorado, USA. Biologia 78(6), 1713–1719. https://doi.org/10.1007/s11756-023-01331-8

Brown, R.W., 1934. The recognizable species of the Green River flora. US Geological Survey Professional Paper 185-C, 44–77. https://doi.org/10.3133/pp185C

Dayvault, R.D., Codington, L.A., Kohls, D., Hawes, W.D., Ott, P.M., Behnke, D., 1995. Fossil insects and spiders from three locations in the Green River Formation of the Piceance Creek Basin, Colorado. In: Averett, W.R., (ed.), The Green River Formation in Piceance Creek and Eastern Uinta Basins. Grand Junction Geological Society, Grand Junction, Colorado, pp. 97–116.

Grande, L., 2013. The lost world of Fossil Lake. University of Chicago Press, Chicago. https://doi.org/10.7208/chicago/9780226922980.001.0001

Hail, W.J. Jr., Smith, M.C., 1997. Geologic map of the southern part of the Piceance Creek Basin, northwestern Colorado. US Geological Survey IMAP 2529. https://doi.org/10.3133/i2529

Jagniecki, E.A., Lowenstein, T.K., 2015. Evaporites of the Green River Formation, Bridger and Piceance Creek Basins: deposition, diagenesis, paleobrine chemistry, and Eocene atmospheric CO2. In: Smith, M.E., Carroll, A.R. (eds), Stratigraphy and Paleolimnology of the Green River Formation, Western USA. Syntheses in Limnogeology, vol 1. Springer, Dordrecht, pp. 277–312. https://doi.org/10.1007/978-94-017-9906-5_11

Johnson, K.R., Plumb, C., 1995. Plant fossils from the Green River Formation at Douglas Pass, Colorado, and Bonanza, Utah. In: Averett, W.R. (ed.). The Green River Formation in Piceance Creek and eastern Uinta Basins. Grand Junction Geological Society, Grand Junction, Colorado, pp. 121–130.

Lawton, T.F., 2008. Laramide sedimentary basins. In: Miall, A.D., (ed.), Sedimentary basins of the world, vol. 5. The Sedimentary Basins of the United States and Canada, Science Direct, pp. 429–450. https://doi.org/10.1016/S1874-5997(08)00012-9

Li, G., Hu, S., Hou, H., Kimura, S., 2019. Heterophylly: phenotypic plasticity of leaf shape in aquatic and amphibious plants. Plants 8(10), 420. https://doi.org/10.3390/plants8100420

Lott, T.A., Manchester, S.R., Dilcher, D.L., 1998. A unique and complete polemoniaceous plant from the middle Eocene of Utah, USA. Review of Palaeobotany and Palynology 104, 39–49. https://doi.org/10.1016/S0034-6667(98)00048-7

Lundell, L.L., Surdam, R.C., 1975. Playa-lake deposition: Green River Formation, Piceance Creek Basin, Colorado. Geology 3, 493–497. https://doi.org/10.1130/0091-7613(1975)3%3C493:PDGRFP%3E2.0.CO;2

MacGinitie, H.D., 1969. The Eocene Green River flora of northwestern Colorado and northeastern Utah. University of California Publications in Geological Sciences 83, 1–203.

O'Sullivan, R.B., 1986. Preliminary geologic map of the Anvil Points Quadrangle, Garfield County, Colorado (1:24000). US Geological Survey Miscellaneous Field Studies Map MF-1882.

Perry, M.L., 1995. Preliminary description of a new fossil scorpion from the middle Eocene Green River Formation, Rio Blanco County, Colorado. In: Averett, W.R., (ed.), The Green River Formation in Piceance Creek and eastern Uinta Basins. Grand Junction Geological Society, Grand Junction, Colorado, pp. 131–133.

Pipiringos, G., Johnson, R.C., 1975. Preliminary geologic map of the Buckskin Point Quadrangle, Rio Blanco County, Colorado: U.S. Geological Survey Miscellaneous Field Studies Map 651.

Remy, R.R., 1992, Stratigraphy of the Eocene part of the Green River Formation in the south-central part of the Uinta Basin, Utah: U.S. Geological Survey Bulletin 1787-BB, 1–79.

Roehler, H.W., 1974. Depositional environments of rocks in the Piceance Creek Basin, Colorado. In: Murray, D.K., (ed.), Guidebook to the energy resources of the Piceance Creek Basin, Colorado: Denver, Colorado, Rocky Mountain Association of Geologists, 25th Annual Field Conference, pp. 57–64.

Santiago-Blay, J.A., Soleglad, M.E., Fet, V., 2004. A redescription and family placement of Uintascorpio Perry, 1995 from the Parachute Creek Member of the Green River Formation (Middle Eocene) of Colorado, USA (Scorpiones: Buthidae). Revista Ibérica de Aracnología 10, 7–16.

Smith, M.E., 2007. Stratigraphy, geochronology, and paleogeography of the Green River Formation, Wyoming, Colorado, and Utah [Ph.D. thesis]: Madison, University of Wisconsin, 318 p.

Smith, M.E., Carroll, A.R., Singer, B.S., 2008. Synoptic reconstruction of a major ancient lake system: Eocene Green River Formation, western United States. Geological Society of America Bulletin 120(1–2), 54–84. https://doi.org/10.1130/B26073.1

Thomaz, S.M., 2025. Asexual reproduction of aquatic macrophytes via stem fragments: A review on determinants of plant fragmentation and propagule dispersal. Hydrobiologia. https://doi.org/10.1007/s10750-025-05942-x

Young, R.G., 1995. Stratigraphy of Green River Formation in Piceance Creek Basin, Colorado. In: Averett, W.R., (ed.), The Green River Formation in Piceance Creek and Eastern Uinta Basins. Grand Junction Geological Society, Grand Junction, Colorado, pp. 1–21.

Wilf, P., 2000. Late Paleocene–early Eocene climate changes in southwestern Wyoming: Paleobotanical analysis. Geological Society of America Bulletin 112, 292–307. https://doi.org/10.1130/0016-7606(2000)112%3C292:LPECCI%3E2.0.CO;2