

Revisions to the fossil sporophyte record of *Marsilea*

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ABSTRACT. The fossil record of *Marsilea* is challenging to assess, due in part to unreliable reports and conflicting opinions regarding the proper application of the names *Marsilea* and *Marsileaceaphyllum* to fossil leaves and leaflets similar to those of modern *Marsilea*. Specimens examined for this study include material assigned to *Marsileaceaphyllum johnhallii*, purportedly the oldest fossil record of a *Marsilea*-like sporophyte from the Lower Cretaceous of the Dakota Formation, Kansas, U.S.A.; leaves and leaf whorls of the extinct aquatic angiosperm *Fortuna* from several Late Cretaceous and Paleocene localities in western North America; and leaves and leaflets resembling *Marsilea* from the Eocene Green River Formation, Colorado and Utah, U.S.A. Literature on the fossil record of *Marsilea* was also reviewed. As a result, several taxonomic changes are proposed. *Marsileaceaphyllum johnhallii* is reinterpreted as an aquatic angiosperm that shares some architectural features with the genus *Fortuna*, although *Marsileaceaphyllum* is here maintained as a distinct genus with an emended diagnosis; under this reinterpretation, the name *Marsileaceaphyllum* can no longer be applied to sporophyte organs with affinities to Marsileaceae. Three valid fossil *Marsilea* species are recognized on the basis of sporophyte material that includes characteristic quadrifoliate leaves and reticulate-veined leaflets: *Marsilea campanica* (J. Kvaček & Herman) Hermsen, comb. nov., from the Upper Cretaceous Grünbach Formation, Austria; *Marsilea mascogos* Estrada-Ruiz et al., from the Upper Cretaceous Olmos Formation, Mexico; and *Marsilea sprungerorum* Hermsen, sp. nov., from the Eocene Green River Formation, U.S.A. The species are distinguished from one another based on leaflet dimensions. Leaves from the Eocene Wasatch Formation, U.S.A., are transferred from *Marsileaceaphyllum* back to *Marsilea*, although not assigned to a fossil species. Finally, an occurrence of *Marsilea* from the Oligocene of Ethiopia is reassigned to *Salvinia*. A critical evaluation of the fossil record of *Marsilea* thus indicates that (1) the oldest fossil marsileaceous sporophytes bearing *Marsilea*-like leaves are from the Campanian; (2) only four credible records of sporophyte material attributable to *Marsilea* are known; and (3) the oldest dispersed *Marsilea* spores are known from the Oligocene.

KEYWORDS: Eocene, Green River Formation, *Marsilea campanica*, *Marsilea sprungerorum*, Marsileaceae, *Marsileaceaphyllum*, Salviniales

INTRODUCTION

Marsilea L., the water clover, is a genus of 45–70 living species of heterosporous, amphibious ferns distributed in tropical to temperate regions worldwide (Tryon & Tryon 1982, Johnson 1986, 1993, Kramer 1990, Lin & Johnson 2013). Amongst ferns, the sporophyte of *Marsilea* is especially distinctive for its superficially four-leaf-clover-like compound leaves (Fig. 1A–E), which, depending on habitat, may be floating or aerial (Gupta 1962, Johnson 1986). The fossil sporophyte record of *Marsilea* may

extend as far back as the Cretaceous, although it is muddled by a long history of misidentifications and misinterpretations (Appendix 1).

Macrofossils attributed to *Marsilea* were first reported in the nineteenth and early twentieth centuries (see Reed 1954, 1965 for a bibliography). Seward (1910) considered some of these early reports unconvincing. A more recent detailed review of the fossil record of *Marsilea* by Skog & Dilcher (1992), later updated by Rich et al. (2001), indicated that much of the

then-known fossil sporophyte material was probably not attributable to the genus (for further comments, see also Collinson 1996, 2001). Most fossil species representing sporophyte material that have at one time been attributed to *Marsilea* can be sorted into several categories: material that is considered possibly or probably marsileaceous, but probably not within *Marsilea*; material that has been reassigned to unrelated taxa (e.g. ginkgophytes, *Hydrangea* Gronov., *Salvinia* Ség.); and remains that have no decisive identification and/or are too poorly known to be considered reliable (Appendix 1; see also critical reviews of the fossil record of *Marsilea* or Marsileaceae by Seward 1910, Collinson 1991, 1996, 2001, Skog & Dilcher 1992, Rich et al. 2001).

Additionally, there are differences of opinion regarding when the name *Marsilea* should be applied to marsileaceous fossil sporophyte material, particularly when that material lacks reproductive structures or is thought to have produced a megaspore consistent with one of the extinct Mesozoic marsileaceous or Marsileaceae-affiliated *sporae dispersae*, that is, *Arcellites* E.L. Miner or *Molaspora* Schemel (e.g. Johnson 1986, Skog & Dilcher 1992, Collinson 1996, Nagalingum 2007, Hermsen et al. 2014). Some recent investigators (Nagalingum 2007, Herman & Kvaček 2010, Hermsen et al. 2014, Vallati et al. 2017) have referred vegetative remains to the fossil genus *Marsileaceaphyllum* Nagalingum, which originally encompassed any sterile fossil marsileaceous sporophyte material that included leaves and/or leaflets (Nagalingum 2007). Other investigators (García Massini et al. 2010, Estrada-Ruiz et al. 2018) have assigned *Marsilea*-like sporophyte fossils that lack reproductive structures or that bear reproductive structures lacking diagnostic characters (i.e. sporocarp teeth, a raphe, and/or *in situ* spores; discussed further below) to *Marsilea*.

The continuing confusion surrounding the nomenclature of fossil sporophyte material bearing or representing *Marsilea*-like leaves and/or leaflets, combined with the length of time that has elapsed since the last comprehensive, critical review, make a fresh assessment of the fossil record of *Marsilea* desirable. In this paper I describe new occurrences of fossil *Marsilea* leaf material from the Eocene Green River Formation of Colorado and Utah, U.S.A., and revise the generic assignments of several other

fossil sporophyte taxa with putatively *Marsilea*-type leaf architecture. Finally, I briefly summarize the state of knowledge of the evolution and paleobiogeography of *Marsilea* from the perspective of this revised fossil record.

IDENTIFYING FOSSIL MARSILEA

Marsilea belongs within Marsileaceae Mirb., a family of heterosporous “water ferns” (order Salviniales) that includes three extant genera (*Marsilea*, *Pilularia* L., *Regnellidium* Lindm.) and approximately 60–75 living species (Smith et al. 2006, Lin & Johnson 2013, Christenhusz & Byng 2016, PPG I 2016). About nine extinct fossil genera are claimed to represent marsileaceous sporophytes, with an additional three or four extinct fossil genera representing dispersed spores (e.g. Paradkar 1971, Chitaley & Paradkar 1972, Lupia et al. 2000, Yamada & Kato 2002, Nambudiri & Chitaley 2004, Nagalingum 2007, Hermsen et al. 2014, Sun et al. 2014, Puebla et al. 2015). Ferns in the family are rooted and rhizomatous (Fig. 1A; Johnson 1986); their leaves have few to no leaflets and are likely evolutionarily simplified from a more complex pinnately compound frond (Pryer & Hearn 2009). Identification of putative vegetative (sterile) sporophyte material representing Marsileaceae in the fossil record is often dependent on leaf and/or leaflet architecture, particularly the overall leaf morphology and/or leaflet venation pattern (e.g. Nagalingum 2007, Hermsen et al. 2014, Sender et al. 2014, Vallati et al. 2017). Leaf characters diagnostic for Marsileaceae were reviewed by Nagalingum (2007) and Hermsen et al. (2014), and are summarized here. The leaves are typically compound with few leaflets (up to six in the fossil genus *Rodeites* Sahni; Paradkar & Barlinge 1981) in an opposite or nearly palmate arrangement (Fig. 1A–E), but filiform in *Pilularia* (see, e.g. Tryon & Tryon 1982, Crouch et al. 2011). The leaflets lack a midvein and have dichotomizing venation. The veins may anastomose rarely (e.g. *Regnellidium*: see esp. Pray 1962, Cúneo et al. 2013) or form a complete reticulum with numerous anastomoses (e.g. *Marsilea*, Fig. 1D). The areoles are fusiform; freely ending veinlets are absent from the areoles (Fig. 1D). A marginal vein is present in leaflets of the modern genera (*Marsilea*, *Regnellidium*), although

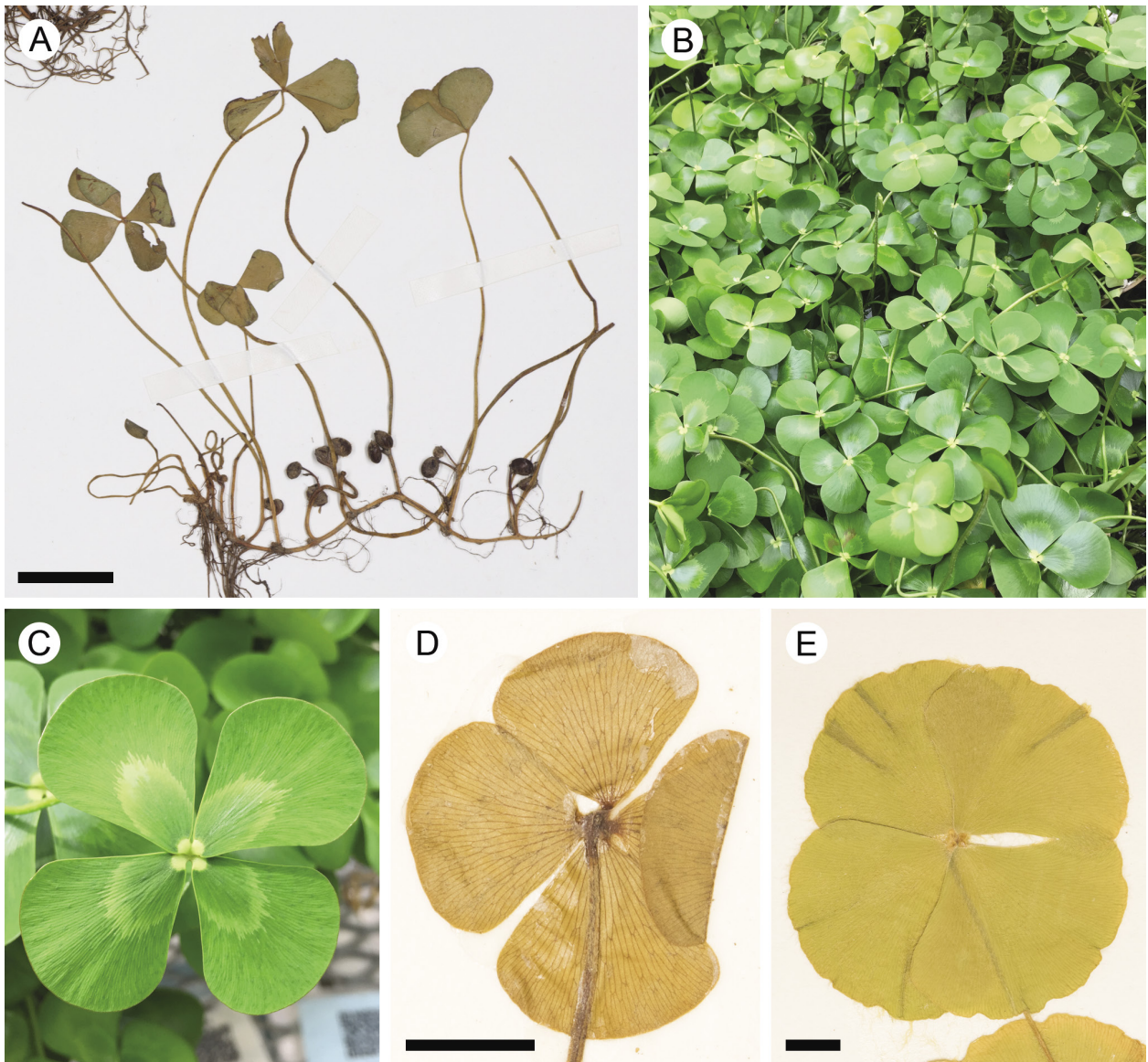


Fig. 1. *Marsilea* sporophyte characters. **A.** *M. quadrifolia* L., sporophyte with rhizome, roots, leaves and sporocarps. BH 000050804 (Juillet 277, France; specimen previously figured by Puebla et al. 2015); **B.** *M. mutica* Mett. (cultivated, L.H. Bailey Conservatory, Cornell University, 2018); **C.** *M. mutica*, leaf (cultivated, L.H. Bailey Conservatory, Cornell University, 2018); **D.** *M. polymorpha* Hook. & Grev., leaf. BH000199641 (G.W. Prescott & R.L. Caylor PZ-108a, Panama); **E.** *M. elata* A. Br. var. *crenata* A. Br., leaf. BH 000068431 (G.H.M. Lawrence 271, cultivated, Quebec). Figure 1A, D, and E used by permission, L.H. Bailey Hortorium, Plant Biology Section, Cornell University (all rights reserved). Scale bars: A = 20 mm; D, E = 5 mm

sometimes absent in fossil forms (e.g. *Regnellites* Yamada & Kato: Yamada & Kato 2002, Sender et al. 2014).

The leaves of *Marsilea* bear four sessile to short-petiolulate leaflets on a very short rachis (Fig. 1A–E; e.g. Gupta 1962, Gaudet 1964, Tryon & Tryon 1982, Johnson 1986, Kramer 1990, Pryer & Hearn 2009, Hermesen et al. 2014, Estrada-Ruiz et al. 2018). The leaflets are obovate to obdeltoid, sometimes described as cuneate or flabellate (Fig. 1A–E); the apical (terminal) leaflet margin is entire (Fig. 1A–D) to subtly to conspicuously toothed (Fig. 1E) or lobed (see also Gupta 1962, Launert 1968, Johnson 1986, Crouch et al. 2011). The leaflet

venation is of a single order, dichotomizing and anastomosing to produce reticulate venation with elongated, often fusiform areoles that become shorter near the apical margin (Fig. 1D; also illustrated by Gaudet 1964, Johnson 1986, Rich et al. 2001, Hermesen et al. 2014, Estrada-Ruiz et al. 2018). The veins end in a delicate marginal vein at the apical (terminal) margin in each leaflet, as best illustrated by Gaudet (1964) and Estrada-Ruiz et al. (2018). The presence and abundance of trichomes is variable, and has been suggested to correlate to the conditions under which the leaf developed (i.e. floating or aerial leaves; Johnson 1986) and/or to the clade of *Marsilea* to which a species

belongs (Nagalingum et al. 2007). The combination of four leaflets per leaf, reticulate leaflet venation and a weak marginal vein distinguishes the foliage of *Marsilea* from that of other Marsileaceae. Although in prior studies leaf and leaflet characters did not completely separate *Marsilea* from *Marsileaceaphyllum* diagnostically (Nagalingum 2007, Herman & Kvaček 2010, Hermsen et al. 2014, Estrada-Ruiz et al. 2018), that issue is rectified with the emendation and reclassification of *Marsileaceaphyllum* provided below.

Marsileaceae are unique in that their spores are produced in sclerified sporocarps (Fig. 1A), which are spherical to reniform and surround two or more bisporangiate sori (Gupta 1962, Johnson 1986, Kramer 1990, Nagalingum et al. 2006). Reliable fossil marsileaceous sporocarps typically have *in situ* spores or are found attached to other organs bearing characters diagnostic for Marsileaceae (however, see Hermsen et al. 2014). *Marsilea* sporocarps often have teeth (one or two pointed projections that occur at the apex of the sporocarp stalk and on the upper surface of the sporocarp); most species also consistently have a sporocarp raphe, or a region where the sporocarp stalk is fused to the sporocarp wall (Gupta 1962, Johnson 1986, Nagalingum et al. 2007, Hermsen et al. 2014). These characters are unique to and apomorphic for “Group II” *Marsilea* (a clade including most of the living species of *Marsilea*) within Marsileaceae (Nagalingum et al. 2007). Thus, they could potentially be used to assign fossil sporocarps to *Marsilea* in the absence of (or in addition to) evidence from other organs (Hermsen et al. 2014). No unequivocal fossil records of *Marsilea* sporocarps are currently known (Appendix 1).

Spores form the bulk of the fossil record of Marsileaceae, and the megaspore record is a key component in understanding the origin and morphological evolution of the group (Lupia et al. 2000, Nagalingum 2007, Hermsen et al. 2014). The marsileaceous megaspore can be identified based on the presence and form of its acrolamella, a proximal extension of the perine (Lupia et al. 2000, Schneider & Pryer 2002, Batten et al. 2011). In living taxa, the acrolamella consists of an inner structure made up of sporopollenin (hereafter, “solid acrolamella” after Schneider & Pryer 2002) surrounded by an outer envelope that becomes gelatinous upon absorbing water (Foster & Gifford 1974,

Schneider & Pryer 2002, Batten et al. 2011). The solid acrolamella is conspicuous and lobed in most genera of Marsileaceae, including *Pilularia*, *Regnellidium*, and the dispersed Mesozoic megaspore genera (i.e. *Arceclites*, *Molaspora*) thought to have affinities to the family (e.g. Collinson 1991, 1996, Lupia et al. 2000, Schneider & Pryer 2002, Batten et al. 2011). *Marsilea* megaspores are prolate, with reticulate perine sculpture, a combination of characters also observed in *Pilularia* (Lupia et al. 2000, Schneider & Pryer 2002); however, *Marsilea* differs in having a relatively flat, ring-like structure at its proximal pole. This structure is considered to be a reduced solid acrolamella (Schneider & Pryer 2002) and is also called a hilum (Lupia et al. 2000).

Marsilea microspores are spherical, with baculate perine sculpture, characters not unique to the genus among Marsileaceae, at least if fossil microspores are considered (Lupia et al. 2000). An acrolamella occurs at least sometimes on marsileaceous microspores, and is either not consistently present or entirely absent on *Marsilea* microspores (Tryon & Lugardon 1991, Lupia et al. 2000, Schneider & Pryer 2002).

MATERIALS AND METHODS

The records indicate that all the Green River Formation *Marsilea* specimens included in this study were collected from Eocene sediments of the Parachute Creek Member, Green River Formation, Colorado and Utah, U.S.A. (Fig. 2). The Parachute Creek Member was deposited in the Uinta and Piceance Creek Basins of western Colorado and eastern Utah and is thought to represent shallow lake and other wetland environments of ancient Lake Uinta (MacGinitie 1969, Johnson & Plumb 1995, Grande 2013). The taxonomic composition of the Parachute Creek/Lake Uinta flora has been extensively documented from multiple localities (e.g. Brown 1934, MacGinitie 1969, Manchester 1989, Johnson & Plumb 1995, Call & Dilcher 1997, Boucher et al. 2003, Manchester et al. 2006, Allen 2015). Other genera described from the localities that yield *Marsilea* leaves and/or leaflets (as identified by locality number rather than locality name; UF = Paleobotanical Collection, Florida Museum of Natural History; UCMP = University of California Museum of Paleontology) include *Cedrelospermum* Saporta (Ulmaceae) from Douglas Creek, Colorado (UF 15727: Manchester 1989), *Populus* L. (Salicaceae) from Handleys, Colorado (UCMP PB02019: Manchester et al. 2006), and *Phoenix* L. (Aracaceae), *Pseudosalix* Boucher et al. (Salicaceae), and *Populus* from Handleys Rainbow UT, Utah (UCMP PB02016: Boucher et al. 2003, Manchester et al. 2006, Allen 2015).

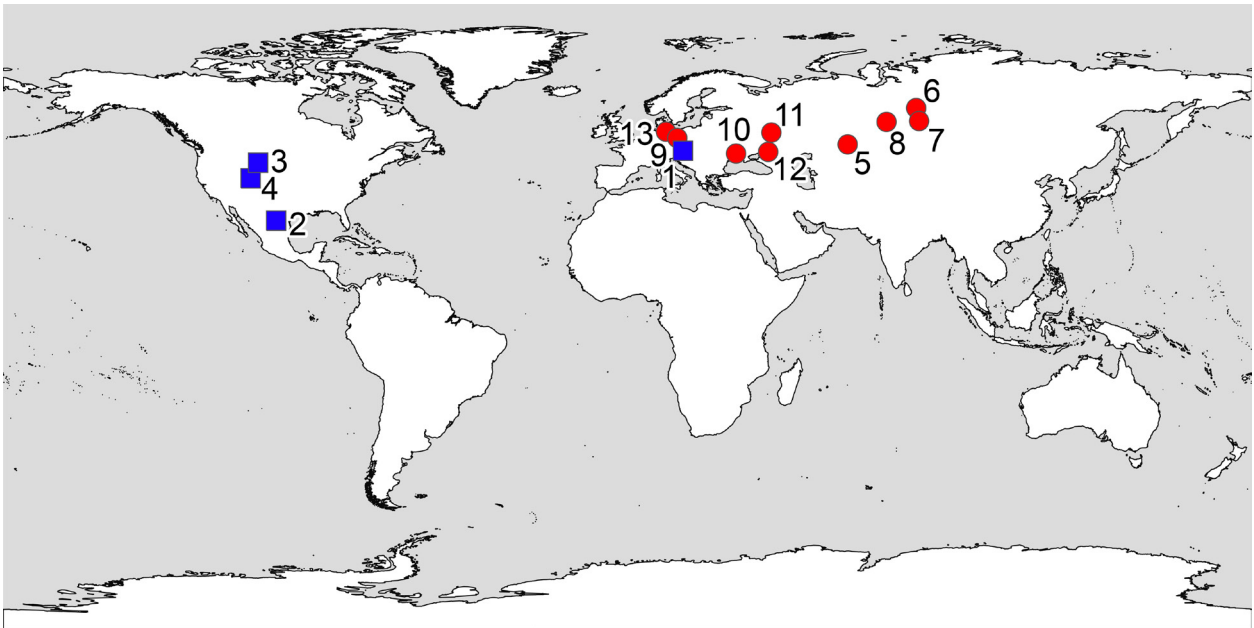


Fig. 2. World map showing distribution of *Marsilea* leaf and leaflet compression and impression fossils (blue squares) and megaspores (red circles). Due to the scale of the map, some localities that occur near one another have been combined. For references, see Appendices 1 and 3. 1. *Marsilea campanica*, Campanian (Upper Austria, Austria); 2. *Marsilea mascogos*, Campanian (Coahuila, Mexico); 3. *Marsilea* sp., Eocene (Wyoming, U.S.A.); 4. *Marsilea sprungerorum*, Eocene (Colorado and Utah, U.S.A.); 5. *Marsilea tertiaria*, Oligocene (Kostanay Region, Kazakhstan); 6. *Marsilea* sp., Oligocene–Miocene (Tomsk Oblast, Russia); 7. *Marsilea* sp., Miocene (Tomsk Oblast, Russia); 8. *Marsilea* sp., Miocene (Omsk Oblast, Russia); 9. *Marsilea dorofeevii* and *Marsilea reticulata*, Miocene (Brandenburg and Saxony, Germany); 10. *Marsilea maeotica* and *M. sarmatica*, Miocene (Mykolaiv and Odessa Oblasts, Ukraine); 11. *Marsilea tambovica*, Miocene (Tambov Oblast, Russia); 12. *Marsilea tertiaria*, Miocene (Rostov Oblast, Russia); 13. *Marsilea dorofeevii*, Pliocene (Mecklenburg-Vorpommern, Germany)

Specimens including a nearly complete compound leaf, a partial leaf and isolated leaflets of *Marsilea* from the Green River Formation examined for this study are housed in the Paleobotanical Collection of the Florida Museum of Natural History (FLMNH, specimen number prefix UF), University of Florida, Gainesville, Florida, U.S.A., and the University of California Museum of Paleontology (UCMP), Berkeley, California, U.S.A. Although several of these specimens had already been identified as *Marsilea* on specimen labels, some had not previously been attributed to this taxon. Contextual specimen information (e.g. formation, locality, collectors) was gathered from specimen labels and/or databases maintained by FLMNH and UCMP (<https://ucmpdb.berkeley.edu>). Another leaf specimen held at the Denver Museum of Nature & Science (DMNH), Denver, Colorado, U.S.A., was identified based on a photograph labeled *Regnellidium* in an online database (paleobotanyproject.org, accessed 7 August 2017). Comparative extant material of *Marsilea* and *Salvinia* illustrated in this paper is held at the L.H. Bailey Hortorium Herbarium (BH), Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York, U.S.A., and the L.H. Bailey Conservatory, Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York, U.S.A. The figured cleared leaf of *Salvinia* was provided by M.A. Gandolfo (Cornell University) and was sampled from a specimen held at BH.

Material relevant to the taxonomic status of *Marsileaceaphyllum* was also studied, including selected specimens of *Marsileaceaphyllum johnhallii* (J.E. Skog

& Dilcher) Nagalingum and *Fortuna* McIver & Basinger. Specimens of *Marsileaceaphyllum johnhallii* are held at FLMNH and are from the Lower Cretaceous (Albian) of the Dakota Formation, Barton County, Kansas, U.S.A. (locality UF 15706; Skog & Dilcher 1992, 1994; for updated age information, see also Wang & Dilcher 2018). A preliminary survey of fossils attributed to *Fortuna marsilioides* (W.A. Bell) McIver & Basinger, *Fortuna* cf. *F. marsilioides*, *Fortuna*, or “*Fortunea*” [sic] was also made based on material held in North American collections. The fossils examined are from the Late Cretaceous (Campanian–Maastrichtian) to Paleocene of Alberta, Canada, and the Paleocene of Montana and Wyoming, U.S.A. Associated data (e.g. geographic and stratigraphic information, localities) were gathered from published literature, specimen labels, and/or databases maintained by the respective collections where the fossils are held. Specimens of *Fortuna* examined for this study and their repositories are listed in Appendix 2 and include specimens from many localities where *Fortuna* is known to occur (see Bell 1949, McIver & Basinger 1993, Gemmill & Johnson 1997, Stockey & Rothwell 1997, Hoffman & Stockey 1999, Wilf 2000, Hoffman 2002). *Fortuna* is additionally reported from Ravenscrag Butte, Paleocene, Ravenscrag Formation, Saskatchewan, Canada (McIver & Basinger 1993), although those specimens were not examined. Stockey and Rothwell (1997) also speculated that *Fortuna* may have been attributed to *Quereuxia* and *Trapago* in the Maastrichtian–Danian of Kamchatka Krai, Russia (see e.g. Golovneva 1991).

Fossil and herbarium specimens were photographed using DSLR cameras (Canon and Nikon, several models),

live material was photographed with an iPhone, and the cleared leaf was scanned on a Canon 9000F Mark ii flatbed scanner. Photomicrographs of fossil *Marsilea* venation were made using a Nikon Digital Sight DS-Fi2 camera head with a Nikon Digital Sight DS-U3 camera control unit attached to a Nikon SMZ1500 stereoscopic microscope. Photomicrographs were captured using NIS Elements BR ver. 4.11.00 software (1991–2012, Laboratory Imaging), which was also used to measure the Green River *Marsilea* specimens. The distribution map (Fig. 2) was created using SimpleMappr (Shorthouse 2010). Locality coordinates used to construct the maps were either taken from collection records or estimated based on locality descriptions in collection records and/or in publications. Plates were constructed using Adobe Photoshop CC.

Terminology used to describe leaves and leaflets was adapted from Ellis et al. (2009) and other sources, as applicable. Plant classification above ordinal level here follows Ruggiero et al. (2015), wherein angiosperms and ferns are recognized at the rank of class (Magnoliopsida and Polypodiopsida, respectively). Ordinal and family-level classification follows Smith et al. (2006) and PPG I (2016), wherein Salviniales is recognized as an order with two extant families (Marsileaceae, Salviniaceae).

SYSTEMATIC PALEONTOLOGY

Class: Magnoliopsida (angiosperms)

Order: Unknown

Family: Unknown

Genus: *Marsileaceaphyllum*
Nagalingum, emend. Hermsen

Emended generic diagnosis. Rhizomatous aquatic plants bearing roots and upright axes at the nodes, upright axes with apical whorls of foliar organs (i.e. leaves or leaflets, identity uncertain). Foliar organs obovate, apex obtuse and rounded, base cuneate, lateral margins straight to slightly convex. Apical margin with broad, rounded teeth, the apex of each tooth retuse (notched) and glandular. Venation actinodromous, major veins ending in a marginal vein inside the apical margin or in a tooth apex; finer veins forming a reticulum; areoles irregularly polygonal; freely ending veinlets absent. Marginal vein nearing or reaching the apical margin at the notch in each tooth.

Comments. The above diagnosis is based on the type and sole species of *Marsileaceaphyllum* here recognized, *Marsileaceaphyllum johnhallii*. Morphotypes and species here

excluded from *Marsileaceaphyllum* include *Marsileaceaphyllum* sp. (Vallati et al. 2017), *Marsileaceaphyllum* sp. B (Nagalingum 2007), *Marsileaceaphyllum* sp. C (Nagalingum 2007), *Marsileaceaphyllum lobatum* Nagalingum (Nagalingum 2007), *Marsileaceaphyllum mahisensis* Hu et al. (Hu et al. 2008, Hu & Taylor 2014), and species and morphotypes of *Marsileaceaphyllum* transferred to *Marsilea* herein (see below).

Type species: *Marsileaceaphyllum johnhallii* (J.E. Skog & Dilcher)

Nagalingum, emend. Hermsen

Fig. 3A–C

Basionym. *Marsilea johnhallii* J.E. Skog & Dilcher (1992), Amer. J. Bot., 79(9), p. 983, figs 1–11.

Synonyms.

- 1994 *Marsilea johnhallii* J.E. Skog & Dilcher. Skog & Dilcher (1994), p. 11; pl. V, figs 20–22.
- 2007 *Marsileaceaphyllum johnhallii* (J.E. Skog & Dilcher) Nagalingum (2007), p. 45.
- 2014 *Marsileaceaphyllum johnhallii* (J.E. Skog & Dilcher) Nagalingum. Hermsen et al. (2014), p. 372.

Emended specific diagnosis. As for the genus.

Holotype. UF 15706-8273. Skog & Dilcher (1992), fig. 1; Skog & Dilcher (1994), pl. V, fig. 20. Held at the Paleobotanical Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

Type locality. UF 15706, Hoisington III, Barton County, Kansas, U.S.A. (Skog & Dilcher 1992, 1994, Wang & Dilcher 2018).

Type stratum & age. Terra Cotta Clay Member, Lower Cretaceous (Albian) of the Dakota Formation (see Wang & Dilcher 2018).

Specimens examined. UF 15706-3058; 15706-8269, 8269'; 15706-8271, 8271'; 15706-8272; 15706-8273 (holotype); 15706-8274, 8274' (paratype); 15706-8275; 15706-11691, 11691' (paratype); 15706-11791 (putative sporocarp); 15706-11792 (putative sporocarp).

Comments. *Marsileaceaphyllum johnhallii* is based upon a suite of specimens collected from Lower Cretaceous (Albian) sediments of the Dakota Formation, Kansas, U.S.A. (Skog & Dilcher 1992, 1994; for updated age

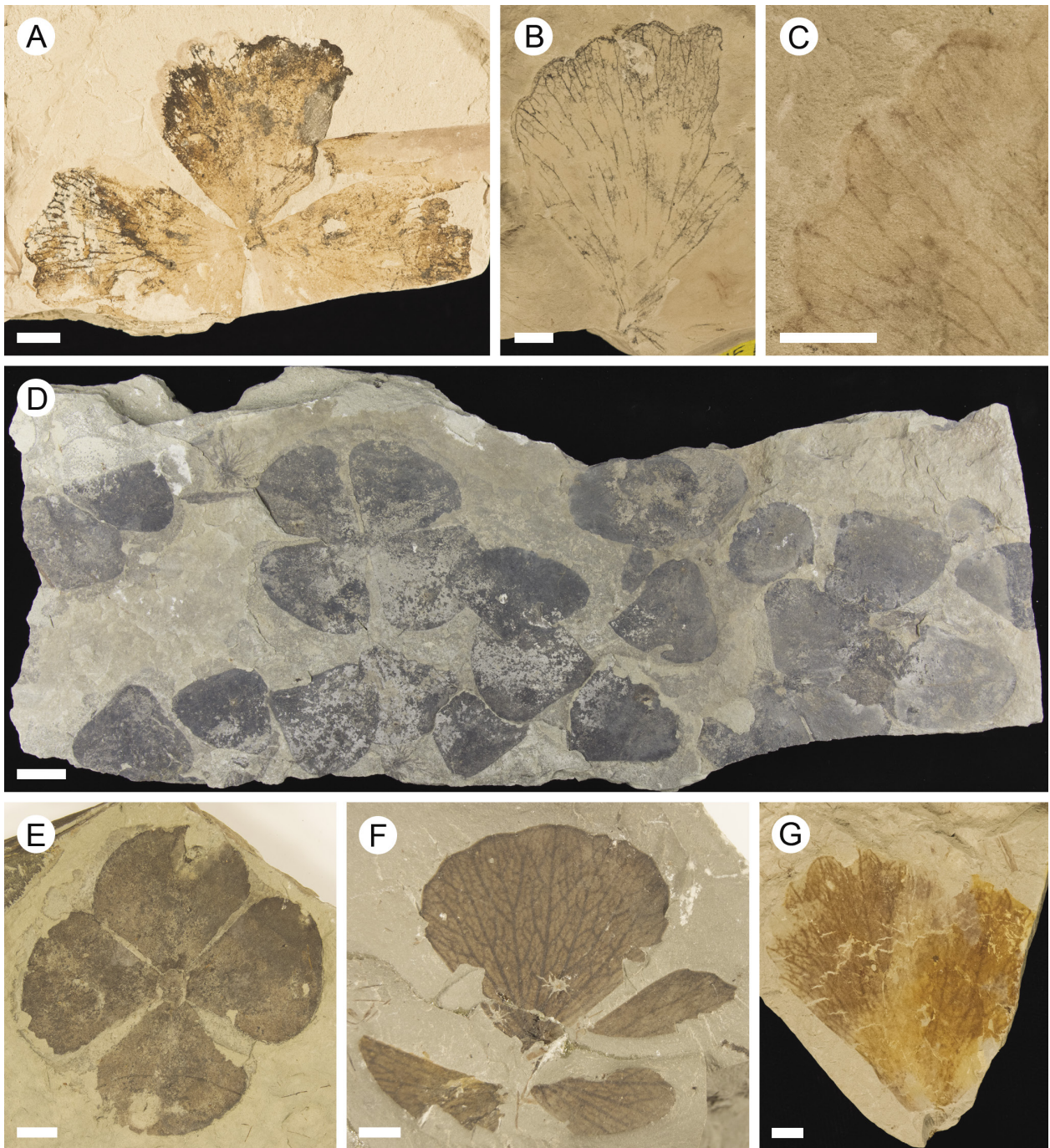


Fig. 3. *Marsileaceae* and *Fortuna*. **A–C.** *Marsileaceae johnhallii*, Hoisington III, Albian, Dakota Formation, Kansas, U.S.A.; **A.** Three leaves/leaflets in an apparent whorl. UF 15706-8269; **B.** Leaf/leaflet showing venation pattern. UF 15706-8272 (specimen previously figured by Skog & Dilcher 1992, 1994); **C.** Detail of apical margin of leaf/leaflet, showing marginal vein and structure of teeth. UF 15706-8271 (specimen previously figured by Skog & Dilcher 1992); **D–F.** *Fortuna marsilioides*, Late Cretaceous–Paleocene, Alberta, Canada; **D.** Slab with rosettes and individual leaves preserved on same plane. Dissected structures are underwater leaves of *Trapago angulata* (Newb.) McIver & Basinger (see Stockey & Rothwell 1997). TMP 1989.057.0015 (Oldman River, Campanian–Maastrichtian, St. Mary River Formation, Alberta, Canada); **E.** Rosette of four leaves showing central bilobed structure. UAPC-ALTA PB-S38798.B (Cardston, Maastrichtian, St. Mary River Formation, Alberta, Canada); **F.** Group of leaves. UAPC-ALTA PB-S12766 (Red Deer River, Paleocene, Paskapoo Formation, Alberta, Canada; specimen previously figured by McIver & Basinger 1993); **G.** *Fortuna* leaf showing pronounced crenations. UF 18123-59579 (Bison Basin, Paleocene, Fort Union Formation, Wyoming, U.S.A.). Scale bars: A, B, C, F, G = 5 mm; D = 20 mm; E = 10 mm

information, see Wang & Dilcher 2018). Skog and Dilcher (1992) originally referred the specimens to *Marsilea* and described the species *Marsilea johnhallii* as an aquatic fern having rhizomes bearing roots and having

compound leaves with four leaflets. Structures that they identified as possible sporocarps were discovered in the same sediments. They noted that Mesozoic dispersed megaspore types considered to have affinities to Marsileaceae

(*Arcellites* and *Molaspora*) also occur in the Dakota Formation (see also Kovach & Dilcher 1988), and suggested that *Molaspora*-type megaspores may have been produced by extinct *Marsilea*-like sporophytes.

Collinson (1996) thought that *Marsilea johnhallii* should be transferred out of *Marsilea* and to a fossil genus if it could be shown to have produced megaspores referable to *Molaspora*. Nagalingum (2007) later erected the genus *Marsileaceaphyllum* as a morphologically heterogeneous taxon encompassing all marsileaceous fossil sporophyte material (species and morphotypes) bearing or consisting of leaves or leaflets but lacking spores and sporocarps; *Marsileaceaphyllum johnhallii* (J.E. Skog & Dilcher) Nagalingum was designated as the type for the new genus. Hermsen et al. (2014) emended *Marsileaceaphyllum* to include solely fossil sporophyte material of leaves or bearing leaves similar to those of *Marsilea*, that is, marsileaceous leaves with four leaflets and a marginal vein. The name *Marsileaceaphyllum* has been applied to three species in addition to *Marsileaceaphyllum johnhallii*: *M. campanicum* J. Kvaček & Herman, *M. lobatum* and *M. mahisensis* (Nagalingum 2007, Hu et al. 2008, Herman & Kvaček 2010, Hermsen et al. 2014). It has also been applied to several morphotypes lacking definitive assignment to a species (Nagalingum 2007, Hermsen et al. 2014, Vallati et al. 2017). Apart from *Marsileaceaphyllum johnhallii*, all *Marsileaceaphyllum* species and morphotypes are based solely upon compound leaves and/or simple foliar structures interpreted as isolated leaflets.

The features of *Marsileaceaphyllum johnhallii* are inconsistent with the characteristics of *Marsilea* and Marsileaceae. Differences include (1) The venation pattern, which consists of more than one order of weakly differentiated veins, primary veins radiating from the base of the foliar structures, and finer veins forming a reticulum (Fig. 3A, B); (2) the shape of the areoles, which are irregularly polygonal (Fig. 3A–C) rather than fusiform (cf. Fig. 1D); and (3) the teeth, which are uniform, notched, and glandular (Fig. 3A–C). Furthermore, this combination of features is more characteristic of the leaf architecture of an angiosperm than one of a fern (see Jud & Hickey 2013). Reinterpretation of *M. johnhallii* as an angiosperm means that other species and morphotypes

still assigned to *Marsileaceaphyllum* require reassignment at genus level, as they are structurally dissimilar from and likely unrelated to the type species of the genus (for further discussion, see Hermsen et al. 2014). The identity of the structures originally considered putative sporocarps of *Marsileaceaphyllum johnhallii* is unknown. Because the “sporocarps” are not attached to the other organs (Skog & Dilcher 1992), it is possible that they were not produced by the same taxon.

It is unclear with which group of angiosperms *Marsileaceaphyllum johnhallii* might be affiliated. No plausible modern relatives have been identified. *Marsileaceaphyllum johnhallii* does, however, share some architectural similarities with the obscure extinct angiosperm taxon *Fortuna marsilioides*, which is characterized by quadrifoliate leaf whorls or rosettes (Fig. 3D, E; McIver & Basinger 1993). The type specimen of *F. marsilioides* was originally interpreted by Bell (1949) as representing whorled appendages, possibly comprising a calyx. McIver & Basinger (1993) later erected the genus *Fortuna* after examining a suite of specimens from Campanian–Maastrichtian and Paleocene deposits of western Canada. Several authors (Bell 1949, McIver & Basinger 1993, Gemmill & Johnson 1997, Herman & Kvaček 2010) have remarked on the superficial resemblance between quadrifoliate *Marsilea* leaves (Fig. 1A–E) and *Fortuna* rosettes/whorls (Fig. 3D, E). Little has been reported on *Fortuna* since its initial description by McIver & Basinger (1993), with only a few papers providing limited additional illustrations, descriptions or interpretations of the genus (Gemmill & Johnson 1997, Stockey & Rothwell 1997, Hoffman 2002).

Marsileaceaphyllum johnhallii (Fig. 3A–C) resembles *Fortuna* (Fig. 3D–G; see also description and figures in McIver & Basinger 1993) in the whorled arrangement of its foliar organs, the overall size and shape of its foliar organs, the presence of a toothed apical leaf/leaflet margin with glandular teeth, the presence of more than one order of venation, and the presence of a strong vein following the apical leaf/leaflet margin. *Marsileaceaphyllum* differs from *Fortuna* in several key ways, however. *Marsileaceaphyllum* apparently has only three leaves (or leaflets) per whorl (Fig. 3A), rather than four. A bilobed or bipartite structure sometimes occurs in the center of complete

quadrifoliate rosettes/whorls of *Fortuna* (Fig. 3E; see also “circular bodies” of McIver & Basinger 1993), although the presence of such a structure in *Marsileaceaphyllum* is more ambiguous (Fig. 3A). *Fortuna* leaves often have inconspicuous teeth (Fig. 3D–F; McIver & Basinger 1993, Hoffman 2002); even when their leaves have large crenations, the teeth lack the pronounced apical notch characteristic of *Marsileaceaphyllum* (cf. Fig. 3B and Fig. 3G). The overall venation pattern differs between the taxa, with *Fortuna* having more clearly differentiated vein orders and more orders of veins (cf. Fig. 3B and Fig. 3F). Finally, the marginal vein is farther from the apical margin in *Marsileaceaphyllum* (Fig. 3B, C) than in *Fortuna* (Fig. 3F, G).

Due to the structural differences between the two taxa, *Marsileaceaphyllum* is here maintained as a genus distinct from *Fortuna*. Whether the similarities between the taxa are due to convergence or relatedness is unclear.

Class: Polypodiopsida (ferns)

Order: Salviniales

Family: Marsileaceae Mirb.

Genus: *Marsilea* L.

Marsilea campanica (J. Kvaček & Herman)
Hermsen, comb. nov.

Basionym. *Marsileaceaphyllum campanicum* J. Kvaček & Herman in Herman & Kvaček (2010), Late Cretaceous Grünbach Flora of Austria, Naturhistorisches Museum Wien, pp. 39–40, text-figs. 7H, 17; pl. 8, figs 1–7.

Synonyms.

1910 *Marsilia Nathorsti* Krasser, nom. nud., in Seward (1910), p. 474.

2004 *Marsilea* sp., Kvaček & Herman (2004), fig. 1b.

2007 *Marsilea campanica* J. Kvaček & Herman, nom. nud., in Herman & Kvaček (2007), fig. 2H.

2014 *Marsileaceaphyllum campanicum* J. Kvaček & Herman. Hermsen et al. (2014), pp. 372–373.

Emended diagnosis. Leaflets 12–40 mm long and 14–44 mm wide. Leaflet shape obovate, apex rounded and obtuse, base cuneate. Leaflet lateral margins straight to convex, apical margin entire to shallowly undulate.

Holotype. NHMW 1999B0057/0509a. Herman & Kvaček (2010), text-fig. 17; pl. 8, fig. 2.

Held in the Department of Geology and Palaeontology, Naturhistorisches Museum Wien, Vienna, Austria (Herman & Kvaček 2010).

Type locality. Grünbach am Schneeberg, Lower Austria, Austria (Herman & Kvaček 2010).

Type stratum & age. Upper Cretaceous (Campanian) Grünbach Formation (Herman & Kvaček 2010).

Comments. The earlier name “*Marsilia Nathorsti*” was coined by Seward (1910, citing pers. comm. by Krasser) in anticipation of a formal description by Fridolin Krasser. Krasser (1906) only mentioned the occurrence of *Marsilea* in the Grünbach flora in a brief note, and no formal description or illustration of the Grünbach species was subsequently published. The name *Marsilea campanica* J. Kvaček & Herman was later applied to the Grünbach material in a figure caption (Herman & Kvaček 2007), but that name was also not validly published, as no description or diagnosis was provided and no type designated (i.e. it is a nomen nudum). The first valid name applied to the Grünbach leaves was thus *Marsileaceaphyllum campanicum* J. Kvaček & Herman (Herman & Kvaček 2010).

Herman and Kvaček (2010) referred the Grünbach specimens to *Marsileaceaphyllum* rather than *Marsilea*, due to the lack of reproductive material and the relatively large size of the fossil species. Since the type species of *Marsileaceaphyllum* can no longer be referred to Marsileaceae, the generic assignment of the Grünbach specimens must be reevaluated. It is appropriate to refer the Grünbach species to *Marsilea* because the leaves have the diagnostic characters of *Marsilea* leaves. The leaves are petiolate and quadrifoliate, with obovate leaflets; the leaflets have a single order of dichotomizing and anastomosing veins and a marginal vein formed by closure of the areoles near the apical margin (Herman & Kvaček 2010). Because the name *Marsilea campanica* J. Kvaček & Herman was not validly published, the specific epithet is available for use in the new combination *Marsilea campanica* (J. Kvaček & Herman) Hermsen.

Marsilea campanica leaves can be distinguished from leaves of other fossil and extant species of *Marsilea* by their unusually large leaflets (Herman & Kvaček 2010). Herman & Kvaček (2010) reported that the leaflet

Table 1. Occurrences of *Marsilea* sporophytes, based on vegetative material bearing characteristic leaflets and accepted as valid in the present study

Name	Age	Location	Leaflet dimensions (mm, L × W)	Reference
<i>Marsilea</i> sp.	Eocene	U.S.A.	20 × 20	Rich et al. 2001
<i>Marsilea campanica</i>	Late Cretaceous	Austria	12–40 × 14–44	Herman & Kvaček 2010
<i>Marsilea mascogos</i>	Late Cretaceous	Mexico	3–19.5 × 2.1–13	Estrada-Ruiz et al. 2018
<i>Marsilea sprungerorum</i>	Eocene	U.S.A.	4.8–16.4 × 3.8–18.3	This paper

dimensions of *Marsilea campanica* are as much as 40 mm long and 44 mm wide. By comparison, in a monograph on *Marsilea* species from the Americas (Johnson 1986) no extant species was reported to have leaflets more than 40 mm in length or width (*M. macropoda* Engelm. ex A. Braun was close, with leaflets up to 35 mm long and 39 mm wide). In a monograph on the species of Africa and Madagascar (Launert 1968), two species were described as having leaflets similar in size to those of *M. campanica*: *M. ehippiocarpa* Alston (up to 40 mm long and 35 mm wide) and *M. macrocarpa* C. Presl (up to 35 mm long and 40 mm wide). The maximum length and width of other fossil *Marsilea* leaflets is 20 mm or less (Tab. 1).

Marsilea sprungerorum

Hermsen, sp. nov.

Fig. 4A–H

Diagnosis. Leaflets 4.8–16.4 mm long and 3.8–18.3 mm wide, L/W ratio 0.9–1.4, glabrous. Leaflet shape obovate to flabellate, apex rounded and obtuse, base cuneate. Leaflet lateral margins straight to slightly concave or convex, apical margin entire.

Description. Leaves compound, petiolate, with four leaflets, leaflets appearing palmately arranged (Fig. 4A, B). Petiole ca 1.2 mm wide and at least 12.2 mm long (Fig. 4A, B). Each leaflet 4.8–16.4 mm long and 3.8–18.3 mm wide (L/W ratio 0.9–1.4), glabrous, obovate to flabellate, apex rounded and obtuse, base cuneate, lateral margins straight to slightly concave or convex, apical margin entire (Fig. 4A–G). Venation dichotomizing and anastomosing, producing a reticulate pattern (Fig. 4A–H). Areoles highly elongated and fusiform basally, becoming shorter apically (Fig. 4A–H), with the areoles bordering the apical margin having pointed basal ends and rounded or truncated apical ends (Fig. 4G, H); linear streaks sometimes occurring within areoles (Fig. 4E–H). Freely ending veinlets absent (Fig. 4G, H). Marginal vein present near the apical leaflet

margin, formed by closure of the areoles near the apical margin (Fig. 4G, H).

Holotype. UF 623-61259, 61259' designated here (Fig. 4A, B). Held in the Paleobotanical Collection of the Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

Type locality. UF 623. Bonanza VII, Uintah County, Utah, U.S.A.

Type stratum & age. Lower to middle Eocene Parachute Creek Member, Green River Formation.

Etymology. The species epithet honors the collectors of the holotype specimen of the species, Mike and Sandra Sprunger.

Paratypes. UCMP 390989a, b (locality UCMP PB02016); UCMP 390990 (locality UCMP PB02019); UF 15727-59581, 59581'; UF 18681-48440; UF 18681-48441; UF 18681-59580, 59580'.

Additional specimen. DMNH EPI.24978 (locality DMNH 2780).

Additional localities. DMNH 2780, Douglas Pass, Colorado. UCMP PB02016, Handleys Rainbow UT, Uintah County, Utah; this locality number has also been reported as Bonanza, Utah (Boucher et al. 2003), and Watson, Utah (Manchester et al. 2006, Allen 2015). UCMP PB02019, Handleys Colorado, Colorado; this locality number has also been reported as Douglas Pass, Colorado (Manchester et al. 2006). UF 15727, Douglas Creek, Rio Blanco County, Colorado; this locality was lumped with MacGinitie's (1969) Wardell Ranch locality (UCMP PA106, UF 18001) in Manchester (1989). UF 18681, Calamity Ridge, Rio Blanco County, Colorado.

Stratigraphic occurrence. All localities are assigned to the Parachute Creek Member, Green River Formation. These sediments are early to middle Eocene (Ypresian to Lutetian) in age (Grande 2013, Smith & Carroll 2015).

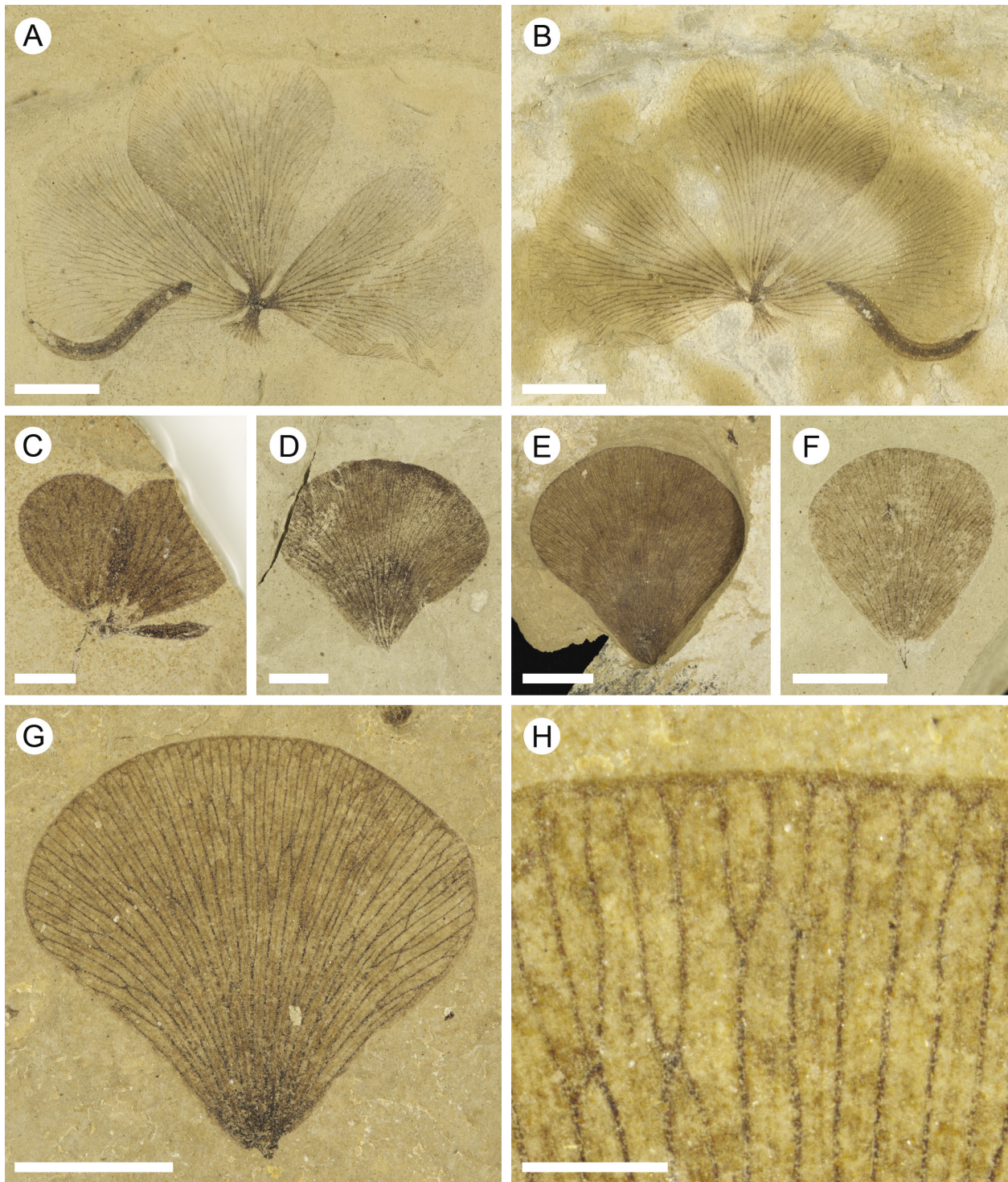


Fig. 4. *Marsilea sprungerorum* Hermsen, sp. nov., early to middle Eocene, Parachute Creek Member, Green River Formation, Colorado and Utah, U.S.A. **A.** Specimen of whole leaf showing four leaflets and lax petiole. Holotype. UF 623-61259'; **B.** Counterpart of specimen shown in A. Holotype. UF 623-61259; **C.** Specimen showing two relatively complete small leaflets and a third partial leaflet. UF 18681-59580; **D.** Leaflet. UCMP 390989b (Locality UCMP PB02016); **E.** Leaflet. UF 18681-48440; **F.** Leaflet. UF 15727-59581'; **G.** Detail of leaflet showing reticulate venation. UF 18681-48441; **H.** Detail of leaflet showing entire margin, reticulate venation, and marginal vein. UF 18681-48441. Scale bars: A, B, D–G = 5 mm; C = 2 mm; H = 1 mm

Comments. *Marsilea sprungerorum* leaves have the essential characters necessary for assignment to *Marsilea*, including quadrifoliate architecture, obovate leaflets in a radial arrangement, a single order of dichotomizing and anastomosing veins, fusiform areoles, no

freely ending veinlets, and a marginal vein (compare Fig. 1 to Fig. 3). The curved petiole preserved on one specimen as well as the entire-margined, glabrous leaflets are consistent with features characteristic of floating leaves of modern *Marsilea* (see, e.g. Gupta

1962, Johnson 1986, Rich et al. 2001). Some of the leaflets show faint linear marks between the veins (Fig. 4E–H). These linear marks could represent abaxially occurring brown- or red-pigmented areas (“suberous streaks” of Launert 1968; “hydropoten” of Johnson 1986) or sclerified “pellucid streaks” (Launert 1968, Crouch et al. 2011). Pigmented streaks are common on floating leaves of *Marsilea* (Launert 1968, Johnson 1986), whereas pellucid streaks are restricted to three Old World species (Launert 1968, Crouch et al. 2011).

Leaves of *Marsilea sprungerorum* can be distinguished from leaves of *Marsilea campanica* based on their typically smaller leaflets, although larger leaflets of *M. sprungerorum* may overlap in size with smaller leaflets of *M. campanica* (Tab. 1). The dimensions of *Marsilea sprungerorum* leaflets largely overlap with the dimensions of leaflets of the fossil taxon *Marsilea mascogos* Estrada-Ruiz et al. (Tab. 1), described from the Upper Cretaceous (Campanian) Olmos Formation of Mexico (Estrada-Ruiz et al. 2018). However, the taxa have subtly different leaflet shapes. My qualitative observations and rough measurements of published images in Estrada-Ruiz et al. (2018) indicate that the leaflets of *M. mascogos* tend to be slightly more elongated than the leaflets of *M. sprungerorum*. This is reflected in the L/W ratio of the maximum leaflet dimensions for each of the species, ca 1.5 in *M. mascogos* and ca 0.9 in *M. sprungerorum* (Tab. 1). The difference in the ages of the specimens also suggests that they represent different species.

***Marsilea* sp.**

Original description. *Marsilea*. Rich et al. (2001), *PALAIOS* 16(6), pp. 610, 611, figs 3, 4B, 4D.

Synonyms.

2007 *Marsileaceaeaphyllum* sp. A. Nagalingum (2007), p. 48.

2014 *Marsileaceaeaphyllum* cf. *campanicum*. Hermsen et al. (2014), p. 373.

Locality. Dry Creek Petrified Tree Environmental Education Area (Bureau of Land Management, United States Department of the Interior), Johnson County, Wyoming, U.S.A. (Rich et al. 2001).

Stratigraphic unit & age. Lower Eocene Wasatch Formation (Rich et al. 2001).

Comments. Rich et al. (2001) originally described this material, from the Eocene Wasatch Formation of Wyoming, U.S.A., as *Marsilea*. Nagalingum (2007) later transferred it to *Marsileaceaeaphyllum*, and Hermsen et al. (2014) emphasized its similarity to *Marsileaceaeaphyllum campanicum* (= *Marsilea campanica* in this paper). Given the age of the material and the region in which it was found, it could be another occurrence of *Marsilea sprungerorum*. Based on their “sinuous” petioles, Rich et al. (2001, p. 610) interpreted the Wasatch leaves as floating leaves.

Family: Salviniaceae Mirb.

Genus: ***Salvinia*** Ség.

***Salvinia* sp.**

Original description. *Marsilea* sp. García Massini et al. (2010), *Palaeontologia Electronica* 13(1, 6A): p. 18, fig. 8.5–8.8.

Locality. CH-79, Margargaria River sections, Chilga, Ethiopia (García Massini et al. 2010, García Massini & Jacobs 2011).

Stratigraphic unit & age. Oligocene, Chilga beds (García Massini et al. 2010, García Massini & Jacobs 2011).

Comments. García Massini et al. (2010) described and illustrated compound leaves and detached leaflets which they attributed to *Marsilea*; these were collected from Oligocene sediments along the Margargaria River in Chilga, Ethiopia. Hermsen et al. (2014) later cast doubt on the assignment of these leaves to *Marsilea*, noting that the shapes of the areoles formed by the veins are not consistent with Marsileaceae. Specifically, the areoles in the Margargaria River leaves are elongated-rectangular to elongated-polygonal rather than fusiform (see fig. 8.5, 8.8 in García Massini et al. 2010).

Based on published illustrations, the Margargaria River leaves are here reinterpreted as leaves of *Salvinia* (Fig. 5A, B), a floating heterosporous fern in the family Salviniaceae (Smith et al. 2006, PPG I 2016). Sporophytes of *Salvinia* are characterized by having simple floating leaves with entire margins and branching underwater leaves that bear sori (Fig. 5A; Tryon & Tryon 1982, Schneller 1990). Specimens originally interpreted as compound

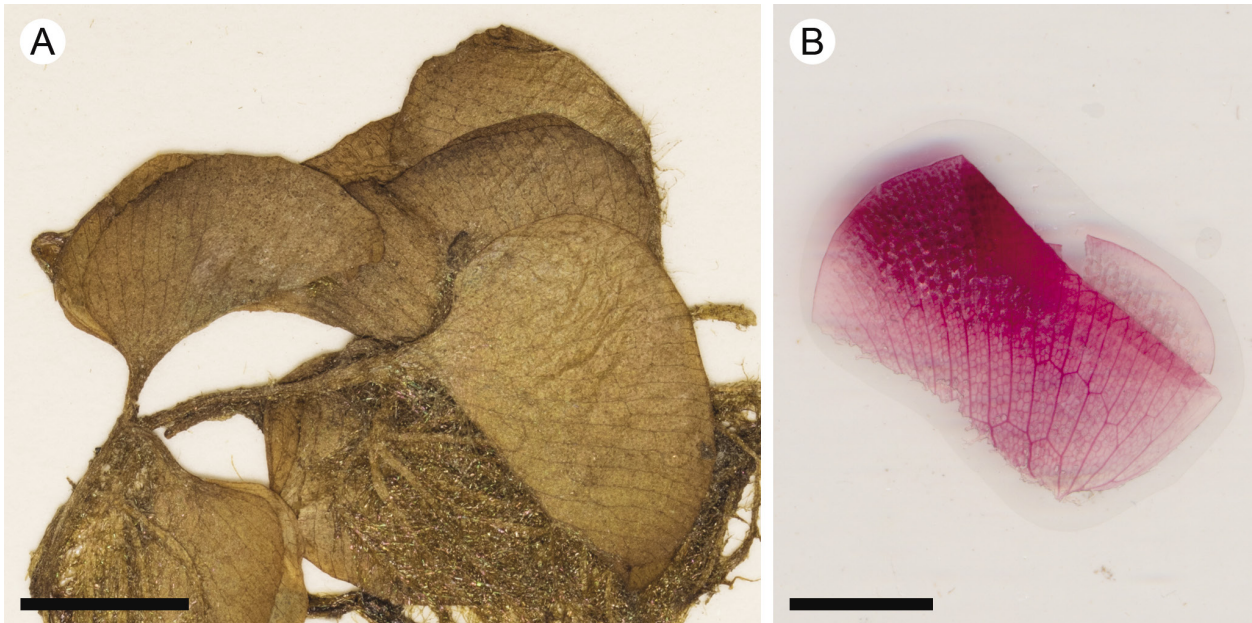


Fig. 5. *Salvinia auriculata* Aubl., leaves. BH 000050807 (Richard R. Halse 5528, cultivated, Oregon). **A.** Conduplicate floating leaves showing polygonal venation pattern; branching structures are underwater leaves; **B.** Cleared floating leaf showing venation pattern. Images used by permission, L.H. Bailey Hortorium, Plant Biology Section, Cornell University (all rights reserved). Scale bars = 5 mm

leaves of *Marsilea* (see fig. 8.6, 8.7 in García Massini et al. 2010) are therefore here reinterpreted as simple, floating *Salvinia* leaves closely clustered on stems (cf. Fig. 5A). The Margargaria River “*Marsilea*” leaves appear to represent floating *Salvinia* leaves in lateral and oblique views, suggesting that they may have been conduplicate leaves of the type observed when *Salvinia* sporophytes occur in dense aggregations, that is, so-called “mat-form” (Mitchell & Tur 1975) or “tertiary” (Hattingh 1961, Julien et al. 2002) plants.

The lamina in floating *Salvinia* leaves has a midrib with a network of anastomosing veins forming areoles on either side (Fig. 5A, B; Forno 1983, Schneller 1990, Pérez-Consuegra et al. 2017). The venation of the Margargaria River “*Marsilea*” leaves shows particular similarity to the venation of conduplicate or tertiary leaves of certain modern *Salvinia* species in which there is a clear gradient in the size of the areoles; large, elongated-polygonal (rectangular to hexagonal) areoles occur nearest the midline along which the leaf folds, with areoles becoming shorter and narrower nearer the margin (Fig. 5A, B; Forno 1983). As the areoles traverse the lamina from midline to margin, an areole may be succeeded by a pair of areoles, each member of the pair about half the width of their subtending areole (Fig. 5B; see also Forno 1983); this regular pattern of areole narrowing by halves is also evident in

the Margargaria River “*Marsilea*” leaves (see fig. 8.5, 8.8 in García Massini et al. 2010).

Notably, García Massini et al. (2010) identified planar floating leaves of *Salvinia* from the Margargaria River flora and *Salvinia* megaspores from the same layers that yielded the “*Marsilea*” leaves (see also García Massini & Jacobs 2011). Flat leaves are produced by modern *Salvinia* sporophytes when they are sparsely distributed and are first occupying a water body (Hattingh 1961, Mitchell & Tur 1975, Julien et al. 2002). Thus, the *Salvinia* and “*Marsilea*” leaves could be two different growth forms or stages of the same species of *Salvinia*.

DISCUSSION

The fossil species *Marsilea campanica* and *M. sprungerorum*, as well as the additional *Marsilea* occurrence reported by Rich et al. (2001), have leaf architecture that places them within the circumscription of *Marsilea*, as discussed above. One final species not treated here, *Marsilea mascogos* from the Campanian Olmos Formation of Coahuila, Mexico, is also referable to *Marsilea* (Estrada-Ruiz et al. 2018). The Olmos Formation material consists of more organs than other fossil *Marsilea* species and occurrences, including partial and complete compound leaves, rhizomes, roots, and a putative sporocarp (Estrada-Ruiz et al.

2018). No co-occurring *Marsilea* or marsileaceous spores (mega- or microspores) have been documented in palynological studies of the Grönbach (Herman & Kvaček 2010), Olmos (Martínez-Hernández et al. 1980), Wasatch (Rich et al. 2001) or Green River Formations (Bradley 1931, Wodehouse 1933, Newman 1974, Cushman 1983).

Placement of these fossils into the genus *Marsilea* contrasts with previous approaches to the classification of marsileaceous sporophyte material taken by Nagalingum (2007) and Hermsen et al. (2014). Those authors referred vegetative sporophyte material bearing or consisting of *Marsilea*-type leaves to a separate fossil genus (*Marsileaceaphyllum*, now considered an angiosperm). At this point, however, no unequivocal evidence or even strong circumstantial evidence (e.g. extinct marsileaceous spore genera macerated from the same deposits that yield fossil *Marsilea* sporophytes) justifies creating one or more new fossil genera to accommodate the fossil *Marsilea* species recognized here. If further analysis or additional specimens of any of these species reveals spore morphology diagnostically distinct from *Marsilea*, it will then be appropriate to segregate that species into a novel fossil genus (see Collinson 1996).

The fossil record of Marsileaceae has been summarized in a number of recent papers (e.g. Collinson 1991, 1996, Lupia et al. 2000, Nagalingum 2007, Hu et al. 2008, Batten et al. 2011, Sun et al. 2014); new reports are rapidly expanding the documented fossil history of the family, particularly the sparse fossil sporophyte record (e.g. Sender et al. 2014, Puebla et al. 2015, Monje-Dussán et al. 2016, Vallati et al. 2017, Estrada-Ruiz et al. 2018). Evidence from fossil sporophytes and dispersed spores indicates that Marsileaceae or their stem lineage originated during the Early Cretaceous or slightly earlier (e.g. Kovach & Batten 1989, 1993, Lupia et al. 2000, Yamada & Kato 2002, Nagalingum 2007). Leaves of *Flabellariopteris mii* Sun, which have strictly dichotomizing venation, dubiously extend the temporal range of Marsileaceae to the Triassic (Sun et al. 2014). The Mesozoic record of fossils affiliated with Marsileaceae consists largely of occurrences of extinct dispersed spore taxa (e.g. Batten & Kovach 1990, Lupia et al. 2000), which are sometimes found in the same deposits as marsileaceous sporophyte fossils (e.g. Nagalingum 2007, Hermsen et al. 2014, Vallati et al. 2017)

and occasionally within fossil sporocarps (e.g. Chitaley & Paradkar 1972, Lupia et al. 2000, Aulenback 2009). Characteristic Marsileaceae-affiliated Mesozoic spore genera (megaspores *Arcellites* and *Molaspora*, microspore *Crybelosporites* Dettmann) probably vanished by the end of the Cretaceous, although there are questionable Paleogene occurrences of the megaspore genera *Arcellites* and *Molaspora* (Kovach & Batten 1989, Collinson et al. 2013). (For the range of *Crybelosporites*, see Lupia et al. 2000.)

Each of the extant genera of Marsileaceae (*Marsilea*, *Pilularia*, *Regnellidium*) has been documented from the fossil record. As previously noted by Cúneo et al. (2013), the occurrence of leaves that have architecture and venation consistent with *Marsilea* (see Kvaček & Herman 2004, Herman & Kvaček 2007, 2010, Estrada-Ruiz et al. 2018) and *Regnellidium* (see Cúneo et al. 2013, 2014, Gandolfo et al. 2014, Puebla et al. 2015) in the Late Cretaceous, clearly indicates that these lineages were distinct by the latter part of the Late Cretaceous (Campanian to Maastrichtian). Furthermore, at least some occurrences of the dispersed megaspore species *Molaspora lobata* (Dijkstra) Hall may be dispersed *Regnellidium* megaspores (Lupia et al. 2000, Cúneo et al. 2013, 2014, Gandolfo et al. 2014; but see Batten et al. 2011 for a contrasting interpretation). Dispersed *Regnellidium* megaspores are definitively recorded beginning in the Eocene (Dorofeev 1981, Batten et al. 2011). In contrast, *Marsilea* megaspores have no morphological equivalents in the Cretaceous or early Paleogene, but are first reported from the Oligocene (Fig. 2; Appendix 3). *Pilularia* is conclusively known only from spores, the oldest being reported from Neogene deposits (e.g. Dorofeev 1981, Kovach & Batten 1989, Batten & Kovach 1990, Velichkevich & Zastawniak 2003, 2007).

Today, *Marsilea* has an extensive global distribution, with species native to each continent except Antarctica (Nagalingum et al. 2007), and with a center of diversity in Africa (Kramer 1990, García Massini et al. 2010). The few known fossil records, which are scattered geographically and stratigraphically (Fig. 2), do not shed much light on the historical biogeography of the genus. This pattern parallels that of the fossil record of *Regnellidium*, although *Regnellidium* differs in having a highly restricted distribution in South

America today (Batten et al. 2011, Cúneo et al. 2013). The reasons for the scarcity of *Marsilea* sporophytes and spores in the fossil record remain elusive, as the plants should have been associated with aquatic environments conducive to fossilization. Collinson (1991) speculated that fossil marsileaceous sporocarps may be rare in part because sporocarps of modern Marsileaceae open quickly in the presence of water. Once the spores are free, gametophyte development, fertilization and initiation of new sporophytes occurs within about 48 hours (Schneider & Pryer 2002). Johnson (1986) observed that *Marsilea* sporophyte populations tend to be ephemeral, lasting only a few years before disappearing; he characterized *Marsilea* as a “colonizing plant” (Johnson 1986, p. 24). Perhaps, then, the depauperate fossil record of *Marsilea* is a function of its ecology and life history, which simply provide limited opportunities for preservation.

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Appendix 1

Marsilea sporophyte fossils and their current status. This table updates the tables of Skog and Dilcher (1992) and Rich et al. (2001), who first provided critical evaluations of the *Marsilea* fossil record by species/occurrence. For a bibliography of early reports, see also Reed (1954, 1965). Location data have been updated to reflect current political boundaries; age assignments have been updated from original sources as noted. Occurrences not attributed to a named species of *Marsilea* have been omitted unless the material was figured. Corrections have been made to some names (i.e. orthography of species epithets). Organ type: L = leaf and/or leaflet; L(P) = leaf (petiole only, for anatomically preserved material); R = rhizome (may have roots); S = sporocarp. The status of some fossil species names is indicated by the following abbreviations: nom. illeg. (nomen illegitimum), nom. nud. (nomen nudum) and nom. inval. (nomen invalidum, for names not validly published that do not clearly fit either of the previous categories)

Name	Organ type(s)	Age	Location	Key reference(s)	Notes & current status
<i>Marsilea?</i>	S	Late Cretaceous?	Australia	Shirley (1902)	Name listed with question mark in original description.
<i>Marsilea</i> sp.	L	Eocene	U.S.A.	Rich et al. (2001)	Valid occurrence.
<i>Marsilea</i> sp.	L	Oligocene	Ethiopia	García Massini et al. (2010)	Floating leaves of <i>Salvinia</i> (see text, this paper).
“ <i>Marselia</i> -like” [sic]	L, R, S	Late Jurassic–Early Cretaceous	India	Banerji (1987, 2004)	Considered plausibly marsileaceous by Skog & Dilcher (1992).
<i>Marsilea andersonii</i> Hollick	L	Late Cretaceous ¹	U.S.A.	Hollick (1904, 1906)	Specimens reexamined by Skog & Dilcher (1992), who considered the affinities of the New York material to be equivocal, and the Massachusetts material to be possible petals.
<i>Marsilea? attenuata</i> (Lesq.) Hollick	L	Late Cretaceous ²	U.S.A.	Lesquereux (1876, 1878), Hollick (1894), Knowlton (1900)	Basionym is <i>Salvinia attenuata</i> Lesq. (Lesquereux 1876, 1878). Knowlton (1900) reported the sole specimen lost and cast doubt on attributions to <i>Marsilea</i> and <i>Salvinia</i> . Sometimes listed as also occurring in Japan (Reed 1954, Gupta 1962), probably a misinterpretation of Florin (1919).
<i>Marsilea bendirei</i> Ward, nom. nud.	L	Miocene ³	U.S.A.	Ward (1885)	Considered to be the basionym for <i>Hydrangea bendirei</i> (Ward) Knowlt. (Knowlton in Merriam 1901; Knowlton 1902). No description or figure for original name. Also previously assigned to <i>Porana bendirei</i> (Ward) Lesq. (Lesquereux 1888).
<i>Marsilea campanica</i> J. Kvaček & Herman, nom. nud.	L	Late Cretaceous	Austria	Herman & Kvaček (2007)	Name coined in a figure caption. Now included in <i>Marsilea campanica</i> (J. Kvaček & Herman) Hermsen, comb. nov.
<i>Marsilea campanica</i> (J. Kvaček & Herman) Hermsen, comb. nov.	L	Late Cretaceous	Austria	Herman & Kvaček (2010), this paper	Basionym is <i>Marsileaceaeophyllum campanicum</i> J. Kvaček & Herman (Herman & Kvaček 2010). For full list of synonyms, see text. Valid species.
<i>Marsilea chitaley</i> Mistri, nom. inval.?	L(P), R	Late Cretaceous–Paleocene ⁴	India		Name proposed in thesis, as cited by Nambudiri & Chitaley (2004).
<i>Marsilea cretacea</i> Heer	S	Late Cretaceous	Greenland	Heer (1882)	Considered equivocal (see Skog & Dilcher 1992).
<i>Marsilea cretacea</i> Velen., nom. nud.	S	Late Cretaceous	Czech Republic	Velenovský (1889)	Synonym of <i>Marsilea perucensis</i> E. Bayer (Frič & Bayer 1900). Velenovský (1889) listed Velenovský as author (possibly in error) and Heer as author of this species in the same publication.
<i>Marsilea fischeri</i> Heer	NA	Recent		Gupta (1962)	Extant, should be <i>M. fischeri</i> Hier. (Skog & Dilcher 1992).
<i>Marsilea (?) grandis</i> (Heer) Heer	L	Early Cretaceous	Greenland	Heer (1874, 1882)	Basionym is <i>Baiera grandis</i> Heer (Heer 1874). Considered a possible ginkgo-phyte by Seward (1927, as <i>Ginkgoites</i> Seward) and Skog & Dilcher (1992, as <i>Baiera?</i> A. Braun).

Appendix 1. Continued

Name	Organ type(s)	Age	Location	Key reference(s)	Notes & current status
<i>Marsilea hickenii</i> Herter	NA	Recent		Gupta (1962)	Extant, not a fossil (Skog & Dilcher 1992).
<i>Marsilea höltingiana</i> Schaff.	NA	Recent		Rich et al. (2001)	Hollick (1904) illustrated leaves of the extant species “ <i>Marsilea höltingiana</i> Scaff.” for comparative purposes. Rich et al. (2001, p. 609) listed it as an “invalid taxon.” No other references were located.
<i>Marsilea intertrappea</i> G.V. Patil & Upadhye	L(P), R	Late Cretaceous ⁴	India	Upadhye & Patil (1979)	Paradkar (1988) suggested that this species be transferred to <i>Rodeites</i> Sahni (Marsileaceae, extinct).
<i>Marsilea johnhallii</i> J.E. Skog & Dilcher	L, R, S?	Early Cretaceous ⁵	U.S.A.	Skog & Dilcher (1992, 1994)	Basionym of <i>Marsileaceaeaphyllum johnhallii</i> (J.E. Skog & Dilcher) Nagalingum. Not a marsileaceous fern, but a probable angiosperm (see text).
<i>Marsilea</i> (?) <i>karaldinensis</i> I.V. Lebedev	L	Jurassic	Russia	Lebedev (1955)	Considered “unidentifiable” by Skog & Dilcher (1992, p. 987).
<i>Marsilea marionii</i> A. Braun, nom. illeg.	S	Oligocene	France	Marion (1872), Braun (1872)	Illegitimate replacement name for <i>Ron-zocarpon hians</i> Marion. Marion (1872) described this taxon as a fruit. Considered equivocal (see Collinson 2001).
<i>Marsilea mascogos</i> Estrada-Ruiz et al.	L, R, S?	Late Cretaceous	Mexico	Estrada-Ruiz et al. (2018)	Valid species.
<i>Marsilea mohgaoense</i> Khubalkar, nom. inval.?	L(P)	Late Cretaceous ⁴	India		Name proposed in thesis, as cited by Nambudiri & Chitaley (2004).
<i>Marsilea nashii</i> Underw.	NA	Recent		Gupta (1962)	Extant, not a fossil (Skog & Dilcher 1992).
<i>Marsilea nathorstii</i> Krasser in Seward, nom. nud.	L	Late Cretaceous	Austria	Krasser, pers. comm. to Seward (1910)	Synonym of <i>Marsilea campanica</i> (J. Kvaček & Herman) Hermsen, comb. nov. Name cited by Seward (1910) in anticipation of description by Krasser. See also Krasser (1906), Herman & Kvaček (2010).
<i>Marsilea neesiana</i> Lindb.		Quaternary?	Russia		Occurrence information based on Reed (1954) and Skog & Dilcher (1992).
<i>Marsilea patnii</i> S.P. Patil et al.	L(P)	Late Cretaceous–Paleocene ⁴	India	Patil et al. (2014)	Fern petiole/stipe with aerenchymatous cortex. Possibly belongs in <i>Rodeites</i> .
<i>Marsilea perucensis</i> E. Bayer	S	Late Cretaceous	Czech Republic	Velenovský (1888, 1889), Frič & Bayer (1900)	Replacement name for <i>Marsilea cretacea</i> Velen. (Velenovský 1889). Originally described and figured as “ <i>Marsilia</i> ? sp.” [sic] by Velenovský (1888). Considered equivocal (see Skog & Dilcher 1992).
<i>Marsilea sahnii</i> Kappate, nom. inval.	?	Late Cretaceous ⁴	India		Invalid name proposed in an abstract according to Srivastava & Guleria (2006).
<i>Marsilea sprungerorum</i> Hermsen, sp. nov.	L	Eocene	U.S.A.	This paper	Valid species.
<i>Marsilea vera</i> Jarm.	L	Late Cretaceous	Kyrgyzstan ⁶	Jarmolenko (1935)	Called a “[d]ubious leaf piece” by Skog & Dilcher (1992, p. 987).

¹ Berry (1915) placed *Marsilea andersonii* in the Upper Cretaceous Magothy Formation.

² According to Stockey et al. (2007), the Point of Rocks locality of Lesquereux (1876, 1878) is likely within the Upper Cretaceous Almond Formation.

³ Knowlton (1902) reported that *Marsilea bendirei* came from Van Horn’s ranch; this locality occurs in the Miocene Mascall Formation (Dillhoff et al. 2009).

⁴ Most Indian fossil *Marsilea* material collected from the Deccan Intertrappean Beds is known to come from Mohgaonkalan (Upadhye & Patil 1979; Nambudiri & Chitaley 2004; Srivastava & Gupta 2006) and has thus been assigned a Late Cretaceous age (see Matsunaga et al. 2018). Two species were assigned a Late Cretaceous to Paleocene age because their locality of origin could not be established (*Marsilea chitaleyi*) or because the precise age of the collection locality is unclear (*M. patnii* at Maraipatan; see Matsunaga et al. 2018).

⁵ Revised age discussed by Wang & Dilcher (2018).

⁶ Age and revised location information after Doweld (2016) and the entry for *Marsilea vera* in the *The International Fossil Plant Names Index* (IFPNI International Editorial Board 2014–2018).

Appendix 2

Specimens of *Fortuna* examined for this study. Specimens listed include floating leaf material. Specimens preserving only rhizomes have been omitted.

Repositories and associated acronyms:

DMNH: Paleobotany Collection, Department of Earth Sciences, Denver Museum of Nature & Science, Denver, Colorado, U.S.A.

TMP: Royal Tyrrell Museum of Palaeontology, Drumheller, Alberta, Canada.

UAPC-ALTA: Paleobotanical Collection, Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada.

UF: Paleobotanical Collection, Florida Museum of Natural History, University of Florida, Gainesville, Florida, U.S.A.

USPC: Paleobotanical Collection, Department of Geological Sciences, University of Saskatchewan, Saskatoon, Saskatchewan, Canada. (These specimens have since been relocated to the Royal Saskatchewan Museum, Regina, Saskatchewan, Canada.)

Identification: *Fortuna marsilioides*

Locality. Oldman River, Late Cretaceous (Campanian–Maastrichtian), St. Mary River and Foremost Formations, Alberta, Canada (TMP); near Cowley, Late Cretaceous (Maastrichtian), St. Mary River Formation, Alberta, Canada (USPC; see McIver & Basinger 1993).

Specimens examined. TMP 1988.122.0004, 1989.057.0001–1989.057.0018 (Fig. 3D shows TMP 1989.057.015); USPC 455-4605, 455-4608. Part-counterpart: USPC 455-4609, 4609'.

Notes. The Oldman River locality is near Cowley, Alberta, Canada, and is the source of the type specimen of *Fortuna marsilioides* (Bell 1949, McIver & Basinger 1993, Hoffman 2002). McIver and Basinger (1993) illustrated all USPC specimens cited here (455-4605, 455-4608, 455-4609, 4609'), as well as a rosette or whorl and bilobed structure that they indicated came from TMP 88.122.4.

Identification: *Fortuna marsilioides*

Locality. St. Mary River Reservoir, Late Cretaceous (Campanian–Maastrichtian), St. Mary River Formation, Alberta, Canada (TMP); Cardston/Spring Coulee, Late Cretaceous (Maastrichtian), St. Mary River Formation, Alberta, Canada (UAPC-ALTA).

Specimens examined. TMP 1989.057.0040; UAPC-ALTA PB-S38793–38797, S48947, S48948, S48950, S48952–S48958, S48963, S48968, S48969, S48971–S48974, S48976–S48978, S48981–S48991, S48993–S49007, S49008.a, S49009.a, S49031, S49043, S49092, S52457, S52469.A, S57604.A. Part-counterpart: UAPC-ALTA PB-S38798.A, B (Fig. 3E); S48949.A, B; S48951.A, B; S48961.A, B; S48962.A, B; S48965.A, B; S48966.A, B; S48967.A, B; S48975.A, B; S48979.A, B; S48980.A, B; S51057.A, B.

Notes. Stockey and Rothwell (1997) reported *Fortuna* from the Cardston flora, although they did not illustrate the material. The Cardston locality is near

the St. Mary Reservoir dam northwest of Spring Coulee, Alberta, Canada (Stockey & Rothwell 1997). The Royal Tyrrell Museum's St. Mary River Reservoir locality is probably in the same vicinity as the University of Alberta's Cardston locality, so the two are grouped together here.

Identification: *Fortuna marsilioides*

Locality. Joffre Bridge Roadcut, Paleocene, Paskapoo Formation, Alberta, Canada.

Specimens examined. UAPC-ALTA PB-S16658, S16660, S16661.

Notes. See Hoffman and Stockey (1999) and Hoffman (2002) for locality details. Hoffman (2002) described *Fortuna marsilioides* from this locality and illustrated two of the specimens listed above (S16660, S16661).

Identification: *Fortuna marsilioides*

Locality. Red Deer River, Paleocene, Paskapoo Formation, Alberta, Canada (McIver & Basinger 1993).

Specimens examined. UAPC-ALTA PB-S8007, S12766 (Fig. 3F). Part-counterpart: UAPC-ALTA PB-S8006.A, B.

Notes. These specimens have conflicting locality information. McIver and Basinger (1993) indicated that all were collected from the Paleocene Paskapoo Formation at the Red Deer River locality in the vicinity of Blackfalds, Alberta. The UAPC-ALTA collections database (last accessed 21 March 2019, <https://www.ualberta.ca/museums/museum-collections/paleobotanical-collection>) indicates that two (S8006, S8007) come from Red Deer River and one (S12766) from Blindman River, Alberta, and that all were collected from the Paleocene Ravenscrag Formation. Since the Paskapoo Formation occurs in parts of Alberta and the Ravenscrag Formation occurs in Saskatchewan (McIver & Basinger 1993, Hoffman 2002), I have followed McIver and Basinger (1993) for the locality and stratigraphic assignment here and in the caption to Figure 3. McIver and Basinger (1993) illustrated these specimens.

Identification: *Fortuna*

Locality. Bison Basin/Buffalo Basin (UF loc. 18123; DMNH loc. 102, 717, 720, 1163, and 1166), Paleocene, Fort Union Formation, Fremont County, Wyoming, U.S.A.: DMNH EPI.8988, EPI.27850–EPI.27856, EPI.27912, EPI.27961, EPI.28124–EPI.28127, EPI.28138, EPI.28140; UF 18123-59579 (Fig. 3G).

Notes. This locality has been called Bison Basin in publications but is called Buffalo Basin on specimen labels. According to Wilf (2000, see accompanying GSA Data Repository item 200014 at <https://www.geosociety.org/datarepository/>), *Fortuna* also occurs in Bison Basin localities DMNH 716, 719 and 1164.

Gemmill and Johnson (1997) and Wilf (2000) attributed the Bison Basin specimens to *Fortuna* cf. *F. marsilioides* and morphotype BB1 or BB01, and collections labels suggest that the DMNH specimens listed above

were examined for one or both studies. The teeth of the Fort Union Formation *Fortuna* specimens tend to be larger than those of the Canadian specimens, and they may represent a distinct species or population.

Although Gemmill and Johnson (1997) indicated that all *Fortuna* leaves from the Bison Basin flora were found in isolation (i.e. as singletons), DMNH EPI.27850 includes three incomplete leaves radiating from a central point in an apparent whorl or rosette. The symmetry of the specimen suggests that there may have been a fourth leaf. Gemmill and Johnson (1997) illustrated one leaf from Bison Basin; the illustrated specimen does not match the specimens examined for this study (no specimen number was published).

Identification: *Fortuna*

Locality. East Fork Razor Creek (UF loc. 18163), Paleocene, Fort Union Formation, Yellowstone County, Montana, U.S.A.

Specimens examined. UF 18163-26101, 18163-26102.

Notes. *Fortuna* has not previously been listed as occurring in the East Fork Razor Creek flora in publications (Manchester et al. 1999, Manchester & Kodrul 2014). Both specimens from UF 18163 consist of whorls or rosettes of four leaves. They appear to be of the same species or population as the Bison Basin specimens.

Appendix 3

Occurrences of fossil *Marsilea* megaspores, some with attached microspores. For a bibliography of reports from the former USSR, see also Batten and Kovach (1990). IFPNI (IFPNI International Editorial Board 2014–2018), Gnibidenko & Semakov (2009) and Fikáček et al. (2011) were sources of supplementary locality information.

Name	Age	Location	References
<i>Marsilea</i> sp.	Oligocene–Miocene	Russia (Omsk Oblast, Tomsk Oblast)	Dorofeev (1963a)
<i>Marsilea dorofeevii</i> Mai	Miocene–Pliocene	Germany	Mai (2000, 2004)
<i>Marsilea maeotica</i> P.I. Dorof.	Miocene	Ukraine	Dorofeev (1951, 1955a, 1981), Negru (1986)
<i>Marsilea reticulata</i> Mai	Miocene	Germany	Mai (1999), Czaja (2003)
<i>Marsilea sarmatica</i> P.I. Dorof.	Miocene	Ukraine	Dorofeev (1955b, 1981)
<i>Marsilea tambovica</i> P.I. Dorof.	Miocene	Russia (Tambov Oblast)	Dorofeev (1981, 1988)
<i>Marsilea tertiaria</i> P.I. Dorof.	Oligocene–Miocene	Kazakhstan, Russia (Rostov Oblast)	Dorofeev (1959, 1963b, 1981)