Early Eocene infructescences from Argentine Patagonia expand the biogeography of Malvoideae.

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ABSTRACT

Premise: Fossil infructescences and isolated fruits with characters of the subfamily Malvoideae, of Malvaceae (Mallow Family), were collected from early Eocene sediments in Chubut, Argentina. The main goals of this research are to describe and place these fossils systematically, and to explore their biogeographical implications.

Methods: Fossils were collected at the Laguna del Hunco site, Huitrera Formation, Chubut, Patagonia, Argentina. They were prepared, photographed, and compared with extant and fossil infructescences and fruits of various families using herbarium material and literature.

Results: The infructescences are panicles that display an alternate arrangement of their fruits. They bear these fruits on short pedicels that are subtended by a bract; the fruits display an infracarpelar disk and split to the base into five ovate sections interpreted as mericarps. Each mericarp is characterized by an acute apex and the presence of a longitudinal ridge. The isolated fruits show the same features as those on the infructescences. The fossils share unique features with members of the cosmopolitan family Malvaceae, subfamily Malvoideae.

Conclusions: The fossils preserved have a unique combination of characters that does not conform to any previously described genus, justifying the erection of the new genus and species, *Uiher karuen*. This new taxon constitutes the first known Malvoideae reproductive fossils of the Southern Hemisphere, expanding the distribution of Malvoideae during the early Eocene.

KEY WORDS: infructescence; Laguna del Hunco; Malvaceae; Mericarps; Patagonia; schizocarp; South America; Southern Hemisphere.

INTRODUCTION

The angiosperm family Malvaceae, commonly known as the mallow family, comprises approximately 4,225 extant species mostly distributed in temperate and tropical regions around the globe (Stevens, 2001; Bayer and Kubitzki, 2003). Malvaceae are characterized by having flowers in terminal or axillary inflorescences on main or lateral shoots and by producing a broad range of fruit types (Bayer and Kubitzki, 2003) including loculicidal capsules and schizocarps (Bayer and Kubitzki, 2003; Areces-Berazain and Ackerman, 2017).

The phylogeny of the family has changed over time, and for the last 30 years taxonomic treatments have considered monophyletic Malvaceae to include the former families Sterculiaceae, Tiliaceae, Bombacaceae, and Malvaceae *s.s.*, nevertheless, the phylogeny of Malvaceae *s.l.* has endured consistent changes (Judd and Manchester, 1997; Bayer et al., 1999; Vogel, 2000; Baum et al., 2004; Tate et al., 2005; Richardson et al., 2015; Carvalho-Sobrinho et al., 2016; Areces-Berazain and Ackerman, 2017; Cvetković, 2021; Xie et al., 2023). Currently, Malvaceae is divided into the subfamilies Byttnerioideae, Grewioideae, Tilioideae, Helicteroideae, Brownlowioideae, Sterculioideae, Dombeyoideae, Bombacoideae, and Malvoideae.

Unfortunately, this new Malvaceae classification clusters taxa with a wide range of morphological features, making it difficult to identify traits unique to the family. Malvaceae's dominant features are alternate phyllotaxis, mucilage cavities, and a calyx composed of five valvate sepals; other common traits include the presence of tufted or stellate hairs, actinomorphic flowers with often convoluted corollas, and stamens connate forming a tube or in bundles (Stevens, 2001; Bayer and Kubitzki, 2003). Common leaf traits include palmate venation, teeth with a medial principal vein, and tooth apices at the ends of looping accessory veins (Hickey and Wolfe, 1975; Carvalho et al., 2011).

The subfamily Malvoideae is the largest clade within Malvaceae and comprises the historical Malvaceae (Malvaceae *s.s.*) as it was circumscribed prior to the addition of the other families, as well as a few other genera (Bayer et al., 1999; Areces-Berazain and Ackerman, 2017). It comprises 110 genera and 1,730 species (Bayer and Kubitzki, 2003), and although it is found worldwide, it is most diverse in the Americas (Stevens, 2001; Bayer and Kubitzki, 2003; Areces-Berazain and Ackermam, 2017; Fig. 1). Members of Malvoideae are generally shrubs and herbs producing schizocarps or loculicidal capsules (Stevens, 2001; Bayer and Kubitzki, 2003).

The fossil record of Malvaceae is mostly represented by pollen, leaves, and wood, and is predominantly based on Northern Hemisphere reports. In the Northern Hemisphere fossil Malvaceae have been recorded in Asia (Chitaley and Nambudiri, 1973; Qiu et al., 2012; Meshram et al., 2013; Shukla et al., 2014; Anberrée et al., 2015; Kapgate, 2017; Xu et al., 2020; Jia et al., 2021; Wang et al., 2021; Del Rio et al., 2022; Manchester et al., 2023), Europe (Kvaček, 2004, 2006; Kvaček and Wilde, 2010; Worobiec et al., 2010), northern Africa (Pan and Jacobs, 2009), North America (Manchester,1992; Wheeler et al., 1994; Estrada-Ruiz et al., 2010), and South America north of the equator (Colombia, Carvalho et al., 2011); whereas those from the Southern Hemisphere are from South America (Anzótegui and Cristalli, 2000; Wilf et al., 2003, 2005; Barreda et al., 2007, 2012, 2020; Ramos et al., 2017), Australia (McCurry et al., 2022), and with one possible leaf in Antarctica (Dutra and Batten, 2000). Remarkably, the Malvaceae fossil fruit record is rather scarce compared to the overall fossil record for the family and comprises only around a dozen genera worldwide (Table 1). The Malvoideae fossil record is even more biased towards the Northern Hemisphere, with only three records from the Southern Hemisphere. There are four occurrences from South America; *Malvaciphyllum* Anzótegui leaves from the Paleocene of Colombia, north of the equator (Carvalho et al., 2011), the Miocene of Argentina, and the Pliocene of Brazil (Anzótegui and Cristalli, 2000), as well as Pleistocene *Bastardiopsis* (K.Schum.) Hassl. wood from Argentina (Ramos et al., 2017).

Among diverse fossils collected at the early Eocene Laguna del Hunco flora, in Chubut, Patagonia, there is a set of infructescence fragments and isolated fruits previously mentioned in Wilf et al. (2005), but not illustrated or taxonomically identified. These infructescences show a unique combination of characters suggesting strong affinities to Malvaceae, subfamily Malvoideae. The principal goals of this contribution are to describe these putative malvaceous fossil infructescences and to evaluate their biogeographical implications for understanding the past and modern distribution of Malvoideae.

MATERIALS AND METHODS

The Tufolitas Laguna del Hunco, Huitrera Formation, Chubut Province, Patagonia, Argentina deposits preserve a caldera lake assemblage deposited during the early Eocene Climate Optimum, with a diverse flora indicative of a mesic rainforest. The age of these deposits is based on multiple $^{40}Ar/^{39}Ar$ analyses from tuff samples below and at various horizons within the 170 m fossil lake sequence, resulting in an age bracket for all but three of the specimens considered here of 52.22$\underline{+}$ 0.22 Ma, the age of a tuff in the middle of the most fossiliferous interval, to the age of the uppermost beds of the underlying ignimbrite analyzed as 52.54 $\underline{+}$ 0.17 Ma (Wilf et al., 2003; Gosses et al., 2021). The remaining three fossils were from 23 meters above the 52.22 ± 0.22 Ma ash layer but within the same paleomagnetic polarity interval (Wilf et al., 2003, Wilf, 2012).

The biota of LH is quite diverse. Faunal fossils include insects such as Mercoptera (scorpionflies; Petrulevičius, 2009), and Anisoptera (dragonflies; Petrulevičius et al., 2010; Petrulevičius and Nel, 2013); along with siluriform fishes (catfish; Azpelicueta and Cione, 2011), pipoid frogs (Báez and Trueb, 1997), turtles (Sterli et al., 2021), and birds (Degrange et al., 2021). Floral fossils from the site are far more numerous. The palynoflora encompasses a wide diversity of spores and pollen, including some Malvaceae pollen (Barreda et al., 2020), while macrofossils include leptopteroid ferns, gymnosperms, and angiosperms. The leptopteroid fern *Todea* Willd. ex Bernh. and the presence of the gymnosperm Podocarpaceae are key contributors to the evidence that suggests the site may have once been a rainforest due to environmental constraints on these groups, particularly the Podocarpaceae (Carvalho et al., 2013; Wilf, 2012; Pujana et al., 2020; Andruchow Colombo et al., 2023). Other gymnosperms found in the flora include cycads (Wilf et al., 2016) and Araucariaceae (Wilf et al., 2014; Rossetto-Harris et al., 2020). Angiosperms include members of Solanaceae (Wilf et al., 2017; Deanna et al., 2020), Winteraceae (Brea et al., 2021), Monimiaceae (Knight and Wilf, 2013), Ripogonaceae (Carpenter et al., 2014), Menispermaceae (Jud et al., 2018), Juglandaceae (Hermsen and Gandolfo, 2016), Akaniaceae (Gandolfo et al., 1988), Fagaceae (Wilf et al., 2019), Myrtaceae (Hermsen et al., 2012), Cunoniaceae (Matel et al., 2022), and Euphorbiaceae (Wilf et al., 2023) among others.

The fossil reproductive material studied herein was collected from four (LH2, LH4, LH6, and LH27) of the thirty-three quarries located at Laguna del Hunco, Huitrera Formation, Chubut Province, Patagonia, Argentina; paleolatitude ~47° S (Wilf et al., 2003, 2005). Seventeen infructescence fragments bearing from two to 58 fruits (on the longest fragment) were examined, as well as seven isolated fruits. Fossils are housed and permanently curated in the paleobotanical collection of the Museo Paleontológico Egidio Feruglio (MEF), Trelew, Chubut, Argentina under the repository prefix MPEF-Pb.

Specimens were compared with several extant families that produce schizocarps or loculicidal capsules and previously described fossils. Extant material was gathered from the herbarium at the L. H. Bailey Hortorium (BH), Plant Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York, USA; the digital collections of the Department of Botany, National Museum of Natural History, Washington DC, USA (https://collections.nmnh.si.edu/search/botany/); and The John G. Searle Herbarium, Field Museum, Chicago, Illinois, USA. Because of the previously established paleobiogeographical connections of Laguna del Hunco to certain areas (Gandolfo et al., 1988, 2011; Hermsen et al., 2011; Wilf, 2012, 2020; Carvalho et al., 2013; Wilf et al., 2014, 2016; Gandolfo and Hermsen, 2017; Deanna et al., 2020; Brea et al., 2021), examination of extant taxa focused on material from southeast Asia, Australia, Africa, South America, and the Pacific islands, but North American, European, and northern Asian material was also examined. Herbarium specimens from BH were imaged using a Nikon DSC 950 camera with a 60 mm Nikkor micro lens (Nikon, Melville, New York, USA) and processed using Smart Shooter 4 software (Tether Tools Phoenix, Arizona, USA). Smithsonian material was accessed via the botanical collection digital search catalog. Field Museum material was imaged by the John G. Searle Herbarium staff. Fossils were imaged using a Nikon SMZ18 under a 1.6x objective feeding to Nikon NIS-Elements BR 5.10.01 software. Some images were cropped, resized, and white balanced in

Adobe Photoshop (Adobe, San Jose, California, USA), but no other manipulations to the images have been done.

SYSTEMATIC PALEONTOLOGY

Order — Malvales

Family — Malvaceae

Subfamily — Malvoideae

Genus — *Uiher* Siegert, Gandolfo, et Wilf gen. nov.

Generic diagnosis — Paniculate infructescences; schizocarps pedicellate, each subtended by a bract at the base of the pedicel, fruit arrangement alternate. Each schizocarp is composed of five mericarps that split from each other completely from the apex to the base; mericarps ovate in shape with an acute apex; longitudinal ridge present on each mericarp.

Type species — *Uiher karuen* Siegert, Gandolfo, et Wilf sp. nov. (Fig. 2, 3).

Etymology — *Uiher*, from the Tehuelche "vessel" referring to the role of the fruits as a vessel of information through time. The Tehuelche are an indigenous tribe that previously inhabited large areas of Patagonia.

Species — *Uiher karuen,* Siegert, Gandolfo, et Wilf sp. nov.

Species diagnosis — As for the genus *Uiher.*

Etymology — *karuen,* "old" (Tehuelche).

Holotype — MPEF-Pb 8352. Museo Paleontológico Egidio Feruglio, Chubut, Trelew, Argentina. (Fig. 2A, C).

Paratypes — MPEF-Pb 8353 (Fig. 2B), MPEF-Pb 8357, MPEF-Pb 8354, MPEF-Pb 8356.

Type locality — Laguna del Hunco quarry LH2, Ypresian (early Eocene), Huitrera Formation, Chubut Province, Patagonia, Argentina

Other localities — Laguna del Hunco, Ypresian (early Eocene), Huitrera Formation, Chubut Province, Patagonia, Argentina. Quarry LH4: MPEF-Pb 465, MPEF-Pb 1241, MPEF-Pb 8150, MPEF-Pb 8151, MPEF-Pb 8152, MPEF-Pb 8163, MPEF-Pb 8164, MPEF-Pb 8165 (Fig. 3B, D), MPEF-Pb 8166, MPEF-Pb 8167, MPEF-Pb 8355, MPEF-Pb 8358, MPEF-Pb 8359, MPEF-Pb 8360, MPEF-Pb 8361, MPEF-Pb 8362; LH 6: MPEF-Pb 8029 (Fig. 3C), MPEF-Pb 8363; LH 27: MPEF-Pb 8168.

Description — The fossil infructescences are incomplete panicles that bear alternately arranged fruits (Fig. 2A, B). The fragments range from 4.4 cm to 6.4 cm in length. Fruits are borne on short pedicels ranging in length from 0.4 mm to 1.6 mm. The pedicels are each subtended by a bract that ranges in length from 0.5 mm to 1.4 mm (Fig. 2A, B). The mean fruit size is 2 mm by 2.1 mm, with length ranging from 1.4 mm to 2.9 mm and width ranging from 1.5 mm to 3.4 mm. The fruits have a superior ovary, display evidence of an infracarpelar disk (Fig. 2C and Fig. 3B, D), and split from the apex to the base completely into five ovate mericarps (Fig. 3C, D). Each mericarp is characterized by an acute apex, rounded base, and the presence of a longitudinal ridge (Fig. 2A, B, C; 3C, D); they have a length ranging from 1.1 mm to 2.6 mm and a width ranging from 0.8 mm to 1.5 mm. Isolated fruits show the same features as those on infructescences.

DISCUSSION

Several families were considered for their potential affinities with *Uiher karuen*. Because both schizocarps and loculicidal capsules are present in multiple lineages of Malvaceae (Bayer and Kubitzki, 2003; Areces-Berazain and Ackerman, 2017), comparisons to *Uiher karuen* were established with members of families that produce either of these fruit types. Families other than Malvaceae that produce infructescences bearing schizocarps include Apiaceae, Geraniaceae, Rutaceae, Rosaceae, and Sapindaceae. Both Apiaceae and Geraniaceae are herbaceous, with schizocarps that split from the base and remain attached at the apex, unlike the Patagonian fossils. Apiaceae schizocarps are composed of only two mericarps, far fewer than the five seen in *Uiher*, and the mericarps are more elongated (Fig. 3C, D; Plunkett et al., 2018). Geraniaceae schizocarps have a unique manner of splitting, wherein each mericarp separates completely from the center of the schizocarp, but remains attached to the persisting style which has split and curled up (Albers and Van der Walt, 2007). The resulting shape is reminiscent of a candelabra. Although the number of mericarps in Geraniaceae and *Uiher* are often the same, the shape of the mericarps is quite different (Albers and Van der Walt, 2007). The Sapindaceae include species that produce schizocarps with samaroid or inflated mericarps (Acevedo-Rodríguez et al, 2011), a trait that *Uiher* does not possess. Some Simaroubaceae produce schizocarps with drupaceous mericarps (Clayton 2011), which *Uiher* lacks.

Other families that occasionally produce schizocarpic fruits are Boraginaceae (Weigend et al, 2016), Capparaceae (Kers, 2002), Celastraceae (Simmons, 2004), Euphorbiaceae (Webster, 2014), Rhamnaceae (Medan and Schirarend, 2004), Rutaceae (Kubitzki et al, 2010), Verbenaceae (Atkins, 2004), and Zygophyllaceae (Sheahan, 2007). However, the fruit morphologies of these families are very dissimilar to those produced by the Patagonian fossil taxon; thus they were discarded before detailed comparisons were performed.

Although we do not interpret *Uiher* as loculicidal capsules, we investigated families that produce this fruit type, to lend support to our interpretation. Families that produce loculicidal capsules with five locules or valves include Meliaceae, Rutaceae, and Lythraceae. Meliaceae species produce three to six valves, but they generally have a large central axis that is visible when the valves are open (Mabberley, 2010); such an axis is not seen in *Uiher.* The family Rutaceae has a variety of fruit types, including capsules with two to five locules; some capsules split loculicidally and some septicidally, and these capsules are generally globose and lacking an acute apex (Kubitzki et al., 2010). Lythraceae produces loculicidal capsules with two to six sections, but these have a persistent floral tube (Graham, 2007), which *Uiher* does not have. All these families were discarded because although the fossils bear some superficial resemblance they have little overlap of characters.

Notably, members of Malvaceae and the Patagonian fossils share several characters, including infructescence type, fruit type, and fruit morphology (the shape and the number of mericarps). Characters that support the placement of *Uiher* within Malvaceae include the superior ovary, the infracarpelar disk, and the presence of bracts subtending the fruits (Fig. 2, 3). The ovary of *Uiher karuen* is interpreted as being superior because there is no evidence of a hypanthium or a surrounding receptacle, and therefore the fossils are considered hypogynous like the majority of the Malvoideae (Kubitzki and Bayer, 2003). In addition, the “bullseye” mark at the bases of the fossil fruits (Fig. 2D, 3D) coincides with the infracarpelar disk found in many Malvaceae species (Krapovickas, 1988). Furthermore, the bracts that are preserved on most but not all infructescences, suggest that they may senesce at maturity as the fruit dries. Subtending bracts of this type are common in Malvaceae (Kubitzki and Bayer, 2003).

As mentioned above, we interpret *Uiher karuen* fruits to be schizocarps but loculicidal capsules were also investigated, as both types of fruit are produced by members of Malvaceae, especially within Malvoideae (Areces-Berazain and Ackerman, 2017). In particular, the ancestral state of Malvoideae is believed to be a five-carpellate capsule (Areces-Berazain and Ackerman, 2017). However, Malvoideae loculicidal capsules almost always bear other features, such as a pronounced calyx or epicalyx, which at least partially covers the capsule (Bayer and Kubitzki, 2003). This is not observed in *Uiher*.

A single specimen (MPEF-Pb 8150; Fig. 3A) revealed the schizocarpic nature of the fruit because it distinctly shows the separation of the ovoid mericarps at the base, both from each other and from the base of the fruit. This supports our interpretation that *Uiher karuen* is a schizocarp. As with schizocarps, loculicidal capsules can separate into ovate sections with an acute apex. However, a loculicidal capsule would maintain the connections of the valves to the base of the capsule, if not to each other, and this trait was not observed in these LH fossils (Fig. 3A). Regardless of fruit type, *Uiher karuen* can confidently be placed within Malvaceae based on the characters preserved.

Comparisons with extant Malvaceae**:** To compare the fossils with members of Malvaceae, the Patagonian fossil fruits were considered here as schizocarpic but were additionally compared to taxa with loculicidal capsules, particularly because schizocarps have likely evolved at least three times in Malvaceae (Areces-Berazain and Ackerman, 2017). Comparisons were established using the features of the inflorescence/infructescence (presence and type, fruit arrangement) and of the fruits (number, shape, presence of an acute apex, and presence of a ridge on each mericarp). The Patagonian fossils share characters with several extant Malvaceae genera, including the infracarpelar disc, an attribute found in extant Malvaceae of Patagonia (Krapovickas, 1988). In particular, within Malvoideae, the genera *Sidalcea* A. Gray*., Tetrasida* Ulbr., and *Wissadula* Medik. share a large number of characters with *Uiher*, all produce schizocarps with mericarps that have external ornamentation that when fossilized could be interpreted as a ridge.

Sidalcea is a Northern Hemisphere genus that shares many characteristics with the fossils, most noticeably the paniculate inflorescence with alternate arrangement of the fruits and the schizocarp fruits (Fig. 4A, B). Mostly, *Sidalcea* schizocarps split into 5 to 9 ovoid mericarps (Fig. 4A, B); in some species, the mericarps are characterized by the presence of longitudinal ridges similar to those seen in *Uiher* (Fig. 3C, D). The fruits of *Sidalcea* sit on similarly short pedicels which are each subtended by a bract; the bract is occasionally missing in some fruits on the same infructescences, suggesting the possibility of senescence at maturity (Fig. 4A, B), another trait seen in *Uiher*. *Sidalcea* does have a persistent calyx around the schizocarp (Bayer and Kubitzki, 2003) which *Uiher* lacks.

Tetrasida is a small genus of species that produce schizocarps composed of five ovate mericarps with an acute apex (fig. 4C). Among *Tetrasida* some species share characters with *Uiher* such as *Tetrasida chachapoyensis* (Baker f.) Fryxell and Fuertes. In this species mericarps bear a longitudinal ornamentation down each mericarp (Fryxell and Fuertes, 1992); however, these schizocarps are borne on long pedicels, rather than the short pedicels as in *Uiher. Tetrasida* also lacks a subtending bract at the pedicel base of each fruit; some also produce a transverse endoglossum that splits the upper parts of the mericarp, leaving an opening (Fryxell and Fuertes, 1992; Bayer and Kubitzki, 2003).

Wissadula also shares some characters with *Uiher*, they produce schizocarps with three to six mericarps with some species producing five like *Uiher.* Similarly, some *Wissadula* species bear their schizocarps on long pedicels, and some species on particularly short pedicels on a spike-like infructescence. Its mericarps, like those of *Uiher*, are often ovoid with an acute apex and a ridge down the center of the mericarp (Fig. 4 D.); but unlike *Uiher*, this ridge often facilitates only a partial septicidal dehiscence of the upper portion of the mericarp (Bayer and Kubitzki, 2003; Bovini and Baumgratz, 2016, De Araújo Masullo et al., 2020).

Unfortunately, due to the few characters that can be scored for the new fossil species, a phylogenetic analysis did not produce reliable results because the fossil species "jumped" from one clade to another within Malvoideae. Problems with a lack of characters in phylogenetic analysis are abundantly documented (see Gauthier, 1988; Nixon, 1996; Escapa and Pol, 2011). Based on the interpretation that *Uiher* produced schizocarps, combined with other characters including infructescence type, mericarp number, and the presence and shape of ridged mericarps, we hypothesize that *Uiher* is likely to be a member of the Malviodeae tribes Malveae or Hibisceae which although no genus or species produces the same set of traits, all of the major traits of *Uiher* can be found among the various members of both tribes.

Comparisons with Malvaceae fossil fruits: The fossil record of Malvaceae fruits is relatively limited (see Introduction). Reliable reports include the genera *Tiliaceaeocarpon* Meshram, Narkhede and Bhowal, *Harrisocarpon* Chitaley and Nambudiri*, Hibiscocarpon* Kapgate, *Firmiana* Marsili*, Burretiodendron* Rehder*, Reevesia* Lindl.*,* Florissantia (Knowlton) Manchester, *Tilia* L. and *Daberocarpon* Chitaley and Sheik (Table 1).

Berry (1925, 1928, 1934, 1938; Fig. 5) described two species of the genus *Malvacarpus* based on fruit remains: *Malvacarpus tertiarius* Berry from Laguna del Hunco, and *Malvacarpus guiñazui* Berry. *M. tertiarius* and *Uiher karuen* are quite different. *M. tertiarius* has nine "carpels" (Fig. 5), which is far more than the five mericarps found in *Uiher*. *M. guiñazui* might have five sections, although it is unclear. The individual sections of both *Malvacarpus* species have starkly different shapes from each other and from *Uiher*. The sections of *M. tertiarius* are thin and tapered at the top and bottom, while the sections of *M. guiñazui* bear distinct apical ornamentation and are directly compared to *Malvocarpum* Hollick by Berry. Because of these differences, *Uiher karuen* cannot be placed within *Malvacarpus*.

Malvocarpon clarum, originally erected by Hollick (1928), was collected at the banks of the Collazo River, Puerto Rico, in sediments of Oligocene age (Nieves-Rivera, 2007). Hollick (1928, p. 214) described it as "consisting of an aggregate of what appears like elongated, apiculate carpels arranged around a common center," yet later on the same page, he referred to it as "the fruit as a whole and also the individual capsules." Based on figures 2 and 3 of Hollick (1928), this fruit can be reinterpreted as probably a schizocarp with individual mericarps, rather than individual capsules; however, further evaluation of *M. clarum* is needed to decipher its morphology.

Tiliaceaeocarpon jamsavlii Meshram represents a six-sided indehiscent capsule with a suggested age of Late Cretaceous (Meshram, 2013), and lacks overlapping features with *Uiher*. *Hibiscocarpon mohgaonensis* Kapgate, referred to as fossil fruit of *Hibiscus esculentus* L., with an unconfirmed Paleocene age (Kapgate 2017), are very similar to those produced by extant *Hibiscus* and are completely different from *Uiher*. *H. mohgaonensis* has single fruits, generally with sepals and stipules below each fruit. *Craigia* spp. W.W.Sm and W.E.Evans are rather prolific in the fossil record when taking into consideration Kvaček et al.'s (2005) reassignment of various fruits and leaves to *Craigia* spp. of the Eocene, Miocene, and Pliocene. *Craigia* spp. and Oligocene *Burretiodendron* spp. fossils are not infructescences and are described as single fruits having winged valves (Kvaček, 2004; Qiu et al., 2012; Anberrée et al., 2015; Xu et al., 2020; Wang et al., 2021; Del Rio et al., 2022), while there is no such wing on *Uiher*. *Firmiana* spp., with examples in the Eocene and mid-Miocene, is a single-valved dehiscent fruit with pinnate venation (Jia et al., 2021; Del Rio et al., 2022) that has no characters in common with *Uiher*. *Reevesia hurnikii* Kvaček, from the early Miocene, represents single fruits that have an acute base with a bulbous apex (Kvaček, 2006), which is the reverse of *Uiher. Florissantia* spp., from the Oligocene, sits on a particularly long pedicel, with large sepals remaining attached to the base of the fruit (Manchester, 1992), neither of these key features are present in *Uiher*. Cretaceous-Paleocene *Daberocarpon gerhardii* possesses ten mericarps, each with an apical awn and a depression in the middle of the schizocarps where the mericarps come together (Manchester et al., 2023). *Harrisocarpon sahnii*, which comes from the same locality as *Daberocarpon gerhardii*, possesses five mericarps but with deep furrows between each mericarp prior to splitting (Chitaley and Nambudiri, 1973; Manchester et al., 2023), compared to *Uiher*'s comparatively shallow furrows (Fig. 3A). *Harrisoncarpon sahnii* also has pinched tips on its mericarps, which *Uiher* lacks.

Palaeoecological and biogeographical implications: The biogeography of species with possible affinity to *Uiher* is broad, with *Sidalcea, Tetrasida,* and *Wissadula* detailed here. *Sidalcea* is native to western North America (Bayer and Kubitzki, 2003; Govaerts, 2023). *Tetrasida* has a very small native range in northwestern South America, including portions of Peru, Ecuador, and Bolivia (Bayer and Kubitzki, 2003; Govaerts, 2023). *Wissadula* has a large native range covering vast parts of tropical and subtropical North and South America as well as Africa, and a more limited range in southern Asia (Bayer and Kubitzki, 2003; Govaerts, 2023). Several species of *Wissadula* are native to Northeastern or Northwestern Argentina, but none range into Patagonia (Bovini and Baumgratz, 2016).

Many plant species found at Laguna del Hunco paleoflora and throughout Patagonia have biogeographic connections to Australasia, Malesia, and northern South America. (Carvalho et al., 2013; Gandolfo et al., 2017; Wilf et al., 2013, 2019, 2023). The extant genera compared to *Uiher* grow in a variety of habitats. This diversity of habitats precludes any meaningful conclusions beyond those drawn from the overall temperate and tropical distribution of Malvoideae and Malvaceae (Stevens, 2001; Fig. 1). In this interpretation, the ecological constraints previously suggested for the locality (Carvalho et al., 2013; Gandolfo and Hermsen, 2017; Barreda et al., 2020; Brea et al., 2021) fall within the broad ecological range indicated by the placement of *Uiher*.

CONCLUSION

Uiher karuen represents the first confirmed infructescence macrofossils of Malvoideae in the Southern Hemisphere. Based on detailed comparisons between *Uiher* and modern families and genera, it is clear that this Patagonian fossil taxon belongs within Malvoideae. Malvoideae and *Uiher karuen* share several characters including paniculate infructescences, short pedicels, subtending bracts, and ovate mericarps with an acute apex and longitudinal ridges which strongly support the placement of *Uiher* in Malvoideae. *Uiher karuen* is the only fossil fruit of Malvoideae in the Southern Hemisphere, where there are only three previously known Malvoideae leaf macrofossils, and one wood macrofossil. The presence of these fossils at Laguna del Hunco expands the evidence for the presence and diversification of Malvaceae and Malvoideae in the Southern Hemisphere as early as the Eocene.

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AUTHOR CONTRIBUTIONS

C.S.:conceptualization, data curation, formal analysis, investigation, methodology, validation, visualization, and writing (original draft, review and editing); M.A.G.: conceptualization, data curation, funding acquisition, methodology, project administration, resources, supervision, validation, and writing (review and editing); P.F. data curation, project administration, validation, and writing (review and editing).

DATA AVAILABILITY

All specimens of the new fossil species *Uiher karuen* are curated at the Museo Paleontológico Egidio Feruglio, Trelew, Chubut, Argentina. Extant material used is curated and housed at BH, Bailey Hortorium (BH), Cornell University, Ithaca, New York, USA, or at the United States National Herbarium (US), National Museum of Natural History, Washington DC, USA.

DECLARATION OF INTERESTS: none

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Table 1: Malvaceae fossil fruits listing genus, first author, location, and age.

Species	First Author	Location	Age
Daberocarpon gerhardii	Manchester 2023	Deccan Intertrappean beds, India	Late Cretaceous – Paleocene
Harrisocarpon sahnii	Manchester 2023 Chitaley 1973	Deccan Intertrappean beds, India	Late Cretaceous - Paleocene
Tiliaceaeocarpon jamsavlii	Meshram 2013	Madhya Pradesh, India	Late Cretaceous – Paleocene
Hibiscocarpon mohgaonensis	Kapgate 2017	Mohgaonkalan, India	Paleocene
Wind dispersed fruits*	Herrera 2014	La Guajira, Colombia	Paleocene
Malvacarpus tertiarius*	Berry 1925	Chubut, Argentina	Eocene
Malvacrpus guiñazui*	Berry 1938	Río Negro, Argentina	Eocene
Craigia sp.	Del Rio 2022	Tibet, China	Eocene
Firmiana sp.	Del Rio 2022	Tibet, China	Eocene
Craigia spp,	Qiu 2012	Hainan, China	Eocene
Florissantia spp.	Manchester 1992	Colorado, Oregon, USA; British Colombia, Canada	Oligocene
Burretiodendron parvifructum	Xu 2020	Guangdong, China	Oligocene
Burretiodendron parvifructum	Anberrée 2015	Yunnan, China	Oligocene
Malvocarpon clarum*	Hollick 1928	Puerto Rico, USA	Oligocene
Reevesia hurnikii	Kvaček 2006	Ústí nad Labem, Czech Republic	Miocene
Firmiana sinomiocenica	Jia 2021	North Gyeongsang, South Korea	Miocene
Tilia asiatica	Jia 2021	North Gyeongsang, South Korea	Miocene
Craigia bronnii	Kvaček 2004	Ústí nad Labem, Czech Republic	Miocene
Craigia lincangensis	Wang 2021	Yunnan, China	Miocene

* Indicates that doubts have been raised about the validity of the assignment to Malvaceae.

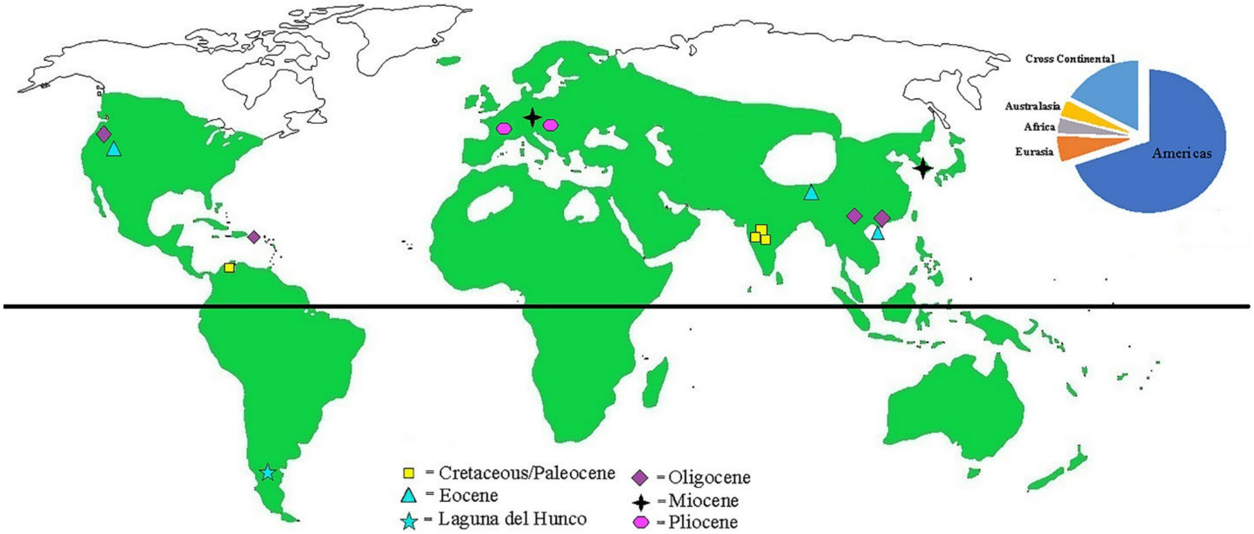

Figure 1. Map of Malvoideae global distribution, with present-day mapped in green. The pie chart indicates the percentage of species native to each region. Symbols indicate fossil fruit occurrences.

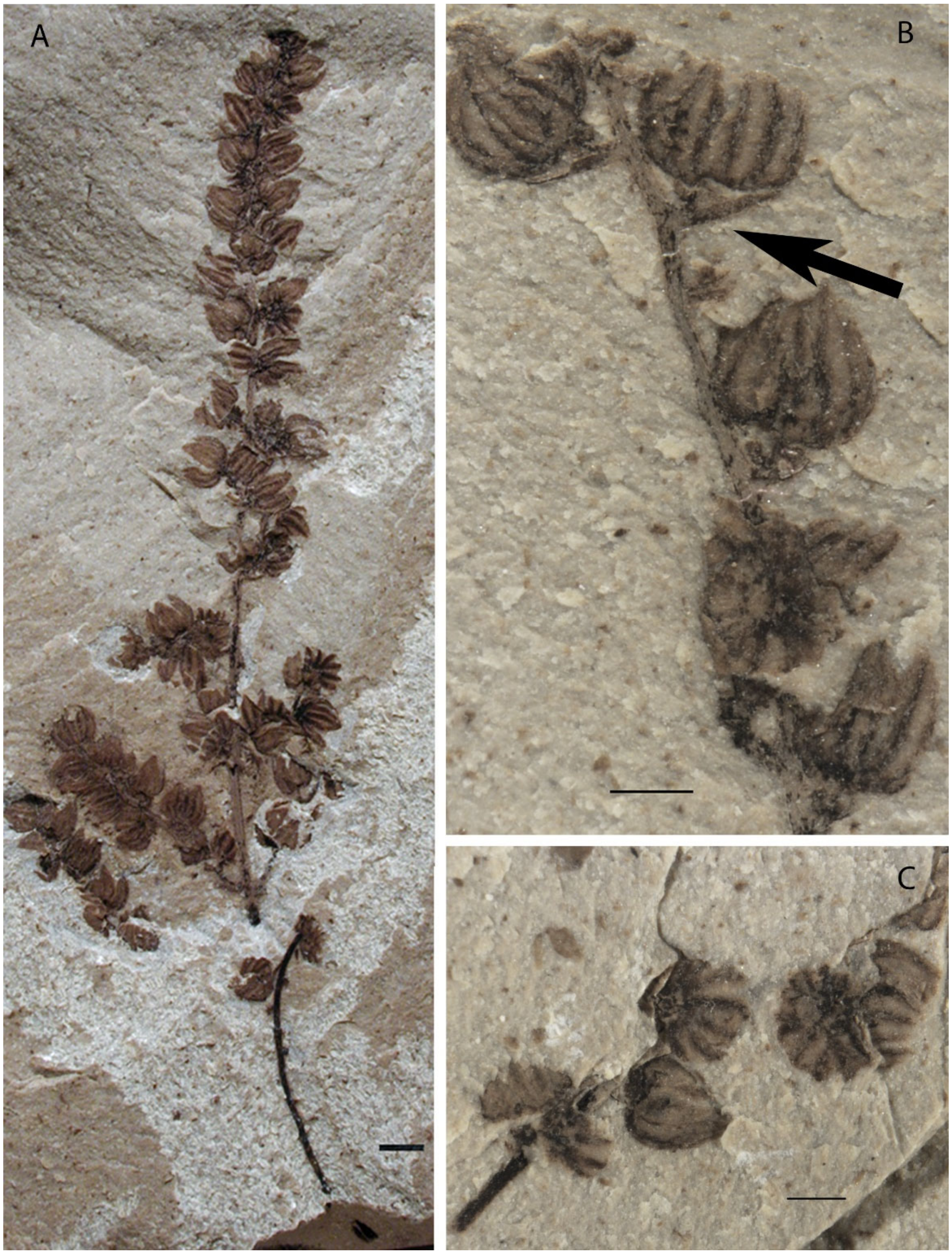

Figure 2. *Uiher karuen* Siegert, Gandolfo, et Wilf, sp. nov. A. MPEF-Pb 8352, Branching infructescence bearing five-parted fruits. B. MPEF-Pb 8353, Infructescence segment showing alternate phyllotaxis of the fruits; the fruits are pedicellate, subtended by bracts (arrow), and variably closed or open. C. Lateral and basal views of several fruits of MPEF- Pb 8352, showing infracarpelar discs. Scale bars = 1 mm.

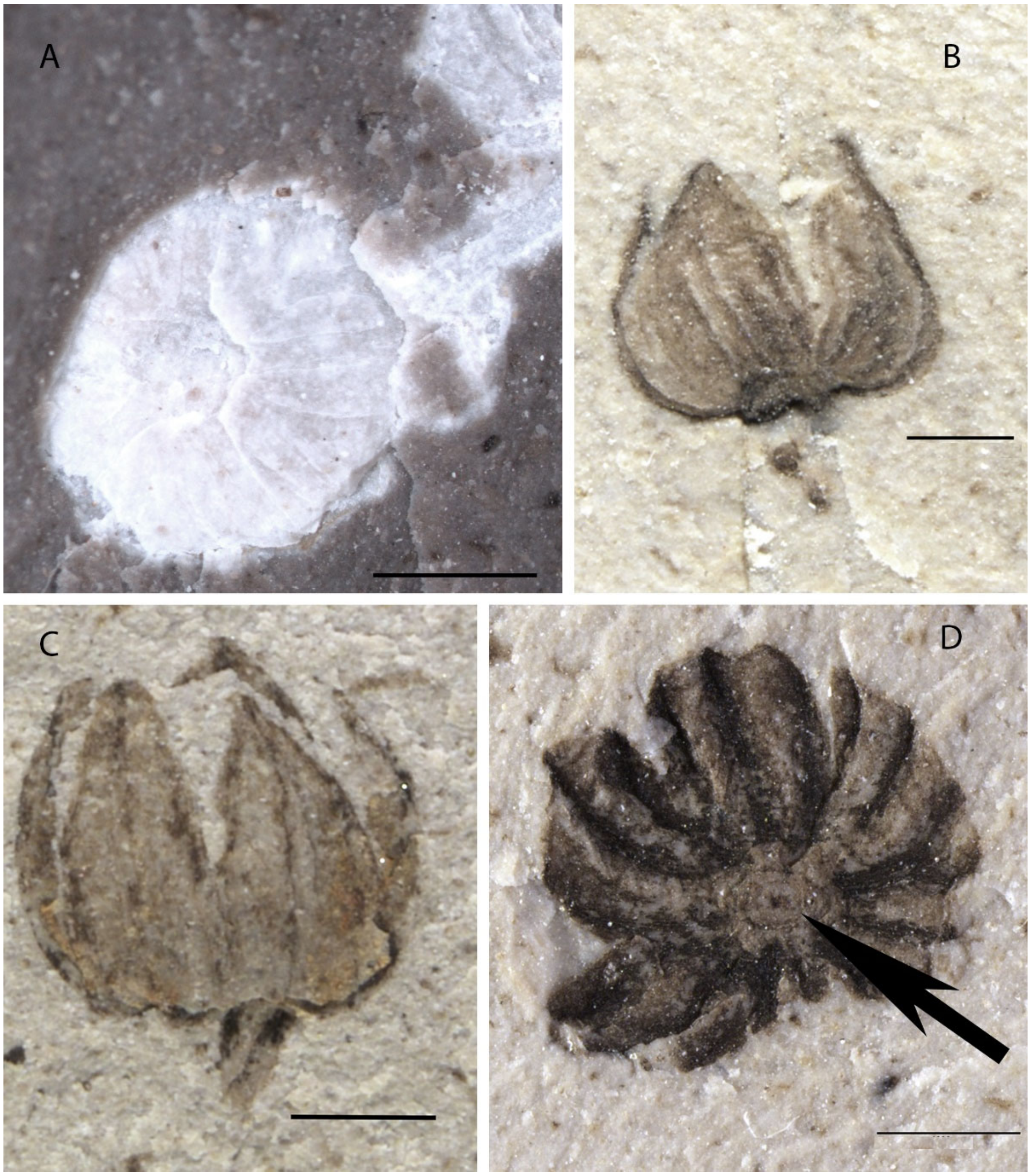

Figure 3. *Uiher karuen* Siegert, Gandolfo, et Wilf, sp. nov. A. Basal view of MPEF-Pb 8150, showing mericarps separating from the base. The white coloration results from silicate mineral replacement of the original compression. B. Lateral view of MPEF-Pb 8165, showing several sections and an infracarpelar disc at the base of the schizocarp. C. Lateral view of MPEF-Pb 8029 opened fruit, showing five sections opening from the apex. Each section is obovoid with an acute apex and a meridional line. D. MPEF-Pb 8165, Detail of the infracarpelar disk, indicated by the arrow. Scale bars = 1 mm.

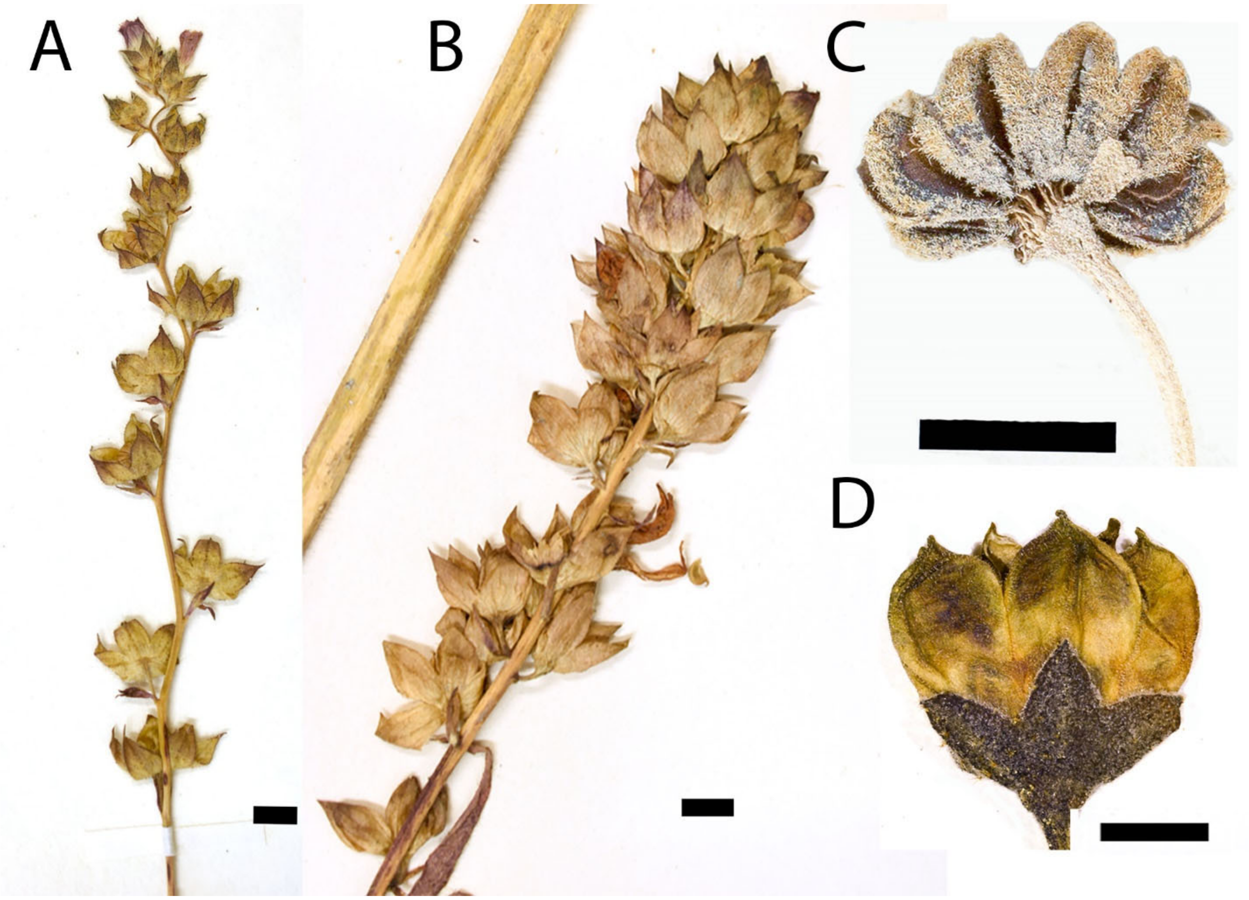

Figure 4. Selected extant members of the subfamily Malvoideae. A. *Sidalcea calycosa* infructescence, BH 000 307 603. B. *Sidalcea hendersonii* infructescence, BH 000 307 614. C. *Tetrasida chachapoyensis* V0243599F D. *Wissadula subpeltata* fruit BH 000 332 340. Scale bars = 0.5 cm.

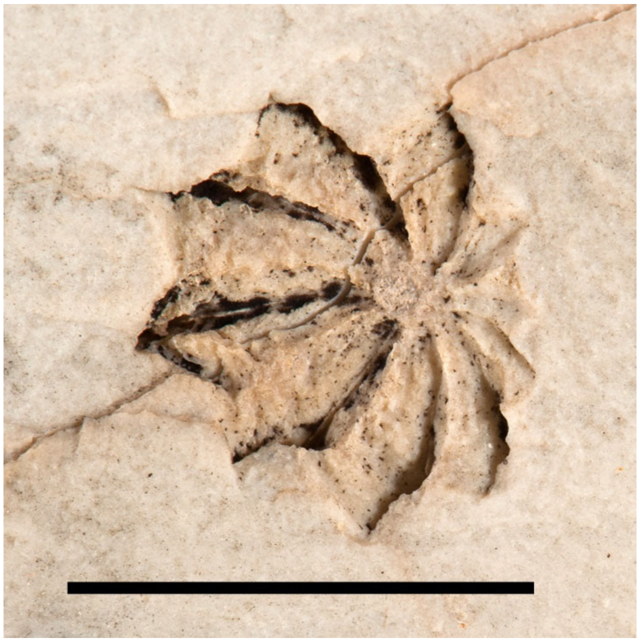

Figure 5. *Malvacarpus tertiarius* holotype specimen (Berry 1925), USNM 219107. Scale bar = 1cm.