Vegetation History and Archaeobotany (2024) 33:489–502
https://doi.org/10.1007/s00334-023-00965-7

ORIGINAL ARTICLE

Pre-Hispanic use of edible *Geoffroea decorticans* fruits in central Argentina - first approximations based on an integrated morphoanatomical and archaeobotanical approach

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Received: 1 March 2023 / Accepted: 6 July 2023 / Published online: 14 October 2023

Abstract

The edible drupe of *Geoffroea decorticans* (Fabaceae) has been used in South America since ancient times. However, and despite its great current cultural importance, there are no details about the past modes of use. In the central mountains of Argentina, micro- and macrobotanical remains of this wild species were recovered from archaeological sites within three subregions. This evidence indicates that the taxon was part of the plants used as food by the communities who inhabited the area in the Late Pre-Hispanic period (LPP, 1,500 – 350 BP). Identifying the culinary practices involving these remains in the past requires an interpretive model built from processing activities currently performed with these fruits, as well as detailed knowledge of the anatomy of these fruits. As part of a major archaeological-ethnobotanical research project, in this work we present a micro-morphological and histological characterization of *G. decorticans* drupes and describe the charred carpological remains recovered from the study area to date. We use these anatomical data, as well as ethnographic information from previous studies, to infer the possible activities and processes that formed the archaeological specimens. The results indicate differences in the processing of *G. decorticans* during LPP at both local and subregional scales and enhance our knowledge about the interrelation between the LPP societies and wild edible plants.

Keywords Carpology · Wild edible plants · Hunter-gatherers · Drupe · Cordoba province · South America

Introduction

Wild edible plants in archaeobotanical studies

Since ancient times, collection and consumption of wild edible plants have been vital activities for many human groups, not only from a nutritional viewpoint but also as an important aspect of their identity (Turner et al. 2011). Wild edible plants have been used by both hunter-gatherer groups and the so-called agrarian peoples and pastoralists and, even for the latter groups, these taxa have played a key role on certain occasions of their social life (e.g. due to insufficient harvests or famine) (Turner et al. 2011; Antolín Tutusaus and Berihuete Azorín 2017).

However, archaeobotanical studies have focused on domesticated plants, whereas wild species and the activities associated with them remain poorly understood (Antolín and Berihuete-Azorín 2017; Korstanje 2017). Thus, considering food as a "total social fact" (Aguirre 2017) through which researchers gain access to different dimensions of a

Communicated by L. A. Newsom.

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society, such bias in the focus of studies has probably made it difficult to understand the dimensions of social life related to the collection of plants in past societies (Antolín Tutusaus and Berihuete Azorín 2017; Korstanje 2017).

In this sense, and due to the constant recovery and identification of evidence of wild plant taxa in different archaeological contexts, studies have been conducted to unravel the role of these species in food over time (Zapata Peña 2000; Capparelli 2011; Antolín and Jacomet 2015; Berihuete-Azorín 2016). An emblematic case of study in South America is the analysis of the use of fruits of wild *Neltuma* Raf. species (which were part of the genus *Prosopis* L., Fabaceae until recently; see Hughes et al. 2022) by the past societies from northwestern Argentina. This research has marked a milestone due to its ethnobotanical, ethnoarchaeological and experimental approach (Capparelli 2007, 2011; Capparelli and Lema 2011). Based on the methodological approach developed by Hillman (1984) and Jones (1984), Capparelli performed an ethnographic immersion in current communities with the aim of finding out about the present modes of use of *Neltuma* pods and answering archaeobotanical questions (Capparelli 2007). Likewise, based on the characterization and carbonization of the processed fruits and processing residues, this author generated an interpretive model that allowed her to determine the post-collection practices applied to the charred macroremains recovered from El Shincal archaeological site (Catamarca, Argentina) (Capparelli 2011; Capparelli and Lema 2011). This investigation required an exhaustive morphoanatomical characterization of the unprocessed fruits (Capparelli 2008).

This line of research laid the foundations for the analysis of changes and continuities in practices with *Neltuma* species which, together with *Geoffroea decorticans* (Gillies ex Hook. & Arn.) Burkart (Fabaceae, "chañar") and *Sarcomphalus mistol* (Griseb.) Hauenschild (Rhamnaceae, "mistol"), are the wild trees with edible fruits of greatest cultural importance in north-central Argentina today (e.g. Montani and Scarpa 2016; Saur Palmieri et al. 2022). In this work, we resume these methodological contributions to study the practices applied to *G. decorticans* by the pre-Hispanic societies of the mountainous region of Córdoba province (central Argentina).

Botanical and ethnobotanical aspects of *Geoffroea decorticans*

G. decorticans is a tree of the Fabaceae family with a wide distribution that includes Peru, Bolivia, Paraguay, Chile, Uruguay and Argentina (Fig. 1a). An indehiscent fruit develops from the papilionaceous flower with superior ovary (Demaio et al. 2015) (Fig. 1b). This fruit is an ovoid-globose drupe, 1.5–3.5 cm long and 1.5–2.4 cm wide (Fig. 1c). When ripe, its epicarp (syn exocarp, *sensu* Font Quer 2001) is smooth and reddish orange (Burkart 1949; Demaio et al. 2015) (Fig. 1d). The mesocarp is pasty, abundant, sweet (Fig. 1e-f), and consists mainly of disaccharides (≈30%) (Orrabalis et al. 2014). The endocarp is ovoid-fusiform, woody, rough, whitish-yellowish, 1.5-2 cm long and 1.2–1.5 cm wide (Fig. 1g). It has a high lignocellulosic content (97%) (Burkart 1949; Orrabalis et al. 2014). It is composed of a labile outer layer and a compact middle layer (Fig. 1h-i). Inside, the stone presents macroscopically visible transverse grooves, covered with a thick, whitish, light and delicate layer (Fig. 1j) (Saur Palmieri et al. 2019). The *G. decorticans* drupe has a single seed, which is exalbuminate and has a wavy surface (Burkart 1949; Kirkbride et al. 2003). The seed is mostly composed of lipids and proteins (Maestri et al. 2001) (Fig. 1k). The type of fruit exhibited by this species (as all the species of the genus *Geoffroea*) is unusual in Fabaceae, since most of the species of this family develop legumes as fruits (legumes are carpological structures that usually split along the two carpel suture lines to release multiple seeds) (Kirkbride et al. 2003).

At present, *G. decorticans* is highly appreciated by various peoples due to the nutritional quality of its fruits and seeds. Fruits are consumed fresh or boiled in several preparations (drinks - *aloja*, *añapa*, desserts - *cocho* and jams - *arropes*) (Villagrán and Castro 2004; Vidaurre et al. 2006; Scarpa 2009; Suárez 2014; Trillo et al. 2014; Montani and Scarpa 2016; Varela et al. 2019). Seeds are consumed raw or roasted and they are obtained by breaking the endocarp with a stick (Arenas 2003). In particular, in the mountain region of central Argentina, *G. decorticans* fruits are mostly consumed as a snack (unprocessed) and used for the preparation of *arrope* (a syrup made by boiling the drupes for several hours) (Arias Toledo et al. 2007; Saur Palmieri et al. 2018, 2019). Thus, this species is one of the best known and most widely used wild edible plants in the study area (Saur Palmieri et al. 2022). Moreover, although the modes of consumption in the past still need to be clarified, it is undeniable that its use has been continuous over time since, at least, the Late Pre-Hispanic period (LPP, 1,500 – 350 BP) (Saur Palmieri 2022; Trillo and López in press).

The Late Pre-Hispanic people of the mountains of central Argentina

In the mountain area of Córdoba province, central Argentina, studies of plant remains have been aimed at unravelling the subsistence system of pre-Hispanic settlers (López 2018). The greatest availability of data comes from occupations during the LPP, corresponding to societies characterized by high residential mobility, occupying different landscapes seasonally. The residential structures of the

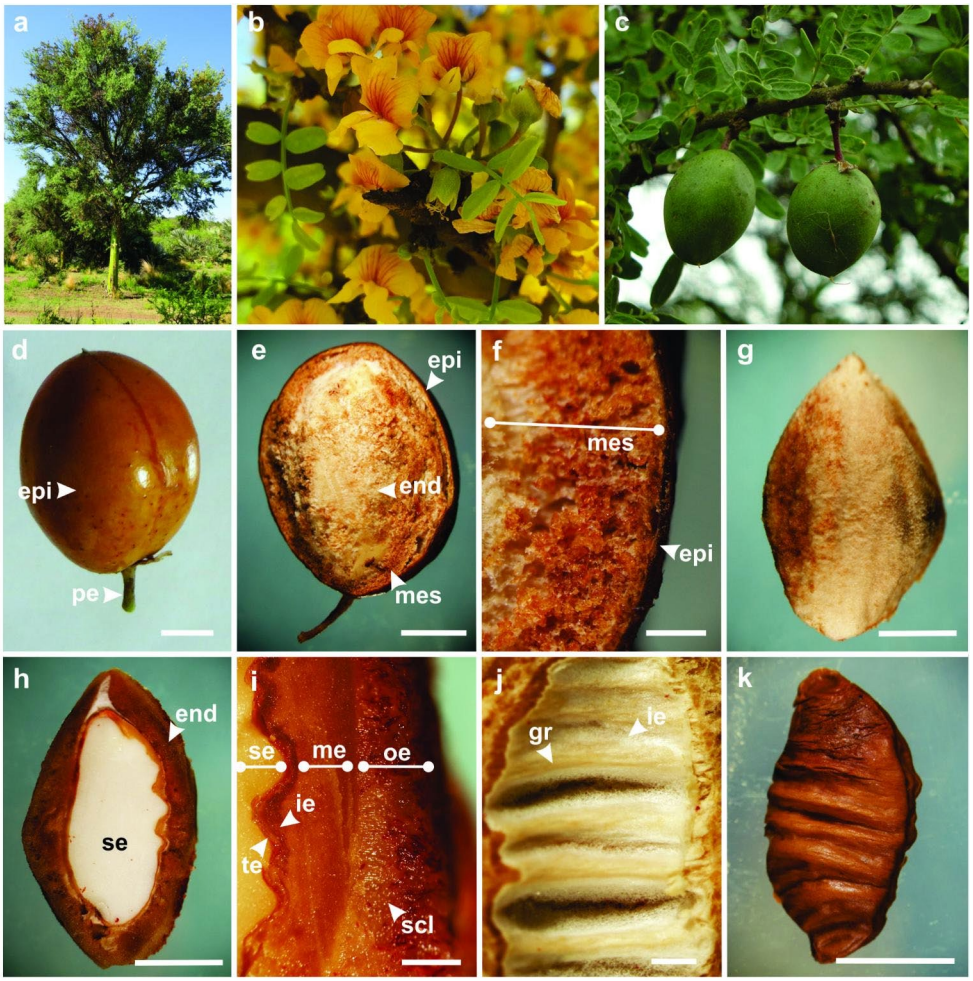

Fig. 1 *Geoffroea decorticans* overview, **a** general appearance of the tree; **b** flowers; **c** immature fruits; **d** ripe fruit; **e** longitudinal section of the fruit; **f** epicarp and mesocarp; **g** external view of the endocarp; **h** longitudinal section of endocarp and seed; **i** detail of endocarp wall; **j** inner side of the endocarp with transverse grooves; **k** seed. *end*, endocarp; *epi*, epicarp; i.e., inner layer of the endocarp; *mes*, mesocarp; *oe*, outer endocarp; *pe*, pedicel; *scl*, sclereids; *se*, seed; *te*, testa. Scale bars **d-e**, **g-h**, k = 5 mm; **f**, i-j = 1 mm (all the photos were taken by VSP)

open-air sites in the valleys are associated with short, seasonal occupations; they were built with perishable materials available nearby, which had low preservation potential. In addition, well-defined hearth features are absent in the sites of this period (Medina et al. 2016). The subsistence strategy was mixed, based on wild plant and animal resources. Agriculture was practiced on a small scale, with minimal labour investment and without irrigation. In the cultivation plots, crops and weeds were combined (Recalde and López 2017; López 2018). Agricultural activity, which was initiated around 1,500 BP, became one of the practices carried out in the process of diversification and intensification of the consumption of resources that had begun towards the end of the Middle Holocene and the beginning of the Late Holocene. (4,000–3,000 BP) (Pastor et al. 2012; Recalde and López 2017).

Archaeobotanical investigations implemented in various archaeological sites located in the mountains of Córdoba identified plants that were included in the diet of pre-Hispanic human groups through the analysis of charred macro- and microremains (phytoliths and starch grains). Thus, fruits, seeds, and underground storage organs of wild taxa, as well as crops and associated weeds, were identified (Recalde and López 2017; López 2018; López et al. 2020; Tavarone et al. 2021).

The archaeological evidence recovered in the three subregions shows that some plant taxa are present in more than one of them; however, there are differences in both the ubiquity and density of certain taxa. These differences suggested the existence of certain differences in the patterns of occupation and subsistence of late pre-Hispanic communities of the mountains of Córdoba. In this sense, how human groups interrelated with their environments would differ between communities from the north subregion and the centre-west of the mountains (Recalde and López 2017; López 2018).

G. decorticans is among the wild taxa that were recovered from sites in central Argentina (López et al. 2020). The archaeobotanical evidence corresponding to this species consists, on the one hand, of microremains found in the dental tartar of individuals from different localities in the mountain sector. This finding confirms the consumption of this edible species during the LPP (Zárate et al. 2020; Tavarone et al. 2021) (Fig. 2). On the other hand, macroremains of this wild plant were recovered, which correspond

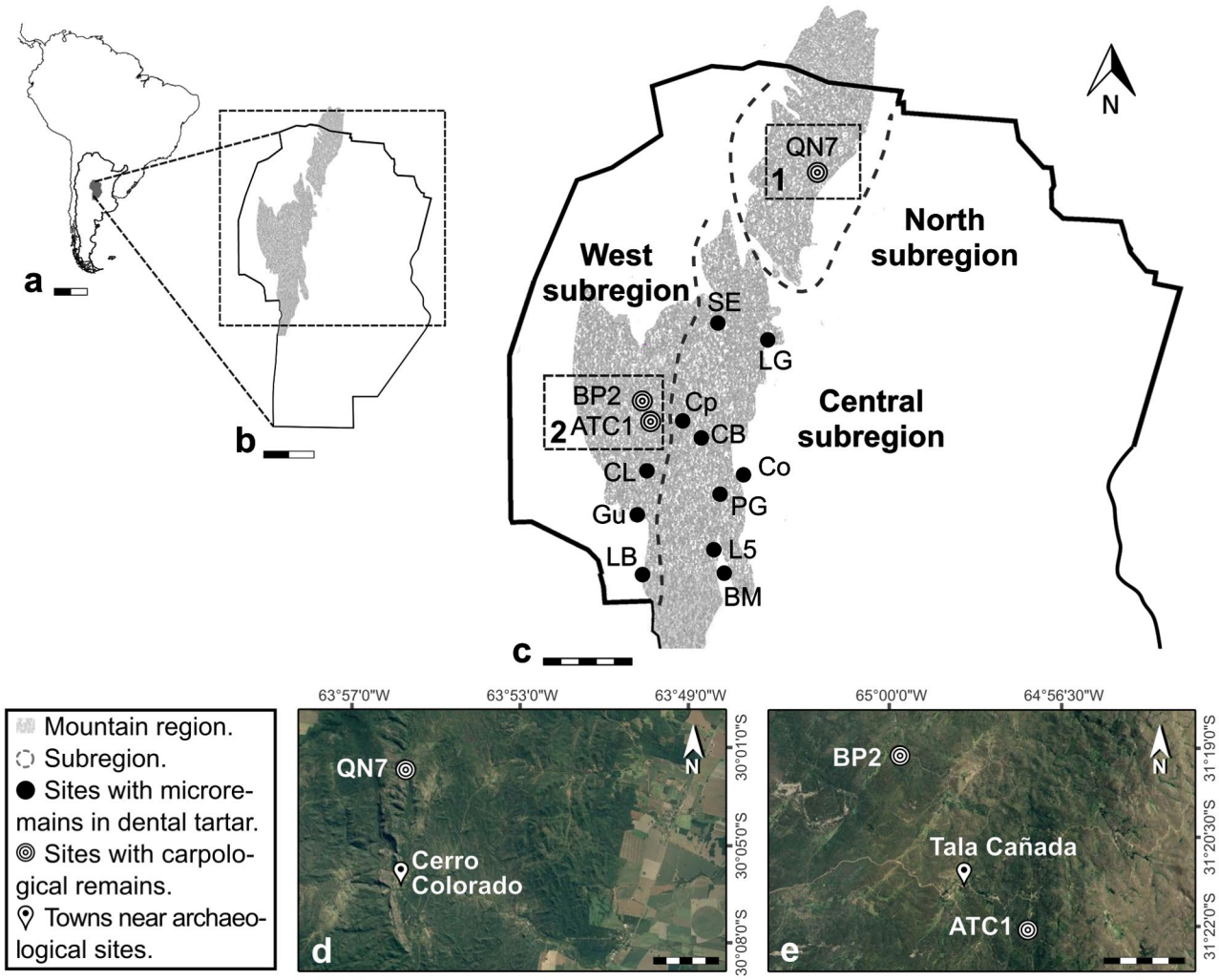

Fig. 2 Location of the archaeological sites of the mountains of central Argentina where remains of *Geoffroea decorticans* were recovered; **a** Córdoba province, Argentina; **b** mountain region (expanded in c); **c** archaeological sites from each subregion (box 1 is expanded in d and box 2 is expanded in **e**); **d** detail of location of QN7 site (north subregion); **e** detail of location of BP2 and ATC1 sites (west subregion). *ATC1*, Arroyo Tala Cañada 1; *BM*, Banda Meridional; *BP2*, Boyo Paso 2; *Co*, Constantinopla 1215; *Cp*, Copina; *CL*, Cañada Larga; *CB*, Cuesta Blanca; *Gu*, Guasmara; *L5*, Loteo 5; *LB*, Loma Bola; *LG*, La Granja; *PG*, Potrero de Garay; *QN7*, Quebrada Norte 7; *SE*, San Esteban. Scale bars **a** – 1,000 km; **b** – 100 km; **c** – 50 km; **d-e**, 2.5 km (**d-e**, satellite photos by Google Earth)

to charred endocarp fragments found in three open-air sites occupied during the LPP: Quebrada Norte 7 (north subregion), Arroyo Tala Cañada 1, and Boyo Paso 2 (located in the west) (López 2018). The presence of these carpological remains suggests a similarity in the role that this species may have played in the subsistence of human groups from the north and west subregions.

It is known that, since ancient times, *G. decorticans* has been used as food by various peoples of South America (Capparelli et al. 2005; Ugalde et al. 2021). Furthermore, macroscopic evidence of *G. decorticans* has been recovered not only from the central region of the mountains of Argentina, but also from numerous sites in the country, corresponding to different chronologies, where carpological remains of this taxon have been found, both dry and charred (e.g. Carrizo et al. 2003; Capparelli et al. 2005; McRostie 2013; Calo 2014; García et al. 2014; Petrucci and Spano 2019; Longo 2021). However, in the absence of interpretive models based on current processing practices, there are no details about the modes of use of these fruits in the past.

The recovery of vestiges of this edible plant in archaeological contexts makes it necessary to generate models that allow us to explain the past modes of processing and consumption used by pre-Hispanic communities, as well as to know the changes and continuities in culinary practices related to the use of these drupes. Thus, in previous work we recorded the activities, from pre-collection to consumption (*sensu* Capparelli and Lema 2010), carried out by the current

communities of the north subzone, and we conducted the first study of the anatomical transformations undergone by these fruits after the culinary practices performed by current inhabitants of the sector (Saur Palmieri et al. 2019). These investigations are part of a major ethnobotanical-archaeological project, in which different analyses are integrated. This work aims to characterize the fruit of *G. decorticans* micro-morphologically and histologically, and to describe the carpological remains of this species recovered from archaeological sites located in Córdoba and occupied during the LPP. We expect to contribute to the generation of interpretative bases for the analysis of past culinary practices involving this fruit.

Materials and methods

Study area

The present work was conducted in the mountains of Córdoba province, in central Argentina. These mountains are formed by three main ranges than run from north to south between 29°00'S and 33°12'S and extend between 64°18'W and 65°29'W (Fig. 2). The highest peak reaches 2,790 m a.s.l. Because of the location of archaeological sites where macroremains identified as *G. decorticans* were recovered, this study focused on the mountain woodland belt that extends from 500 to 1,300 m a.s.l. The vegetation in this zone belongs to the Chaco Serrano district, dominated by a xerophytic to subxerophytic woodland intermingled with shrublands and grasslands (Giorgis et al. 2017). Several edible plant species, including *G. decorticans*, are distributed in this region (Saur Palmieri et al. 2022).

We delimited three analytic subregions in the mountain region according to those demarcated by Recalde and López (2017) based on probable differences in modes of subsistence of the past communities. Thus, the north subregion includes the Sierras del Norte range, while the centre subregion comprises the territory between the eastern slope of the Sierras Grandes and the western slope of the Sierras Chicas. The west subregion covers the eastern slope of the Sierras Grandes range (Fig. 2).

Histological characterization of unprocessed fruits of *G. decorticans*

To study the morphoanatomy of the drupe of *G. decorticans*, ripe fruits were collected from different subregions of Córdoba province and fixed in FAA (formaldehyde, acetic acid, alcohol). Due to the uneven hardness of the different parts of the fruit, they were separated for characterization: (1) fruit wall (epicarp and mesocarp), (2) endocarp and (3) seed. Endocarps were previously softened by soaking in 30% hydrochloric acid for 72 h (D'Ambrogio de Argüeso 1986). For histological examination of the material, longitudinal and transverse sections were made using classical techniques (D'Ambrogio de Argüeso 1986; Zarlavsky 2014). Temporary slides were prepared by free hand sectioning, stained with basic fuchsin and astra blue, and mounted in 50% glycerin jelly. To obtain permanent slides, the material was dehydrated in a series of ethyl alcohol and xylene, embedded in paraffin, and then sectioned with a rotary microtome (Zarlavsky 2014). Slides were stained with basic fuchsin and astra blue and mounted with Canada balsam. In addition, the epidermis was separated from the fruit wall using the peeling technique. This technique consists of inserting a histological needle under the epidermis and gently pulling it with fine-tipped forceps to remove it, observe it under the microscope and then characterize it (Zarlavsky 2014). Images were taken using a Primo Star-Carl Zeiss light microscope and a Nikon Coolpix 5200 digital camera.

Archaeological sites of Córdoba with macroremains of *G. decorticans*

To date, carpological remains of *G. decorticans* have been recovered from three archaeological open-air sites: Quebrada Norte 7 (QN7), Boyo Paso 2 (BP2) and Arroyo Tala Cañada 1 (ATC1) (Fig. 2). The former is located in the north subregion and the latter two are located in the west sector.

QN7 is located 5 km north of Cerro Colorado village (Sierra del Norte, Río Seco department) at 600 m a.s.l. It has been interpreted as an open-air settlement associated with potentially agricultural land and grinding areas located near rock shelters with rock-art in the hills surrounding the site. Radiocarbon dates situate the site chronologically at 1,250 ± 80 BP (LP-3212, charcoal) and 405 ± 21 BP (AA107245, maize grain) (Recalde and López 2017). In the 15 m^2 excavated and 6,000 l of sieved sediment, a high density of archaeological materials was found: lithic artifacts, ceramic fragments, and faunal and botanical remains. Among the latter, 441 charred macroremains were recovered, corresponding to local wild resources and domesticated species. Therefore, this is the site where the largest number of carpological remains has been found in Córdoba. Likewise, species not found so far in other sites in the region have been previously recovered in QN7. Such is the case of the remains of wild plants like *Lithraea molleoides* (Vell.) Engl., *Condalia* sp. and *Schinus* cf. *areira* L., crops like *Chenopodium quinoa* Willd. cf. var. *quinoa*, as well as its associated weed *C. quinoa* Willd. var. *melanospermum* Hunz. Likewise, a carpological remain of *G. decorticans* was recovered (Recalde and López 2017; López 2018), which was analysed in this work.

BP2 is located in Salsacate valley, near Tala Cañada village (Pocho department) at 1,160 m a.s.l. This site has been interpreted as a successively occupied campsite for medium- to long-term periods. The presence of 23 superimposed post molds, not arranged in a clear pattern, indicates the overlapping of temporary residential structures, built of perishable materials and with low investment in effort. Pollen indicators suggest continuous human occupation and the three consolidated floors found were dated to 750 ± 70 BP (LP-2932, charcoal), 1,060 ± 50 BP (LP-3122, charcoal) and 1,500 ± 80 BP (LP-3107, charcoal). In addition, a high amount of archaeological material was recovered in the 9,500 l of sieved sediment, including projectile points, bone and lithic artifacts, anthropomorphic figurines and animal and botanical remains (Medina 2015; Medina et al. 2016, 2017). The analysis of botanical evidence showed the presence of crops (*Zea mays* L. and *Phaseolus vulgaris* L.) and wild plants. Among the latter are *Neltuma* sp. (= *Prosopis* sp.), *Sarcomphalus mistol* and the carpological specimen identified as *G. decorticans* (López 2018), which was analysed in the present study.

Finally, ATC1 is located near BP2 (at 1,325 m a.s.l.). In this site, the domestic area was adjacent to farming plots. Within the domestic area, a consolidated floor, dated to 900 ± 70 BP (LP-1511, charcoal), was found; it presents several post-molds. Parallel furrows were detected transversal to the slope of the land, as if the plot had been ploughed with hoes. This feature was dated to 1,028 ± 40 BP (AA64820, bean) (Pastor 2007–2008). Phytoliths of *Z. mays* and *P. vulgaris* leaves were recovered from the sediment obtained from the furrows, indicating on-site cultivation of these crops (Pastor and López 2010). Macroremains identified as *Phaseolus lunatus* L. and *P. vulgaris* were found in about 8,000 l of sieved sediment. Furthermore, a fragment of *G. decorticans* endocarp, which was examined in this work, was also recovered (López 2018).

Description of *G. decorticans* carpological remains

The micro-anatomical results obtained in the first part of this work were used to describe the three macroremains recovered to date from Córdoba sites (QN7, ATC1 and BP2). These specimens were systematically sampled by fine sieving with 2–1 mm mesh and previously identified as *G. decorticans* by López (2018). Photographs were taken with an Olympus SZX16 stereomicroscope coupled to an Olympus DP71 digital camera.

Results

Fruit anatomy

Transverse sections of the epicarp showed a remarkably thick cuticle covering a single-layered epidermis (Fig. 3a-b). Epidermal cells are rectangular and flattened in transverse section (Fig. 3b), but polygonal on surface view (Fig. 3c). Isolated stomata were also observed in the epidermis (Fig. 3a, d). Below the epidermis, there is a multilayered (10–12 cell layers thick) hypodermis of collenchyma. Hypodermal cells are periclinally elongated and have thickened, non-lignified walls and dense content (Fig. 3a-b). The mesocarp is composed of several layers of large, thin-walled parenchyma cells (Fig. 3a). In the innermost area of this tissue, fibre bundles (4–5 cells thick) (Fig. 3e) and numerous sclereids, occurring singly or in small groups, were observed (Fig. 3f).

The endocarp is divided into three parts: external, middle and internal. The external endocarp corresponds to the area that contacts the mesocarp and is composed of rectangular sclereids that are arranged perpendicularly to the endocarp surface (Fig. 3g-i). The middle endocarp is very compact and hard. Its outer part is composed of short and rounded sclereids that are wide in cross section, with thickened cell walls and small lumen. These sclereids are regularly arranged, parallel to the surface of the endocarp and perpendicular to the external endocarp cells (Fig. 3h-i). Towards the interior of the pit, the arrangement of the middle-endocarp sclereids becomes disorganized and the sclereids intermingle with bundles of fibres arranged in non-uniform directions. Besides, their contours become reduced and irregular as the cell wall becomes thinner and the lumen widens (Fig. 3j). The internal endocarp is composed of 5–7 layers of ordered fibres, arranged perpendicularly to the major axis of the endocarp (Fig. 3g-k). Elongated, very thin-walled parenchyma cells are observed internally covering the endocarp; these cells have wide intercellular spaces, which give this part of the tissue the lax, light and delicate appearance that is observed macroscopically (Fig. 3k).

The seed presents an exotesta that covers the cotyledons (Fig. 3l). This outer stratum is composed of a layer of thick-walled cells arranged in a palisade; below them, there is a layer of hourglass cells, with a star-shaped cross section and wide intercellular spaces (Fig. 3m-n). The mesotesta consists of thin-walled parenchyma cells that are loosely and periclinally arranged. This medial portion of the testa changes in thickness (from 4 to 5 to 7–8 cell layers), marking the visible grooves on the seed surface (Fig. 3o). The single-layered endotesta presents elongated parenchyma cells. The embryo is straight and the cotyledons exhibit an isolateral structure with small vascular bundles.

Description of carpological remains

The macroremains recovered from the archaeological sites of Córdoba correspond to three charred endocarp fragments that differ in their macroscopic characteristics and in the degree of fragmentation.

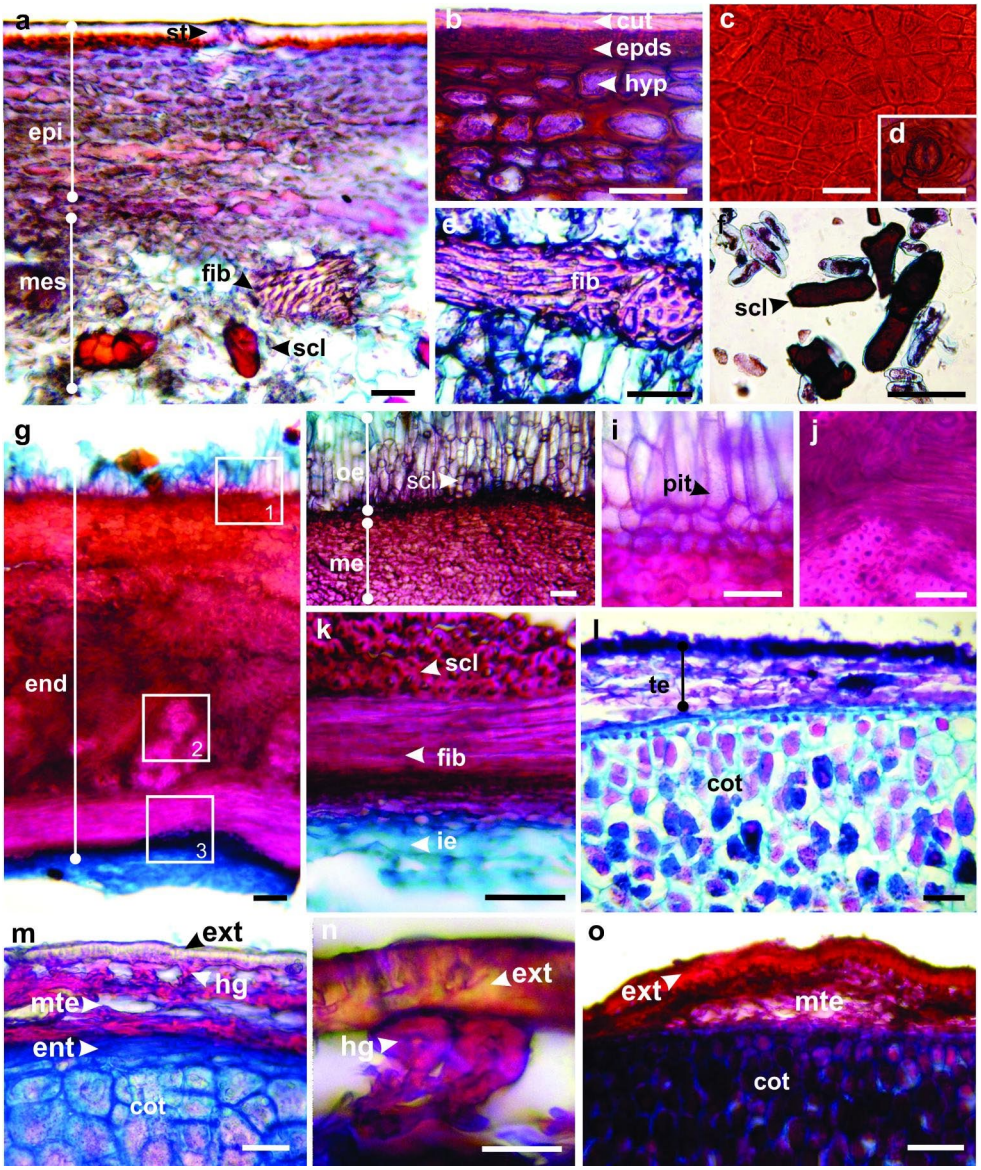

Fig. 3 Histology of *Geoffroea decorticans* fruit; **a** transverse section of the fruit wall; **b** detail of epicarp; **c** surface view of epidermal cells; **d** stoma; **e** mesocarp fibers; **f** mesocarp sclereids; **g** transverse section of the endocarp (box 1 is expanded in h, 2 in j and 3 in k); **h** (detail of box g1) outer and middle endocarp; **i** outer endocarp sclereids. **j** (detail of box g2) middle endocarp; **k** (detail of box g3) fibres of middle endocarp, and inner endocarp; **l** transverse section of the seed; **m** detail of testa; **n** hourglass cells in transverse section; **o** testa at an undulated site of the seed. *co*, cotyledon; *cut*, cuticle; *end*, endocarp; *ent*, endotesta; *epds*, epidermis; *epi*, epicarp; *ext*, exotesta; *fib*, fibres; *hg*, hourglass cells; *hyp*, hypodermis; i.e., internal endocarp; *me*, middle endocarp; *mes*, mesocarp; *mte*, mesotesta; oe, outer endocarp; *pit*, pits; *scl*, sclereids; *st*, stomata; *te*, seminal testa. Scale bars **a-m**, o = 50 µm; n = 25 µm (the photos were taken by the VSP and NED)

Specimen from QN7

This macroremain is 0.46 × 0.44 × 0.12 cm in length, width and thickness, respectively, and is partially charred. On its inner side, the typical transversal grooves of the endocarp of this species are evident (Fig. 4a). The internal layer of the endocarp has a vitreous shine. This parenchyma tissue does not cover the entire internal surface of the fragment. On the contrary, it is fragmented and alternates with sectors that lack brightness, corresponding to the middle layer (Fig. 4b). The external face of the fragment is smooth and no traces of mesocarp or fused material are detected on its surface. No rectangular sclereids arranged perpendicularly to the surface were observed, indicating that the outer endocarpic layer is absent (see Fig. 3h). For this reason, it is concluded that the external portion of the carpological remain corresponds to the middle part of the stone (Fig. 4c). In addition, the edges of the specimen are irregular, with a solid appearance due to the arrangement of the sclereids of the middle layer of the endocarp (Fig. 4d).

Specimen from BP2

This macroremain is 1.42 × 1.03 × 0.57 cm in length, width and depth, respectively, and is partially charred. It corresponds to half of an endocarp, separated longitudinally from the other half by the suture line. It is not fragmented. On the inside, the characteristic transverse grooves of the species are observed (Fig. 4e). Covering these striations is a matte, thin and consistent layer that we identified as the seminal testa, which is detached from any other component of the seed (Fig. 4e-f). The external side of the specimen is mostly

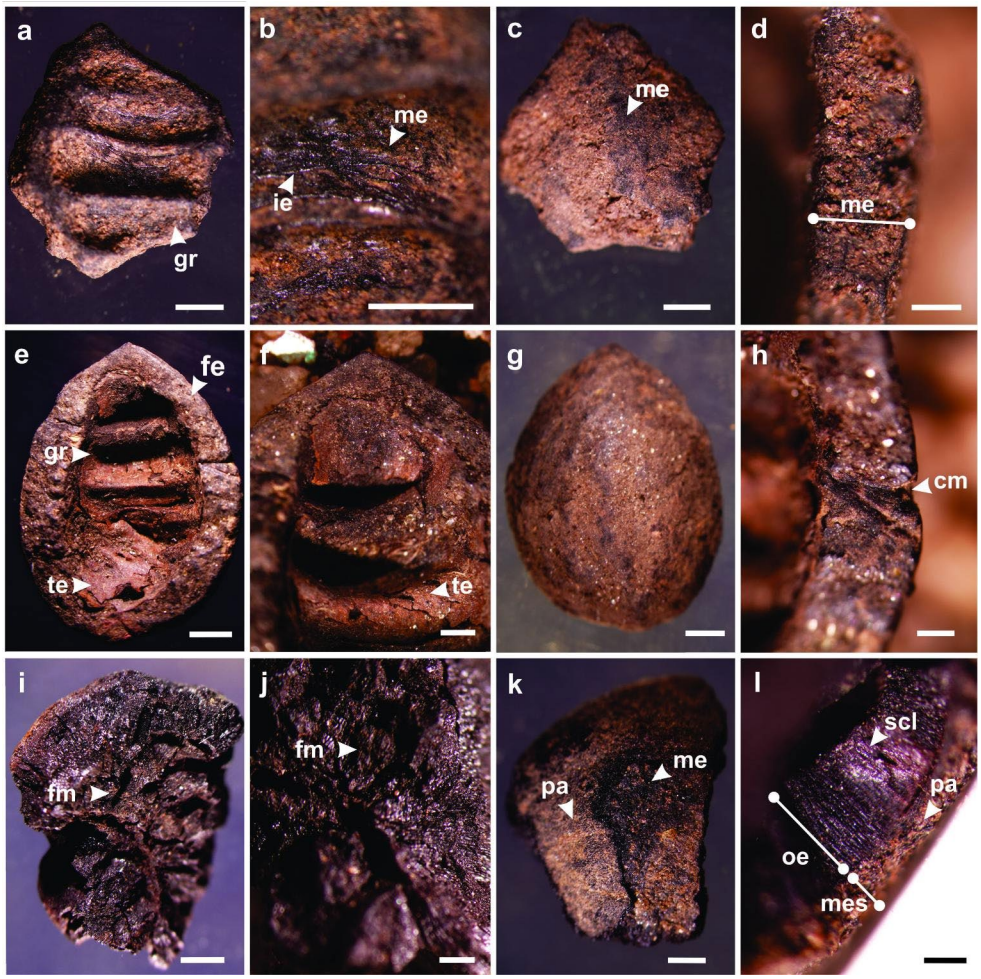

Fig. 4 Carpological remains of *Geoffroea decorticans* recovered from the archaeological sites of the mountains of central Argentina a-d QN7 specimen. **a** inner side of the endocarp fragment; **b** detail of inner side; **c** outer side corresponding to the middle layer of the endocarp; **d** detail of edge. **e-h** BP2 specimen. **e** inner side; **f** detail of the inner side; **g** outer side corresponding to the outer layer of the endocarp; **h** detail of the flat edge with a straight notch. **i-l** ATC1 specimen. **i** inner side of the endocarp fragment; **j** detail of inner side; **k** outer side with mesocarp patina covering the endocarp outer layer; **l** detail of the edge. *cm*, "cut marks"; *gr*, groove; *fe*, flat edge; i.e., inner endocarp; *mes*, mesocarp; *mm*, fused material; *me*, middle endocarp; *oe*, outer endocarp; p.a., patina; *scl*, sclereids; *te*, testa. Scale bars a, c, f, h-i, k-l = 1 mm; b, d, j = 0.5 mm; e, g = 2 mm

smooth, with very slight roughness typical of that part of the endocarp (Fig. 4g). The edge of the specimen, which corresponds to the carpellar suture line, is mostly regular and flat. It also presents a "V"-shaped notch, with two facets, whose edges are straight and defined; the notch is oriented perpendicular to the longitudinal axis of the endocarp (Fig. 4h).

Specimen from ATC1

The carpological remains from this site correspond to an endocarp that split into two fragments while it was manipulated for analysis. The fragments are totally charred and are $0.75 \times 0.5 \times 0.37$ and $0.7 \times 0.6 \times 0.32$ cm in length, width and depth, respectively. The inner side of both fragments is irregular and exhibits abundant, fused, voluminous material with a vitreous lustre (Fig. 4i-j). Although it is not possible to individualize cell layers in this structure, due to their relative location they would correspond to the seed and, possibly, to the innermost layers of the endocarp. The outer side is smooth and corresponds to a thick mesocarp patina. In some sectors of the surface, this tissue is detached, making the outer layer of the endocarp visible. That layer has a rough appearance (Fig. 4k). Both the patina and the sclereids of the outer endocarp are observed at the edge of the fragments (Fig. 4l).

Discussion

Implications of the morphoanatomical approach

G. decorticans stands out for its fleshy and indehiscent fruit, which has a hard endocarp and a single seed, unlike the legume of most species of the Fabaceae family to which it belongs (Kirkbride et al. 2003). Although some authors refer to this carpological structure as a "nutlet" (Kirkbride et al. 2003) or as a "drupaceous fruit" (Ireland and Pennington 1999; WFO 2023), the specific bibliography of the genus classifies it as a "drupe" (Burkart 1949; De Lima 1989). Here, we follow the latter classification.

The histological results of the present work allow us to establish certain similarities between the drupe of *G. decorticans* and those of other Fabaceae with the same type of fruit. For example, species of the *Andira* genus also present

subepidermal collenchyma and solitary sclereids in the mesocarp. Both taxa present a hard endocarp on the outside and, on the inside, a spongy parenchyma layer (as a "seed cushion") that dries out and becomes "papery" at maturity (Pennington and Gemeinholzer 2000).

Moreover, the deep knowledge of the morphoanatomy of the carpological structures of *G. decorticans* contributes to the understanding of current culinary practices carried out in the mountains of Córdoba, which have been documented in previous works. For example, local residents indicated the need to soften the wall of the fruit through boiling, a technique that would ensure the extraction and utilization of the sugars present in the pulp (Saur Palmieri et al. 2019). The present description of the thick collenchymatous hypodermis, which makes the fruit wall rigid, supports the prolonged boiling recorded ethnographically. In addition, the double sclerenchymatous layer of the endocarp described in this study explains its great hardness, which is a characteristic that was recorded in ethnobotanical interviews. This trait also explains why this lignified structure does not break down after the different activities involved in the production of *arrope* and in direct consumption (Saur Palmieri et al. 2019). Besides, it has been postulated that washing the fruits before the initial boiling would produce the detachment of the epidermal trichomes (Saur Palmieri et al. 2019) described by Flores and Vignale (2010). However, these structures were absent at the mature stage of the (unprocessed) fruits analysed in the present study. On the contrary, preliminary observations made of immature fruits suggest that there would be trichomes on the fruit surface, which would disappear with the complete ripening of the epicarp, without mediating culinary activities.

The integration of the descriptive data of the fruits of *G. decorticans* and of the samples obtained during the production of syrup presented previously (see Saur Palmieri et al. 2019), contributes to the interpretation of the cellular structures of the charred carpological remains as well as to the inference of possible past practices. The following section details these interpretative advances.

What do the *G. decorticans* carpological remains from the central mountains of Argentina reveal?

A first observation of the three archaeological specimens of *G. decorticans* recovered in Córdoba to date reveals that, although there is great heterogeneity in their general appearance, they all correspond to endocarp fragments. That is, the epicarp and mesocarp of the fruits were removed in the past, in different amounts, and only the stone persisted. However, and although some practices ethnographically surveyed for this species in the region generated endocarps devoid - to varying degrees - of the superficial tissues of the fruit (e.g. manual crushing for the production of *arrope* and direct consumption), in no case were broken pits evident (Saur Palmieri et al. 2019). In this sense, given this dissimilarity between the traits described in processed fruits and dried residues produced by current activities and those traits found in carpological remains, it is necessary to investigate other processes involved in the formation of archaeological macroremains. In addition, the different characteristics exhibited by the archaeological specimens suggest the action of diverse factors in their formation. Each of the carpological remains is discussed below based on the analysis carried out in this work and on previous information.

The QN7 specimen is reduced to a small fragment (its length represents approximately 25% of an entire endocarp); in addition, its endocarpic layers are separated. Since the results of the analysis based on current culinary activities did not show these types of feature in the reference material (Saur Palmieri et al. 2019), we hypothesized the intervention of taphonomic and/or post-depositional processes in the formation of this macroremain, which would have acted on an entire stone. A possible explanation is that this drupe may have been consumed as a snack (unprocessed). Then, the incidental dumping of the residue from this practice on the hearth would have contributed to charring of the endocarp. After the weakening of the rigid structure of the endocarp, post-depositional processes (e.g. trampling) may have been involved. However, due to the aforementioned dissociation of cell layers, the outer side of the fragment is composed of the middle cell layer. Thus, it is impossible to study the surface of the outer layer of the endocarp and to assess the arrangement of the mesocarp. Therefore, the fact that this endocarp was almost completely devoid of pulp on its surface, as it is observed in current specimens from the residue of direct consumption, cannot be confirmed (see Saur Palmieri et al. 2019).

Another possible explanation to the formation of the QN7 specimen is that a culinary activity may have been performed during the LPP, which has not been considered until now in the interpretive model because it is not currently carried out in the localities near the archaeological site (Saur Palmieri et al. 2019). Such is the case of the crushing of whole fruits in the mortar, which probably contributes to the breaking of the pits. This activity has been recently documented in another sector of the mountains of Córdoba (Saur Palmieri et al. 2022) and has been also recorded in the manufacture of fermented beverages in the north of Argentina (Arenas 2003; Suárez 2014). In this case, the endocarp would have fragmented due to this post-harvest processing before its contact with domestic fire and its subsequent deposition.

Based on the two hypotheses raised about the formation of the QN7 carpological remain, the question arises as to

whether the endocarp breakage was generated during an incidental human activity (i.e. prior to its carbonization) or if it was the product of postdepositional/taphonomic processes (i.e. after carbonization). To answer this question, ongoing studies involve the incorporation of new post-harvest practices in the interpretive model (does crushing in a mortar really cause the stones to break?). Likewise, experimental approaches have been carried out in which the carpological material is exposed to heat sources to try to replicate as closely as possible the appearance of the charred archaeological specimen (Saur Palmieri 2017; Saur Palmieri et al. 2017). However, conclusive results are still not available. At the same time, it is necessary to evaluate the behaviour of the stones and their fragments under these conditions, as has been done for other drupes (i.e. hazelnut, López-Dóriga 2015).

The specimen recovered from BP2 presents four key features to begin the interpretation of the possible practices and/or processes that were involved in its formation. First, the absence of the external soft tissues of the fruit on the endocarpic surface suggests the direct consumption of this drupe in the past, since this specimen looks like the residue produced when the fruit is consumed directly (reference material) (Saur Palmieri et al. 2019). Second, the opening of the endocarp along the carpellar suture line, generating two symmetrical halves with flat edges (one of them being the carpological remain analysed), is compatible with the natural process of seed germination, as indicated by preliminary observations carried out by one of the authors of this work. Likewise, the adherence of the seed coat to the internal surface of the stone has also been observed after the emergence of *G. decorticans* seedlings (Sofía Machado personal communication). Third, the typology of the notch observed on the flat edge is similar to those described as "cut marks" on faunal remains (e.g. Lyman 1994; Morales 2015; Barkai et al. 2017). For this reason, the anthropogenic origin of this trait is proposed. It may have been generated by using a sharp instrument to cause the opening of the lignified structure and extract the edible seed. Although it is known that current human groups use the seed, which is obtained by breaking the endocarp with a stick (Arenas 2003), there are no ethnographic data that reflect the use of instruments with sharp tips for this purpose. Anyway, in the sites inhabited during the LPP, artifacts have been recovered, such as bone awls, which could have caused the described type of notch (Medina et al. 2014).

Consequently, different practices and processes could have been involved in the formation of the carpological specimen of the BP2 site. Although certain traits are compatible with non-anthropogenic processes (e.g. opening along the suture line, adherence of the seminal testa), other facts are strong indicators of human action, such as the recovery of the endocarp in a context of human occupation during the LPP (arrival of the specimen at the site), its carbonization (which refers to contact with a past hearth), the absence of surface tissues of the pericarp (which indicates the consumption of the fruit without processing), and the cut mark probably involved in the procurement of the seed for ingestion. However, future studies involving the experimental opening of stones in multiple ways will further evaluate and clarify these possibilities.

The ATC1 specimen differs from QN7 and BP2 remains in the presence of the continuous patina of mesocarp on its surface, among other factors. This feature has not been observed in the current dry reference material (Saur Palmieri et al. 2019). Nevertheless, what happens after exposure to a heat source in the surface tissues covering the pits that remain after manual crushing and direct consumption is still unknown. Likewise, besides the ongoing carbonization experiments under controlled conditions (Saur Palmieri 2017; Saur Palmieri et al. 2017), further studies are necessary to know the circumstances that produce the fusion of the internal structures of the endocarp and the seed (as observed in the carpological remain of ATC1), and thus clarify the history of this archaeological specimen from the LPP to the present.

In summary, although there is direct evidence of the consumption of *G. decorticans* in the mountains of central Argentina during the LPP (Tavarone et al. 2021), the practices applied to these fruits are still uncertain. Although reference material was generated to unravel these pre-Hispanic activities (Saur Palmieri et al. 2019), both the small amount of macroscopic remains of this species and the ambiguity of its morphological features have made its interpretation difficult. Future studies that incorporate other culinary activities (i.e. crushing in a mortar) into the interpretive model that has already begun to be built based on taphonomic factors (i.e. carbonization, Saur Palmieri 2017; Saur Palmieri et al. 2017), will allow us to make progress in this regard. Specifically, forthcoming studies will make it possible to replicate in the reference material those features found in the macroremains and will develop a better approach to past practices.

In addition, the significant differences in the characteristics of the three carpological remains suggest a possible diversity of practices in the past, although those activities have not been specified yet. Such divergence in the past activities applied to *G. decorticans* would have occurred both locally and regionally, since both specimens from the west sites (BP2 and ATC1, which are very close geographically), are very different from each other, as well as from the specimen recovered in the North (QN7). Therefore, and despite the small number of macroremains of this plant found to date, such dissimilarity of the specimens supports the hypothesis of subregional divergences in the modes of

use of the natural commons during the LPP proposed by Recalde and López (2017).

In the central sector of the mountains, the absence of charred macroremains of *G. decorticans* stands out (Recalde and López 2017), despite the recovery of phytoliths in dental tartar related to this taxon. Definitely, the microremains indicate the consumption of this plant by the people who lived in this subregion during the LPP. However, this evidence does not allow us to specify the frequency of consumption (Pearsall 2016) and it has not been possible to elucidate any associated culinary practices (Tavarone 2019). However, the fact that carpological remains of *G. decorticans* were not recovered, even when an adequate archaeobotanical methodology has been applied and macroremains of other species have been found (see López 2018; López et al. 2020), could indicate the modes of use of these fruits in that sector. Specifically, and considering that carbonization is the taphonomic factor that has allowed the conservation of macroremains in the mountains of central Argentina (López 2018), in this subzone, processing and consumption practices possibly did not allow the proximity and/or contact of the drupes of *G. decorticans* with fire. This would have hindered its carbonization and, therefore, its preservation to the present, which translates into the absence of this taxon in the macrobotanical record. That is, were these drupes consumed predominantly uncooked (e.g. as a snack) and outside the residential site (i.e. away from the domestic hearth)? This possibility also suggests differences in the culinary activities involving this taxon between the north and west subregions, where the charred specimens analysed in this work were recovered, and the central sector of the mountains. What is this probable differential mode of use of the fruits between subregions indicating in relation to the flexible subsistence system proposed by Medina et al. (2016) for the entire mountainous region of Córdoba? The continuation of the systematic archaeobotanical works will probably allow us to find a greater amount of macroscopic material to perform a deeper analysis of the practices carried out with this species at different geographical scales.

Conclusions

This work, focused on *G. decorticans*, is within the framework of the studies conducted to characterize the interrelationship between human communities and wild food plants in Córdoba over time. Thus, progress has been made in the knowledge of the morphoanatomical, ethnobotanical and archaeobotanical aspects of this species, in an integrated way.

First, the complete study of the histology of the *G. decorticans* fruit is of great taxonomic importance. The Fabaceae family is characterized by the production of legumes (Kirkbride et al. 2003; Judd et al. 2007). For this reason, and since the genus *Geoffroea* is a representative that diverges in this feature due to the presence of a drupe (Burkart 1949; De Lima 1989), the results of this work enrich the knowledge of the carpological structures of taxa that share a phylogenetic origin.

Second, this microanatomical research of the fresh and unprocessed fruits, carried out to answer archaeological questions, has established an analytical basis for the study of the traits acquired by these drupes after different human practices. Hence, it has allowed us to understand the histological foundation of the processing techniques documented in previous ethnobotanical works (through participant observation and in-depth interviews), related to the production of *arrope* in the north of the mountains of central Argentina (Saur Palmieri et al. 2019).

Third, the in-depth knowledge of the fruit of *G. decorticans* contributed to the description and interpretation of macroscopic archaeological material of this species recovered from three sites in the mountainous sector of Córdoba. The observation of traits that diverged from those recorded in the unprocessed reference material, was a key factor in the analysis of the possible past practices applied to the drupes. Consequently, both the dissociation of endocarpic layers in the QN7 specimen and the internal adherence of the seed testa in the BP2 macroremain would have gone unnoticed without detailed knowledge of the stone microanatomy. These features triggered questions and hypotheses about the processes and activities involved in the origin of the carpological remains. Additionally, we hope that this work contributes to the interpretation of the past uses of this wild species that is present in the archaeological record not only from the central mountains but also from other regions of Argentina and other South American countries (e.g. Carrizo et al. 2003; Capparelli et al. 2005; McRostie 2013; Calo 2014; García et al. 2014; Petrucci and Spano 2019; Longo 2021).

Despite the evidence that indicates the consumption of *G. decorticans* in the mountains of Córdoba during the LPP (i.e. microremains recovered from dental tartar, carbonized macroremains), how pre-Hispanic communities used the fruits of this species is still uncertain. However, it is known that studies on consumption of wild species contribute to the knowledge of the dimensions of social life that are often little explored (Antolín Tutusaus and Berihuete Azorín 2017). In the mountains of central Argentina, the predominant role of gathering in the flexible subsistence system in that period (Medina et al. 2016, 2020) reinforces the importance of studying wild edible plants. Despite the low number of carpological remains of this species found in the region to date, certain differences in the evidence analysed have been

revealed in this work (i.e. divergences in the characteristics of the specimens from different sites and subzones). Those differences have made it possible to reinforce and reformulate the hypothesis previously proposed about the different patterns of occupation of the sites between subregions of the mountain area (Recalde and López 2017; López 2018).

According to Berihuete-Azorín (2016), it is particularly difficult to interpret the presence of wild species in the archaeological record, especially due to the different routes of entry of these taxa to the sites. In addition to the problems to verify its anthropogenic origin, it is not always easy to define whether a plant structure was incorporated as a product, by-product, or residue. However, the interdisciplinary ethnobotany-archaeology-morphoanatomy approaches are valuable in this sense, due to the contributions they make, sometimes as hypotheses, and other times as new questions (Capparelli 2008, 2011; Capparelli and Lema 2011; López et al. 2011). In particular, in-depth knowledge of the morphoanatomy of the carpological structures of the taxa that are part of the archaeological record of a site is crucial for two reasons: to accurately identify the taxa (generic, specific and even sub-specific levels) (Hillman et al. 1993; Lema 2011), and to analyse the transformations the carpological material undergoes through anthropogenic practices (Capparelli 2008; López-Dóriga 2015).

Finally, several factors highlight the importance of these studies: the study taxa have historically been neglected by archaeobotanical research (as has happened with wild plants, see Antolín Tutusaus and Berihuete Azorín 2017); the use of these plants was predominant in the past study period (as occurs with wild taxa, specifically *G. decorticans*, in Córdoba during the LPP; López 2018; Medina et al. 2016, 2020); and most importantly, these plants are being revalued and claimed by current local communities as part of their strategies to defend their territories (Saur Palmieri and Galasse Tulián 2021).

Acknowledgements We thank Alejandra Trenchi who helped us to capture images with the stereomicroscope; Sofía Machado provided information about germination; and Andrea Recalde, Matias Medina and Sebastian Pastor allowed us to incorporate to our study the archaeobotanical material recovered from the sites under their direction. Jorgelina Brasca edited the English style. This research was funded by Secretaría de Ciencia y Tecnología-Universidad Nacional de Córdoba (Res. 233/20) and Consejo Nacional de Investigaciones Científicas y Técnicas (doctoral scholarship).

Author contributions All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by VSP, NED and MLL. The first draft of the manuscript was written by VSP and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This study was funded by Secretaría de Ciencia y Tecnología-Universidad Nacional de Córdoba (Res. 233/20) and Consejo Nacional de Investigaciones Científicas y Técnicas (doctoral scholarship).

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