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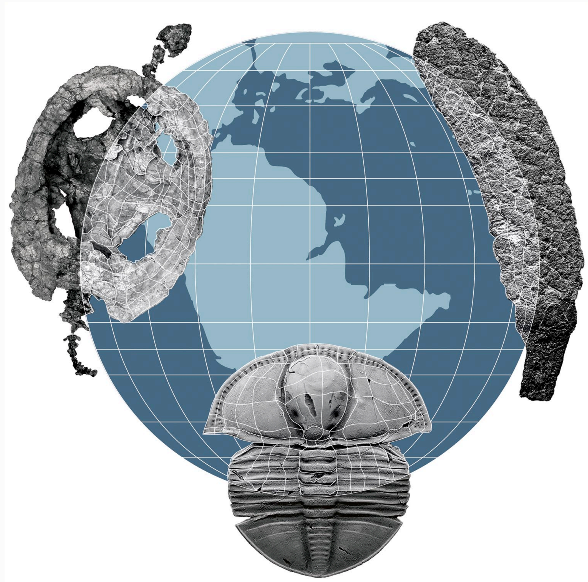

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HEPATICITES (MARCHANTIOPHYTA) IN THE LOWER PERMIAN ARROYO TOTORAL FORMATION (LA RIOJA PROVINCE, ARGENTINA)

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Introduction

Extant bryophytes include near 15000 species divided into three major groups: hornworts, liverworts and mosses (Crandall-Stotler *et al*., 2009). Although the fossil record of this group starts in the Ordovician, the macrofossil remains are scarce and include some examples that are often considered ambiguous (Schuster, 1984), especially in the Paleozoic. In contrast to this, after the Jurassic and especially into the Cenozoic the abundance of bryophyte remains increases and the fossilization in amber or as permineralizations allows more detailed studies of these groups (Frahm, 2003; Taylor and Taylor, 2012; Tomescu, 2016). The difference between the extant and the extinct record is noticeable, now is under discussion if this difference is caused by their preservation potential or the lack of specialists in the group (Tomescu, 2016 and references therein).

In South America, the record of bryophytes starts in the Paleozoic; macrofossil remains are known and only three species were formally recognized, from the Lower Carboniferous of Bolivia (Cardoso and Iannuzi, 2004), the Upper Carboniferous of Argentina (Ottone and Archangelsky, 2001), and the Carboniferous and Lower Permian of Brazil (Ricardi-Branco *et al*., 2016). In Argentina, other remains were identified and reported by Frenguelli (1951) and di Paola *et al.* (1996). Given this scarce fossil record in Western Gondwana, any new bryophyte fossil from South America is highly relevant.

Floristic assemblages of the Lower Permian Arroyo Totoral Formation, from the Paganzo Basin, were previously described by Archangelsky and Arrondo (1973), Cúneo (1984), Barreda and Césari (1995), Cúneo and Archangelsky (1996), Coturel and Gutierrez (2014), among other summaries and mentions. This flora is characterized by the presence of glossopterids (*Gangamopteris* McCoy and *Glossopteris* Brongn.), *Botrychiopsis plantiana*

(Carruthers) Archangelsky and Arrondo, conifers (*Ferugliocladus riojanus* Archangelsky and Cúneo), cordaiteans, ferns (*Asterotheca* Presl.) and sphenopsids (Coturel and Gutiérrez, 2014).

Here we report the first liverwort fossils from the Arroyo Totoral Formation and discuss their importance for the fossil record of the group, their paleoecology, and compare them with coeval South American occurrences.

Geological settings

The Arroyo Totoral Formation (Andreis et al., 1984) crops out south of Sierra de los Llanos, in the eastern sector of the Paganzo Basin, southeastern La Rioja Province, where it lies unconformably on the crystalline basement and is overlain by the La Colina Formation (Permian, Limarino and Page, 1999; Gutiérrez et al., 2006). The unit is also recorded in the Cerro Horcobola, where it is overlain by the Patquía Formation (Permian, Alvarez and Fernández-Seveso, 1987). The Arroyo Totoral formation is referred to the Lower Permian *Gangamopteris* Biozone (Archangelsky et al., 1996). The sequence is characterized by the abundance of shales and sandstones accumulated in lacustrine systems associated to floodplains.

The fossil material was collected in the median levels of the Arroyo Totoral Formation near the Anzulón River, in a small outcrop near its type locality, at 30°49'31.32"S - 66°17'22.26"W (Figure 1, Map). The fossiliferous layers consist of greenish-gray shales with parallel lamination, which also contain conifers (*Ferugliocladus*), glossopterids (*Glossopteris* and *Gangamopteris*), cordaiteans, equisetaleans and ferns (Coturel and Gutiérrez, 2014).

MATERIAL AND METHODS

The fossil material is preserved as a compression and consists of thalloid plant remains associated with a gymnosperm branch (Fig. 2.1). Similar branches from the same level are assigned to *Ferugliocladus* (an early conifer). The systematic treatment is based on Frey and Stech (2009). A Nikon SM2800 stereomicroscope attached to a Nikon DS-Fi1-U2 and a Canon Powershot S5IS digital camera were used for analysis and imaging. Small fragments of the fossil were mechanically extracted with the aid of needles and tweezers. Subsequently they were mounted on standard stubs with adhesive tabs for anatomical analysis under scanning electron microscope (Phillips XL30 SEM, at the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Buenos Aires, Argentina). Line drawings were made using Adobe CS3 Photoshop and Illustrator software. The sample is deposited in the Palaeobotany Collection of CCT-CRILAR, La Rioja Province, under the label CRILAR-PB.

SYSTEMATIC PALEOBOTANY

Phylum MARCHANTIOPHYTA Stotler & Crand.-Stotl., 1977

Genus ***Hepaticites*** Walton, 1925

Type species. *Hepaticites langii* Walton, 1925

Hepaticites sp.

Figure 2.1–3

Sample. CRILAR-PB 1124

Description. The specimen consists of the part and counterpart of one thallus preserved as a compression, with basal isotomous dichotomous branching; branching angles range from 10° to 20° (Fig. 2.1). Branches dichotomize again at the middle and/or top of their length. The fragment is 24 to 28 mm long overall, with branches of different lengths. The width of the thallus varies from 1 to 1,7 mm (Table 1), with the width independent of branching order. Margins are entire, and the apical portions lobed with each apex rounded. The costa (midrib) is conspicuous, 0,2–0,3 mm wide; it runs along the entire thallus but without reaching all the way to the apices. Incompletely preserved cellular patterns suggest quadrangular cells in the thallus wings and narrower, elongated cells in the midrib (Fig. 2.3-4).

***Discussion*.** Fossils with simple morphology and few diagnostic characters are associated with problems in identification at high taxonomic levels. One example of this is the case of *Rhodeopteridium* sp. (in Uhl *et al.* 2016) a tracheophyte frond fragment first described as *Hepaticites* by Ricardi-Branco *et al.* (2011). The most impressive evidence of the real nature of the Brazilian material is the presence of tracheids (Uhl *et al*., 2016, fig. 7). We underwent the extraction of the carbonized mid-vein material of a small fragment, but the results were inconclusive.

Lacking the anatomical evidence, we compared our samples with the illustrations of Ricardi-Branco et al. (2011), and we found significant differences in the plants, which are supported by the samples added in Uhl *et al.* (2016). The "thallus" displayed in fig. 2.1 of Ricardi Branco *et al.* (2011) has the same length as our material, but differs because it is possible to see the anisotomous ramification of the frond, with the alternate arrangement of the last order pinnules. Moreover, only the terminal segments of the Brazilian specimens

exhibit isotomous dichotomy, whereas in the liverworts this is the principal type of ramification. These architectural traits of *Rhodeopteridium* fronds are more obvious in the specimens illustrated by Uhl *et al.* (2016: fig. 6). That ramification is different from that of the material described here, where instead of pinnately dissected leaves, we have a few basal isotomous dichotomies and the same type of division is repeated in the terminal portions of the thallus, resulting in a rosette-shaped small plant.

The delicate thallus differentiated into wings and midrib suggests that the fossil is a simple thalloid liverwort. The lack of reproductive structures and of unequivocal cellular detail constrains the taxonomic assignment to *Hepaticites*.

Hepaticites is a genus created to include "fossil bearing evidence of a relationship to the living Hepaticae … if the knowledge of their structure is too incomplete to warrant the use of a distinctive generic term" (Walton, 1925 *in* Oostendorp, 1987). The last International Code of Nomenclature (McNeill *et al.*, 2012) allows the utilization of fossil-taxa to include different parts, life-history stages or preservation states of a single taxon in different names (Art. 12.8) or the same name (Art. 1.2), so given that the studied material is a single, sterile individual, we concur with the practice of including incompletely preserved specimens in *Hepaticites*, until better specimens allow for reassignment to other taxa.

One species of *Hepaticites* is recognized in South America: *H. simpliciformis* from the Lower Carboniferous Siripaca Formation (Bolivia). *H. simpliciformis* was described as a thalloid, prostrate plant with entire and parallel margins, midrib continuous and the most conspicuous character: the presence of thin linear ribs, diagonal in the lamina. Our sample is larger (see Table 1) and lacks the linear ribs in the lamina. The comparison with other

species of this genus is inconclusive, so we prefer to refer to the genus and maintain an open specific assignation.

DISCUSSION and CONCLUSIONS

Paleoecological considerations

Habit. With approximately 5000 extant species currently recognized, liverworts compose a diverse lineage of land plants, represented on every continent and in nearly all ecosystems (Frey and Stech, 2009; Vanderpoorten and Goffinet, 2009). Liverworts are most abundant in relatively moist areas, while some of them can resist desiccation and have been found in deserts. Simple thalloid liverworts in general occur on soil, and leafy liverworts on rock, bark or leaves, but almost as an exception among thalloid liverworts *Metzgeria* Raddi mostly includes epiphytic species (Vanderpoorten and Goffinet, 2009). It is noteworthy that in our sample, the liverwort seems to be surrounding a small conifer branch. However, given the allochthonous nature of the plant assemblage, association on the bedding plane cannot be taken as unequivocal evidence for association between the two plants during life.

Paleoenvironment. After the Carboniferous glaciations, the climate in the Paganzo Basin underwent transition to a semi-arid to arid climate, by the middle Permian (Limarino *et al*., 2013). The Arroyo Totoral Formation was assigned to the postglacial stage, which in the Eastern Paganzo basin was more humid than in the western sector, at least in the paleovalleys that developed in the Sierra de los Llanos sector (Limarino *et al*., 2013).

The presence of thalloid liverworts in the Arroyo Totoral Formation supports the interpretation of local humid conditions in the Sierra de Los Llanos area, complementary to the development of arid to semiarid environments in other localities of the Paganzo Basin.

The arid environmental conditions developed later in this sector, during deposition of the La Colina Formation (Limarino *et al*., 2013).

The record of liverworts

The small size and the fragility inherent to the thin thallus and the lack of lignified tissues makes the bryophytes a difficult group to find in the fossil record, especially when we look far away from the Cenozoic times and from exceptional preservation as permineralization or amber. Or, at least, that is the traditional explanation for the sparse fossil record of this group of plants. Tomescu (2016) points to evidence demonstrating that the preservation potential of bryophytes is better than traditionally thought and suggests that a major problem leading to the relative rarity of bryophyte fossils is the lack of specialists, and after studying this material we agree with this view.

In this respect, South American Paleozoic sequences, historically less studied than European ones, have yielded a very small number of bryophyte fossils, namely five mosses and two liverworts (Ottone and Archangelsky, 2001; Cardoso and Iannuzi, 2004; Christiano de Souza *et al.*, 2012; Ricardi-Branco *et al*., 2016; Bippus *et al.*, 2017); and other undetermined bryophytic macrofossils from Argentina (Frenguelli, 1951; de Paola *et al.,* 1996), which should be revised. The presence of *Hepaticites* in the Arroyo Totoral Formation adds to the diversity of the fossil assemblage in this unit, as well as to the record of Paleozoic bryophyte fossils in South America. This improves our knowledge of the bryophyte fossil record in the Late Paleozoic of South America and suggests that focused searches could provide evidence of a wider distribution of this cryptic group in these ancient times.

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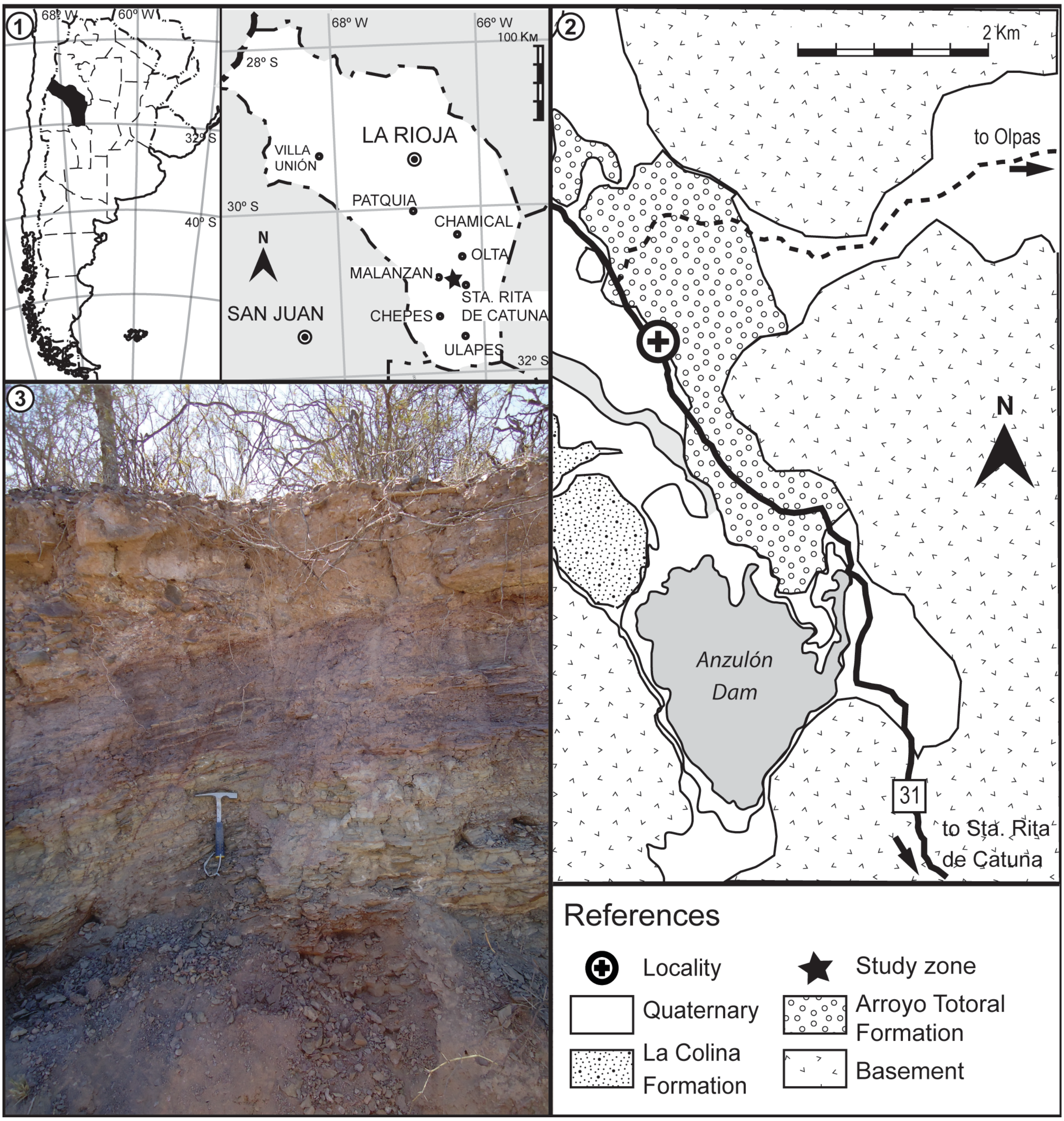
FIGURE CAPTIONS

FIGURE 1. **1.1-2**, Geological map (**1.1**) of the locality, and general La Rioja Province map (**1.2**); **1.3**, view of the outcrop.

FIGURE 2. *Hepaticites sp*. CRILARPB 1124, **2.1** Thallus associated to a gymnosperm branch; **2.2**, line drawing of the bryophyte remains; **2.3-4**, detail of two thalli showing the midrib and the cellular contour. Scale: 10 mm in 2.1, 1 mm in 2.3-4.

Table 1. Comparison of different species of *Hepaticites* with the new sample.



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PATQUIA
CHAMICAL
OLTA
MALANZAN
STA. RITA DE CATUNA
CHEPES
ULAPES
SAN JUAN
N
2
2 Km
to Olpas
N
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31
to Sta. Rita de Catuna
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Study zone
Quaternary
Arroyo Totoral Formation
La Colina Formation
Basement
3

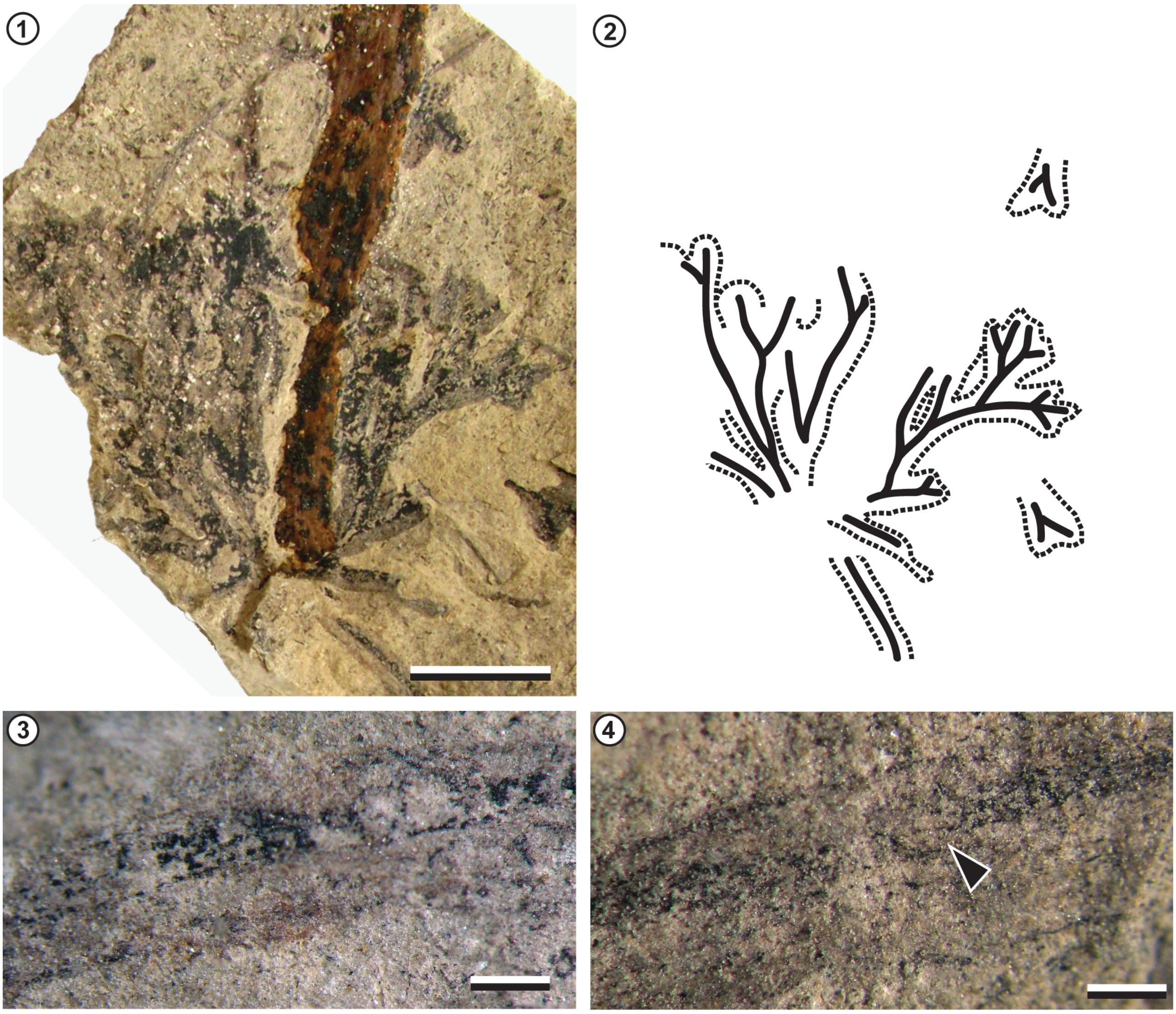
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TABLE 1 – Comparison of different species of **Hepaticites**

Species	*Branching*	*Size (width, in mm)*	*Wings*	*Margin*	*Midrib*	*Rhizoids*
CRILAR PB 1124	*dichotomous*	*1–3*	*quadrangular cells*	*entire*	*conspicuous*	*not found*
Hepaticites simpliciformis	*dichotomous*	*6–8*	*polygonal cells, with ribs*	*entire*	*conspicuous*	*not recorded*
Hepaticites hepaticus	*dichotomous*	*9*	*unistratose*	*entire*	*unistratose, 2 mm thick*	*awl-shaped*
Hepaticites langi	*dichotomous*	*0,6*	*multistratose, cells slightly elongated parallel to the axis*	*entire*	*absent*	*unicellular, smooth-walled*
Hepaticites metzgerioides	*dichotomous*	*10*[(1)]	*unistratose, cells isodiametric*	*entire*	*thick, with elongated cells*	*smooth-walled*
Hepaticites umariensis	*dichotomous*	*2*[(2)]	*?multiestratose*	*entire*	*conspicuous*	*unknown*

From Walton (1925, 1928: fig. 3); Oostendorp (1987); Chandra (1995: pl. 1 fig. 4); Cardoso and Iannuzzi (2004); Ricardi Branco et al. (2011)