Systematic palaeontology (Palaeobotany)

Marchantiopsid colonization mats from the Upper Aptian–Lower Albian of the Escucha Formation (Oliete Sub-Basin, Iberian Ranges, eastern Spain)

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Abstract

In the Oliete Sub-Basin, the Escucha Formation has been divided into three different lithologic intervals, from base to top: E1 (heterolithic with coal), E2 (mainly sandstones), and E3 (claystones). At the upper part of the interval E2, a grey-silty lithosome has been recognized, corresponding to a low-energy sedimentary environment related to a sandy shoal. In this lithosome, marchantiopsid-rich beds extending up to tens of square metres have been preserved. The plant association consists of well-developed mature gametophytes of complex thallose liverworts with thalli radial, dichotomous branched, rosette forming, prostrate and, in most cases, with gemmae cups located on their dorsal surface. The occurrence of scattered individuals forming distinct rosettes that, in many cases, are interlocked or interwoven and the loose arrangement of the association, along with sedimentological characteristics, allows us to interpret these liverworts-rich beds as monospecific colonization mats at early stages of colonization, in which marchantiopsids played the role of pioneers. In addition, the high proportion of gemmiferous individuals provides significant information on the environmental conditions and the effectiveness of colonization by asexual diaspores. Specimens have been assigned to family Marchantiaceae owing to their morphological features. Although liverworts colonization mats have been mentioned from the Albian of Antarctica, no fossil record of these existed at lower palaeolatitudes or in the Upper Aptian–Lower Albian. In addition, no previous record of clonal communities of plants derived from gemmae exists. Due to the latter, the occurrence of the studied colonization mats becomes of prime importance.
To cite this article: C. Diéguez et al., C. R. Palevol 6 (2007).

Résumé

Colonisation par des tapis de marchantiopsides dans l'Aptien–Albien de la formation d'Escucha (sous-bassin d'Oliete, chaîne Ibérique, Espagne orientale). Dans le sous-bassin d'Oliete, la formation d'Escucha a été divisée en trois différents intervalles lithologiques, qui sont de bas en haut : E1 (hétérolytique, à charbon), E2 (essentiellement gréseux) et E3 (roches argileuses). À la

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partie supérieure de l'intervalle E2, un lithosome silteux gris a été reconnu comme correspondant à un environnement sédimentaire de basse énergie, en liaison avec un haut-fond sableux. Dans ce lithosome, des lits riches en marchantiopsides, se développant jusqu'à des dizaines de mètres carrés, ont été préservés. L'association végétale consiste en des gamétophytes matures bien développés, d'hépatiques complexes à thalles, formant des rosettes à branches radiales dichotomiques, couchées et, dans la plupart des cas, avec des réceptacles à gemmules sur leur surface dorsale. La présence d'individus dispersés formant des rosettes distinctes qui, dans de nombreux cas, sont emboîtées ou entrelacées, et l'arrangement lâche de l'association, ainsi que les caractéristiques sédimentologiques autorisent à interpréter ces lits riches en hépatiques comme des tapis de colonisation monospécifiques, dans une étape précoce de colonisation, au cours de laquelle les marchantiopsides jouent le rôle de pionniers. En outre, la proportion élevée d'individus à réceptacles gemmifères fournit une information significative sur les conditions environnementales et l'efficacité de la colonisation par diaspores asexuées. En raison de leurs traits morphologiques, des spécimens ont été rapportés à la famille des Marchantiaceae. Bien que des tapis de colonisation par des hépatiques aient été mentionnés dans l'Albien de l'Antarctique, aucun enregistrement fossile de ceux-ci n'existe à des paléolatitudes plus basses ou à l'Aptien Supérieur–Albien Inférieur. En outre, aucun précédent enregistrement de communautés végétales clonales par gemmules n'existe. En raison de cela, l'exemple des tapis de colonisation étudié ici revêt une importance primordiale. ***Pour citer cet article : C. Diéguez et al., C. R. Palevol 6 (2007).***

1. Introduction

Marchantiophyta are small herbaceous plants that have complicated life cycles with gametophyte generation dominance and occur in colonies with a clonal nature.

This group has been recognized as the most basal monophyletic lineage of embryophytes by means of morphological cladistic analysis [28,29,45], combining rRNA and morphology analyses [23,28], and different molecular studies [8,13,14,19,34–37].

In spite of their presumed long history on Earth, their fossil record is scarce and scattered. The poor representation of liverworts in the fossil record has been mainly attributed to their habit (delicate tissues and simple structures) along with other factors, such as lack of recognition, as well as habitat preferences and sedimentary processes [5]. In relation to the former factor, it has been demonstrated [15] that the preservation potential of liverworts is similar to that of other tracheophytes.

Within Marchantiopsida, the class Marchantiales gathers primarily plants of permanent or seasonally moist open habitats from lowland tropics to temperate and Alpine regions and include gregarious, fast-growing invasive species that form clonal colonization and expansion mats. There exists in literature innumerable brief allusions to liverworts as pioneers, but to date we have not found a detailed or extended study of the matter.

Liverwort-rich beds have been reported from the Triassic of Australia [49] and New Zealand [32], the Albian of southeastern Australia [9] and Antarctica [5]. Some of them [5] were interpreted as colonization mats.

2. Material and methods

The material consists of in situ specimens that expand over an exposed area of approximately $42 \, m^2$ and hand samples preserved as compressions–impressions.

Photography and examination of specimens were made with an Olympus Zeiss stereomicroscope and measures with a Leica MZ 16 A. In addition, the material was examined with a Quanta 200 scanning electron microscope at 25 kV.

Hand samples were photographed with a Canon Eos 300D digital camera under low-angle incident light.

3. Geological setting

The studied area is placed in the Iberian Range (eastern central Spain, Fig. 1).

This study is focused on the Escucha Formation [1] deposited in the extensional Oliete sub-basin during Late Aptian–Albian (Fig. 2A and B). This sub-basin, which measures $1500 \, km^2$, was active from the Early Barremian to the Early–Middle Albian [27,46]. In this area, after the development of carbonate Urgonian platforms during the Aptian, a strong change in sedimentary conditions resulted in high siliciclastic input, and sedimentation took place under continental and coastal conditions.

4. The Escucha Formation

Plant remains have been recorded from an outcrop of the Escucha Formation (Fig. 3) in the southern sector of
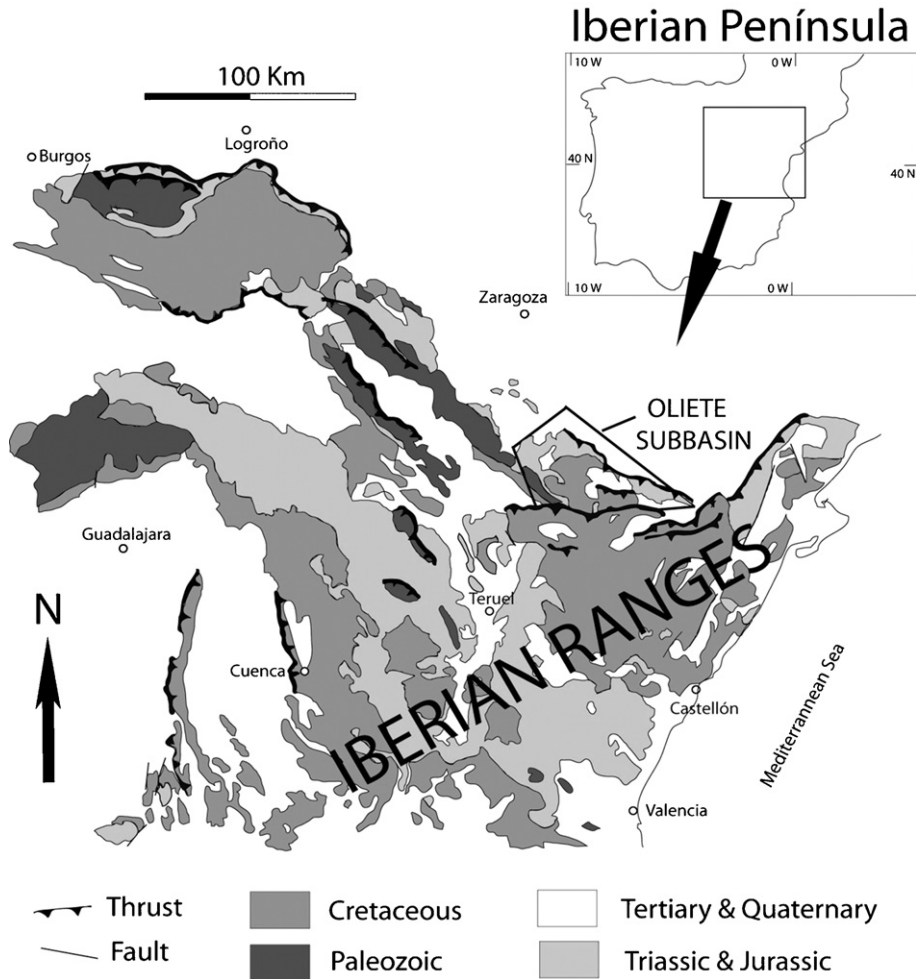
Fig. 1.   Geological map of the Iberian Range showing the location of the Oliete Sub-basin.
Fig. 1.   Carte géologique de la chaîne Ibérique, montrant la localisation du sous-bassin d'Oliete.

the Oliete sub-basin. It is a heterolithic unit dominated by very well sorted fine sand and clay, with coal-bearing deposits in its lower part. Pardo [31] has dated this unit in the Oliete sub-basin as Late Aptian. The Escucha Formation lies upon limestones and marls of the Urgonian Platform (Aptian), and is covered by sandstones of the Utrillas Formation (Fig. 2A) [31,38]. The Escucha Formation has been traditionally ascribed to deltaic-estuarine environments [39]. However, recent studies have demonstrated that transgressive sedimentary environments (e.g., barrier-island systems) developed in the Oliete sub-basin at least during the lower part of the Escucha Formation's deposition [42]. The Escucha Formation has been divided into three different lithologic sub-units, from base to top: E1 (heterolithic with coal), E2 (mainly sandstones), and E3 (claystones) (Fig. 2B). At the upper part of the sub-unit E2, a grey-silty lithosome has been recognized, corresponding to a low-energy sedimentary environment related to a sandy shoal. Plant remains have been recovered from silty and muddy grey sediments deposited in the shoreline of a restricted bay-lagoon [41].

5. Palaeogeography and palaeoclimatology

The Escucha formation was deposited in extensional sub-basins bounded by palaeogeographic highs produced by listric and block-rotation faults [31,38]. Both location of the major faults and depocentre distribution for this unit have been established from isopach maps and stratigraphical correlations, leading to the conclusion that block rotation by listric faults played an important role [39]. Outcrop-scale syn-rift features demonstrate that syn-sedimentary extensional tectonics acted at a
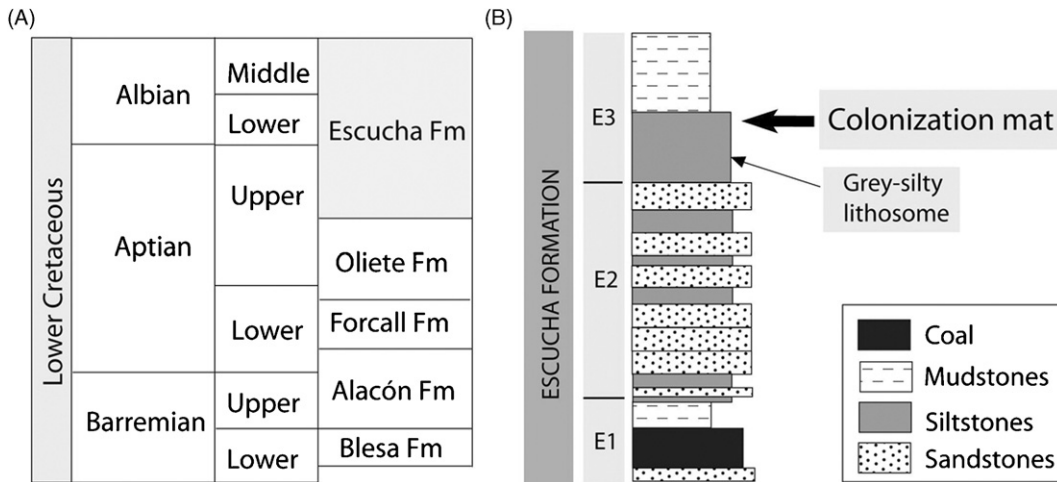
Fig. 2.   (**A**) Chronostratigraphic chart of the Lower Cretaceous at the Oliete sub-basin. (**B**) Local stratigraphic section of the Escucha Formation in the Oliete sub-basin showing the location of the colonization mat.
Fig. 2.   (**A**) Diagramme chronostratigraphique du Crétacé inférieur dans le sous-bassin d'Oliete. (**B**) Coupe stratigraphique locale de la formation Escucha dans le sous-bassin l'Oliete, montrant la localisation du tapis de colonisation.

great variety of scales during the deposition of the Escucha Formation [44].

During the deposition of the Escucha Formation, the studied area was located at a palaeolatitude of 25°N to 30°N [26,48], i.e. at the boundary of the Northern Hot Arid belt (NHA) and of the Northern Mid-latitude Warm humid belt (NMW) [7,47]. The Escucha Formation deposition occurred during a significant climate change in the Iberian Basin [43]. This climate change towards the mid-Cretaceous to more arid and hot conditions is marked by the transition from humid intervals with coal-bearing deposits and coarser siliciclastic deposits at the base of the Escucha Formation to an arid

environment [43]. This palaeoclimate change has been related to a process in which the connection of the North and South Atlantic initiated an equatorial humid climate belt that forced arid belts towards higher latitudes [7,43].

6. Sedimentology

The colonization surface developed during an arid stage in the shoreline of a restricted by-lagoon, in which silty and muddy deposits developed (grey-silty lithosome in Figs. 2B and 3) [41]. Deposits display three different sedimentary facies: Facies A is formed by lenticular stratification. Grey to black mudstones display
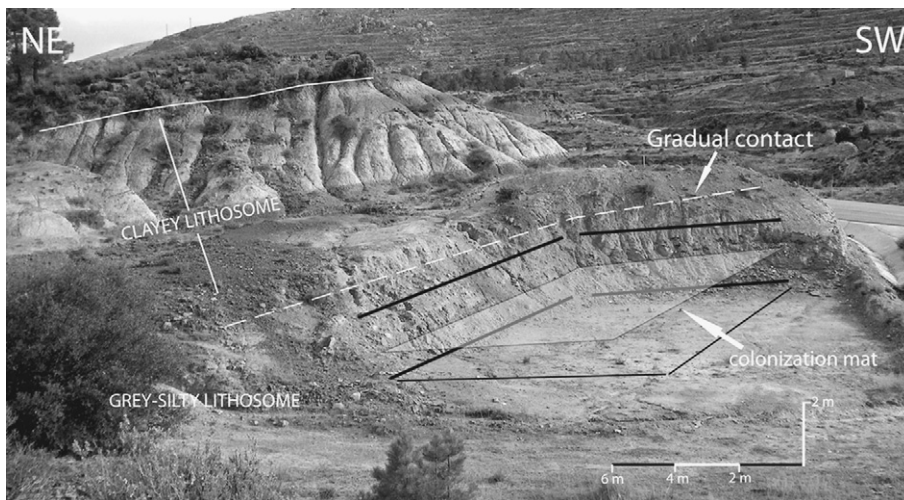

Fig. 3.   Studied outcrop. The colonization mat expands over an area of more than 42 m^2 (minimum exposure).
Fig. 3.   Affleurement étudié : le tapis de colonisation se développe sur une surface de plus de 42 m^2 (exposition minimum).
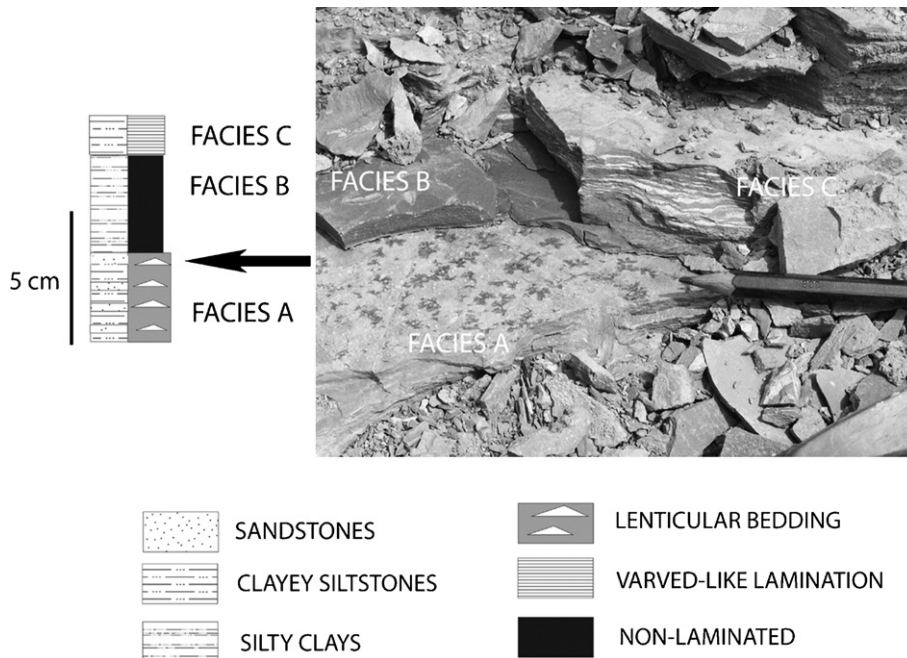
Fig. 4.   Detailed stratigraphic section, showing the main sedimentary facies and the location of the hepatophytic colonization mat. See text for explanation.

Fig. 4.   Coupe stratigraphique détaillée montrant les principaux faciès sédimentaires et le tapis de colonisation hépatophyte. Voir le texte pour plus de détails.

sandy lenses of white fine-grained sandstones. Lenticular stratification can be developed in a great variety of environments, in which fluctuations of energy occur [17,40]. The occurrence of non-rhythmically laminated mud resembling tidal deposits described by [6] and the occurrence of tidal rhythmites as those described by [16] point to a tidal influence during sedimentation that favoured alternating traction (sand) and suspension (mud) deposition.

Facies B is formed by dark-grey to black massive mudstones, from which bioturbation and fossils are completely absent. Massive mudstones were deposited in quiet water under stagnant conditions. The occurrence of undisturbed lamination suggests that bottom conditions were periodically anoxic and/or with an absence of biota [21,30].

Facies C is composed of sand-streaked to laminated mudstones, with laminae maximally a few millimetres thick; sandy laminae become more frequent upwards; animal fossils and bioturbation are completely absent. The sandy streaks and lamination of Facies C probably represent material transported into the muddy area during high-energy events (e.g., storm weather: [30]).

The occurrence of liverworts colonization mat in the upper part of Facies A (Fig. 4) suggests that periods of temporal subaerial exposure took place in a shoreline of a relatively shallow water body. The complete absence of both aquatic faunal remains and bioturbation was probably due to high rates of sedimentation, bottom anoxia and variable salinity.

7. Palaeobotanical description

The liverwort-rich horizon (Fig. 3) is comprised of specimens that have a flattened, typically prostrate dorsal-ventral orientation and spreading rosette-like thalli, which are almost identical to marchantialean gametophytes, except the absence of midrib.

Specimens (Fig. 5) present ecostate, ribbon-shaped thalli, with straight margins up to 4.5 mm in length and 1.5 mm in width, dichotomously branched. Branches are about 2 mm long and 1.5 mm wide and rounded at the tip.

Scattered at irregular distances over the dorsal epidermis of the thalli, rounded outline structures were observed, which correspond to pits of about 0.2 mm (Fig. 6) in outer diameter. These structures have been interpreted as the air pores that open into the characteristic air chambers of the Marchantiales. Each air chamber contains columns of photosynthetic cells and facilitates gas exchange and water relations [12]. The air chambers' walls protect the assimilatory tissue
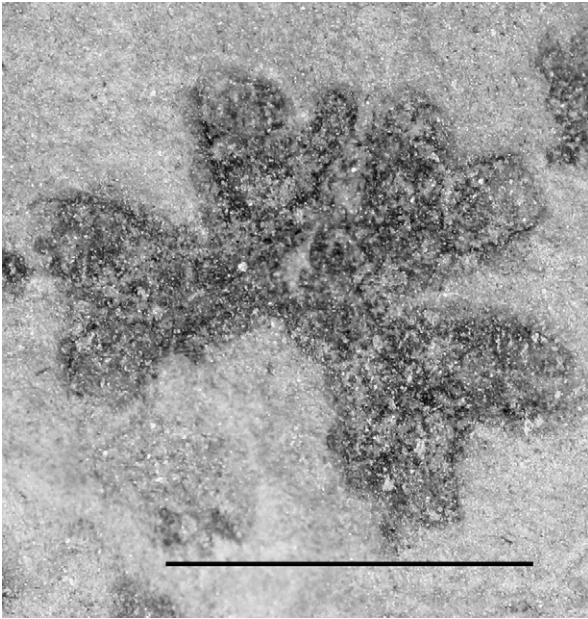
Fig. 5.　Isolated specimen, showing dichotomously branched habit. Scale bar: 5 mm.
Fig. 5.　Spécimen isolé montrant l'habitus en branches dichotomiques. Barre d'échelle : 5 mm.

for undue evaporation. Unlike the stomata of vascular plants, which close in dry weather, the air pores of liverworts have a limited ability to regulate the opening size, since a certain capacity of movement was observed [50].
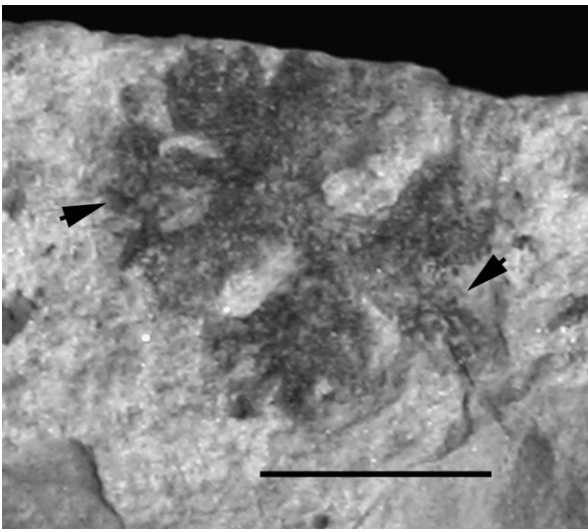

Fig. 6.　Isolated specimen, in which air pores (arrows) and epidermal cellular pattern are evident. Scale bar: 5 mm.
Fig. 6.　Spécimen isolé, dans lequel s'observent des pores contenant de l'air (flèches) et un réseau de cellules épidermiques. Barre d'échelle : 5 mm.
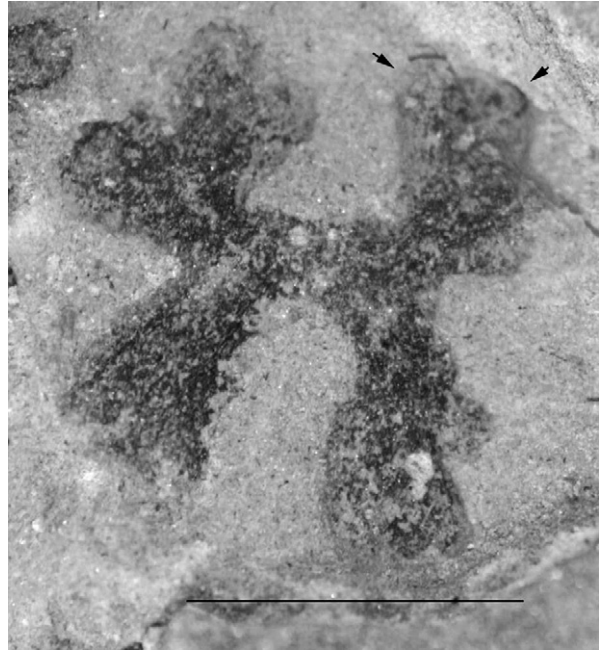

Fig. 7.　Cup-shaped scyphula (arrows) located at the tips of branches. Scale bar: 5 mm.
Fig. 7.　Scyphula en forme de cupule (flèches), au sommet des branches. Barre d'échelle : 5 mm.

The most noteworthy aspect is the presence of distally rounded or cup-shaped structures with fringed margins about 0.7 to 0.9 mm of diameter in the outer part and up to 0.4 mm in its inner part, with entire margins (Fig. 7). These represent scyphulae in which gemmae have developed. These structures are splash cups that are the best-known method for vegetative dispersal, since they can disperse their carried contents up to 60 cm [3].

Gemmae cups of the studied material showed some differences in shape and size. There existed three typologies:

- rounded about 0.9 mm in diameter, with a central pore of 0.5 mm in diameter;
- rounded up to 2.6 mm in outer diameter and 1 mm in inner diameter;
- cup-shaped, about 1.9 mm high and 1.4 mm wide (Fig. 8). After comparison with extant material, these differences have been interpreted as different stages of maturation.

Within living Marchantiopsida, only *Marchantia* and *Lunularia* produce gemmae cups. Morphological differences between gemmae cups of *Marchantia* (bowl-shaped cups) and *Lunularia* (crescent-shaped cups) have
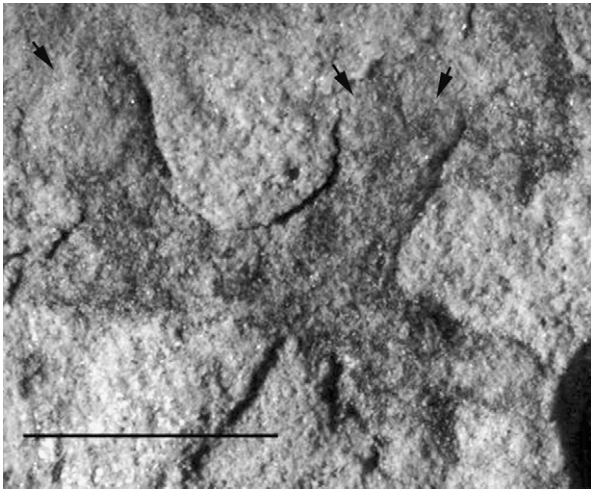
Fig. 8. Gemmae cups (arrows) at different stage of maturation. Scale bar: 5 mm.
Fig. 8. Réceptacles à gemmules (flèches), à différents stades de développement. Barre d'échelle : 5 mm.

led us to conclude that the fossil material is related to the first extant genera.

Included in the sediment amongst the specimens, dispersed lenticular gemmae of 20 μm in diameter occurred (Fig. 9).
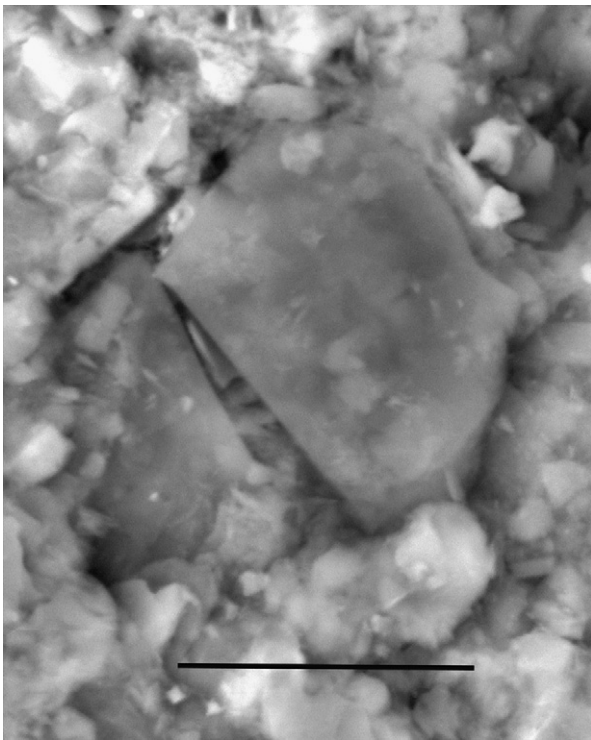

Fig. 9. Dispersed lenticular gemmae. Scale bar: 20 μm.
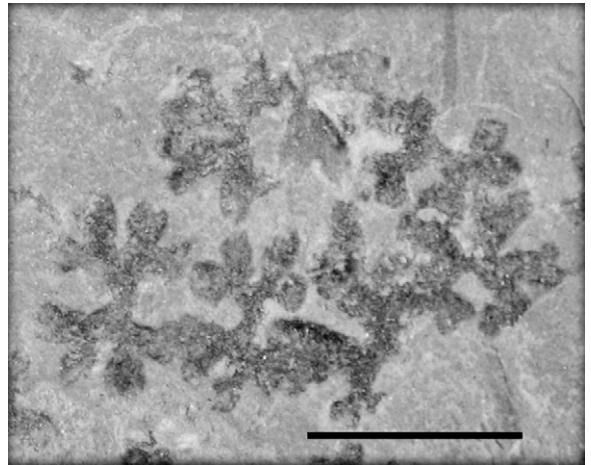Fig. 9. Gemmules lenticulaires dispersés. Barre d'échelle : 20 μm.

Fig. 10. Group of specimens interlocked by their tips. Scale bar: 5 mm.
Fig. 10. Groupe d'individus emboîtés par leurs sommets. Barre d'échelle : 5 mm.

Lenticular gemmae are produced and dispersed by wind or raindrops from gemmae cups to form new individuals, which allow the plant to reproduce asexually in places where sexual reproduction is unsuccessful and to colonize an area very rapidly, because they are generally are produced earlier and faster than spores.

Asexual reproduction in extant liverworts is more common than sexual reproduction. In many taxa, the maintenance of populations depends, almost exclusively, on asexual reproduction, since it is an adaptative strategy in severe conditions [10].

The specimens spread over an area of unusual size and under similar environmental conditions, in which no other plants occurred.

The bryophyte community was formed by solitary plants, plants interlocked by their tips and plants interwoven (Figs. 5, 6, 10, and 11). They were physiologically independent of and genetically identical to their mother plants, since they proceeded from gemmae. They were thus stands, even though individuals are not interconnected [20,22]. The loose arrangement of specimens indicates an early stage of colonization. The majority of the living Marchantiaceae shows a life form consisting of mats according to Magdefrau's [25] classification. In this life form, the growth of plants gives rise to colonies in which their thalli and branches lie mainly in one plane, whether interlocked or parallel and extending horizontally over the substratum [11].

8. Discussion

Palaeogeographical [7,47] and sedimentary data [43] indicate that the studied colonization mats were formed

Fig. 11.   Group of interwoven individuals. Scale bar: 5 mm.
Fig. 11.   Groupe d'individus entrelacés. Barre d'échelle : 5 mm.

under hot and dry environmental conditions. Morphological characteristics of the specimens and type of reproduction, along with the traits of life form, corroborate the fact that mats makers underwent severe conditions. The xerophytic characteristics shown are succulent thallus, presence of air pores and air chambers, and exclusive asexual reproduction that implies a reduction in the amount of water required, concomitant with the partial reduction of sporophytes. In addition, it has been demonstrated [4] that the production of gemmae is an adaptative strategy in severe conditions.

No fossil record of liverwort-rich horizons exists in the palaeogeographic low-latitude zones located in arid climatic belts (Fig. 12). However, liverwort mats were described [5] in sediments from the Late Albian of Alexander Island, Antarctica, a zone included in the Southern High-Latitude Temperate humid belt.

Comparison between the marchantiacean mats here described and those from Alexander Island reveals great differences, as much in the individuals as in the structure of population.

The first difference refers to systematic assignation. Due to their morphological traits, to the presence of air chambers and gemmae cups, the here-studied mat-producers are assignable to family Marchantiaceae

1. Scania, Sweden. Early Jurassic
2. Podolia, Ukrania. Middle Devonian
3. Teruel, Spain. Late Aptian-Albian
4. Zirab, Iran. Late-Triassic-Early Jurassic
5. Kutch, India. Early Cretaceous
6. South Africa. Berriasian-Valanginian
7. Victoria, Australia. Late Albian
8. Tasmania, Australia. Albian
9. Southland, New Zealand. Triassic
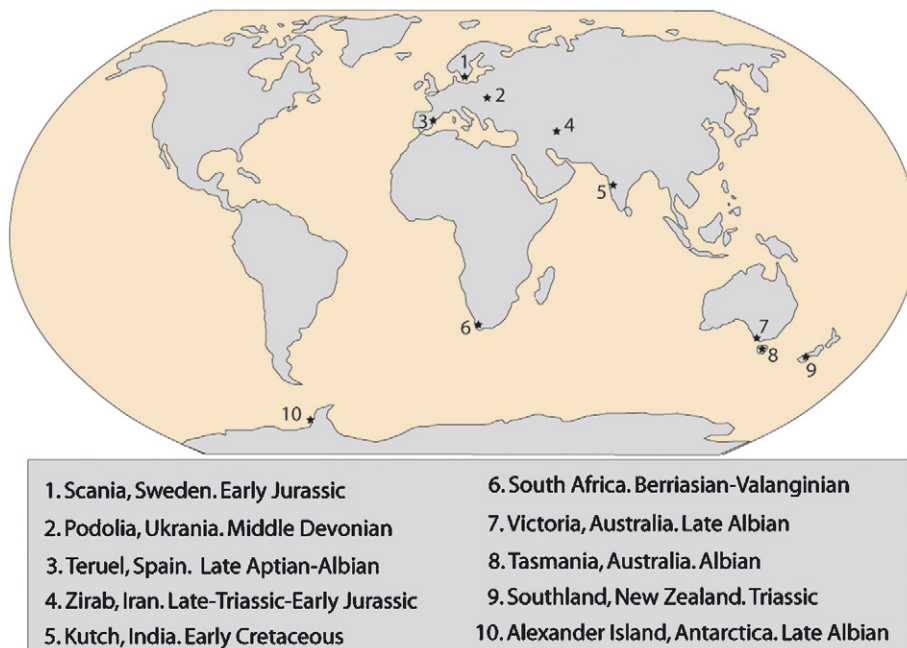10. Alexander Island, Antarctica. Late Albian

Fig. 12.   Palaeogeographic reconstruction and palaeoclimate-belt distribution for the Albian (modified after [7,47]). Stars point out the palaeosetting of some Cretaceous hepatophyte outcrops.
Fig. 12.   Reconstitution paléogéographique et répartition selon une ceinture paléoclimatique pour l'Albien (modifié d'après [7,47]). Les étoiles montrent les lieux d'installation de quelques affleurements crétacés hépatophytes.

without any doubt. In the case of liverwort communities from Alexander Island, the mats were formed by *Thallites bicostatus, Thallites sp.* and *Marchantites rosulatus*. The form genus *Thallites* was proposed [51] for those specimens that showed characters that agree equally with algae and hepatics, namely *incertae sedis*. About *Marchantites*, it is a form genus established for specimens with obscure characters included in Marchantiales. In relation to the population, this is not described, but the author interpreted these liverwort-rich horizons as colonization mats because of the occurrence of individual plants that rarely overlap, showing clearly their outline and little evidence of competition. This arrangement of specimens cannot be considered as a mat, in accordance with the Magdefrau's classification of life forms.

The authors also summarize diverse liverwort-rich beds from the Middle Devonian of Podolia [18], from the Triassic of Australia [49] and New Zealand [33], from the Rhaetian–Liassic of Skromberga (province of Scania) [24], from the Berrisian–Valangian of South Africa [2], and from the Albian of southeastern Australia [9]. After comparison, the liverwort-rich horizon from South Africa seems to be close to marchanticean mats from the Escucha Formation, except as regards the palaeoclimate.

9. Conclusions

The morphological characteristics of the majority of the specimens, such as their growth form and life form, large number, area occupied, and the evident stage of asexual reproduction, combined with the occurrence of gemmae and the absence of other plant remains, allow us to recognize this liverwort-rich horizon as an in situ clonal colonization mat, formed by the growth of marchantiacean plants.

The arid palaeoclimates pointed out by means of available sedimentological data are in accordance with the results of the study of palaeobotanical data.

The marchantiacean community studied represents a xerotermophylous community, well adapted to dry and hot conditions, in which the loose arrangement of individuals indicates an early stage of colonization.

Acknowledgements

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