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Palaeont. afr., **19**, 21—30 (1976)

A REVIEW OF THE BRYOPHYTA FROM THE UPPER TRIASSIC MOLTENO FORMATION, KARROO BASIN, SOUTH AFRICA

by

Heidi M. Anderson

ABSTRACT

The Bryophyta from the Upper Triassic, Molteno Formation, Karroo Basin, South Africa are reviewed. Two species of liverworts, *Marchantites cyathodoides* (Townrow) comb. nov., *M. tennantii* sp. nov. (with possible fertile structures), and one species of moss, *Muscites guescelini* Townrow (with impressions of antheridia) are described. A single specimen is referred to *Thallites* sp. A. A total of 49 specimens are available, 11 from Townrow's collection and 38 from the present collection. These are derived from a total of six separate localities.

INTRODUCTION

The occurrence of bryophytes in the Molteno Formation follows the pattern of sparse representation established for other floras. Since the detailed account of one moss and one liverwort species by Townrow (1959) the Molteno material rates amongst the better known fossil bryophyte records. The present review has been necessitated by the recent additions resulting from an extended collecting programme.

The fossil record of pre-Tertiary Bryophyta is very limited (Lundblad, 1954; Jovet-Ast, 1967; Lacey, 1969). The earliest known bryophyte material is recorded from the Upper Devonian (Grambast and Lacey, 1967). By Upper Carboniferous times the Hepaticopsida (liverworts) and Bryopsida (mosses) are known as two well differentiated groups.

It is important to remember that the classification of living genera and species depends largely on microscopic details of the gametophyte and sporophyte. These details are mostly absent in fossil material, which makes the classification of fossil bryophytes unsatisfactory and they are thus largely placed in form genera.

On rare occasions well preserved material has allowed careful study and comparison with modern bryophytes. Such examples are *Naiadita* (Hepaticopsida) described by Harris (1939) from the Rhaetic of England, *Ricciopsis* (Hepaticopsida) described by Lundblad (1954) from the Rhaeto-Liassic of Sweden, and various moss genera belonging to the Sphagnales and Bryales described by Neuberg (1960) from the Permian of Russia. The Molteno forms described by Townrow (1959) also fall into this category.

BRYOPHYTA OCCURRENCE

The occurrence of Bryophyta in the Triassic of Gondwanaland is briefly considered. Besides the four species (total of 49 specimens) reviewed in this paper from the Molteno, there are only two further records known to the author:

Marchantites cyathodoides — Townrow, 1959, p. 3;
Brookvale plant bed, Hawkesbury Sandstone, Sydney Basin, Australia; Middle Triassic (1 specimen).

Thallites sp. — Jain and Delevoryas, 1967, p. 565;
Minas de Petroleo, Cacheuta Basin, Argentine; Upper Triassic (2 specimens on one slab).

This apparent paucity of bryophytes from the Triassic of Gondwanaland (excluding the Molteno) is most likely a reflection of the need for more intensive collecting.

MATERIAL

The only Molteno bryophyte material described to date derives from the Upper Umkomaas locality (Townrow, 1959). In the present paper additional material (38 specimens) is recorded and described from Upper Umkomaas and a further five localities (Table 1). This constitutes the sum of the available specimens resulting from an extensive collecting programme from 42 localities (Anderson, 1974). The bryophytes were mainly obtained from localities where comprehensive collecting has been undertaken, i.e. Little Switzerland, Upper Umkomaas and Dordrecht II (more than a thousand specimens overall have been catalogued from each). The majority of Bryophyta derive from Dordrecht II (21 specimens). This is due both to the abundance of the material that has been quarried and to the clarity of the impressions which render the small specimens more recognisable. The bryophyte specimens from the present collection are housed at the Bernard Price Institute for Palaeontological Research, Witwatersrand University.

Table 1

Molteno Bryophyta

Note: Townrow (1959) collection is indicated by the figures in brackets

	Hepaticopsida		*Bryopsida*	*?Bryophyta*
Locality	*Marchantites cyathodoides*	*Marchantites tennantii*	*Muscites guescelini*	*Thallites sp. A*
Little Switzerland	2		4	
Upper Umkomaas	3 (4)		3 (7)	
Sani Pass			1	
Dordrecht II		2	21	
Molteno I				1
Vineyard I			1	

EXPLANATIONS TO ILLUSTRATIONS

The photography of certain specimens was difficult as they consist of black compressions set in a black matrix. Generally the best results for these were obtained by photography under Xylol. Equipment used included a 35 mm camera with macrolens and bellow attachment, a Zeiss stereo microscope with camera adaptor, and an Aristophan camera. All the specimens are firstly illustrated natural size and backed up by various magnifications indicated on the photographs (i.e. 1 ×, 5 ×, etc.). The specimens are catalogued both according to a collecting number (indicated by locality code and number) and a publication number (indicated by BPI (Pal) PB 104–124, 152–156). These are indicated on the photographs by a pair of numbers: the upper being the collecting number and the lower the publication number.

The line drawing (Figure 1) represents a composite reconstruction based on the part and counterpart of the holotype of *Marchantites tennantii*. The drawing was made by direct trace from photographs and the details checked under binocular microscope.

CLASSIFICATION

Where possible the classification used in the most recent comprehensive review of the fossil Bryophyta (Jovet-Ast, 1967) has been followed. Certain anomalies were, however, encountered.

The form genus *Hepaticites* was placed in the order Jungermanniales under "Genres Incertae Sedis" by Jovet-Ast (1967). Following this, *H. cyathodoides* Townrow would fall in the Jungermanniales. This is contrary to Townrow (1959) and Lacey (1969). Townrow suggested a strong affinity to the Marchantiales and Lacey regarded it as the earliest acceptable record of this order. Walton (1925) furthermore suggested that only those fossil liverworts which bore undoubted affinities to the Marchantiaceae should be included in genus *Marchantites*. As some of the Molteno forms show such affinities they are classified in the genus *Marchantites* rather than in the more general form genus *Hepaticites*.

The genus *Thallites* Walton 1925 was placed in the family Marchantiaceae by Jovet-Ast (1967) which is incorrect when Walton's (1925) original diagnosis is considered: "Fossils in which the plant body is of a thalloid form, as may be found in the Algae, Bryophyta, or sometimes in higher groups; but possessing no characters by which they may be assigned to any one of these groups to the exclusion of all the others". According to this definition it is doubtful whether *Thallites* may even be included in the Bryophyta.

The genus *Muscites* Brongniart 1929 was placed under "Bryophyta Incertae Sedis" by Jovet-Ast (1967). As this genus is a form genus for fossil mosses it is here suggested that it should rather be placed under the class Bryopsida as Incertae Sedis.

The Molteno species are classified below. As the fossil species are incompletely known, it has been thought advisable not to place them in families.

Phylum: Bryophyta Schimper 1879.
Class: Hepaticopsida Rothmaler 1951.
Order: Marchantiales Engler 1892.
Genus: *Marchantites* (Brongniart, 1849) Walton 1925.
Species: *M. cyathodoides* (Townrow, 1959) comb. nov. *M. tennantii* sp. nov.
Class: Bryopsida Rothmaler 1951.
Order: Incertae sedis.
Genus: *Muscites* Brongniart 1829.
Species: *M. guescelini* Townrow 1959.
Phylum: (possibly allied to the Bryophyta)
Genus: *Thallites* Walton 1925.
Thallites sp. A.

Marchantites cyathodoides (Townrow) comb. nov.
Plate I, Figures 1–10.

Type material: Holotype — Townrow, 1959, Plate IA, number 13929, housed in the South African Museum, Cape Town. Locality: Upper Umkomaas, Natal. Molteno Formation.

Molteno material:

(a) Locality: Little Switzerland.
Slabs: PB 104 (N-L.Sw. 1046) PB 106 (N-L.Sw. 383).
preservation: compressions.

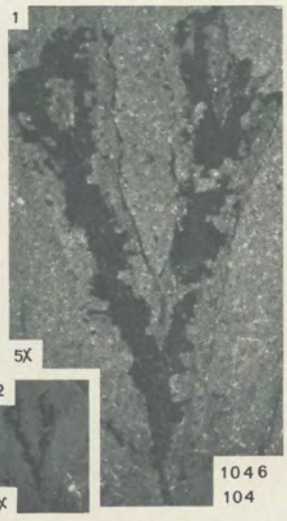
(b) Locality: Upper Umkomaas.
Slabs: Townrow (1959) collection now consisting of microscope slides, 13927–13930 (South African Museum, Cape Town). PB 107 (N-U.U. 1158) PB 108 (N-U.U. 1018), PB 109 (N-U.U. 1157).
Preservation: compressions.

Diagnosis: Townrow, 1959, page 2.

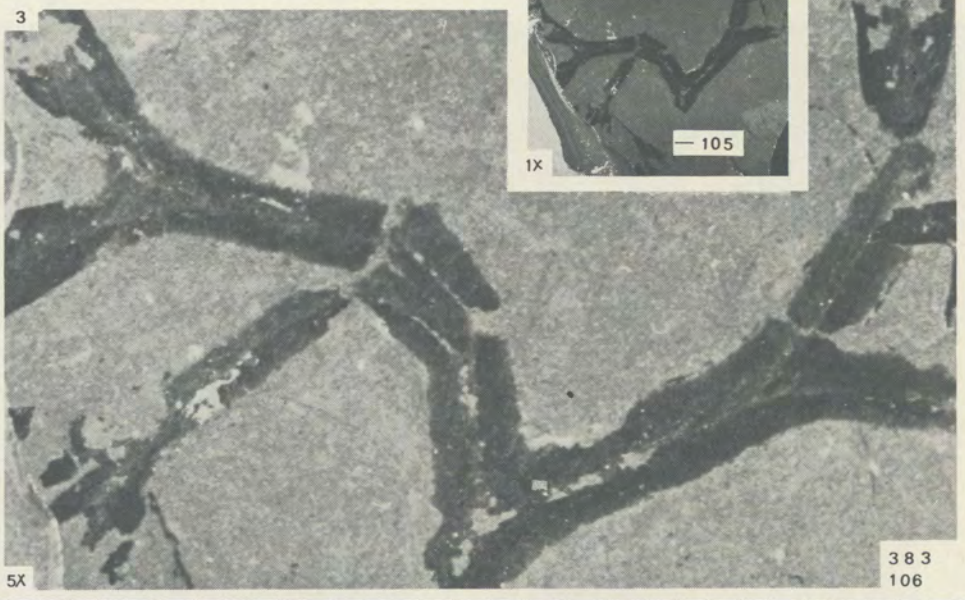
Discussion: Townrow (1959) preferred to place the species in the non-commital genus *Hepaticites* and to indicate its similarity with the extant liverwort *Cyathodium* in his choice of the specific name *cyathodoides*. It is here felt that this species can safely be placed in the genus *Marchantites* (Brongniart) Walton. The prostrate forked thallus, a conspicuous midrib, rhizoides, possible air chambers and central scales all indicate an affinity with the Marchantiaceae.

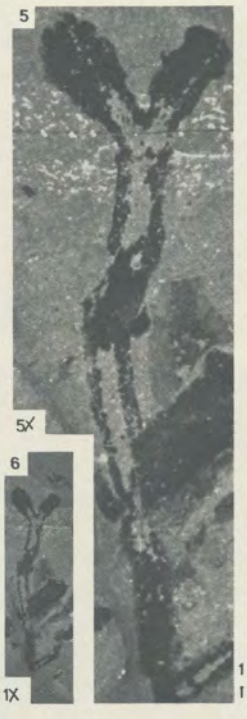
PLATE I

MARCHANTITES CYATHODOIDES

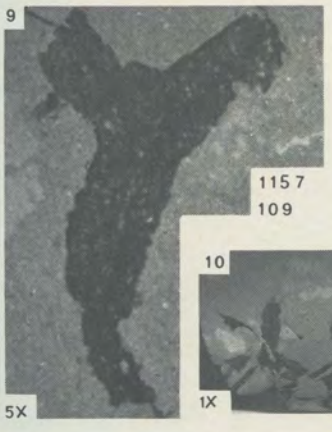


Little Switzerland N—L.Sw.









Upper Umkomaas N—U.U.

THALLITES SP A

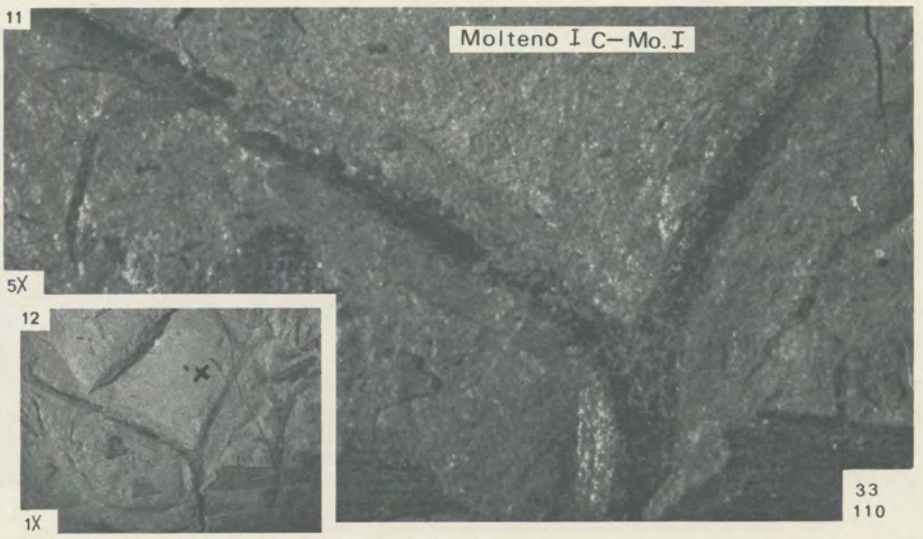




Figure 1. *Marchantites tennantii*, a composite reconstruction based on the part and counterpart of the holotype (PB 111).

In view of Townrow's (1959) detailed microscopic study none of the new specimens (all compressions) have been macerated. The most complete specimen available, i.e. from Little Switzerland (Plate I, Figures 3 and 4) shows a three-fold dichotomy but no true apex. Two clear apices are present (Plate I, Figures 5 and 6) amongst the Upper Umkomaas specimens. The portions of thalli shown in Plate I, Figures 8 and 7 have probably been derived from the same parent plant.

Townrow (1959) recorded five specimens but only four are available at the South African Museum, Cape Town. The whereabouts of the remaining specimen is unknown.

Marchantites tennantii sp. nov.
Plate I, Figures 1–11; Figure 1.

Type material: Holotype PB 111 (C-Dt.II 1035a, b). Locality: Dordrecht II (Birds River), Eastern Cape. Molteno Formation. The species is named in gratitude to the family Tennant on whose farm the locality is situated.

Molteno material: The specimen listed above and PB 112 (C-Dt.II 275'y') which is provisionally referred to this species. Both specimens are preserved as impressions.

Diagnosis: Plant thalloid, dichotomising every 4 to 8 mm, thallus lobes diverging at between 50° to 70°, margin partially undulating, width 2,5 to 4 mm. Midrib conspicuous, 1 mm wide, extending almost to apex, bearing an imprint, probably caused by ventral scales. Lateral wings of thallus 0,75 to 1,5 mm wide, bearing a clear imprint of polygonal areas; these occur in rows arching from midrib to about 30° to meet the margin at 80°. Rhizoids and internal structure unknown.

Discussion: This species can safely be placed in the order Marchantiales (Watson, 1975, pers. comm.). It has thus been placed in the genus *Marchantites* rather than the noncommital genus *Hepaticites* because it has a prostrate forked thallus, a conspicuous midrib, polygonal areas and probable ventral scales. The species is unfortunately not suitably preserved for study of the internal structures, e.g. air chambers. This lack of detail makes a meaningful comparison with modern genera and species impossible.

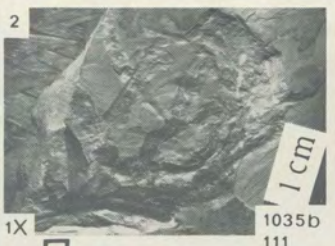
The holotype (Plate II, Figures 1–9) is a very clearly preserved impression. The thallus bears an imprint of apparent cellular structures. These are referred to as

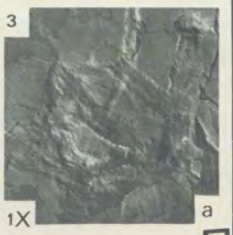
PLATE II

MARCHANTITES TENNANTII

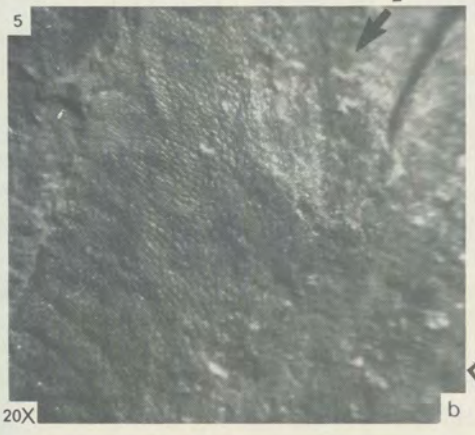
Dordrecht II C–Dt II





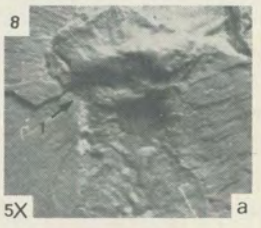


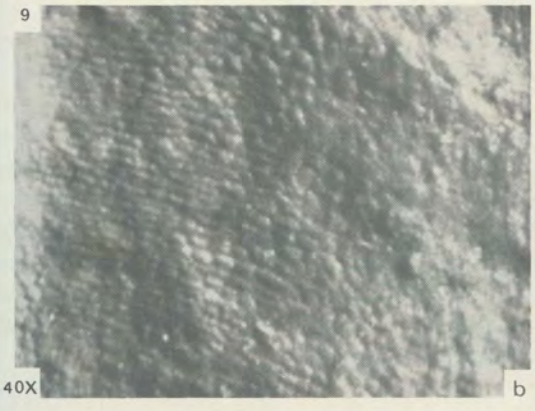














polygonal areas (Plate II, Figures 5 and 9) as there is no evidence that they represent individual cells. Similar polygonal areas (multicellular) are common in the modern Marchantiaceae. Watson (1957, pers. comm.) noted that the size and pattern of the polygonal areas of the holotype was much in accord with that found in several modern liverworts of the order Marchantiales, e.g. *Reboulia hemispherica.*

In an effort to obtain further structural details (e.g. to check the existence of a pore in the polygonal areas) a latex pull was made from the holotype and examined by SEM (Chaloner and Gay, 1972). Besides obtaining a greater magnification of the grooves demarcating the polygonal areas, no details were visible. The sediment encrusting the liverwort at the time of deposition was apparently sufficiently fine to carry the impressions of polygonal outlines, but not any of the more detailed structures.

The part and counterpart of the holotype both appear to represent the dorsal side only of the liverwort (Plate II, Figures 1 to 3). No rhizoids have been found and the presence of ventral scales is inferred from the irregular nature of the midrib region. Townrow (1959) also regarded the specimens of *M. cyathodoides* as preserved dorsal side up and was able to demonstrate this by making balsam transfers. Based on this he suggested that they were preserved *in situ.*

The wings of the thallus appear to be very thin and are probably only a few cells thick. The distinct curved lines on the wings (Plate II, Figures 5 and 6) probably indicate that the thallus wings were slightly corrugated. The latter feature occurs in certain extant species.

Of particular interest are certain apices (numbered in clockwise direction on Figure 1) in this liverwort. The first apex (see also Plate II, Figures 4, 7 and 8) shows a slight depression from which arises a distinctly elevated portion of thallus which is here interpreted as possibly representing an immature archegoniophore or antheridiophore. Certain apices (numbers 6 and 7) do not show this complexity of structure but show instead a gradual weakening of the midrib and continuation of the lateral wings to form a relatively unbroken curve at the apex. Another possibility is that apices numbers 1 and 2 show the initials of a dichotomous branch, as is clearly seen closely behind apices numbers 3 and 4. It is uncertain whether number 5 is a true apex or a broken portion of the thallus. At the points numbered 8–10 the thallus appears to continue. However, to avoid damaging the specimen these areas were not further exposed. At all the other points (numbers 1–7) every effort was made to clear the covering rock.

As this specimen consists only of an impression there is no way of checking microscopically whether certain of these apices actually represent archegoniophores or antheridiophores. Such structures have been specially noted, however, because the known fossil record of pre-Tertiary liverworts, with apparently only one exception, *Naiadita lanceolata* Harris (1939) from the Rhaetic of South West England, is devoid of fertile structures. Good fertile structures occur (gemmae cups and antheridiophores) in fossil liverworts from the Eocene of France, e.g. *Marchantites sezannensis* and *Marchantia munieri* Jovet-Ast (1967).

This species is close to *M. cyathodoides* which Townrow (1959) has compared with other similar liverworts, fossil and modern. The species is distinguished from *M. cyathodoides* by the somewhat wavy thallus margin (as opposed to a smooth one) and in the greater width of the thallus (4 mm in contrast to 2 mm). The absence of internal structure in this species rules out a comparison of microscopic characters. This species also shows a resemblance to *Thallites barwoni* (Medwell) Lundblad 1955 recorded from Victoria, Australia by Medwell (1954). However, *T. barwoni* has a thallus margin regularly dentate and the size is about twice as large as the Molteno specimen.

Muscites guescilini Townrow 1959
Plates III–V

Type material: Holotype — Townrow, 1959, Plate IC, number 13931, housed in the South African Museum, Cape Town. Locality: Upper Umkomaas, Natal. Molteno Formation.

Molteno material:

(a) Locality: Little Switzerland.
Slabs: PB 105 (N-L.Sw. 383), PB 113 (N-L.Sw. 685), PB 114 (N-L.Sw. 821), PB 115 (N-L.Sw. 904 a–h).
Preservation: compressions.

(b) Locality: Upper Umkomaas.
Slabs: Townrow (1959) collection consisting of microscope slides, 13931–13936, 14070, South African Museum, Cape Town: PB 116 (N-U.U. 1156), PB 117 (N-U.U. 1160), PB 118 (N-U.U. 1161a, b).

(c) Locality: Sani Pass.
Slab: PB 119 (N-S.P. 191a, b).
Preservation: compression.

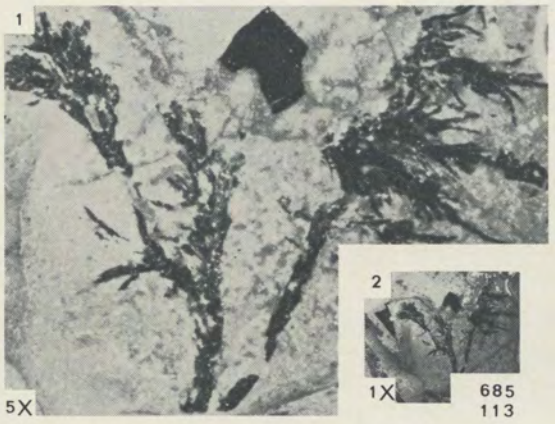
(d) Locality: Dordrecht II.
Slabs: PB 120 (C-Dt.II 687), PB 121 (C-Dt.II 1040a, b), PB 122 (C-Dt.II 286), PB 123 (C-Dt.II 691c), PB 124 (C-Dt.II 457a, b), PB 152 (C-Dt.II 1037), PB 153 (C-Dt.II 285a, b), PB 154 (C-Dt.II 456a, b), PB 155 (C-Dt.II 1038), PB 156 (C-Dt.II 1033). Unfigured specimens are C-Dt.II 283–4, 458, 485, 1029–1032, 1034, 1036, 1039, 1093.
Preservation: impressions.

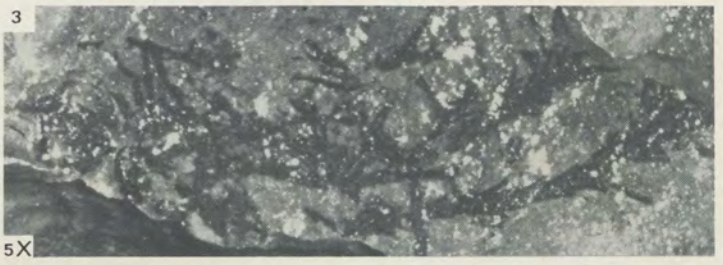
(e) Locality: Vineyard I.
Slab: C-Vy.I 163a, b (not figured).
Preservation: impression.

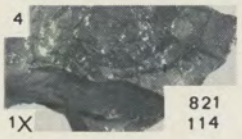
Diagnosis: Townrow, 1959, p. 12.

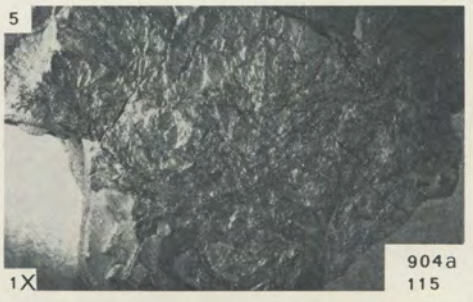
Discussion: Townrow (1959) based this species on material from Upper Umkomaas. He recorded 15 specimens, 12 of which were made into balsam transfers. Seven specimens are housed in the South African Museum, Cape Town. A note by Townrow accompanying the specimens records that the specimen illustrated in Figure 2E disintegrated while being mounted and no longer exists. What has become of the remaining seven specimens is not known. Further material is here noted from the type locality and from an additional four localities.

MUSCITES GUESCELINI



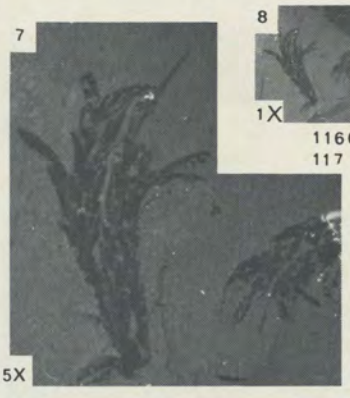


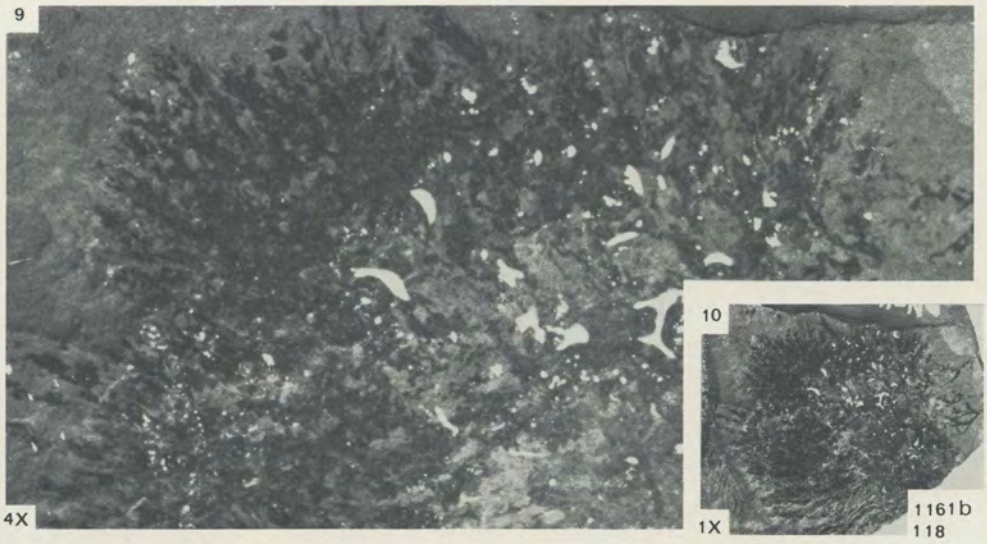




Little Switzerland N– L. Sw.







Upper Umkomaas N– U. U.

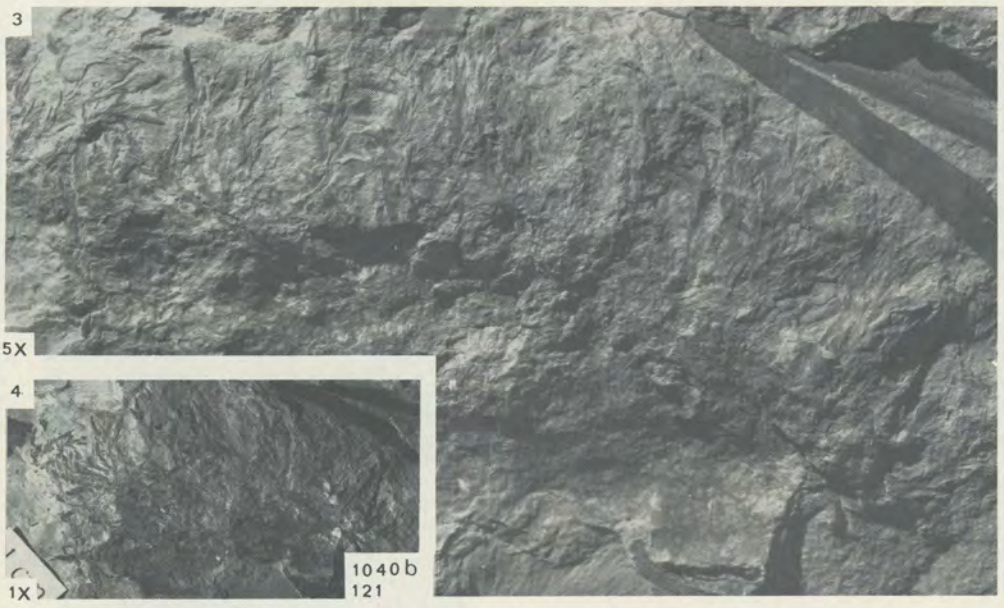




Sani Pass N– S. P.

MUSCITES GUESCELINI


1
5X
2
1X
687
120

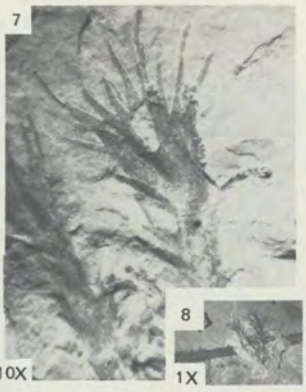

3
5X

4
1X
1040b
121


9
5X

10
1X
457
124

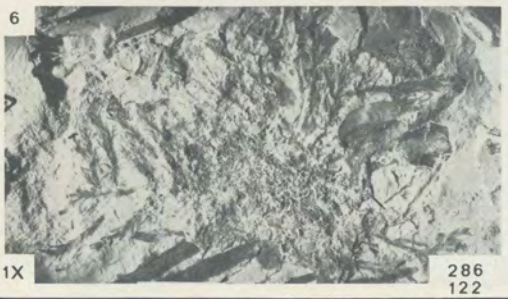

5
10X


7
10X

8
1X
691c
123


11
5X

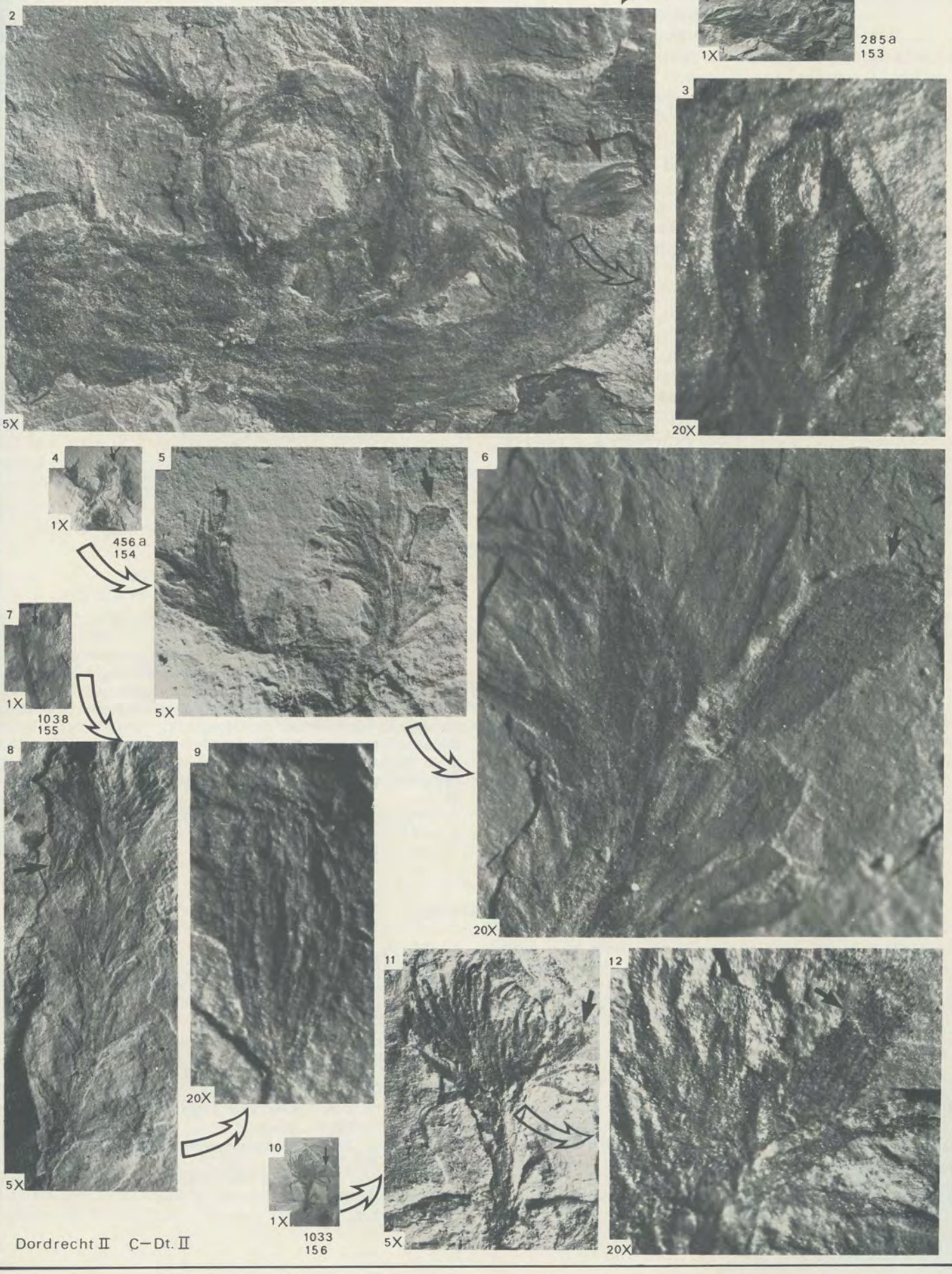
12
1X
1037
152


6
1X
286
122

Dordrecht II C–Dt II

PLATE V

MUSCITES GUESCELINI



Dordrecht II C–Dt. II

As Townrow (1959) has made a very detailed microscopic study of the species, no attempt has been made to repeat this.

The majority of the new material comes from Dordrecht II and this, like the rest, is closely comparable to *M. guescelini*. The leaves are borne spirally, vary from 1–2 mm in length and have no nerve (Plate IV, Figures 5 and 7). Townrow (op. cit.) noted that leaves became more oblong apically. Certain tips show distinctly elongated leaves (Plate IV, Figure 7) while leaves of a more oblong nature also occur (Plate IV, Figure 9). Townrow (op. cit.) noted that leaf shape varied considerably in his specimens.

The new material includes eight moss cushions (clusters) which were probably preserved *in situ*. The best examples are from Upper Umkomaas (Plate III, Figures 9 and 10) and Dordrecht II (Plate IV, Figures 4 and 6). In each of these the radiating branches of the gametophyte are clearly visible. In the moss cushions (Plate III, Figures 5, 6 and 9) the leaves are not clearly preserved and these fossils appear to have been partially eroded by water action. This probably occurred recently, when the fossiliferous horizon became exposed to water seepage. In contrast to these, the moss cushion from Dordrecht II shows some extremely well preserved leaves (Plate IV, Figures 3 and 5). Some good branched specimens also occur from Little Switzerland (Plate III, Figure 1) and Dordrecht II (Plate IV, Figures 9 and 11).

Of particular interest are certain probable fertile structures encountered at the Dordrecht II locality. These have all been figured, while of the remaining material from Dordrecht II (total 17 specimens) only a selection has been illustrated. A probable fertile structure enclosed by numerous (5?) leaves and possibly attached by a short stalk to the stem of one of the branches of a small moss cluster occurs (Plate V, Figures 1, 2 and 3). This inference is drawn from the fact that in modern mosses the fertile structures are usually provided with some protection.

The remaining structures all resemble moss antheridia.

The extant antheridium "is a delicate sac enclosing antherozoid mother cells and, ultimately, male gametes. In form it varies from subglobose, through ovoid to ellipsoid; the wall of the sac is almost always one layer of cells and the whole structure is borne on a stalk of varying length" (Watson 1964). The probable moss antheridia here recorded are 1,5 to 2 mm long and thus similar in size to those of modern *Polytrichum commune* which are 1,5 mm in length. Two of these appear to be attached near the apical portion of a stem (Plate V, Figures 6 and 11), while the third lies apparently detached near the apex of a stem (Plate V, Figure 8). The best preserved specimen shows faint striations indicating cell structure (Plate V, Figure 6). Similar striations also occur in another specimen (Plate V, Figure 12). On the remaining specimen fairly deep grooves are visible (Plate V, Figure 9).

Thallites sp. A
Plate I, Figures 11 and 12

Molteno material:
Locality: Molteno I.
Slab: PB 110 (C-Mo.I 33'x').
Preservation: impression.
Discussion: The slab shows two similar specimens alongside one another (Plate I, Figure 11) aligned in the same direction. The central dark midrib area and the transparent wing (Plate I, Figure 12) indicate that it may be a liverwort; but in the absence of further details, e.g. rhizoids, its affinity remains obscure. Since only a single specimen is available no specific name is appended.

ACKNOWLEDGEMENTS

This paper is dedicated to Dr. Edna Plumstead who introduced me to palaeobotany. I am grateful to Dr. E. V. Watson, Reading University, England for useful taxonomic suggestions regarding the new liverwort described herein. I would like to thank Family Tennant who gave so much aid and hospitality while collecting at Dordrecht II, the Monuments Commission and Forestry Department for necessary permits, and the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand for facilities. For photographic assistance I am grateful to Mr. Thompson, Zoology Department, University of the Witwatersrand; National Institute of Mettalurgy; Mrs. Adele Romanowski and Dr. R. Ellis, Botanical Research Institute. Finally a special thank you to my husband, family and friends who have helped and encouraged me in so many ways and made this work possible.

REFERENCES

ANDERSON, H. M. (1974). A brief review of the Flora of the Molteno Formation (Triassic), South Africa. *Palaeont. afr.*, **17**, 1–10.

CHALONER, W. G. and GAY, M. M. (1972). Scanning electron microscopy of latex casts of fossil plant impressions. *Palaeontology*, **16(3)**, 654–659.

GRAMBAST, L. J. and LACEY, W. S. (1967). Bryophyta and Charophyta. *In* The Fossil Record, pp. 211–217. Geological Society of London.

HARRIS, T. M. (1939). *Naiadita*, a fossil Bryophyte with reproductive organs. *Annales Bryologici, Leiden, Holland*, **12**, 57–70.

JAIN, R. K. and DELEVORYAS, T. (1967). A middle Triassic flora of the Cacheuta Formation from Minas de Petroleo, Argentina. *Palaeontology*, **10(4)**, 564–589.

JOVET-AST, S. (1967). *Bryophyta. In* Traité de Paleobotanique, **2**, 2–186, (E. Boureau, Ed.) Paris, Masson.

LACEY, W. S. (1969). Fossil Bryophyta. *Biol. Rev.*, **44**, 189–205.

LUNDBLAD, B. (1954). Contributions to the geological history of the Hepaticae. Fossil Marchantiales from the Rhaetic-Liassic coal mines of Skrombérga (Prov. of Scania), Sweden. *Svensk Bot. Tidskr.*, **48(2)**, 381–517.

MEDWELL, L. M. (1954). A review and revision of the flora of the Victorian Lower Jurassic. *Proc. R. Soc. Vict.*, **65(2)**, 63–111.

NEUBERG, M. F. (1960). Leafy mosses from the Permian deposits of Angarida. *Trudy geol. Inst. Leningr.*, **19**, 1–104 (in Russian).

TOWNROW, J. A. (1959). Two Triassic Bryophytes from South Africa. *Jl S. Afr. Bot.*, **25**, 1–22.

WALTON, J. (1925). Carboniferous Bryophyta 1. Hepaticae. *Ann. Bot.*, **39**, 563–572.

WATSON, E. V. (1964). *The structure and life of Bryophyta.* Hutchingson University Library, London.